Rates and modes of body size evolution in early carnivores and herbivores: a case study from Captorhinidae

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Body size is an extremely important characteristic, impacting on a variety of ecological and life-history traits. It is therefore important to understand the factors which may affect its evolution, and diet has attracted much interest in this context. A recent study, examining the evolution of the earliest terrestrial herbivores in the Late Carboniferous and Early Permian, concluded that in the four herbivorous clades examined there was a trend towards increased body size, and that this increase was more substantial than that observed in closely related carnivorous clades. However, this hypothesis was not based on quantitative examination, and phylogenetic comparative methods provide a more robust means of testing such hypotheses. Here, the evolution of body size within different dietary regimes is examined in Captorhinidae, the most diverse and longest lived of these earliest high fibre herbivores. Evolutionary models were fit to their phylogeny to test for variation in rate and mode of evolution between the carnivorous and herbivorous members of this clade, and an analysis of rate variation throughout the tree was carried out. Estimates of ancestral body sizes were calculated in order to compare the rates and direction of evolution of lineages with different dietary regimes. Support for the idea that the high fibre herbivores within captorhinids are being drawn to a higher adaptive peak in body size than the carnivorous members of this clade is weak. A shift in rates of body size evolution is identified, but this does not coincide with the evolution of high-fibre herbivory, instead occurring earlier in time and at a more basal node. Herbivorous lineages which show an increase in size are not found to evolve at a faster rate than those which show a decrease; in fact it is those which experience a size decrease which evolve at higher rates. It is possible the shift in rates of evolution is related to the improved food processing ability of the more derived captorhinids rather than a shift in diet, but the evidence for this is circumstantial.

1   Rates and modes of body size evolution in early carnivores and herbivores: a case study from

2   Captorhinidae

4   Keywords: "Captorhinidae", "Body Size", "Rate", "Evolution", "Diet", "Herbivore"

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11   ABSTRACT

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14   history traits. It is therefore important to understand the factors which may affect its evolution,

15   and diet has attracted much interest in this context. A recent study, examining the evolution of

16   the earliest terrestrial herbivores in the Late Carboniferous and Early Permian, concluded that in

17   the four herbivorous clades examined there was a trend towards increased body size, and that this

18   increase was more substantial than that observed in closely related carnivorous clades. However,

19   this hypothesis was not based on quantitative examination, and phylogenetic comparative

20   methods provide a more robust means of testing such hypotheses. Here, the evolution of body

21   size within different dietary regimes is examined in Captorhinidae, the most diverse and longest

22   lived of these earliest high fibre herbivores. Evolutionary models were fit to their phylogeny to

23   test for variation in rate and mode of evolution between the carnivorous and herbivorous

24   members of this clade, and an analysis of rate variation throughout the tree was carried out.

25   Estimates of ancestral body sizes were calculated in order to compare the rates and direction of

26   evolution of lineages with different dietary regimes. Support for the idea that the high fibre

27   herbivores within captorhinids are being drawn to a higher adaptive peak in body size than the

28   carnivorous members of this clade is weak. A shift in rates of body size evolution is identified,

29   but this does not coincide with the evolution of high-fibre herbivory, instead occurring earlier in

30   time and at a more basal node. Herbivorous lineages which show an increase in size are not

31   found to evolve at a faster rate than those which show a decrease; in fact it is those which

32   experience a size decrease which evolve at higher rates. It is possible the shift in rates of

33   evolution is related to the improved food processing ability of the more derived captorhinids

34   rather than a shift in diet, but the evidence for this is circumstantial.

35   **Introduction**

37   Body size is among the most important traits of an organism (Bell 2014). It influences,

38   amongst other things, an organism's potential diet range (Sinclair et al. 2003), the habitats it may

39   occupy, its energy requirements (Oksanen et al 1982), its ability to defend against predation

40   (Roff 1992), its development (Gillooly et al. 2002) and viable reproductive strategy (Tuomi

41   1980). As such, a great deal of effort has been put into understanding the patterns and processes

42   in body size evolution and how this varies between clades, through time, and between different

43   ecological groups.

44   In a recent paper, Reisz & Fröbisch (2014) examined body-size evolution in the earliest

45   terrestrial herbivorous vertebrate. During the first establishment of terrestrial ecosystems in the

46   Carboniferous and Early Permian, high-fibre herbivory appeared independently in at least four

47   different lineages: Edaphosauridae and Caseidae from the synapsid (mammal-line) amniotes,

48   Captorhinidae from the sauropsid (reptile/bird-line) amniotes and Diadectidae from the stem-

49   amniote diadectomorph lineage. Reisz & Fröbisch (2014) noted that, in these four families, the

50   evolution of herbivory appeared to be consistently correlated with increased body size. The

51   earliest members of each of these four clades are considered to be small carnivores or

52   insectivores, and the herbivorous members of these clades appeared in each case to be noticeably

53   larger than their carnivorous ancestors. Moreover, they suggested that there was more

54   pronounced increase in body size in the herbivorous members of these clades than in closely

55   related carnivores.

56   An association between herbivory and large body size has been noticed in other clades

57   e.g. mammals (Gaulin 1979; Fleming 1991; Isbell 1998; Price & Hopkins 2015), birds (Morton

58   1978; Dudley & Vermeij 1992; Klasing 1998) and lizards (Pough 1973; Schluter 1984; Cooper

59   & Vitt 2002). Two possible explanations have been offered for the association. The first is based

60   on the Jarman-Bell Principle (Geist 1974), originally used to explain body size evolution in

61   ungulates but since applied to other clades (e.g. Gaulin 1979; Fleming 1991; Isbell 1998). This

62   principle posits that, since smaller animals have higher metabolic energy requirements relative to

63   their body size, smaller herbivores are limited to more easily digestable plant material such as

64   roots and fruits. Larger members of a herbivorous clade have lower energy requirements relative

65   to their body size, and so are able to subsist on less digestable plant material such as leaves.

66   Since less digestable plant material is more abundant, those able to subsist on it (the larger

67   herbviores) have a selective advantage over their smaller relatives

68   The second explanation for the association between large body size and herbivory,

69   dubbed the abundance-packet size hypothesis by Olsen (2015), is based on the absolute nutrient

70   requirements rather than nutrient requirements relative to body size. A lineage which increases in

71   mass will require larger amounts of food. Therefore, the lineage must either feed on larger prey

72   (macro-carnivory) or find a more abundant food source such as plant material. It should be noted

73   that the abundance-packet size hypothesis differs from the Jarman-Bell Principle in the proximal

74   cause for the association between herbivory and larger body size; the Jarman-Bell principle

75   posits that in a herbivorous lineage there will be a selective pressure towards larger body size,

76   while the abundance-packet size hypothesis posits that in a lineage with a large body size there

77   will be a selective pressure to a more herbivorous diet.

78   Reisz & Fröbisch (2014) did not quantitatively test their hypothesis that the earliest

79   herbivores showed a greater trend towards larger body size than the carnivores; rather it was

80   tentatively suggested based on a visual examination of plotting diet and body size over a

81   phylogeny. Such inferences do need to be rigorously tested, however; for example, a more

82   detailed examination of body-size evolution in Therizinosaurs showed that previous assumptions

83   of a trend towards large body size in these herbivorous theropods was unfounded (Zanno &

84   Makivicky 2012).

85   Of the four clades examined by Reisz & Fröbisch (2014), the captorhinids provide the

86   best case study for testing their theory. They are the longest lived of the clades, surviving from

87   the late Carboniferous until the end of the Permian. They are also the most speciose, with more

88   than 25 species currently described. Moreover, a recently published and comprehensive (19

89   captorhinid terminal taxa) phylogeny exists, well resolved and with reasonably high node

90   supports (Reisz et al. 2015), providing an excellent framework for an analysis of body-mass

91   evolution.

92   The captorhinids were the most diverse sauropsid clade in the Paleozoic. They first

93   appear in the fossil record in the Virgilian aged Hamilton Quarry of Kansas (Müller & Reisz

94   2005) before diversifying during the early Permian. By the Middle Permian they had achieved a

95   global distribution, being known from North America, Europe, Asia and Africa. The first

96   herbivorous members of this clade appeared during the Kungurian (Doddick & Modesto 1995).

97   Crucial to the evolution of herbivory in captorhinids were the multiple rows of maxilliary and

98   dentary teeth. This feature first appeared in the insectivore/omnivore *Captorhinus* (Doddick &

99   Modesto 1995) but in the high-fibre herbivorous taxa up to 11 rows of bullet-shaped maxilliary

100   teeth, combined with a propalineal motion of the lower jaw, form an effective grinding and

101   shredding surface for processing plant material (Modesto et al. 2007).

102   Here I examine changes in rate and mode of the evolution of size in captorhinids. In

103   particular the evolution of the carnivorous and herbivorous members is compared, in order to test

104   the hypothesis of Reisz & Frobisch. The applicability of the Jarman-Bell Principle and the

105   abundance-packet size hypothesis to captorhinid evolution is also examined.

106

107   **Materials and Methods**

108

109   Proxy for body size

110

111   The estimation of body mass in extinct organisms is unsurprisingly difficult, in the

112   absence of a complete skeleton and soft tissue. Some workers have attempted volumetric

113   reconstructions (e.g. Colbert 1962; Hurlbert 1999; Motani 2001), but these require relatively

114   complete skeletons and are not useful in examinations of body mass spanning entire clades. Most

115   other estimates have used a single measurement as a proxy for mass e.g. dorsal centrum cross

116   section (Romer & Price 1940), humerus and femur shaft circumference (Campione & Evans

117   2012). This of course requires those taxa not possessing the necessary elements to be ignored,

118   but in large analyses e.g. Benson et al. (2014) on dinosaurs, a small number of deletions should

119   not mask the overall pattern.

120   Since Captorhinidae are a small clade (18 taxa included in the most comprehensive

121   phylogenetic analysis) useful proxies for body size are limited by the available material. Due to

122   the fact that all terminal taxa analysed by Reisz et al. (2015) possess skull material, but only a

123   limited number have postcranial material preserved, it was decided to use the skull length as a

124   proxy for size. While cranial material is not often used in calculations of body mass, a precise

125   mass in grams is not necessary for the analyses herein; an estimate of relative difference in size

126   is the most important. It is obviously possible for skull size to vary relative to the rest of the

127   body, but comparison of skull measurements to postcranial measurements for those taxa which

128   preserve both indicate that, in captorhinids at least, this does not appear to be a serious concern

129   (see measurements provided by Reisz & Fröbisch 2014). Using skull material allows the study to

130   be as comprehensive as possible. Only two taxa are not represented by a skull complete enough

131   to measure the length (*Captorhinikos valensis* and *Gansurhinus quingtoushanensis*), and both of

132   these do preserve skull material, so an estimate of skull length could be obtained by comparing

133   the length of elements preserved in these taxa to the length of elements preserved in closely

134   related taxa.. The skull lengths were log transformed prior to analysis (see supplementary

135   materials for skull-length data).

136

137   Phylogeny and Time Calibration

138

139   The most recent and comprehensive phylogeny of captorhinids (Reisz et al. 2015) formed

140   the basis of the analyses presented herein. The phylogeny contains 19 captorhinid taxa, of which

141   6 are considered high-fibre herbivores (Figure 1). The phylogeny was time calibrated using the

142   method of Brusatte et al. (2008) in the R 3.03 (R Core Team 2014) package paleotree (Bapst

143   2012); zero-length branches resulting from inconsistencies between the order of branching and

144   the order of tip appearance in the fossil record were eliminated by sharing the zero-length

145   branches equally along the non-zero-length branch immediately ancestral to them. While other

146   time calibration methods are available for use on extinct datasets (for summary see Bapst 2014a;

147   b), the use of the Brusatte et al. method is less subjective than the addition of arbitrary amounts

148   of time to zero-length branches. Meanwhile, methods like the Cal3 method (Bapst 2013) are not

149   suitable for datasets with poor sample size and low resolution. After time calibration, the non-

150   captorhinid outgroups (*Paleothyris* and *Protorothyris*) were dropped.

151   To resolve the uncertainty surrounding the age ranges of taxa, 100 time calibrated trees

152   were generated using the method of Pol & Norrell (2006). For each tree, the ages of each taxon

153   were drawn at random from a uniform distribution of the full possible age range. A single age

154   was drawn for singletons, a first and last appearance for taxa represented by more than one

155   specimen. Subsequent analyses were performed on all 100 trees to assess the impact of uncertain

156   age ranges (see supplementary materials for trees in nexus format). Since the Reisz et al.

157   phylogenetic analysis found two most parsimonious trees (MPTs, differing in the position of

158   *Opisthodontosaurus*), 50 of these 100 trees were based on one MPT, 50 the other.

159

160   Models of Rate and Mode of Evolution

161

162   *Model fitting*

163   When examining the evolution of a continuous trait such as body size and comparing it in

164   different clades, ecological groups or time periods, one must consider both the rate and the mode

165   of evolution. Models such as Brownian motion (BM) assume evolution via a statistically random

166   walk with a constant normally distributed deviate from the observed morphology. In

167   macroevolutionary processes, this can result from randomly varying selection a lack of selective

168   pressure in any particular direction and a lack of variation in rate (Mooers et al 1999; Pagel

169   1997; Pagel 1999). As such, a clade evolving by simple Brownian motion will show no

170   directional trend in trait mean, but instead the trait variance will increase through time. More

171   complicated models can add parameters to provide a more detailed simulation of evolution. One

172   can, for example, incorporate a directional trend to the BM model; the trait variance will still

173   increase through time, but the mean will either increase or decrease. The Ornstein Uhlenbeck

174   (OU) model incorporates an adaptive optimum to which trait values are drawn; the further a

175   lineage strays from this optimum, the more strongly it is drawn back (Hansen 1997). Once the

176   trait has reached the adaptive optimum, it will show a constant variance and mean through time.

177   Rate variation has also been examined, such as in the early burst (EB) model (Harmon et al.

178   2010), where rate of change decreases exponentially from an initial maximum, causing the

179   increase in trait variance to be rapid in the early history of a clade, but to then slow. Further

180   models have been developed allowing shifts in either rate or mode of evolution between clades

181   (O'Meara et al. 2006; Thomas et al. 2009) or at specific points in time (Slater 2013).

182   Maximum likelihood was used to fit three sets of models to the observed size estimates,

183   with the Akaike weights used to deduce which model in each category fits best. The three

184   categories represent 1) models of the evolution of the continuous trait (body size) alone; 2)

185   models of the co-evolution of body size with a dietary regime; 3) models of the evolution of

186   body size subjected to external influences at specific times.

187   The models in the first category included Brownian motion, Brownian motion with trend,

188   Ornstein Uhlenbeck, the TM1 model and the SURFACE model. Under the TM1 model the trait

189   evolves by Brownian motion, but one or more heritable shifts in rate may occur at any node. If a

190   shift occurs at a node, an increase or decrease in rate is deduced for all lineages descended from

191   that node (Thomas et al. 2009). Under the SURFACE model, the trait evolves under an OU

192   process, but one or more shifts in adaptive peak may occur at any node; that is, the descendants

193   from the node at which the shift occurs will be drawn to a different trait value (Ingram & Mahler

194   2013). These five models represent models where captorhinid body size evolution is independent

195 of any specified factor; evolution is either consistent across captorhinids, or can shift but at

196 entirely unspecified points. The BM and BM with trend models were fit using the fitContinuous

197 function in the R package Geiger (Harmon et al. 2008); the OU model using the functions in the

198 package OUwie (Beaulieu et al. 2012); the TM1 model using the transformPhylo.ML function in

199 the package motmot (Thomas et al. 2009); the SURFACE model using the runSurface function

200 in the package surface (Ingram & Mahler 2013).

201   The models in the second category allow different rates or modes of evolution to occur

202 under different dietary regimes. Three such models are tested: BM-V OU-M and OU-MV. Under

203 the BM-V model, body size evolves by Brownian motion but with rates of evolution differing

204 between the carnivorous lineages and the herbivorous lineages. The OU-M model represents

205 body size evolution under an OU process, but with the different dietary regimes drawn to

206 different adaptive optima. The OU-MV model is similar to the OU-M model, but allows a

207 change in rate of evolution as well as adaptive optimum under different dietary regimes. All

208 three of these models were fit using the functions in the R package OUwie.

209   The third category of models tests for the possibility of extrinsic influences on the

210 evolution of body size in captorhinids; that is, changes in rate or mode are related to a change in

211 the organism's environment (both biotic and abiotic) rather than any evolutionary innovation

212 within the clade itself. Were this to be the case, one would expect a shift in rate or mode to occur

213 at a specific point in time, and affect all lineages after this point, rather than affecting all taxa

214 descended from a specific node. The captorhinids evolved at a time of great changes in

215 environment. Throughout the late Carboniferous and Permian, there was a trend towards a

216 warmer, dryer climate (Rees et al. 2002). At the end of the Carboniferous, there was a collapse in

217 the equatorial rainforest and a shift towards seasonally dry climates (DiMichelle et al. 2006;

218   2009). This coincided with, and possibly caused, a radiation in amniotes (Sahney et al. 2010). In

219   the Early Permian, during the Sakmarian stage, there was an abrupt shift towards higher

220   temperatures and accelerated deglaciation (Montanez et al. 2007), possibly coinciding with a

221   brief drop in amniote diversity (Brocklehurst et al. 2013). During the Kungurian and Roadian

222   there was transition from an early Permian fauna dominated by pelycosaurian-grade synapsids

223   and abundant amphibians to a Middle Permian fauna dominated by therapsids, possibly

224   accompanied by a mass extinction event (Sahney & Benton 2008; Benson & Upchurch 2013;

225   Brocklehurst et al. 2013; Brocklehurst et al. in press).

226   Slater (2013) described models to test the possibility of shifts in rate or mode coinciding

227   with a specific point in time. The Rate Shift (RS) model assumes evolution by Brownian motion,

228   but with a shift in rate at a specified point in time. The Ecological Release (ER) model allows a

229   shift in mode at the specified time from OU to BM. Both of these models were tested four times,

230   each with a different time specified for the shift to occur. The four times were the late Gzhelian

231   (coinciding with the rainforest collapse and amniote radiation), the end of the Sakmarian

232   (coinciding with the temperature spike), the early Kungurian and early Roadian (the time of the

233   tetrapod faunal turnover and Olson's extinction).

234   Having found the best fitting model in each of these three categories, these three models

235   were compared to find a single model which overall best fits the evolution of body size in

236   captorhinids.

237

238   *Rate variation*

239   When considering the evolution of a trait such as size, one cannot only consider shifts in

240   the rate. Increasing the rate of evolution under a BM model increases the rate of evolution in

241   both directions, towards larger and smaller. In order to examine whether there is indeed a greater

242   tendency towards larger body size in the herbivorous captorhinids, one must ascertain 1) whether

243   rates of increase in size of herbivores are greater than rates of increase in carnivores; 2) whether

244   rates of decrease in size of herbivores are less than rates of decrease in carnivores, and 3)

245   whether rates of increase in size of herbivores are greater than rates of decrease. Such an

246   examination requires a method which can assess rate variation along every branch in the

247   phylogeny. The method of Venditti et al. (2011) was used to assess rate variation across every

248   branch of the phylogeny. An MCMC analysis was carried out in BayesTraits V2.0 to calculate

249   the pattern of rate variation which best fits the body size data to the time calibrated phylogeny.

250   BayesTraits also scales the branch lengths of the phylogeny to represent rate variation. This

251   method has an advantage over similar methods (e.g. Mooers et al. 1999) in that it allows the

252   scaling of not only individual branches, but the equal scaling of all branches within an entire

253   clade, thus taking into account the possibility of rate heritability.

254   Along with the rate values calculated using the Venditti et al. method, each branch was

255   assigned an inferred diet based on likelihood ancestral state reconstruction, and a direction of

256   evolution (increase or decrease in size). The direction was deduced from ancestral state

257   reconstruction of size, assuming evolution by BM but rescaling the branch lengths to represent

258   the rate variation calculated in BayesTraits. The rates of both increase and decrease in body size

259   in carnivores and herbivores were compared using the Mann Witney U test, calculated in R.

260

261   **Results**

262

263   The model from the first category (models of evolution independent of diet or extrinsic

264   events) which best fits the body size data and phylogeny of captorhinids is the TM1 model

265   representing a rate shift at a specific node in the tree (Figure 2a). This model has a median

266   Akaike weight score of 0.94. In all but three of the 100 time calibrated trees this model has a

267   higher Akaike weights score than all the others, and in 83 the Akaike weight score is above

268   0.8.The majority of analyses (91) suggest this rate shift was an increase occurring at the same

269   node: the clade containing *Captorhinus, Captorhinikos valensis, Labidosaurus* and the

270   Moradisaurinae (Figure 3), although there are a minority where the rate increase is found to have

271   occurred only in the genus *Captorhinus*. This indicates the uncertainty surrounding the ages of

272   taxa is influencing the results.

273   The best model from the second category (coevolution of body size and diet) which best

274   fits the body size data and phylogeny of captorhinids is, in all 100 of the time calibrated

275   phylogenies, the OU-M model (Figure 2b). In all 100, it is found that the herbivorous lineages

276   have are being drawn to a higher adaptive peak of body size than the carnivorous lineages. This

277   model receives an Akaike weight score of above 0.8 in 78 of the tested phylogenies, and has a

278   median Akaike wight score of 0.84.

279   The best model from the third category (coevolution of body size and diet) is the Rate

280   shift model, with a rate increase occurring at the end of the Sakmarian stage (Figure 2c). The

281   median Akaike weights score of this model is only 0.63, indicating greater uncertainty when

282   choosing between these models. There are 6 of the 100 time calibrated trees where a rate shift at

283   the end of the Sakmarian fits the body size data less well than an ecological release (a shift from

284   evolution under an OU process to a BM process) during the Kungurian or Roadian.

285   When the three best fitting models from each category are compared, it is the TM1 model

286   with a rate increase at the node indicated in figure 3 which is overall found to best fit the

287   captorhinid body size data, with a median Akaike weights score of 0.85 (Figure 2d). It should be

288   noted that this median Akaike weights score, while high, is not overwhelming. Only in 59 of the

289   100 time calibrated trees is the score over 0.8, and it is over 0.9 in only 37. The OU-M model

290   received the second highest median Akaike weight score of 0.14%, but receives a score of above

291   50% in 14 of the 100 time calibrated trees (see supplementary data). This indicates that the

292   uncertainty surrounding the ages of certain fossils is affecting the results. However, the majority

293   (86) of the trees best fit a BM model with a rate shift at the clade indicated rather than a higher

294   adaptive optimum for herbivores (see supplementary data). In none of the 100 time calibrated

295   phylogenies is the RS model with a rate shift at the end of the Sakmarian found to be a better fit

296   the either of the other two.

297   The variable rates analysis indicates that the mean rate of size increase in herbivores is

298   higher than that of carnivores, and the Mann Whitney U test suggests the difference is significant

299   (Table 1). However, there are also herbivorous lineages which show a decrease in size, and the

300   Mann Whitney U test suggests that the rate of decrease is also significantly faster in herbivores

301   than carnivores (Table 1). The rates of increase in size of herbivores was found to be lower than

302   rates of decrease (albeit not significantly), while in carnivores the reverse was found; rates of

303   increase in size are higher than rates of decrease, although again, not significantly (Table 1).

304

305   **Discussion**

306

307   Reisz & Frobisch (2014) put forward two theories about body size evolution in early

308   herbivores. First, they suggested that herbivorous clades showed a trend towards increased body

309   size. Second they suggested that this increase was more pronounced in herbivores than in closely

310   related carnivores. Support for these hypotheses depends on observing one or more of these three

311   possible results: 1) the Ornstein Uhlenbeck model with a variable trait optimum would be the

312   evolutionary model best fitting the size data, and the trait optimum would be higher in herbivores

313   than in carnivores; 2) the herbivorous branches which show an increase in size would have a

314   faster rate of change than the carnivorous branches showing an increase; 3) the herbivorous

315   branches which show a decrease in size should have a slower rate of change than the carnivorous

316   branches showing a decrease.

317   Support for a variable optimum OU model being the best fitting is equivocal due to the

318   uncertainty surrounding the age ranges. In most of the 100 sets of ages tested it is not the best

319   supported model. In fact the best supported model for size evolution is the TM1 model

320   incorporating a shift towards higher rates of size evolution, and this shift does not coincide with

321   the evolution of herbivory. Instead it occurred earlier, probably during the Sakmarian or

322   Artinskian. The node at which this shift is inferred to have occurred does contain the herbivorous

323   members of Captorhinidae, but also includes three species of *Captorhinus* and *Labidosaurus*

324   *meachami* (Figure 3), neither of which is considered to be a high-fibre herbivore (Dodick &

325   Modesto 1995; Modesto et al. 2007).

326   The results of the variable rates analysis in BayesTraits may be represented as a heat map

327   (Figure 4), in which high rates are represented by hot colours (purple and red). The results

328   indicate an increase in rates of size evolution at the same node identified by the model fitting

329   analysis. The greatest rate increase is identified in three tip branches: those leading to

330   *Captorhinus aguti, Captorhinus magnus* and *Captorhinikos valensis*. Ancestral size

331   reconstruction indicates that the size change on the branch leading to the herbivorous

332   *Captorhinikos valensis* was an extremely rapid decrease (Figure 5). Another herbivorous taxon

333   which shows high rates of body size evolution (albeit not so high as *Captorhinikos valensis*) is

334   *Gansurhinus*. Again, this herbivore is found to be experiencing a rapid decrease in body size.

335   Overall, the variable rates analysis also fails to support a tendency towards larger body

336   size in herbivores. The rates of evolution along the herbivorous branches of the Captorhinidae

337   are found to be, on average, higher than those of carnivores, but this increase in rate applies in

338   both directions: both towards larger and smaller sizes (Figure 6, Table 1). While this has resulted

339   in comparatively large sizes in herbivorous taxa such as *Moradisaurus*, *Rothianiscus* and

340   *Labidosaurikos*, all of which have skull lengths above 200mm, extremely rapid rates of

341   decreasing body size are also observed in herbivorous taxa such as *Captorhinikos valensis* and

342   *Gansurhinus* (Figure 5). Moreover, while herbivorous taxa do have a higher mean rate of skull

343   size evolution than the carnivorous taxa, both the variable rates analysis and the model fitting

344   analysis indicate that the shift in rate of evolution did not coincide with the evolution of high

345   fibre herbivory, but instead occurred earlier in time and at a node containing both carnivorous

346   and herbivorous taxa (Figure 2). The results support neither a general trend towards larger size in

347   herbivorous captorhinids nor an adaptive optimum of larger size; decreases in body size of high-

348   fibre herbivores occur no less rapidly than increases. In fact, the results directly oppose Reisz &

349   Frobisch's hypothesis that there was a more pronounced trend towards increased body size in

350   herbivores than in carnivores. The rate of size evolution in the high-fibre herbivores is found to

351   be higher in branches which decrease in body size than in those which increase (Figure 6),

352   although the difference is not significant, possibly due to the low sample size (Table 1).

353 Meanwhile the converse is found to be true in the carnivorous lineages; body size evolution is

354 faster in lineages which show an increase (although the difference is lowest of those tested and is

355 again not significant).

356   These results allow the rejection of the Jarman-Bell Principle as governing body size in

357 Captorhinidae. The Jarman-Bell Principle posits a selective pressure towards large body size

358 within an already herbivorous lineage. Therefore, were it applicable to captorhinids, one would

359 expect the OU-M model, with the herbivorous captorhinids being drawn to a higher body size

360 than carnivores, to best fit the captorhinid data, and one would expect the herbivorous

361 captorhinids to show higher rates of increase in body size than decrease. Neither of these

362 predictions is borne out by the data. The OU-M model cannot be completely rejected due to the

363 uncertainty surrounding the ages of taxa, but it is not the best fitting model in most cases.

364 Meanwhile, herbivorous captorhinids show some extremely rapid decreases in body size, while

365 most of the herbivorous lineages which increase in body size do so gradually (with the exception

366 of the lineage leading to *Labidosaurikos*).

367   Rejection of the abundance-packet size hypothesis is more difficult. This hypothesis

368 posits that lineages with a larger body size should experience a selective pressure towards a more

369 herbivorous diet, but does not preclude the possibility of herbivorous lineages returning to a

370 smaller body size. The transition to herbivory does appear to have occurred in lineages of above

371 average size, which would support this hypothesis. One should note, however, the uncertainty

372 surrounding how many transitions to herbivory there were and where they occurred (Figure 1). It

373 is unclear whether *Captorhinikos chozaenesis* represents a separate evolution of herbivory, or if

374 *Labidosaurus* represents a reversal to a more omnivorous diet.

375   Since the evolution of herbivory may be rejected as the cause of this shift in rate of body-

376   size evolution, an alternative explanation is necessary. Changes in rate and mode of evolution

377   can either be intrinsic, relating to the evolution of a "key" morphological, behavioural or

378   developmental innovation, or extrinsic, relating to a change in environment. An extrinsic cause

379   would be supported if a shift in rate or mode occurred at a specific time rather than in a specific

380   clade. This does not appear to be the case in the Captorhinidae; models involving a temporal

381   shift in rate and mode fit the captorhinid phylogeny worse than the TM1 model. Therefore an

382   intrinsic cause must be sought; one must consider the morphological variations within

383   captorhinids.

384   One feature which characterises the more derived captorhinids is the increased efficiency

385   of food processing. Multiple tooth rows have evolved at least twice; in *Captorhinus aguti* and in

386   the clade containing *Captorhinikos chozaensis* and the Moradisaurinae, although the lack of this

387   feature in *Labidosaurus* leads to uncertainty over the optimisation of this character (Figure 6).

388   The evolution of the propalineal motion of the lower jaw is another innovation which would

389   improve food processing in this clade. The ability to perform such a motion has been suggested

390   in *Captorhinus* (Heaton 1979), *Labidosaurus* (Modesto et al. 2007) *Captorhinikos valensis*

391   (Modesto et al. 2014) and the Moradisaurinae (Dodick & Modesto 1995), a distribution which

392   corresponds with the position of the inferred rate shift. One might reasonably suggest that the

393   improved food processing could have widened the range of ecological niches available to

394   captorhinids. Basal captorhinids were limited to a "grab and gulp" feeding habit, indicated by the

395   simple conical teeth and suitable only for capturing small, non-resisting prey such as

396   invertebrates (Hotton et al. 1997). The inferred evolution of propalineal jaw motion coincides

397   with the node at which the rate shift occurred, and the majority of taxa descended from this node

398   possess multiple tooth rows. The transition to a dentition and jaw morphology allowing

399   processing of food after capture widens the diet available for both carnivorous and herbivorous

400   forms; in carnivores it allows the capture of larger, more resistant prey and the detatchment of

401   pieces for mechanical processing, while in herbivores it aids the digestion of tough fibrous plant

402   material whilst reducing the need for gut fermentation inferred for more bulky herbivores such as

403   caseids. One might therefore infer an "ecological release" as the increased food processing

404   ability permitted captorhinids to explore as-yet untried ecological niches, increasing the rate

405   body size evolution in both directions.

406   There are difficulties with conjecturing a causal relationship between the evolution of the

407   specialised jaw motion and the rate shift. One must remember this evidence is purely

408   circumstantial. Moreover the propalineal motion is in some cases difficult to infer; one can

409   deduce its presence from wear patterns on the teeth (Heaton 1979; de Riqles & Taquet 1982), but

410   such data is not always available and morphological correlates must be found. Dodick &

411   Modesto (1995) suggested the increased length of the articulation between the lower jaw and the

412   quadrate could be such an indicator, as could the vaulting of the skull roof which allows the

413   required angle of adductor musculature. However, these lines of evidence conflict in the case of

414   *Captorhinus*; the tooth-wear patterns suggest the ability to perform the jaw motion (Heaton

415   1979), but *Captorhinus* lacks the supposed morphological correlates (Dodick & Modesto 1995).

416   Despite these uncertainties a causal relationship between the evolution of improved oral

417   processing equipment and increased rate of body size evolution is an extremely tempting one.

418   Further confirmation could be provided by examination of other taxa with multiple rows of teeth

419   and the specialised jaw motion. *Baeotherates fortsillensis*, for example, was not included in the

420   analysis of Modesto et al. (2014), on which that of Reisz et al. (2015) is based, due to the lack of

421   material, but the single dentary preserved shows tooth morphology similar to *Captorhinus aguti*

422   (May & Cifelli 1998), and so could provide further information on the evolution of multiple

423   tooth rows in non-herbivorous taxa. Meanwhile, taxa such as *Gecatogomphius kavejevi*,

424   *Kahneria seltini* and *Captorhinikos parvus* would deliver further data on body size evolution in

425   the herbivorous taxa. Modesto et al. (2014) suggested further preparation of these taxa would be

426   required before attempting to fit them in a phylogenetic analysis.

427   It is necessary to conclude with an acknowledgement that, while this study does cast

428   doubt on the general hypothesis of Reisz & Frobisch (2014) that the earliest herbivores showed a

429   pronounced trend towards larger body size, one should be careful about expanding the inferences

430   presented here to other clades. Multiple clades evolved herbivory independently, and they all

431   show great variation in size, tooth morphology and environmental preference. Nevertheless this

432   study strongly highlights the need for quantitative examinations of evolution. It is difficult to

433   make inferences about evolutionary patterns and processes with visual examinations of trait data

434   divided into coarse categories. In clades where a comprehensive, well supported phylogeny

435   exists, a great variety of tools are available to test such hypotheses and provide robust

436   confirmation.

437

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439

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444

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583   herbivores. Proceedings of the Royal Society B 280:1-8.

584 **Figure Captions**

585

586 Figure 1

587 Title: The phylogeny of Captorhinidae, illustrating the evolution of high-fibre herbivory.

588 Legend: Two of the 100 time calibrated phylogenies used in this analysis. The thick branches

589 indicate the observed range for non-singleton taxa. The tip labels in green indicate those taxa

590 inferred to have a high-fibre herbivorous diet. The pie charts represent the probability of each

591 dietary regime inferred for each node, deduced by maximum likelihood ancestral state

592 reconstruction using the ace function in the R package ape. A) MPT 1: *Opisthodontosaurus* is the

593 sister to the clade containing *Rhiodenticulatus* and all captrorhinids more derived. B) MPT 2:

594 *Opisthodontosaurus* is the sister to *Concordia*.

595

596 Figure 2

597 Title: The fit of models of body size evolution to the phylogeny of Captorhinidae

598 Legend: Boxplots showing the distribution of 100 Akaike weight values calculated for each

599 model representing the fit of each model of body size evolution to the 100 time calibrated

600 phylogenies. A) Category 1 models (Evolution of body size alone). B) Category 2 models

601 (coevolution of body size with herbivory. C) Category 3 models (evolution of body size with

602 shifts in rate or mode at specified points in time). D) Comparison of the best fitting models from

603 each of the three categories. The abbreviation Gzh, Sak, Kun and Roa represent the time at

604 which the shift in rate/ mode occurred in the RS and EC models. Gzh – end of the Gzhelian; Sak

605 – end of the Sakmarian; Kung – beginning of the Kungurian; Road – beginning of the Roadian.

606 Other abbreviations as in the main text.

607

608   Figure 3

609   Title: The shift in rate of body size evolution, identified by fitting the TM1 model to the

610   phylogeny of Captorhinidae

611   Legend: Two of the 100 time calibrated phylogenies of Captorhinidae, with the location of the

612   rate increase indicated by the red branches. The branch lengths here represent the time until the

613   first appearance of the taxa. A) MPT 1. B) MPT 2

614

615   Figure 4

616   Title: Variation in rates of body size evolution within Captorhinidae, illustrated as a heat map.

617   Legend: Two of the 100 time calibrated phylogenies of Captorhinidae, illustrating variation in

618   rates of body size evolution identified using the method of Venditti et al. (2011). The branch

619   lengths here represent the time until the first appearance of the taxa. A) MPT 1. B) MPT 2

620

621   Figure 5

622   Title: The evolution of body size through time of the Captorhinidae.

623   Legend: Two of the 100 time calibrated phylogenies, illustrating both the age and inferred body

624   size of each node. Ancestral body sizes are reconstructed using likelihood, assuming evolution

625   by Brownian motion but scaling the branches to represent rate variation. Herbivorous lineages

626   are coloured green. As the analyses do not take into account changes occurring within the

627   observed ranges of the species, the observed ranges are here shown to experience no changes in

628   body size. A) MPT 1. B) MPT 2

629

630 Figure 6

631 Title: The evolution of multiple tooth rows in the Captorhinidae.

632 Legend: Two of the 100 time calibrated phylogenies used in this analysis. The tip labels in red

633 indicate those taxa with multiple tooth rows. The pie charts represent the probability of an

634 ancestral morphology including multiple tooth rows, deduced by maximum likelihood ancestral

635 state reconstruction using the ace function in the R package ape. A) MPT 1. B) MPT 2

636

637 Table 1

638 Title: Results of Mann Witney U tests

639 Legend: Values of W and p-values resulting from the Mann Whitney U test comparing rates of

640 lineages evolving in different directions and under different dietary regimes.

641

1

The phylogeny ofCaptorhinidae, illustrating the evolution of high-fibre herbivory.

Two of the 100 time calibrated phylogenies used in this analysis. The thick branches indicate the observed range for non-singleton taxa. The tip labels in green indicate those taxa inferred to have a high-fibre herbivorous diet. The pie charts represent the probability of each dietary regime inferred for each node, deduced by maximum likelihood ancestral state reconstruction using the ace function in the R package ape. A) MPT 1: *Opisthodontosaurus* is the sister to the clade containing *Rhiodenticulatus* and all captrorhinids more derived. B) MPT 2: *Opisthodontosaurus* is the sister to *Concordia* .

A.

Gansurhinus

Rothianiscus

Moradisaurus

Labidosaurikos

Captorhinikos valensis

Labidosaurus

Captorhinikos chozensis

Captorhinus magnus

Captorhinus aguti

Captorhinus laticeps

Saurorictus

Protocaptorhinus

Romeria texana

Romeria prima

Reiszorhinus

Rhiodenticulatus

Opisthodontosaurus

Concordia

Thuringothyris

Kasimovian	Gzhelian	Asselian	Sakmarian	Artinskian	Kungurian	Roadian	Wordian	Capitanian	Wuchiapingian	Changhsingian
Carboniferous		Permian								

300   290   280   270   260

B.

Gansurhinus

Rothianiscus

Moradisaurus

Labidosaurikos

Captorhinikos valensis

Labidosaurus

Captorhinikos chozensis

Captorhinus magnus

Captorhinus aguti

Captorhinus laticeps

Saurorictus

Protocaptorhinus

Romeria texana

Romeria prima

Reiszorhinus

Rhiodenticulatus

Opisthodontosaurus

Concordia

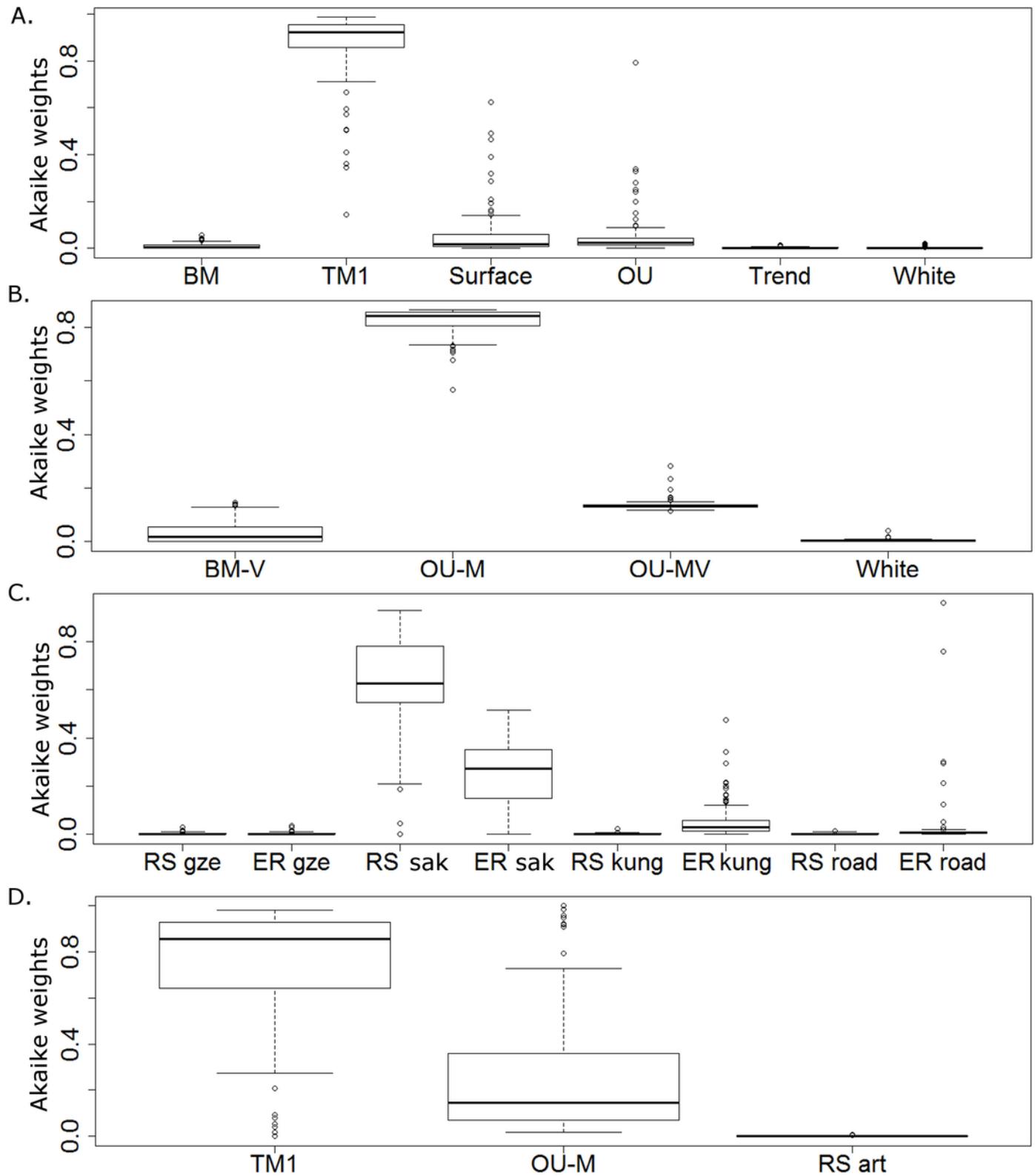
Thuringothyris

Kasimovian	Gzhelian	Asselian	Sakmarian	Artinskian	Kungurian	Roadian	Wordian	Capitanian	Wuchiapingian	Changhsingian
Carboniferous		Permian								

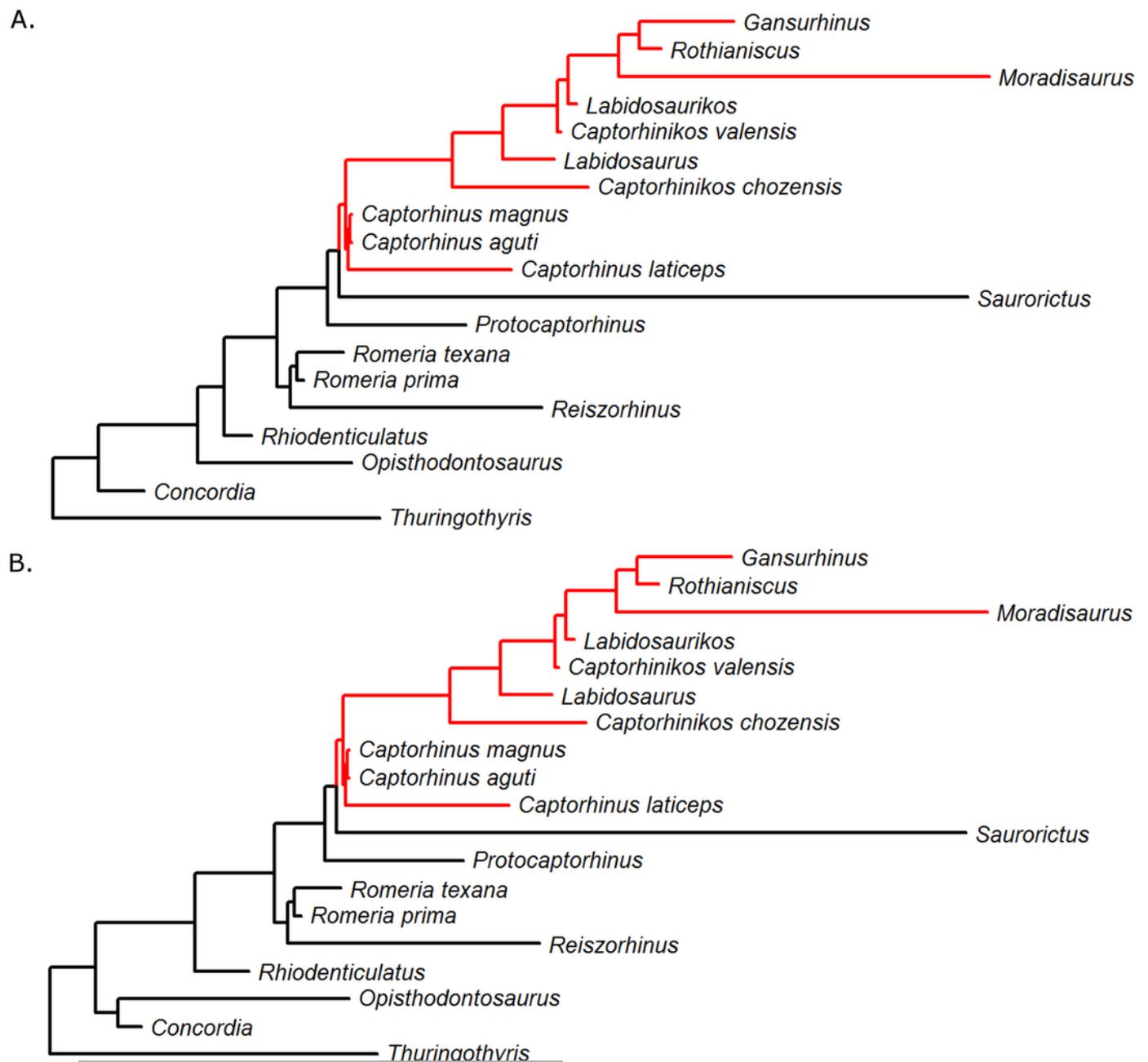
300   290   280   270   260

2

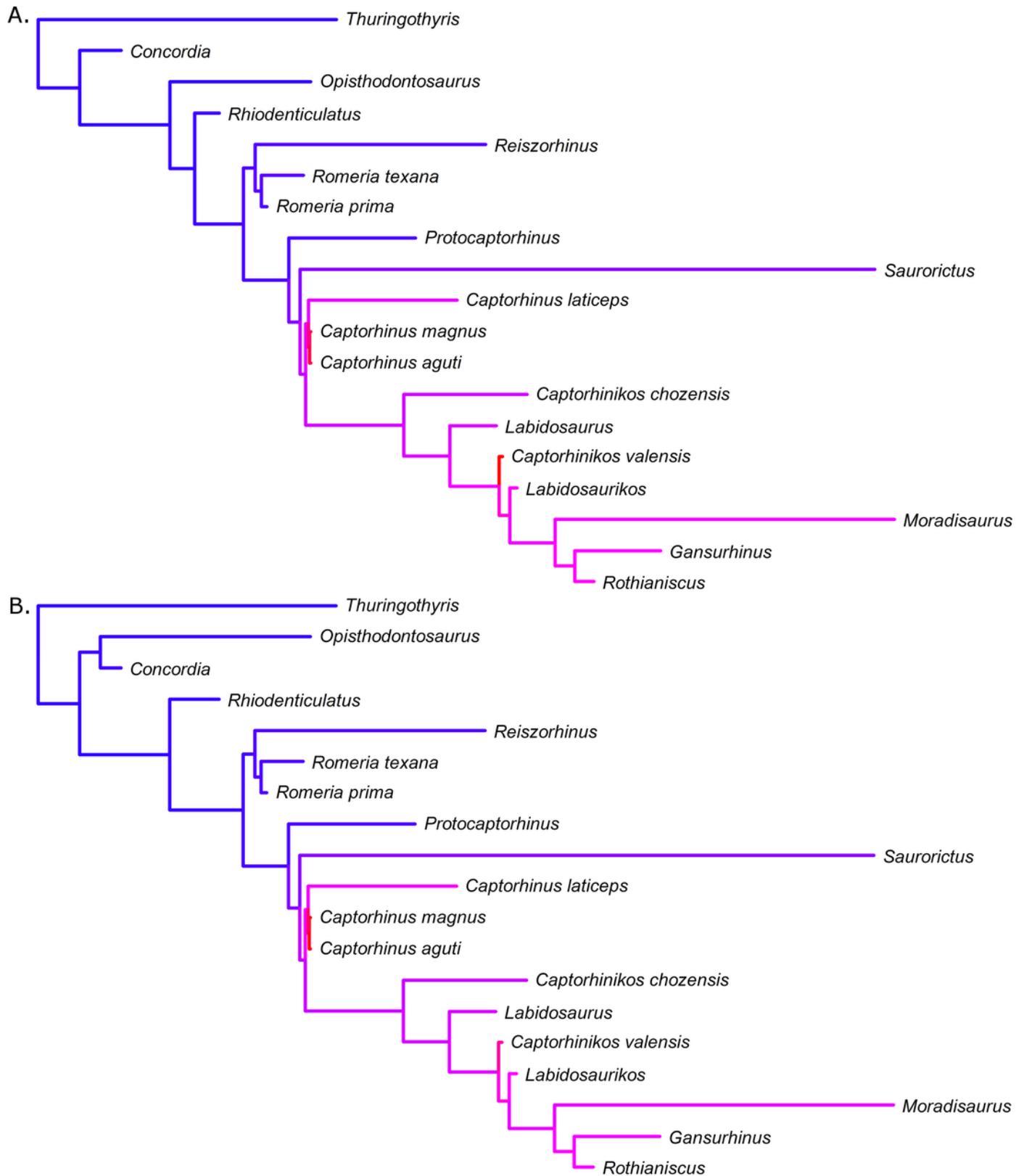
The fit of models of body sizeevolution to the phylogeny of Captorhinidae

Boxplots showing the distribution of 100 Akaike weight values calculated for each model representing the fit of each model of body size evolution to the 100 time calibrated phylogenies. A) Category 1 models (Evolution of body size alone). B) Category 2 models (coevolution of body size with herbivory. C) Category 3 models (evolution of body size with shifts in rate or mode at specified points in time). D) Comparison of the best fitting models from each of the three categories. The abbreviation Gzh, Sak, Kun and Roa represent the time at which the shift in rate/ mode occurred in the RS and EC models. Gzh – end of the Gzhelian; Sak – end of the Sakmarian; Kung – beginning of the Kungurian; Road – beginning of the Roadian. Other abbreviations as in the main text.

3

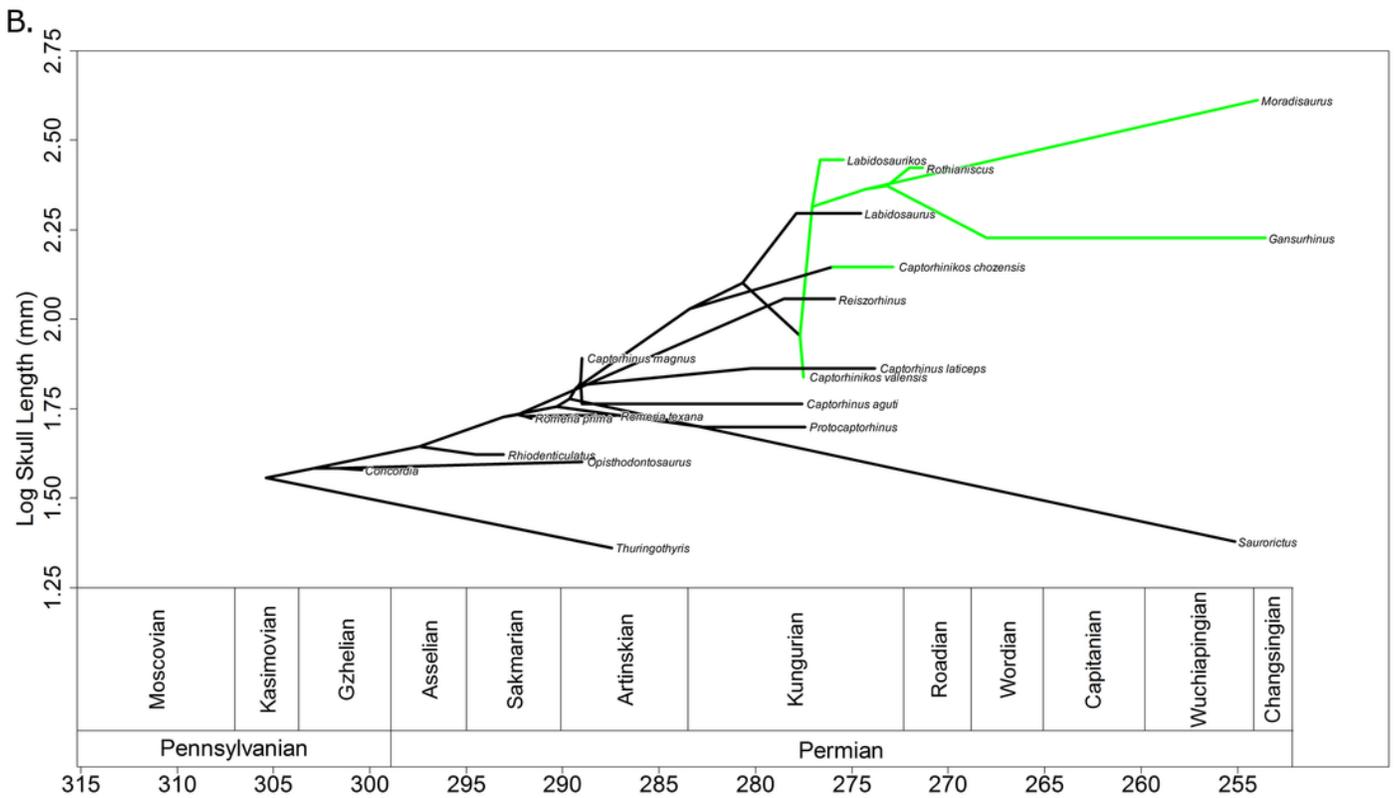
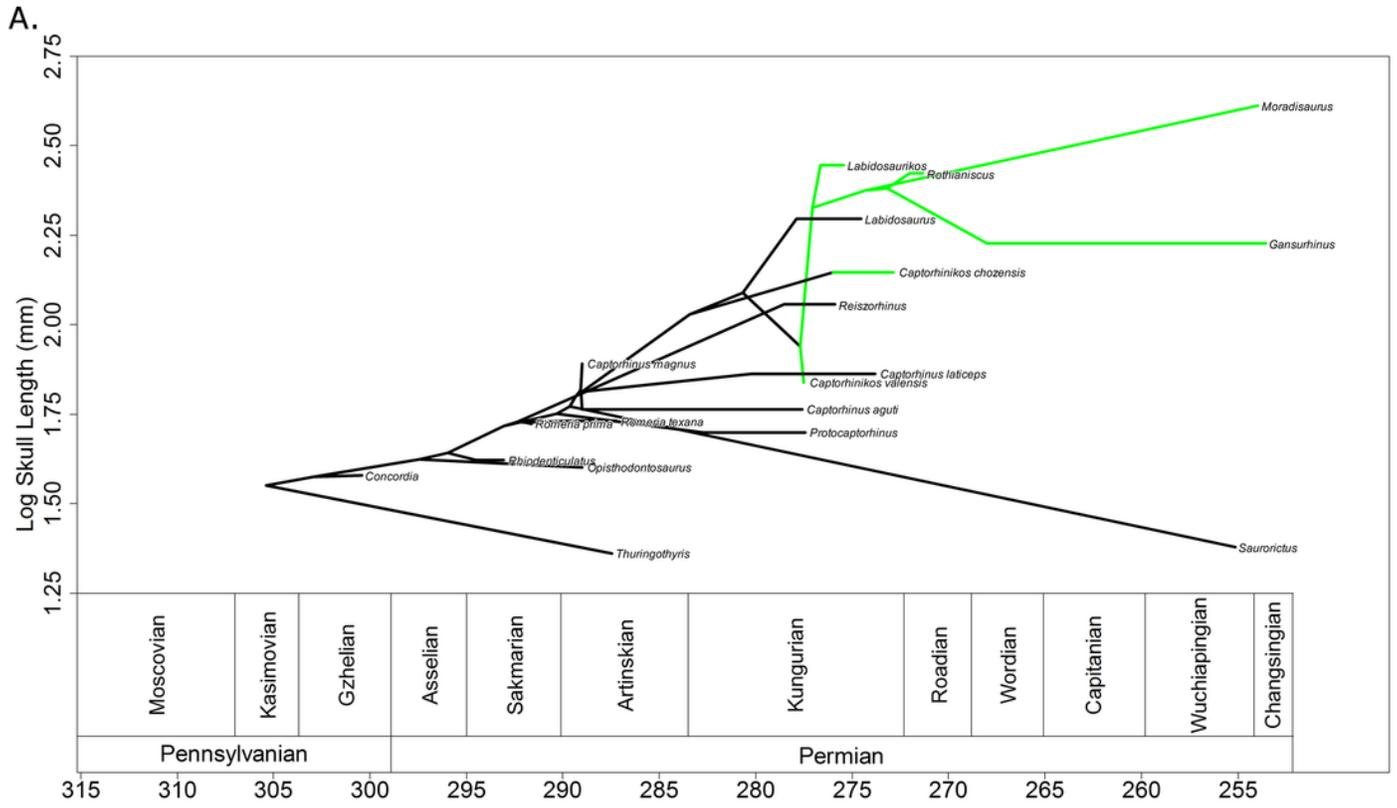
The shift in rate of body size evolution, identified by fitting the TM1 model to the phylogeny of Captorhinidae

Two of the 100 time calibrated phylogenies of Captorhinidae, with the location of the rate increase indicated by the red branches. The branch lengths here represent the time until the first appearance of the taxa. A) MPT 1. B) MPT 2

4

Variation in rates ofbody size evolution within Captorhinidae, illustrated as a heat map.

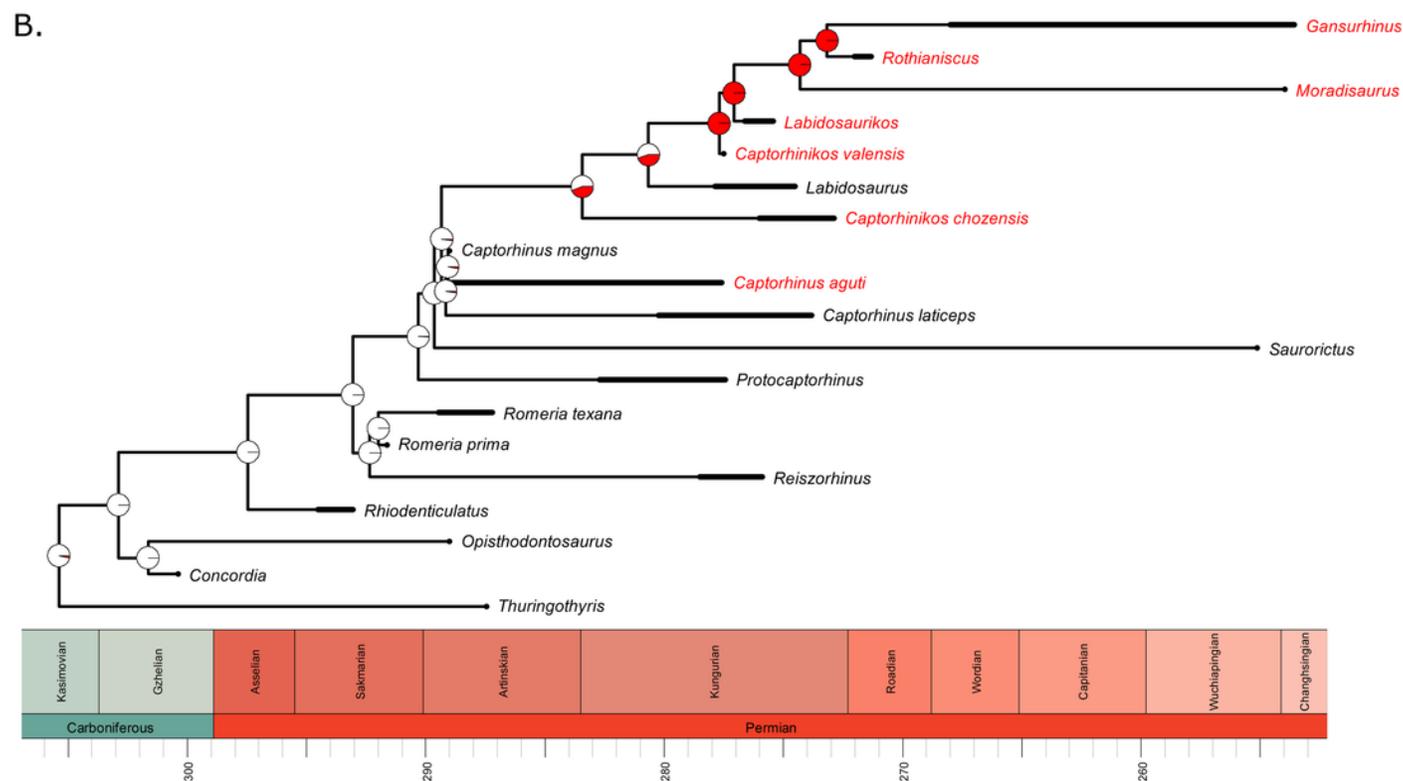
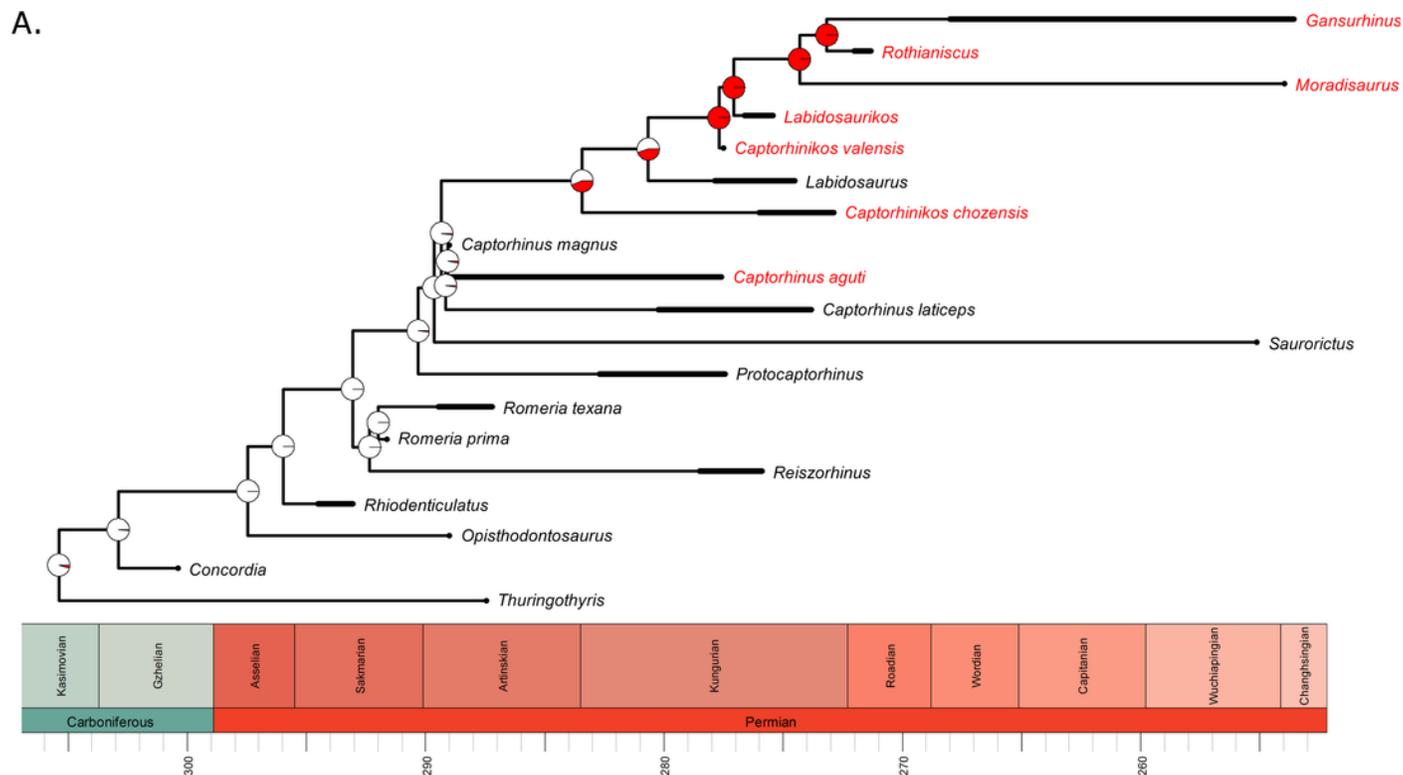
Two of the 100 time calibrated phylogenies of Captorhinidae, illustrating variation in rates of body size evolution identified using the method of Venditti et al. (2011). The branch lengths here represent the time until the first appearance of the taxa. A) MPT 1. B) MPT 2.

5

The evolution of body size through time of the Captorhinidae

Two of the 100 time calibrated phylogenies, illustrating both the age and inferred body size of each node. Ancestral body sizes are reconstructed using likelihood, assuming evolution by Brownian motion but scaling the branches to represent rate variation. Herbivorous lineages are coloured green. As the analyses do not take into account changes occurring within the observed ranges of the species, the observed ranges are here shown to experience no changes in body size. A) MPT 1. B) MPT 2.

The evolution of multiple toothrows in the Captorhinidae.

Two of the 100 time calibrated phylogenies used in this analysis. The tip labels in red indicate those taxa with multiple tooth rows. The pie charts represent the probability of an ancestral morphology including multiple tooth rows, deduced by maximum likelihood ancestral state reconstruction using the ace function in the R package ape. A) MPT 1. B) MPT 2.

A.

B.

Results of Mann Witney U tests

Values of W and p-values resulting from the Mann Whitney U test comparing rates of lineages evolving in different directions and under different dietary regimes

Comparison of rates	Sample size	Median of rates	W	P-value
Herbivorous branches decreasing in size vs Carnivorous branches decreasing in size	3 vs 9	4.144 vs 1.234	25	0.036
Herbivorous branches increasing in size vs Carnivorous branches increasing in size	9 vs 15	3.674 vs 1.308	104	0.029
Herbivorous branches increasing in size vs Herbivorous branches decreasing in size	9 vs 3	3.674 vs 4.144	22	0.146
Carnivorous branches increasing in size vs Carnivorous branches decreasing in size	9 vs 15	1.308 vs 1.234	52	0.379