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Figure #	Figure title One sentence only	Filename This should be the name the file is saved as when it is uploaded to our system. Please include the file extension. i.e.: <i>Smith_ED</i> <i>Fig1.jpg</i>	Figure Legend If you are citing a reference for the first time in these legends, please include all new references in the Online Methods References section, and carry on the numbering from the main References section of the paper.
Extended Data Fig. 1	Maximum parsimony strict consensus tree	Extended_Data_1.tif	Strict consensus of 16 MPT's recovered from maximum parsimony analysis , each with 1558 steps (consistency index 0.2356, retention index 0.5934, rescaled consistency index 0.1398). Figures above the nodes are Bremer support indices; figures below the nodes are bootstrap support indices. Bremer support below 2 or bootstrap support below 50 is omitted.
Extended Data Fig. 2	Bayesian maximum clade credibility tree (Mkv)	Extended_Data_2.tif	Maximum clade credibility tree recovered from Bayesian analysis using the non-time calibrated Mkv model . Figures adjacent to the nodes are the posterior probability value of the node.
Extended Data Fig. 3	Bayesian MCC tree (FDB) with node ages (median and 95% HPD)	Extended_Data_3.tif	Maximum clade credibility tree recovered from Bayesian analysis using the time calibrated fossilised-birth-death model with median node ages . Yellow horizontal bars represent 95% highest posterior density (HPD) interval at node age. Red figures adjacent to nodes are the median node ages. Abbreviations: Lopin. = Lopingian, Mid. = Middle, Miss. = Mississippian.

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Item	Present?	Filename This should be the name the file is saved as when it is uploaded to our system, and should include the file extension. The extension must be .pdf	A brief, numerical description of file contents. i.e.: <i>Supplementary Figures 1-4, Supplementary Discussion, and Supplementary Tables 1-4.</i>
Supplementary Information	yes.	Ford_Benson_2019_Supplementary_Information.pdf	Supplementary Discussion 1-3
Reporting Summary	yes	nr-reporting-summary.pdf	

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7 The phylogeny of early amniotes and the affinities of Parareptilia
8 and Varanopidae

9

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14

15

16 **Amniotes include mammals, reptiles and birds, representing 75% of**
17 **extant vertebrate species on land. They originated around 318 million**
18 **years ago (early late Carboniferous) and their early fossil record is**
19 **central to understanding the expansion of vertebrates in terrestrial**
20 **ecosystems. We present a new phylogenetic hypothesis that challenges**
21 **the widely-accepted consensus about early amniote evolution, based on**
22 **parsimony analysis and Bayesian inference of a new morphological**
23 **dataset. We find a reduced membership of the mammalian stem-lineage,**
24 **which excludes varanopids. This implies that evolutionary turnover of**
25 **the mammalian stem-lineage during the early/middle Permian transition**
26 **(273 Ma) was more abrupt than has previously been recognised. We also**
27 **find that Parareptilia are nested within Diapsida. This suggests that**
28 **temporal fenestration, a key structural innovation with important**
29 **functional implications, evolved fewer times than generally thought, but**
30 **showed highly variable morphology among early reptiles after its initial**
31 **origin. Our phylogeny also addresses controversies over the affinities of**
32 **mesosaurids, the earliest known aquatic amniotes, which we recover as**
33 **early-diverging parareptiles.**

34

35 The current paradigm of early amniote evolution was established in the late
36 20th century^{1,2}. It includes a deep crown-group dichotomy between Synapsida
37 (total-group mammals) and Reptilia (total-group reptiles, including birds),
38 followed by an early divergence of Parareptilia from all other reptiles

39 (Eureptilia)^{3,4}. More recent phylogenetic analyses have mostly focused on
40 relationships within subgroups^{e.g.5-7}. As such, interrelationships among major
41 groups, representing the deepest evolutionary divergences of amniotes, have
42 not been extensively tested for over a decade⁸, although some recent studies
43 have voiced uncertainties^{9,10}.

44
45 Patterns of temporal fenestration have been central to hypotheses of early
46 amniote evolution since the earliest studies¹¹ up to the present¹². Temporal
47 fenestrae are openings in the skull that are important attachment sites for jaw
48 closing (adductor) muscles¹³ and show substantial variation among extant
49 amniotes¹⁴. The origin of fenestration is linked to diversification of feeding
50 styles during the invasion of terrestrial ecosystems¹⁵. In the classical
51 paradigm, synapsids, including mammals, have a single temporal opening
52 whereas crownward Reptilia, including most extant reptiles, have two
53 openings (the 'diapsid' condition)¹⁶, and stem-group amniotes plus many early
54 reptiles, parareptiles and turtles, lack temporal openings altogether (the
55 'anapsid' condition)¹⁷. However, subsequent discoveries have complicated
56 this pattern. For example, many parareptiles possessed a single temporal
57 fenestra, located laterally^{18,19}, as a possible synapomorphy of the group²⁰.
58 Furthermore, both molecular and morphological studies have recovered
59 turtles, which lack fenestrae, as diapsids^{21,22,23}, implying the secondary loss of
60 both upper and lower fenestrae. This suggests that evolutionary patterns of
61 temporal fenestration are at least as labile as those of other skeletal traits.

62
63 We compiled a phylogenetic dataset of 294 discrete morphological characters
64 by comprehensive review and synthesis of previous studies, together with 21
65 new characters, drawn from across the skeleton. Unlike previous phylogenetic
66 studies^{2,3,12}, our character list codes occurrences of temporal fenestration
67 without imposing *a priori* hypotheses of homology between openings in the
68 skulls of distinct species (e.g. "Lateral temporal fenestra: absent (0), present
69 (1)"). As already recognised by some previous studies, this widespread
70 existing approach to coding temporal openings makes strong assumptions
71 that may impose bias on the results of phylogenetic analysis^{24,25}. To address
72 this, we use two suites of characters describing distinct, local observations of
73 similarity between the skulls of fenestrated taxa (see Methods). One suite
74 encodes the participation of key bone surfaces in temporal openings,
75 including both fenestrae and emarginations (which topologically are ventrally-
76 open fenestrae). The other encodes the contacts between key bone surfaces
77 on elements that typically surround temporal openings.

78
79 Our analysis includes 66 early fossil members of the amniote crown-group,
80 and four crownward members of the amniote stem-group, giving a total of 70
81 operational taxonomic units. The goal of our study is to examine the deep
82 divergences of the amniote crown-group. Therefore, our taxon sample
83 focuses on early-diverging and chronologically older members of crown-group
84 subclades. We excluded recumbirostrans from our analysis. Recumbirostrans
85 have generally been assigned to non-amniote microsaurids, but were recently
86 recovered as early crown-group amniotes²⁶. The possible relationship of
87 recumbirostrans with amniotes is of great interest. However, our dataset is

88 currently not suited to test their hypothesised affinities as it includes few non-
89 amniotes.

90

91 Our study uses parsimony analysis and two forms of Bayesian inference: (1)
92 analysis using the Mkv model of morphological character state evolution
93 (referred to as our 'Mkv' analysis); and (2) analysis using a relaxed Mkv
94 morphological clock model incorporating information on taxon ages using the
95 fossilised-birth-death process (referred to as our 'FBD' analysis) (see
96 Methods). We find a pattern of deep amniote divergences that is only broadly
97 consistent with previous work. Our discussion, below, emphasises important
98 topological differences that question our current understanding of early
99 evolutionary events on the lineages leading to both mammals and to crown-
100 group reptiles.

101

102 Results

103

104 All our analyses recover parareptiles + neodiapsids as a monophyletic group
105 within Diapsida (Fig. 1 and Extended Data 1–3). These findings differ sharply
106 from the current consensus in which parareptiles are the earliest diverging
107 reptiles, and are sister to a monophyletic Eureptilia comprising captorhinids,
108 'protorothyridids' and diapsids³. We instead find captorhinids as the earliest
109 diverging reptiles, with protorothyridids, araeoscelidians and varanopids as
110 successively more proximate clades to the group comprising parareptiles +
111 neodiapsids. We propose the name Neoreptilia for this group (Fig. 1), defined
112 as the most recent common ancestor of *Procolophon trigoniceps* Owen 1876
113 and *Youngina capensis* Broom 1914 plus all of its descendants. Neoreptilia is
114 supported by eight unambiguous synapomorphies, including a single median
115 embayment of the posterior skull margin (ch.5), the absence of caniniform
116 teeth (ch.31), a smooth posterior surface of the supraoccipital (ch.106), a
117 single coracoid ossification (ch.244) and subequal extensions of the distal
118 condyles of femur (ch.276). Bremer support for Neoreptilia is 2 (parsimony
119 analysis), and Bayesian posterior probabilities are 0.57 (Mkv) and 0.40 (FBD).

120

121 The hypothesis that parareptiles are sister to 'Eureptilia' requires between 19
122 and 48 additional steps compared to the most parsimonious trees (MPT)
123 returned by parsimony analysis (MPT length = 1558 steps; Extended data 1).
124 The null hypothesis that these trees are statistically equivalent to the MPTs is
125 statistically rejected ($p = 0.0002$ – 0.0117) or near-rejected, attaining marginal
126 non-significance when the basal captorhinid *Thuringothyris* is constrained to
127 be a member of Neoreptilia ($p = 0.0630$; based on non-parametric statistical
128 testing; see Supplementary Information 8). Hypothesis testing of the Mkv
129 analysis very strongly rejects the null hypothesis H_0 ($2 \times$ the marginal log
130 likelihood, or \log_e , = 11.64). The FBD analysis also rejects the null hypothesis
131 H_0 ($2 \times \log_e = 5.16$) (see Methods and Supplementary Information).

132

133 Our FBD analysis provides an estimated age of the basal divergence of
134 crown-group amniotes into Synapsida and Reptilia (the mammal/bird split) of
135 331–319 Ma (95% Highest Posterior Density; median = 324.51 Ma, see
136 Extended Data 3), pre-dating the earliest fossils (318 Ma)²⁷ and consistent
137 with the mean molecular clock divergence time estimate of 326 Ma (354-

138 311Ma)²⁸. We find a median divergence time estimate of parareptiles from
139 neodiapsids of 308.65 Ma, implying a ghost lineage of only 5 million years for
140 parareptiles, based on the age of the oldest known member of the group²⁹.
141 This compares to a ghost lineage of around 20 million years if parareptiles are
142 considered in their conventional position as the earliest diverging group of
143 reptiles.

144
145 We find Varanopidae, including the early Permian amniote *Orovenator*
146 *mayorum*, as sister to Neoreptilia (Fig. 1 and Extended Data 1-3). Varanopids
147 have long been considered as synsapsids^{12,30}, but we find good support for
148 varanopids as reptiles, with Bremer support of 5 and Bayesian posterior
149 probabilities of 0.99 (Mkv) and 0.95 (FBD) for the inclusive clade Varanopidae
150 + Neoreptilia. This clade is supported by ten unambiguous synapomorphies,
151 including a long, narrow posterolateral process of the frontal (ch.66), a narrow
152 temporal ventral bar (ch.74), an edentulous ectopterygoid (ch.145),
153 holocephalous trunk ribs (ch.225), the absence of a supraglenoid foramen
154 (ch.239), a poorly developed trochlea and capitellum of the humerus (ch.247)
155 and a low cnemial crest of the tibia (c.282). The hypothesis that varanopids or
156 that individual varanopid species are synsapsids requires between 27–34
157 additional steps in parsimony analysis and is rejected by both parsimony ($p =$
158 0.0003–0.0037) and Bayesian hypothesis testing methods, which are very
159 strongly in favour of the hypothesis that varanopids are nested within Reptilia,
160 ($2 \times \log_e \text{BF}$ for Mkv =41.12, for FBD = 12.74 - see methods and
161 Supplementary Information).

162
163 Our results provide strong posterior support for some hypothesised
164 relationships, including the monophyly of Amniota, Captorhinidae,
165 Araeoscelidia, Neodiapsida, and synsapsid subclades such as Caseasauria
166 and the clade of Ophiacodontidae + Edaphosauridae + Sphenacodontia (Fig.
167 1). However, we also find relatively weak support for some traditionally well-
168 established clades, such as Synsapsida and Parareptilia, and several nodes
169 along the reptilian stem-lineage, which have posterior probabilities <60% in
170 our FBD analysis (Fig. 1).

171 172 Discussion

173
174 The sister relationship between parareptiles and neodiapsids, and their
175 relationship to Varanopidae, implies a single origin of temporal fenestration
176 before the common ancestor of these clades (Fig.2). This reduces the number
177 of independent acquisitions of temporal fenestration inferred among major
178 groups of early amniotes from three implied by classical hypotheses^{1,3}
179 (independently in synsapsids, parareptiles and diapsids) to two (one in
180 synsapsids, one in diapsids; Fig. 2). Diapsids, including neoreptiles, most likely
181 represent a single origin of lateral temporal fenestration. Fenestral
182 morphology nevertheless shows considerable homoplasy in this group,
183 including changes to the surrounding bones, multiple origins or losses of the
184 upper temporal fenestra and subsequent losses of fenestration (Fig. 3; and
185 see^{25,31}). This contrasts with previous hypotheses, in which the distinct
186 morphologies of varanopid, parareptile and diapsid fenestrae were considered
187 to reflect their independent evolutionary origins.

188

189 Our tree implies that reptilian fenestration first appeared in Diapsida
190 (araeoscelidians + varanopids + neoreptiles) as a lateral opening with
191 participation of the squamosal, jugal, postorbital, and possibly quadratojugal
192 (Fig. 3). The absence of this opening in the chronologically late araeoscelidian
193 *Araeoscelis* suggests a secondary loss³² (though alternatively this opening
194 might have originated in varanopids + neodiapsids with independent
195 acquisition in the early araeoscelidian *Petrolacosaurus*). The lateral opening
196 was retained in most younger diapsids, with independent reductions or losses
197 in several groups of parareptiles: millerettids, mesosaurids, nycteroleterids
198 and pareiasaurs. An upper opening is present in Neodiapsida, is possibly in
199 the varanopid *Orovenator* (in which the temporal region is incomplete³³), and
200 is present in araeoscelidians, resulting in an early example of a 'diapsid'
201 condition in *Petrolacosaurus*³⁴ that is likely only analogous to the condition in
202 neodiapsids. The lower temporal opening was further modified by loss of the
203 lower temporal bar in neodiapsids, resulting in a widespread 'euryapsid'
204 condition that might be primitive for crown-group reptiles³¹. Loss of the lower
205 temporal bar also occurred in procolophonoid parareptiles (Fig. 3; owenettids
206 + procolophonids). Other modifications of fenestral patterns are present in
207 both reptiles and synapsids, including the appearance of an accessory
208 fenestra in ophiacodontid synapsids^{30,35}, and partial division of the lower
209 opening in the parareptile *Delorhynchus cifelli*³⁶ (Figs 2-3).

210

211 Extensive variation in early reptile fenestration during a short interval of their
212 early evolution is striking. This is especially true by comparison to its apparent
213 conservatism in many younger groups, including major clades of extant
214 amniotes such as mammals, birds and crocodylians. Distinct aspects of
215 fenestra morphology correspond to different sites of muscle attachment and
216 have implications for jaw function and therefore feeding^{13,14,37}. High early
217 variation in reptilian temporal fenestration from a single ancestor may
218 therefore be a key aspect of the early ecological diversification of reptiles.
219 How this occurred could be partly explained by recent observations of large
220 variation in fenestra morphology during post-hatching ontogeny in some early
221 reptiles. For example, the lateral temporal fenestra becomes subdivided by a
222 posterior extension of the jugal during ontogeny in the parareptile
223 *Delorhynchus cifelli*³⁶, and the anterior extension of the supratemporal
224 increases in size during ontogeny of *Eunotosaurus africanus*, encroaching
225 into and substantially reducing the size of the upper temporal fenestra²³. In
226 light of this, it is possible that heterochrony, involving modifications of post-
227 hatching ontogenetic changes in morphology, played an important role in
228 facilitating early evolutionary transitions between morphologically distinct
229 patterns of fenestration, including both closure of a subdivision of temporal
230 fenestrae.

231

232 The affinities of the secondarily aquatic Mesosauridae, represented by the
233 genera *Mesosaurus* and *Stereosternum* in our analysis, have been
234 controversial. Recent analyses have found mesosaurids as either a sister to
235 all other reptiles or as parareptiles^{9,10}. We recover mesosaurids as
236 parareptiles in all analyses, and under all interpretations of their pattern of
237 temporal fenestration (Fig. 1 and Extended Data 1-3; also see Supplementary

238 Information). Our results are consistent with both previous hypotheses, either
239 that mesosaurids possessed temporal fenestrae or that they represent an
240 early example of secondary loss of fenestration in parareptiles.

241

242 The sister relationship of neodiapsids and parareptiles in our analyses may
243 have intriguing implications regarding hypotheses of turtle origins (also see
244 ref.⁹). These have been highly debated, with conflicting hypotheses arising
245 from palaeontological^{24,38,39,40} and molecular phylogenetic analyses.
246 Molecular studies provide strong evidence that turtles are the sister of
247 Archosauromorpha, and therefore deeply nested within Neodiapsida^{21,22} (see
248 position of crown-group reptiles as indicated on Fig. 3). Most recently, the
249 middle/late Permian *Eunotosaurus africanus*, which was earlier regarded as a
250 parareptile^{41,42}, has been proposed as a stem-group turtle²³ and the affinities
251 of *Eunotosaurus* are therefore of pivotal interest. If *Eunotosaurus* indeed is a
252 parareptile (and therefore not a neodiapsid) then it cannot be a stem-group
253 turtle, unless current molecular studies^{21,22} are shown to be in error. The
254 taxon sample of our dataset is not yet sufficient to address this issue, which
255 we believe requires more detailed morphological study of both parareptiles
256 and *Eunotosaurus*. Furthermore, since we assume a monophyletic reptilian
257 crown-group within Neodiapsida, our topology has no implications for the
258 timing of the origins of the reptile crown group (Lepidosauromorpha
259 +Testudinata + Archosauromorpha).

260

261 The extinction of most ‘pelycosaur’-grade synapsids in the late early Permian
262 (Cisuralian), and their replacement in global faunas by therapsids in the early
263 middle Permian (Guadalupian)⁴³, involved wholesale turnover of evolutionary
264 lineages following a long period of around 30 million years in which
265 pelycosaurids were abundant (late Carboniferous–early Permian). This was a
266 transformative event in the evolution of terrestrial ecosystems, and of the
267 mammalian stem-lineage⁴⁴. Understanding of this transition is complicated by
268 the geographic structure of the fossil record: ‘pelycosaur’-yielding fossil sites
269 of the Cisuralian are exclusively at low palaeolatitudes in warm ever-wet
270 environments whereas therapsid-rich assemblages of the Guadalupian are
271 predominantly from temperate palaeolatitudes^{44,45,46,47}. Furthermore, the
272 enigmatic early Permian synapsid *Tetraceratops insignis* has been identified
273 either as the earliest-diverging therapsid^{48,49} or as a non-therapsid
274 sphenacodontian^{50,51}. *Tetraceratops* may therefore indicate the occurrence of
275 therapsids late in the early Permian, which is also indicated by the timing of
276 the therapsid ghost-lineage, although it does not on its own suggest
277 substantial diversification of therapsids prior to the middle Permian.

278

279 Two groups that have typically been regarded as pelycosaur-grade synapsids
280 co-occur with therapsids in the Guadalupian: caseids, with a short temporal
281 duration in the early Guadalupian and varanopids, which persisted to the
282 latest Guadalupian⁵². Our finding that varanopids are not synapsids therefore
283 substantially reduces the duration of ‘eupelycosaur’ co-occurrence with
284 therapsids in these biota to a short interval at the start of the middle Permian
285 (Fig. 4). This makes the Cisuralian–Guadalupian turnover event more
286 pronounced than was previously recognised (by e.g. ^{43,44}).

287

288 The origin of amniotes was a landmark event in the evolution of terrestrial
289 ecosystems, providing a foundation for the tremendous ecological diversity of
290 extant land vertebrates^{53,54}. Taken together, our findings suggest that reptiles
291 achieved greater diversity than previously recognised in the early Permian,
292 and challenges the existing narrative of early amniote classification and
293 evolutionary history. Improved resolution of the deep phylogenetic
294 divergences among amniotes will enable more detailed characterisation of the
295 dynamics of this evolutionary radiation and of the origins of well-defined
296 reptilian groups that persist to the present.

297 Methods

298
299 **Phylogenetic analysis.** This was performed using both maximum parsimony
300 and Bayesian inference. Both methods were used in order to present a fully
301 comprehensive series of results, particularly in light of recent conflicting
302 opinions on the comparative performance of both methods for discrete
303 morphological datasets^{55,56,57,58}. Furthermore, the estimation of branch
304 lengths derived from Bayesian analysis using a fossilised birth-death (FBD)
305 model (see below) can offer insights into macroevolutionary patterns and the
306 timing of major evolutionary divergence, and have been used in this study to
307 estimate rates of evolution. The topologies recovered using both maximum
308 parsimony analysis and Bayesian inference are fundamentally similar in
309 respect to higher taxonomic levels, although several differences are evident
310 (see Fig.1 and Extended data 1-3).

311 **Construction of morphological dataset.** We compiled a comprehensive
312 taxon list, encompassing a broad range of early amniotes, with the aim of
313 resolving relationships among higher taxonomic groups. The sample was
314 focused on the basal chronologically early members of each clade (see on-
315 line data). In total, 70 taxa were selected, including 4 species of stem-group
316 amniotes (*Gephyrostegus*, *Seymouria*, and the diadectomorphs *Tseajaja* and
317 *Limnoscelis*) and 66 species that have previously been considered as crown-
318 group amniotes. Most operational taxonomic units (OTUs) were selected at
319 species level, with six taxa considered at the generic level to improve scoring
320 completeness (*Seymouria*, *Ophiacodon*, *Dimetrodon*, *Araeoscelis*,
321 *Proterosuchus* and *Romeria*). All OTUs are Carboniferous or Permian in age,
322 with the exception of those representing archosauromorphs (*Prolacerta*
323 *broomi* and *Proterosuchus* spp) and procolophonoids (*Procolophon*
324 *trigoniceps* and *Owenetta kitchingorum*), from the earliest Triassic, and
325 *Candelaria barbouri*, from the Ladinian, Middle Triassic. All OTUs were scored
326 for 294 discrete characters, and all characters are parsimony informative,
327 although limited non-parsimony informative scoring has been retained in
328 some multistate characters for information purposes. The character list was
329 assembled by undertaking a comprehensive review of key phylogenetic
330 studies on stem-amniotes⁵⁹, early amniotes^{1,2,3}, early
331 synapsids^{60,61,62,63,64,65,66}, parareptiles^{67,68,69}, diapsids^{70,71,72,73,74} and
332 captorhinids^{75,76,77,78}. There are 21 new characters; eight
333 (75,76,77,85,86,89,90,95) represent a novel series of characters describing
334 temporal fenestration and emargination, together with seven new characters
335 of the mandible (165,176,177,175,182,196,197), three of the palate

336 (134,135,139) and one each for the maxilla (40), prefrontal (62) and manus
337 (266). The new characters, together with the characters derived from previous
338 studies, were compiled in to a single database from which 294 characters
339 were selected, with the omission of similar or redundant characters, or those
340 that were parsimony uninformative. There are 55 multistate characters, all of
341 which are unordered. Equal weighting was applied across all characters. A full
342 character list with annotations on their use in previous analyses, optimisation
343 and, where appropriate, explanatory comments are provided in the on-line
344 data package, along with a character-taxon matrix.

345 **Parsimony analysis.** This was performed in TNT v.1.5-beta⁷⁹, using the new
346 technology driven search with sectorial, drift and tree fusing algorithms, set at
347 an initial level of 100, with 1000 random additional sequences and the
348 minimum tree length searched for 100 times. *Gephyrostegus bohemicus* was
349 set as the out-group. No constraints were applied to the original analysis. The
350 resulting 18 most parsimonious trees (MPTs) of 1558 steps were then
351 subjected to an additional round of tree bisection reconnection (TBR) branch
352 swapping, with no additional trees recovered. Decay indices (Bremer support)
353 also were calculated in TNT v.1.5-beta. Bootstrap analysis (100 replicates, full
354 heuristic search) was performed using PAUP*v.4.0a for Macintosh⁸⁰. Since
355 the setting in TNT in respect to character optimisation is restricted to
356 unambiguous synapomorphies (i.e. where ACCTRAN and DELTRAN agree),
357 the parsimony analysis was also performed in PAUP*v.4.0a, using a heuristic
358 search and TBR, with 1000 random additional replicates, resulting in 18 MPTs
359 of 1558 steps. The ACCTRAN/DELTRAN optimisations of character states
360 were subsequently produced, which are detailed in Supplementary Data. The
361 retention index (RI), consistency index (CI) and rescaled consistency index
362 (RCI) were also calculated in PAUP*v.4.0a. The tree topology, tree length and
363 number of MPTs recovered in PAUP*v.4.0a were identical to those recovered
364 in TNT v.1.5-beta. The nexus file for the character-taxon matrix is provided in
365 the on-line data package.

366 **Non-time calibrated Bayesian analysis.** We performed a Bayesian analysis
367 using the Mkv model with the new dataset of 294 discrete morphological
368 characters and 70 OTUs, using MrBayes v3.2.6⁸¹. The 'standard' datatype
369 was used for morphological data, and the coding was set at 'variable', i.e. only
370 variable characters being sampled, with rates set to a gamma distribution
371 (alpha=1). Gamma distribution modifies the Mkv substitution model to allow
372 variation in the rates of evolution among characters⁸². The alpha parameter
373 determines one aspect of the shape of the gamma distribution.
374 *Gephyrostegus* and *Seymouria* were constrained as the out-group taxa. The
375 Mkv model analysis was performed with 2 runs of 4 chains each (one 'cold',
376 three 'heated'), with temperature set at 0.10. The analysis was run for 50
377 million generations, sampling every 500th generation, with a burn-in of the
378 first 2,500 sampled trees (25%). The effective sample size (ESS) for the two
379 parameters (Tree Length and shape of gamma distribution) were in excess of
380 60,000, and the average potential scale reduction factor (PSRF) was < 1.001.
381 Scripts for all Bayesian analyses are available in the on-line data package.

382 **Time calibrated Bayesian analysis with Fossilised-Birth-Death model.**

383 We performed a second Bayesian phylogenetic analysis on the new amniote
384 dataset with a Fossilised-Birth-Death prior^{83,84}, using a relaxed clock model
385 (rates=gamma, coding=variable, clockvarpr=igr). The ages of all OTUs were
386 specified using a uniform distribution (see on-line data for age ranges).
387 Options specifying proportional sampling of extant taxa (sampleprob) were
388 omitted since the analysis is limited to fossil data. The setting for the tree age
389 prior, the age of the most recent common ancestor of the tree, was set to
390 offsetexponential (x,y), where x is the oldest fossil in the taxon list (*Hylonomus*
391 *lyelli* 318.1 Ma), and y the mean density of the cumulative density function
392 between the oldest taxon and earliest putative date of the appearance of a
393 common tree ancestor (in this case the earliest Carboniferous, 358.9 Ma).
394 Two runs, each consisting of 4 chains at a temperature of 0.10, were
395 performed for 50 million generations, and sampled every 500th generation,
396 with a burn-in of the first 2,500 sampled trees (25%). The ESS was greater
397 than 200 for all tested parameters and an average PSRF was < 1.001 on all
398 parameters.

399 **Constraint analysis – parsimony.** A series of additional parsimony analyses
400 were run, which included topological constraints, to compare tree lengths of
401 alternative phylogenetic hypotheses. Pairwise Templeton tests were used to
402 statistically compare the topologically-constrained analyses to the most
403 parsimonious trees. The Templeton test is a non-parametric statistical test
404 (Wilcoxon signed-rank test) adapted to phylogenetic data⁸⁵. It uses a critical
405 threshold applied to the P-value (P=probability) to accept or reject the null
406 hypothesis that both topologies are statistically equivalent explanations of the
407 data. The rejection of the null hypothesis (with a critical one-tailed p-value
408 below 0.05) implies that the most parsimonious tree topology is a (statistically)
409 significantly better explanation of the data than the constrained tree topology.
410 Templeton tests for a one-tailed P-value were performed in PAUP* v.4.0a for
411 Macintosh⁸⁰. The phylogenetic hypotheses (null hypotheses) tested by this
412 method were (i) all varanopids, including *Orovenator*, are positioned within a
413 monophyletic Synapsida (i.e. to the group containing caseosaurs +
414 ophiacodontids + edaphosaurids + sphenacodontians), (ii) captorhinids are
415 recovered as the sister taxon to ‘protorothyridids’ + diapsids within a
416 monophyletic Eureptilia (see Supplementary Information for further details).
417

418 **Constraint analysis – Bayesian inference.** We tested hypotheses of
419 monophyly in various groups by calculating the marginal log likelihoods of
420 constrained topologies for each phylogenetic hypothesis, using the stepping-
421 stone sampling method⁸⁶ in MrBayes v3.2.6⁸¹. We used equally informed
422 priors on topology space for both the H₀ and H₁ models, as suggested by ref
423 ⁸⁷, to avoid bias towards the constrained analysis. The alternative hypotheses
424 tested were the same as those detailed under parsimony above. Interpretation
425 of the results, based on 2 x log_e BF, is in accordance the guidelines of ref ⁸⁸
426 (see Supplementary Information for further details).
427

428 Author contributions

429

430 DPF and RBBJ conceived the project. DPF collected the data and conducted
431 the phylogenetic analysis and hypothesis testing. DPF and RBBJ designed
432 and produced the figures. DPF and RBBJ wrote the manuscript.
433

434 Data availability: The data used in this study, including the character list,
435 character/taxon matrix, full taxon list with sources and missing data metrics,
436 age range notes for the FBD analysis and the NEXUS and Bayesian scripts
437 have been archived and are available via Dryad on-line data storage¹⁰⁴. All
438 other data supporting the findings of this study are available in the
439 Supplementary Information file.
440

441 Competing interests: The authors declare no competing interests.
442

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795 Figure legends

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798 Figure 1

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800 **Fig.1. Maximum clade credibility tree recovered from Bayesian analysis**
801 **using the time calibrated fossilised-birth-death model.** Figures adjacent to
802 nodes are the posterior probability value of the node. Abbreviations: Lopin. =
803 Lopingian, Mid. = Middle, Miss. = Mississippian.

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807 Figure 2

808 **Fig. 2. Phylogeny of major clades of early amniotes, showing two origins**
809 **of temporal fenestration in synapsids (green) and reptiles (magenta).**

810 Topology based on all analyses. Key to skull elements: green=jugal,
811 magenta=quadratojugal, yellow=squamosal, blue=postorbital,
812 orange=parietal. Figures adjacent to nodes are posterior probabilities for
813 Bayesian analyses: Mkv non-time calibrated/FBD. UTF=upper temporal
814 fenestra. Diagrams of amniote skulls are not to scale and have been redrawn
815 based on the following reconstructions: *Seymouria*⁸⁹, *Limnoscelis*⁹⁰,
816 *Varanosaurus*³⁵, *Edaphosaurus*⁶³, *Dimetrodon*³⁰, *Eothyris*⁹¹, *Ennatosaurus*⁹²,
817 *Captorhinus*⁹³, *Protorothyris*⁹⁴, *Petrolacosaurus*³⁴, *Araeoscelis*³²,
818 *Archaeovenator*⁶⁴, *Aerosaurus*⁹⁵, *Millerosaurus*⁹⁶, *Acleistorhinus*⁶⁷,
819 *Youngina*⁹⁷, *Claudiosaurus*⁹⁷.

820

821 Figure 3

822 **Fig. 3. Phylogeny of early reptiles, showing changes in temporal**
823 **fenestration.** Topology based on all analyses. Key to skull elements:
824 green=jugal, magenta=quadratojugal, yellow=squamosal, blue=postorbital,
825 orange=parietal, purple=supratemporal. Diagrams of amniote skulls are not to
826 scale and have been redrawn based on the following reconstructions (where
827 not cited in Fig. 2): *Orovenator*⁹⁸, *Mycterosaurus*⁹⁹, *Belebey*⁶⁸, *Mesosaurus*⁹,
828 *Macroleter*¹⁰⁰, *Emeroleter*¹⁰¹, *Candelaria*¹⁰², *Nyctiphruetus*¹⁰³, *Milleretta*⁹⁶,
829 *Colobomycter*⁶⁹, *Delorhynchus*¹⁹.

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833 Figure 4

834 **Fig. 4. Phylogeny of major clades of early amniotes showing wholesale**
835 **turnover of the mammalian total-group (Synapsida) during the early–**
836 **middle Permian transition.** The duration of coexistence between
837 ‘eupelycosaur’ and therapsids is reduced by the finding that varanopids are
838 reptiles and not synapsids. Synapsid lineages are shown in green, diapsids in
839 magenta.

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