

Wright & Wagner

Quantitative Phylogenetic Models of Punctuated Change

1 Quantitative Models for Distinguishing Punctuated and Continuous-Time Models

2 of Character Evolution and Their Implications for Macroevolutionary Theory.

3 April M. Wright

4 Peter J. Wagner

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6 RRH: PUNCTUATED CHANGE AND PHYLOGENY

7 LRH: APRIL M. WRIGHT & PETER J. WAGNER

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9 *April M. Wright, Department of Biological Sciences, Southeastern Louisiana*
10 *University. Hammond, Louisiana 70402*

11
12 *Peter J. Wagner, Department of Earth & Atmospheric Sciences, and School of*
13 *Biological Sciences. 316 Bessey Hall, University of Nebraska, Lincoln USA 68588.*
14 *Email: pjwagner3@gmail.com*

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16 **Non-technical Summary**

17 Punctuated Equilibrium predicts a distribution of anatomical change that is
18 fundamentally different from the models used in studies of relationships among
19 species. We present a model to assess relationships that assumes punctuated
20 change. We apply this model to a dataset of strophomenoid brachiopods to
21 demonstrate that a model of punctuated change fits better than a model of
22 continuous-time (“phyletic gradualism”) change in this group. Notably, because the
23 punctuated model posits elevated speciation rates early in the strophomenoid
24 history, the model also posits elevated rates of change among the early
25 strophomenoids relative to later ones. This corroborates notions for what causes
26 bursts of anatomical evolution rooted in ecological theory rather than evolutionary
27 developmental theory. More basically, it emphasizes that paleontologists should
28 consider both punctuated and continuous-time models when assessing relationships
29 and other aspects of macroevolutionary theory.

30

31 **Abstract**

32 The recent proliferation of quantitative models for assessing anatomical character
33 evolution all assume that character change happens continuously through time.

34 However, punctuated equilibrium model posits that character change should be
35 coincide with cladogenetic events, and thus should be tied to origination rates.
36 Rates of cladogenesis are important to quantitative phylogenetics, but typically
37 only for establishing prior probabilities of phylogenetic topologies. Here, we
38 modify existing character likelihood models to use the local cladogenesis rates
39 from Bayesian analyses to generate the amounts of character change over time
40 dependent on origination rates, as expected under the punctuated equilibrium
41 model. In the case of strophomenoid brachiopods strop from the Ordovician, we
42 find that Bayesian analyses strongly favor punctuated models over continuous-time
43 models, with elevated rates of cladogenesis early in the clade's history inducing
44 frequencies of change despite constant rates of change per speciation event. This
45 corroborates prior work proposing that the early burst in strophomenoid disparity
46 reflects simply elevated speciation rates, *which in turn* has implications for
47 seemingly unrelated macroevolutionary theory about whether early bursts reflect
48 shifts in intrinsic constraints or empty ecospace. Future development of punctuated
49 character evolution models should account for the full durations of species, which
50 will provide a test of continuous change rates. Ultimately, continuous change vs.
51 punctuated change should become part of phylogenetic paleobiology in the same
52 way that other tests of character evolution currently are.

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Introduction

Eldredge and Gould's (1972) proposal that anatomical change commonly is "punctuated" rather than distributed continuously through time inspired a flurry of research. Although early research focused on particular case studies documenting examples of gradual (e.g., Gingerich 1979; Sheldon 1996) or punctuated (Cheetham 1986; Polly 1997) change, more recent studies have focused on the ubiquity of punctuation and stasis relative to continuous, anagenetic change (e.g., Hunt 2013; Hunt et al. 2015). Other work focused on the implications of punctuated change for the interface between macroevolution and processes such as selection (e.g., Lande 1976). However, the macroevolutionary implications of punctuated vs. continuous-time models go beyond how speciation itself works. This was first realized for trends over time (Eldredge and Gould 1972; Stanley 1975), as state-dependent origination and extinction rates (i.e., species selection *sensu lato*) can induce the same patterns as frequent shifts to particular conditions. The possibility of punctuated change has necessary implications for patterns of morphological evolution: punctuated change coupled with elevated cladogenesis rates should induce rapid increases in disparity and apparently high rates of anatomical change per million years even if the rates of change per speciation event remain constant (Foote 1996b; Congreve et al. 2021).

That macroevolutionary implications of punctuated change dovetail into methodological implications for how we conduct phylogenetic analyses with anatomical data. This goes beyond the co-occurrence of ancestor and descendant species that led to the initial recognition of punctuated equilibrium (Eldredge 1971) or the expected differences in tree-shapes that we expect from punctuated equilibrium and continuous-time models of character change (Wagner and Erwin 1995). Quantitative phylogenetic methods consider not only topologies, but also rates of change and divergence times (e.g., Lewis 2001). Rates of cladogenesis are important in Bayesian phylogenetic analyses: but to establish prior probabilities of divergence times and tree shapes (e.g., Heath et al. 2014), not for evaluating character evolution. Under punctuated models, cladogenesis rates would also affect the likelihoods of character change rates and divergence times simply because even if a rate-of-change parameter remains constant, then the expected amount of change over two different branches with the same duration t will be different if those two branches span intervals with different cladogenesis rates. Innumerable paleobiological studies suggest that cladogenesis rates vary substantially over time (e.g., Foote et al. 2018; Foote 2023; Foote et al. 2024). It is already standard

91 practice for phylogenetic studies to consider a range of possible models of
92 character evolution and diversification simply because we cannot know in advance
93 which set of assumptions maximizes the probability of our observed data or our
94 possible inferences (see, e.g., Wright et al. 2021). Thus, even if speciation models
95 are not a focus of a study that we are conducting, then speciation models might still
96 represent an important nuisance parameter that we need to accommodate to test
97 seemingly unrelated macroevolutionary hypotheses.

98
99 We have three goals in this paper. First, we shall elaborate upon a punctuated
100 analog to the Mk model (Lewis 2001) that is commonly used in phylogenetic
101 studies (see also Wagner and Marcot 2010). We will also present means of
102 applying this to existing Bayesian phylogenetic packages such as RevBayes
103 (Höhna et al. 2016). Second, we will then apply this approach to Ordovician
104 strophomenoid brachiopods (Congreve et al. 2015), which represents a clade
105 displaying an early burst of disparity that coincides with elevated rates of
106 cladogenesis. We will use this example to examine the possible implications of
107 punctuated change models when testing “intrinsic constraint” vs. “empty
108 ecospace” explanations for early bursts (Congreve et al. 2021). Third and finally,
109 we will discuss how future alterations of phylogenetic methods might take into
110 account the stasis component of punctuated equilibrium.

111 112 **Methods**

113 *Continuous-Time vs Punctuated Change in Phylogenetic Models*

114 Macroevolutionary theory and systematic methods often represent two sides of the
115 same coin: most (if not all) conflicting ideas about ways in which organisms
116 evolve predict different relationships between phylogeny and observable data.
117 Models of character evolution exemplify this. The most common method for
118 anatomical data is Lewis’ (2001) Mk model. Here, the likelihood of a specific
119 combination of relationships, diversification times and rate of change is the
120 Poisson probability of net stasis or ultimately transitioning to another state is given
121 by:

$$122 \quad e^{Qc} \quad \text{(eqn. 1)}$$

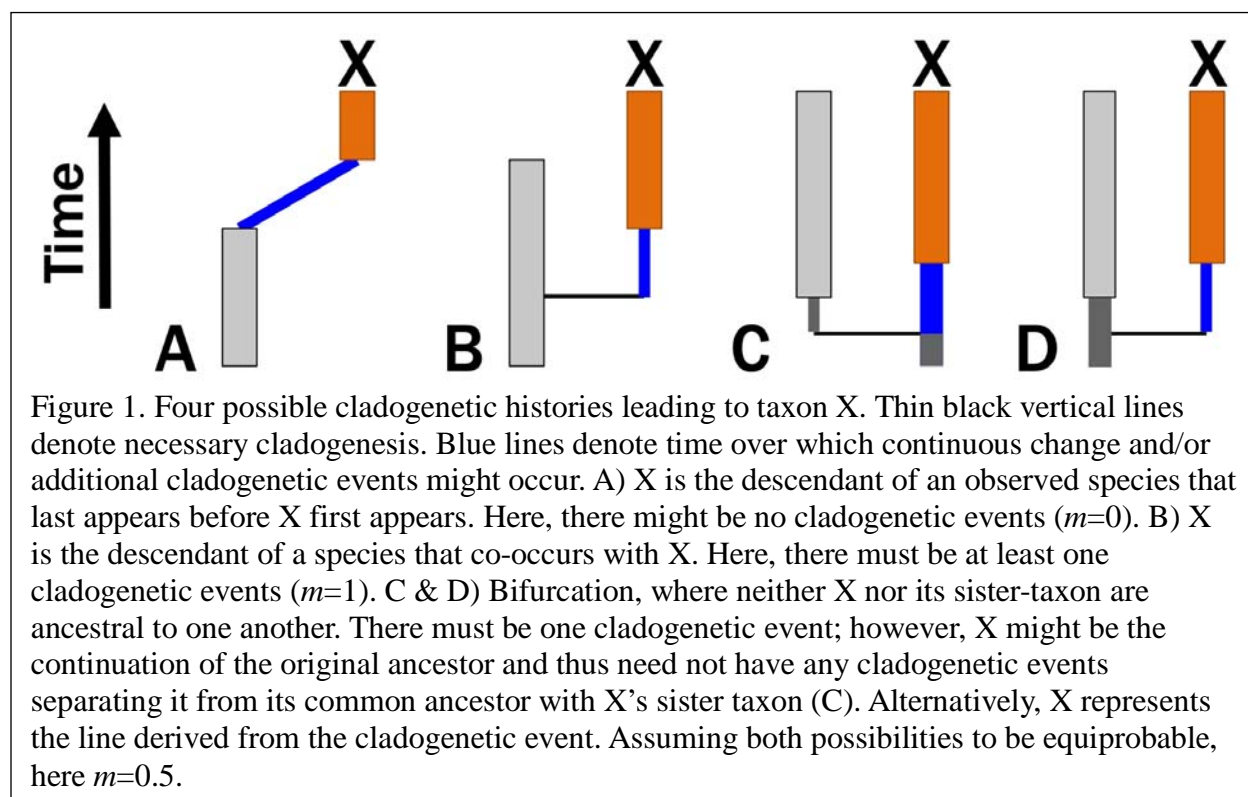
123 where Qc in its simplest form is a transition matrix:

$$124 \quad Q_C = t \times \begin{pmatrix} -\alpha & \alpha & \alpha \\ \alpha & -\alpha & \alpha \\ \alpha & \alpha & -\alpha \end{pmatrix} \quad \text{(eqn. 2)}$$

125 with t being the amount of time over which a character might change (e.g., the
126 span between a divergence time and the first appearance of a taxon), α is the
127 instantaneous (Poisson) rate of change, and αt therefore is the expected amount of
128 change. (It is unnecessary to place t outside of the matrix and using αt or $-\alpha t$ in

129 each cell will yield the same results; we use this form because phylogenetic
130 analyses vary t and α independently, and because the scripts for performing these
131 analyses require separating α and t .) Following matrix exponentiation, the
132 probability of net stasis is $\frac{1+(k-1)e^{-k\alpha t}}{k}$ and the probability of any transition is
133 $\frac{1-e^{-k\alpha t}}{k}$ where k is the number of character states (e.g., 3 in equation 2; Lewis
134 2001). Note that the probability of net stasis is not the Poisson probability of no
135 change ($e^{-\alpha t}$) but instead is the probability of starting at State X and ending at State
136 X. This is because ‘no change’ can be accomplished in two ways: because of truly
137 no character change or because 2+ characters changes ultimately led to reversal.
138 Thus, for a binary character, the probability of net stasis is the Poisson probability
139 of zero changes plus the summed probabilities of all even numbers of change.
140 Similarly, the probability of “ultimate” transition for a binary character is the
141 summed probability of all odd numbers of changes. When there are 3+ states, these
142 probabilities are weighted by the probability that (say) 3 changes will lead back to
143 the original state or from State X to State Y. More complex variants of the Mk
144 model exist that allow for biased state transitions (including driven trends *sensu*
145 McShea 1994), variation in probabilities of state transitions over phylogeny
146 (Nylander et al. 2004; Wright et al. 2016) and correlated character change (e.g.,
147 Billet and Bardin 2018). However, these variants all assume that anatomical
148 change can happen at any point in time rather than being concentrated in speciation
149 events.
150

151 Because punctuated models posit that change is limited to cladogenetic events, we
152 might expect a punctuated analog to the Mk model to use binomial/multinomial
153 probability. However, this would require that we know the number of cladogenetic
154 events that occur over some duration t . If cladogenesis itself is a continuous time
155 process with rate λ , then the expected number of events over time t is λt . If we
156 incorporate the probability of change per branching event is ε , then the expected
157 amount of change over time t is simply $\varepsilon \lambda t$. This led Lewis (2001: pg. 917) to
158 suggest that the Mk model accommodates punctuated change, making no
159 assumptions about how the change is distributed across a given branch. This will
160 be true only for punctuated anagenetic change in which change is neither
161 continuous over time nor attached to cladogenetic events (Wagner and Marcot
162 2010). This differs from Eldredge & Gould's model, which posits that cladogenesis
163 and anatomical change have a common cause. Phylogenetic topologies will imply
164 some minimum number of cladogenetic events, m , which means that expected
165 change is $\varepsilon(m+\lambda t)$. We can assume $m=0$ only for a possible anagenetic topology
166 (Fig. 1A). Given a budding cladogenetic topology (Fig. 1B), $m=1$ for the branch
167 leading to the daughter species and expected change is $\varepsilon(1+\lambda t)$. Given a bifurcating
168 pattern between two true-sister taxa, there are two possibilities for any one branch
169 (Figs. 1C-D). There must be one branching event, but we usually will have no
170 reason to think that the "necessary" branching event leads to either branch: it might
171 be either a continuation of the ancestral line or it might be the product of



172 cladogenesis. Thus, this prior probability of that the necessary cladogenetic event
173 leads to the branch in question is 0.5 and expected change now is:

174 $\frac{(\varepsilon[1+\lambda t])+(\varepsilon[0+\lambda t])}{2} = \varepsilon(0.5 + \lambda t)$. This effectively makes the minimum number of
175 branching events leading to either of two true sister taxa $m=0.5$ and the expected
176 number over branch duration $t = 0.5 + \lambda t$. A key difference that emerges is that even
177 if $t=0$, the expected change is greater than zero given any phylogenetic topology in
178 which there must have been at least one cladogenetic event (i.e., $m=0.5$ or 1.0).

179
180 Following Wagner and Marcot (2010), a “true” punctuated equilibrium analog to
181 the Mk model in its simplest form is given by:

182

$$183 \quad Q_P = t \times \begin{pmatrix} -\varepsilon \left(\frac{m+\lambda t}{t} \right) & \varepsilon \left(\frac{m+\lambda t}{t} \right) & \varepsilon \left(\frac{m+\lambda t}{t} \right) \\ \varepsilon \left(\frac{m+\lambda t}{t} \right) & -\varepsilon \left(\frac{m+\lambda t}{t} \right) & \varepsilon \left(\frac{m+\lambda t}{t} \right) \\ \varepsilon \left(\frac{m+\lambda t}{t} \right) & \varepsilon \left(\frac{m+\lambda t}{t} \right) & -\varepsilon \left(\frac{m+\lambda t}{t} \right) \end{pmatrix} \quad (\text{eqn. 3})$$

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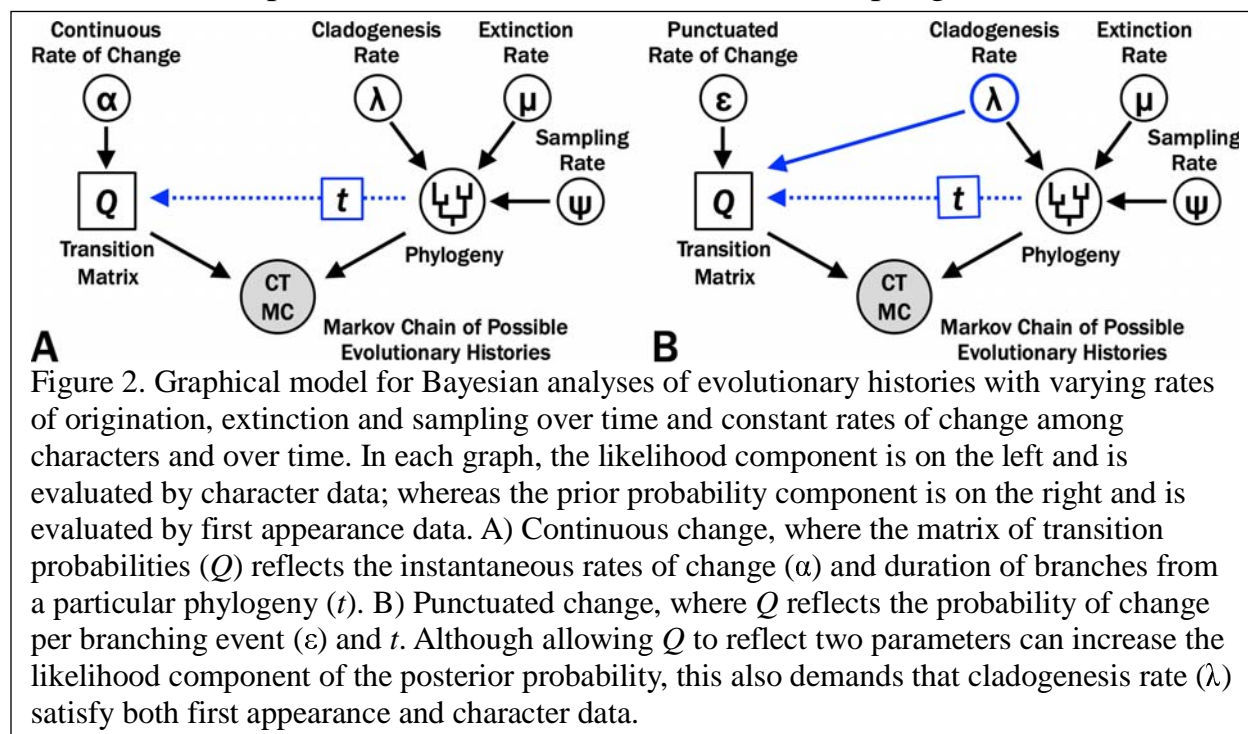
185 with the probability of net stasis is $\frac{1+(k-1)e^{-k\varepsilon(m+\lambda t)}}{k}$ and the probability of
186 “ultimate” transition is $\frac{1-e^{-k\varepsilon(m+\lambda t)}}{k}$. We would accommodate more complex
187 models of character state transitions such as those outline above by varying ε in the
188 same way that those models vary α .

189
190 *Cladogenesis rates*

191 Two issues immediately arise from tying expected character change to rates of
192 cladogenesis (λ). One is whether allowing two parameters (λ and ε) instead of just
193 one (α) to generate the likelihoods of possible evolutionary histories might unduly
194 bias tests towards favoring punctuated equilibrium models. Another is how we go
195 about including λ in phylogenetic analyses. Because the latter informs on the
196 former, we will first review how Bayesian analyses incorporate diversification and
197 sampling rates.

198
 199 Bayesian phylogenetic analyses such as the Fossilized-Birth-Death (FBD) model
 200 (e.g., Heath et al. 2014) assess the prior probability of branch durations on
 201 phylogenetic topologies based on rates of cladogenesis (λ), extinction (μ) and
 202 sampling (ψ) (Fig. 2). ψ alone affects the probability that we fail to sample either
 203 an earlier member of a lineage or some direct ancestor to one or more sampled taxa
 204 over time t (Wagner 1995a; Foote 1996a). λ affects the probability that 0...N
 205 cladogenetic events will happen over that time, and the combination of λ , μ and ψ
 206 affect the probability that we would fail to sample any descendants of each
 207 cladogenetic event (Foote et al. 1999; Stadler 2010; Bapst 2013; Didier et al.
 208 2017). Thus, λ has a major effect on the posterior probability of a tree regardless of
 209 the model of character change (Fig. 2A) and using λ to co-determine expected
 210 character change does not introduce any new parameters our model (Fig. 2B).

211
 212 As described elsewhere (e.g., Wright 2019; Wright et al. 2021; Wright et al. 2022),
 213 we can make numerous modifications to the basic models illustrated in Figure 2
 214 that relax assumptions about homogeneity of rates. We would make identical
 215 modifications to both the continuous-time and punctuated models in Figure 2 in
 216 order to allow for rate variation among characters (e.g., Gamma or lognormal vs.
 217 invariant rates; e.g., Yang 1994; Harrison and Larsson 2015) or over the phylogeny
 218 (e.g., relaxed vs. strict clocks; e.g., Sanderson 1997; Drummond et al. 2006).
 219 “Skyline models” (e.g., Stadler 2011; Stadler et al. 2013; Warnock et al. 2020)
 220 allow for the temporal variation in diversification (or sampling) rates of the sort



221 that innumerable paleobiology studies document (e.g., Krug and Jablonski 2012;
222 Alroy 2015; Foote et al. 2018; Lowery and Fraass 2019; Foote 2023; Foote et al.
223 2024). Under Skyline FBD models, an X million year branch duration in an
224 interval with high λ usually will have a lower probability than will an X million
225 year duration in an interval with low λ (see Wagner 2019). This is where the
226 continuous-time and punctuated models might yield very different results,
227 particularly if we are using “strict clock” models for both α and ε . Variation in λ
228 over time will allow shifts in expected amounts of change per million years even
229 under constant ε . However, λ is simultaneously evaluated by the prior probabilities
230 of branch durations: as λ increases, the probability of shorter branches increases
231 and as λ decreases, the probability of shorter branches increases (see, e.g., Wagner
232 2019). Thus, we cannot freely vary λ to maximize how well constant (“strict
233 clock”) ε maximizes the probability of the character data. Instead, the punctuated
234 model should result in high posterior probabilities relative to the continuous-time
235 model *only if increasing or decreasing origination rates to improve likelihood*
236 *given character data also improves prior probabilities given stratigraphic data.*
237

238 *Data and Analyses*

239 We examine 37 Ordovician genera from the brachiopod superfamily
240 Strophomenoidea based on character data published by Congreve et al. (2015).
241 Strophomenoids appear during the Middle Ordovician and are one of the two
242 superfamilies (along with the Plectambonitoidea) that contribute most to the
243 diversification of “articulate” brachiopods during the Great Ordovician
244 Biodiversification Event (Harper et al. 2013). Congreve et al. (2021) show that the
245 clade displays a classic “early burst” of morphological disparity and that this
246 coincides with elevated rates of change per million years given phylogenies
247 consistent with the cladogram published by Congreve et al. (2015). However, those
248 elevated rates coincide with similar peaks in origination rates, leading Congreve et
249 al. (2021) to suggest that the early burst might reflect elevated frequencies of
250 punctuated change rather than changes in the basic evolvability strophomenoid
251 shells. The former interpretation is more in keeping with predictions of “empty
252 ecosystems” driving morphological change rather than “relaxed intrinsic
253 constraints” (see, e.g., Valentine 1969, 1980) and thus highlights the potential
254 importance of being able to distinguish between continuous-time and punctuated
255 character change models when addressing other macroevolutionary issues.
256

257 We conduct analyses in RevBayes (Höhna et al. 2016). The following aspects of
258 the punctuated and continuous-time analyses are identical for both analyses. Both
259 analyses assume lognormal rate variation among characters, as prior analyses
260 indicate that this fits better than Gamma or invariant distributions (Wagner 2012,

261 Harrison and Larsson 2015). Both used a 12-bin Skyline model, with
262 chronostratigraphic partitions reflecting the Ordovician stage-slices proposed by
263 Bergström et al. (2009) and the Ordovician timescale given in Gradstein et al.
264 (2020), although after lumping some of the relatively brief stage-slices (see
265 Congreve et al. 2021). We seeded sampling (ψ) and origination (λ) rates based on
266 birth–death–sampling analyses published in Congreve et al. (2021) but allowed to
267 vary over the analyses. Following Wright et al. (2021), we did not have extinction
268 (μ) vary independently of origination; instead, we use a separate turnover
269 parameter that follows a lognormal distribution matching substage variation in
270 turnover (μ/λ) shown in empirical studies. Finally, the upper and lower bounds of
271 the first appearance times for the analyzed taxa reflect the earliest and latest
272 possible dates of the oldest species in each genus based on data in the Paleobiology
273 Database (PBDB). However, instead of the dates given by the PBDB, we use an
274 extrinsic database (see Congreve et al. 2021) that restricted possible first
275 appearances to conodont or graptolite zones, with the ages of those zone again
276 derived from Gradstein et al. (2020). We could not implement the complex
277 compound Beta distributions for possible first appearance dates used in Congreve
278 et al. (2021); therefore, the analyses assumed a uniform distribution of possible
279 ages within those upper and lower bounds (see Barido-Sottani et al. 2019).

280
281 For the purposes of this study, we use invariant rates (= strict clocks) for both
282 continuous–time (α) and punctuated (ε) rates of change. The sole difference in the
283 two sets of analyses is that in the punctuated analysis, the rate of character change
284 was set by ε , the “local” cladogenesis rate (λ_i) and the minimum branching events
285 (m). For branches spanning 2+ stage-slices, the expected change from cladogenesis
286 in addition to m is given by:

$$\varepsilon \times \sum_{i=1}^n \lambda_i t_i$$

287 (eqn. 4)

288 with $\sum t_i$ equaling the branch duration. We accomplished this by: 1) dividing each
289 branch into 100-kyr intervals; 2) referring to the origin time of each branch on each
290 particular phylogeny; and, 3) setting the rate of change to $\varepsilon \lambda_i$ where λ_i is the
291 origination rate during that 100-kyr time slice (see supplementary material). We set
292 m to 0.5 for all branches because this was a genus-level analysis and we had no
293 strong intuition of which branches the cladogenetic events should sit on. Even if a
294 particular phylogeny has: 1) one genus as ancestral to another; and, 2) both genera
295 co-existing, then it is possible that the branching event allowing 2+ lineages to co-
296 exist happened within the paraphyletic genus while the “derived” genus represents
297 greater amounts of continuous anagenetic change. This neglects the possibility that

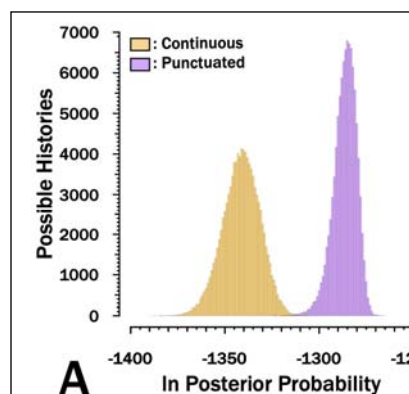
298 an ancestral genus might disappear prior to the first appearance of the derived
299 genus. Unfortunately, Bayesian analyses currently have no way to accommodate
300 last appearance data. Fortunately, initial analyses (e.g., Congreve et al. 2015) do
301 not suggest this happened within the clade and most of the genera have wide
302 ranges with apparent close relatives usually co-existing. As we will discuss below,
303 this is an area that requires further development.

304
305 We set up each of our models in RevBayes 1.2.1 (Höhna et al. 2016). We ran the
306 models until convergence, as assessed in the software tracer (about 1 million
307 generations per estimation). RevBayes returns both trees and parameter estimates
308 in a tab-separated format. We then processed results in the R programming
309 environment (R Core Team 2018).

310

311 **Results**

312 *Relative Success of Continuous-Time and Punctuated Models*



A Figure 3. Distribution of results saved from 10^6 total generations predict the character matrix and the log prior probabilities describing corresponding phylogeny given strophomenoids.

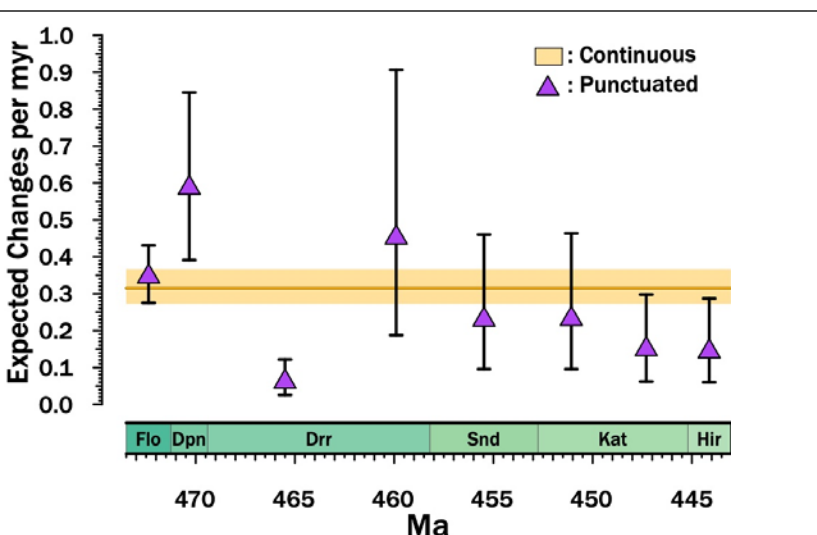
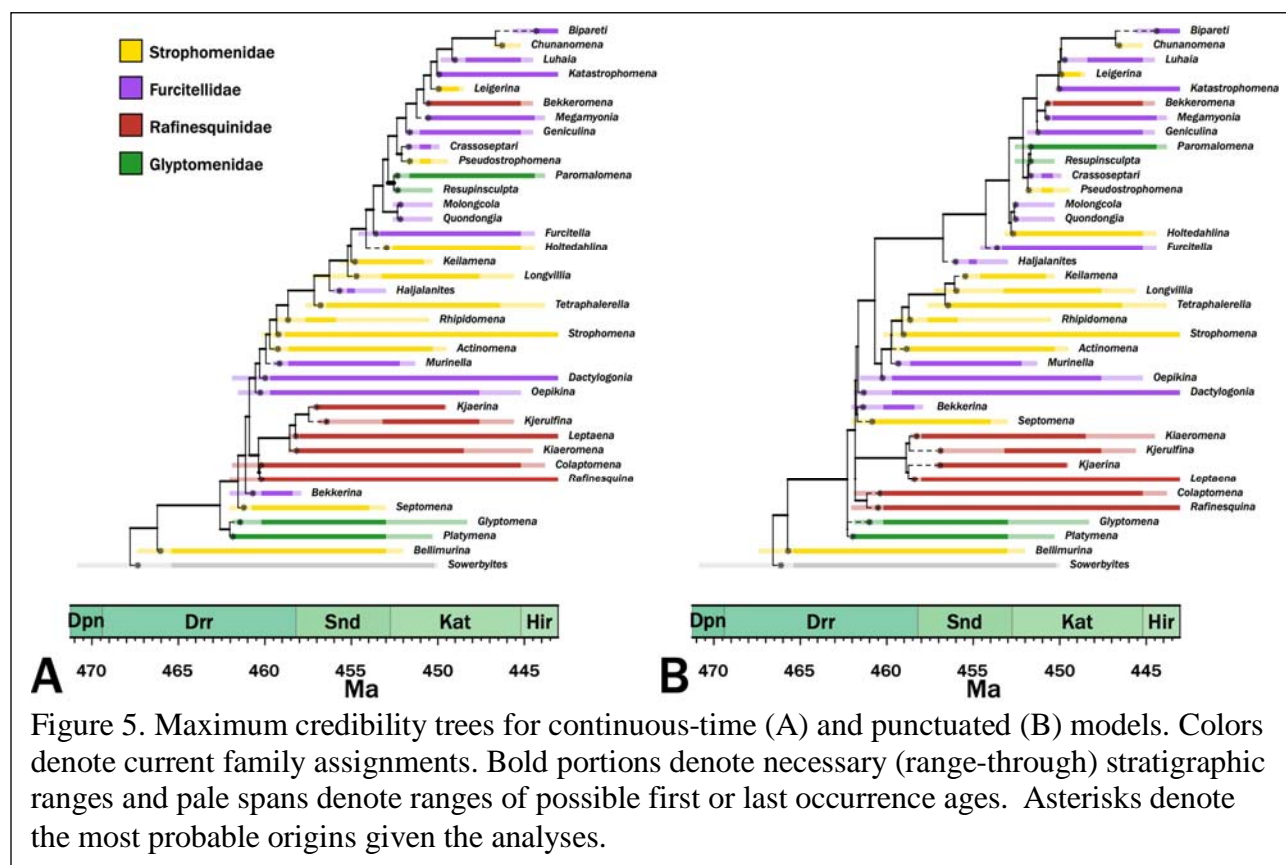


Figure 4. Implied rates of character change per million years. Dark orange line gives the median α from the MCMC runs with the 25th \square 75th percentile distributions shown by the pale orange bar. Purple triangles give the median $\epsilon\lambda_i$ from the MCMC runs with brackets encompassing the 25th \square 75th percentile distributions, with λ_i being the cladogenesis rate for the stage-slice in question. These therefore are directly proportional to the distribution of λ within and among stage-slices. For each MCMC iteration, α and ϵ reflect the median of the lognormal distributions of rate. Finally, note that this excludes the effect of the minimum number of branching events, which means that each branch is expected typically 0.21 changes in the punctuated models in addition to those expected from $\epsilon\lambda_i$. Note that most MCMC iterations place the divergence of the analyzed taxa in the earliest Darriwilian (Drr) or latest Dapingian (Dpn); thus, the Darriwilian through Hirnantian points are the ones of primary interest to this study.

313 Evolutionary histories of
 314 strophomenoid
 315 brachiopods with
 316 punctuated change are
 317 much more probable
 318 than are those with
 319 continuous change (Fig.
 320 3A). In general, the most
 321 probable histories
 322 assuming continuous
 323 change are only slightly
 324 better than are the least
 325 probable histories
 326 assuming punctuated

327 change. The difference in summed posteriors is large, with the log of the
 328 differences >48 ; this resulting Bayes Factor indicates very strong support for the
 329 punctuated model (Kass and Raftery 1995). The distribution in log-posteriors is
 330 much more peaked and restricted for the punctuated model than for the continuous-
 331 time model. Because the MCMC analyses achieve solid convergence under both
 332 models (Supplemental Figure 1), we have no reason to suspect that longer runs
 333 would find continuous histories that rival or exceed the best punctuated histories.

334
 335 The difference in log-posterior probabilities is driven much more by the differences
 336 in log-likelihoods than in differences in log-priors (Figs. 3B vs. 3C). This can be
 337 seen in both the differences in values and in how much more constrained and



338 peaked the punctuated posteriors and likelihoods are relative to the continuous
 339 posteriors/likelihoods. However, we see the same pattern (albeit less dramatically)
 340 for the priors: the prior probabilities of the phylogenetic topologies under
 341 punctuated histories tend to be both higher and more concentrated around the
 342 central values. This indicates that the punctuated histories do both a better job of
 343 predicting the distribution of character state combinations *and* the distributions of
 344 first appearances among those character state combinations than do continuous
 345 histories. The difference in prior probability is driven predominantly by the prior
 346 probabilities of the origination rate, branch durations, and fossil age intervals.

347
 348 *Apparent Rates of Character Change*

349 Both models employ strict clocks (i.e., the same rates of character change over the
 350 entire tree), which means that either α (continuous-time) or ε (punctuated) are the
 351 same on all branches. However, heterogeneity in cladogenesis rates (λ) over
 352 stage slices results considerable temporal variation in expected rates of change
 353 per million years under the punctuated model (Fig. 4). the Dapingian and late
 354 Darriwilian (Dw3 of Bergström et al. 2009) both elevate expected change
 355 substantially under the punctuated model despite constant ε . Conversely, relatively

356 low cladogenesis rates in the Late Ordovician yield an apparent quiescence in
357 expected amounts of change.

358

359 *Phylogenetic Relationships*

360 The maximum credibility trees given continuous and punctuated change histories
361 are generally similar, differing more in implied divergence times than in cladistic
362 relationships (Fig. 5). Both trees imply similar patterns of polyphyly among three
363 of the families while suggesting that one (the Rafinesquinidae) is one taxon away
364 from monophyletic.

365

366 **Discussion**

367 *Punctuated Character Change among Strophomenoid Brachiopods.*

368 Our analyses strongly support the notion that anatomical change within the
369 Ordovician Strophomenoidea is attached to speciation rates and thus consistent
370 with the punctuated equilibrium model. The elevated likelihoods of punctuated
371 histories indicate that the variation in “rates” of change over time generated by
372 temporal variation rates in branching rates do a very good job of predicting
373 anatomical evolution among strophomenoids. It is equally noteworthy that the
374 prior probabilities are generally better given punctuated change histories than
375 given continuous change histories. As we note above, demanding that origination
376 rates predict both branch durations and the distribution of character states among
377 taxa is essentially double jeopardy for the origination rate parameter. In particular,
378 if character change is continuous and cladogenesis rates vary, then intervals of high
379 cladogenesis should generate many short branches with little character change.
380 High rates of cladogenesis elevating the priors under the punctuated model will
381 receive reduced likelihoods due to the lack of change. Conversely, low rates of
382 cladogenesis predicting reduced change along branches will elevate the likelihoods
383 but reduce the priors.

384

385 Our results also suggest that the range of data that we can use to assess punctuated
386 change vs. continuous change models is broader than we usually assume.

387 Traditionally, these analyses have focused on species-level studies that relied on
388 contrasting (lack of) change within lineages with apparent change between
389 lineages. Here, we can show at the genus level that explicitly tying rates of change
390 to cladogenesis rates greatly elevates the likelihoods and posterior probabilities of
391 evolutionary histories, and thus is sufficient for assessing a key component of the
392 punctuated equilibrium model.

393

394 *Macroevolutionary implications*

395 This study corroborates Congreve's et al. (2021) suggestion that the elevated rates
396 of change per million years underlying a burst of disparity during the later
397 Darriwilian among early strophomenoid brachiopods was driven at least in part by
398 punctuated change coupled with elevated cladogenesis. This coincides with the
399 peak of the final phase of the Great Ordovician Biodiversification Event in which
400 origination rates were very high for numerous groups (see, e.g., Servais et al. 2010,
401 Stigall 2018, Thomas et al. 2021). These patterns in turn relates to "loose genes"
402 vs. "empty ecospace" notions of what might drive early bursts in disparity
403 (Valentine 1969, 1980). Because "diversity-dependent-" models such as logistic
404 diversification generate elevated cladogenesis rates (λ) under empty ecospace
405 scenarios, we expect punctuated change plus rapid radiation to generate high
406 disparity. Of course, this is an incomplete representation of the empty ecospace
407 model, as the original concept focused on relatively lax selection allowing more
408 change than "usual" rather than on elevated cladogenesis rates (e.g., Valentine
409 1969). Thus, like the "loose gene" models, the empty ecospace model posies (or
410 can posit) elevated α or ε as well as elevated λ . Were the point of this paper to fully
411 evaluate strophomenoid evolution during the GOBE, the next step would be to use
412 "relaxed clock" models (see Wright et al. 2021) in which ε varied over time in
413 order to assess whether we do see declining amounts of change per speciation
414 event over time. Moreover, because alterations of modularity or other variations of
415 "loose gene" models might help trigger adaptive radiations (e.g., Wagner and
416 Müller 2002), one would need to partition characters based on inferred ecological
417 roles in order to better distinguish between reduced internal constraints or relaxed
418 ecological restrictions drives elevated ε (e.g., Foote 1994; Wagner 1995b;
419 Ciampaglio 2002, 2004; see, e.g., Wright et al. 2021). However, the primary point
420 for this study is that speciation models are be a critical nuisance parameter when
421 trying to distinguish between basic explanations for rapid increases in
422 morphological disparity. At least in the case of Ordovician strophomenoids,
423 elevated early disparity is at least partially explained solely by elevated punctuated
424 speciation.

425

426 *Effects on Inferred Phylogeny*

427 The maximum credibility trees under both continuous change and punctuated
428 change are generally similar, which indicates that the basic patterns are embedded
429 in the character state and stratigraphic range data. We obviously cannot know
430 which tree is more accurate. However, trees from punctuated change histories
431 generally display shallower divergence times and shorter branch durations than do
432 trees from continuous change histories, which is expected if the punctuated change
433 model is generally more accurate than is the continuous change model (Wagner
434 2000; Wright and Lloyd 2021). Trees from punctuated change history also tend to

435 be somewhat more symmetrical (= “balanced”, i.e., possessing greater proportions
436 of sister taxa that are both clades rather than one clade and one analyzed taxon)
437 than are trees from continuous change histories (Colless imbalance = 0.20 given
438 punctuated; Colless imbalance = 0.35 given continuous-time where 1.0 means a
439 completely “pectinate” or imbalanced tree; Colless 1995), which also is expected if
440 the punctuated model is generally more accurate than is the continuous change
441 model (Huelsenbeck and Kirkpatrick 1996). Although the differences between the
442 maximum credibility trees (and thus the preponderance of the probable trees used
443 to generate those maximum credibility trees) are not great, the fact that they exist
444 suggests that punctuated vs. continuous change represents yet another set of
445 parameters that paleophylogeneticists should consider when assessing phylogeny
446 for its own sake (see Warnock and Wright 2020; Wright et al. 2021).

447

448 *Future Developments: the importance of stratigraphic ranges beyond first*
449 *occurrences*

450 One obvious “flaw” with our approach is that it focuses solely on what happens
451 “between” taxa on a phylogeny by basically treating each taxon as existing in a
452 single point in time somewhere between the lower and upper bound of its first
453 appearance. However, it is quite common for marine invertebrate species to have
454 substantial durations that range through multiple chronostratigraphic boundaries.
455 This in itself has been critical to understanding punctuated equilibrium as it
456 indicates both stasis and situations where one or more long-ranging species gives
457 rise to 1+ daughter species while still persisting (Eldredge 1971). Warnock et al.
458 (2020) lay the groundwork for taking into account stratigraphic ranges beyond the
459 first occurrence in an effort to improve the estimates of extinction and sampling
460 rates for the prior probability of phylogenies. Here, we will outline two other ways
461 in which this should be done to better assess continuous change vs. punctuated
462 change models.

463

464 As we note above, the ability of our approach to recognize punctuated change
465 without needing to examine stasis within lineages should expand our ability to test
466 for punctuated character change. The flip-side to this is that being able to modify
467 our tests to account for potential stasis within lineages should greatly expand the
468 power of the tests that we propose. This will be particularly true for species-level
469 analyses where the punctuated equilibrium model predicts that a morphospecies
470 duration reflects only extinction rates (μ) whereas- the continuous change model
471 predicts that a morphospecies duration reflects both μ and the continuous rate of
472 change (α). The probability of observed stasis for one character within a lineage
473 with N finds is:

474
$$\prod_{n=1}^{N-1} \frac{1+(k-1)e^{-k\alpha t_i}}{k} \quad (\text{eqn. 5})$$

475 where t_i is the time that elapses between find n and find $n+1$ and $\frac{1+(k-1)e^{-k\alpha t_i}}{k}$ is
476 the probability of net stasis over t_i given the number of states and α . This
477 introduces an obvious difficulty: just as we know only the upper and lower bounds
478 of possible ages for the first appearance, we will have only upper and lower bounds
479 on the ages of subsequent occurrences. Moreover, even if we have detailed
480 biochronological ordinations of a clade's species (see, e.g., Guex and Davaud
481 1984; Alroy 1994; Sadler et al. 2003), then we often will still have numerous finds
482 that cannot be ordered relative to others, resulting in numerous possible
483 combinations of finds. One "shortcut" that is conservative with respect to the
484 continuous change model is to use only the first and last appearances, and thus set
485 t_i to the duration of the lineage (Wagner and Marcot 2010). This will mean
486 including upper and lower bounds of last appearances and varying both over
487 MCMC searches. By adding this to the likelihood component of Bayesian
488 phylogenetic analyses, the stratigraphic ranges of individual species offer a test of
489 α in addition to the distributions of branch durations and character state
490 combinations.

491
492 A directly related issue to stasis and prolonged stratigraphic ranges / temporal
493 durations is the possibility of budding cladogenesis. Indeed, it is often forgotten
494 that the study initiating the punctuated equilibrium debate was a "tree-based" study
495 in which phylogenetic reconstruction of Devonian trilobites suggested that
496 ancestral species survived extinction rates and sometimes generated what we now
497 call polytomies on cladistic depictions of relationships (Eldredge 1971). The
498 maximum credibility trees given either punctuated or continuous change models
499 (Fig. 5) both include the same improbable pattern: numerous long-ranging genera
500 are not reconstructed as "ancestral" (paraphyletic) relative to any other genera (see,
501 e.g., Foote 1996a; Fig. 1C-D). The same issue would be true if this were a
502 species-level phylogeny with numerous long-ranging genera: just as α predicts
503 character change over a species' lifetime, λ predicts that the lineage should be just
504 as prone to giving rise to new species as are the unsampled ancestral lineages
505 linking species on a phylogeny (Wagner and Erwin 1995). There are two issues
506 here. One, because current programs such as RevBayes do not include information
507 about stratigraphic ranges, the MCMC searches could not consider that (say)
508 *Strophomena* was still present when *Rhipidomena* or *Tetraphalerella* appeared, and
509 thus could not consider potentially more probable phylogenies in which one or
510 both taxa "bud" directly from *Strophomena*. Two, the longer a lineage (or group of
511 closely related lineages) persists, the more sampled descendants we expect them to

512 generate. This means that the prior probability of a polytomy with (say)
513 *Strophomena* linked as an ancestor to 2+ descendant species should increase as
514 durations increase (see, e.g., Wagner 2019). Trees lacking such polytomies but still
515 including long-lived species should have lower prior probabilities than should
516 trees placing such species at the “node” of polytomies with descendants appearing
517 at different time over the species’ histories. Note that the mode of speciation itself
518 is not important here: under low rates of continuous change, we will expect
519 accidental “stasis” sometimes, and the same expectations would apply to them.
520 However, because we expect species with long durations relative to origination
521 rates to be more common under punctuated models than under continuous change
522 models, accommodating “natural polytomies” should be more important when
523 change was punctuated.

524

525 **Conclusions**

526 Punctuated equilibrium presents a model of character evolution that is
527 fundamentally different than the continuous change models currently used in
528 Bayesian and likelihood phylogenetics. In the case of strophomenoid brachiopods
529 from the Ordovician, punctuated character models imply evolutionary histories that
530 are both more probable and more likely than do continuous change models.
531 Moreover, the punctuated model combined with variable diversification rates over
532 time at least partly accounts for an early burst in strophomenoid disparity purely
533 from elevated speciation rates early in the groups history that elevate the expected
534 numbers of changes per million years without changing the expected numbers of
535 changes per speciation event. Thus, concerns about whether speciation and
536 character change are continuous or punctuated transcends theoretical interest in
537 how speciation operates: it is an important nuisance parameter that can affect our
538 conclusions about hypotheses stemming from seemingly unrelated
539 macroevolutionary theory.

540

541

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548

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550

551 **Data Availability Statement.** Data available from the Dryad Digital Repository
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554

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Literature Cited

556 Alroy, J. 1994. Appearance event ordination: a new biochronologic method.
557 *Paleobiology* 20:191 – 207.

558 ————. 2015. A more precise speciation and extinction rate estimator.
559 *Paleobiology* 41:633 – 639.

560 Bapst, D. W. 2013. A stochastic rate-calibrated method for time-scaling
561 phylogenies of fossil taxa. *Methods in Ecology and Evolution* 4:724–733.

562 Barido-Sottani, J., G. Aguirre-Fernández, M. J. Hopkins, T. Stadler, and R.
563 Warnock. 2019. Ignoring stratigraphic age uncertainty leads to erroneous
564 estimates of species divergence times under the fossilized birth-death
565 process. *Proceedings of the Royal Society B: Biological Sciences*
566 286:20190685.

567 Bergström, S. M., X. Chen, J. C. Gutiérrez-Marco, and A. Dronov. 2009. The new
568 chronostratigraphic classification of the Ordovician System and its relations
569 to major regional series and stages and to $\delta^{13}\text{C}$ chemostratigraphy. *Lethaia*
570 42:97–107.

571 Billet, G., and J. Bardin. 2018. Serial homology and correlated characters in
572 morphological phylogenetics: modeling the evolution of dental crests in
573 placentals. *Systematic Biology* 68:267 – 280.

574 Cheetham, A. H. 1986. Tempo of evolution in a Neogene bryozoan: rates of
575 morphologic change within and across species boundaries. *Paleobiology*
576 12:190 – 202.

577 Ciampaglio, C. N. 2002. Determining the role that ecological and developmental
578 constraints play in controlling disparity: examples from the crinoid and
579 blastozoan fossil record. *Evolution and Development* 4:170 – 188.

580 ————. 2004. Measuring changes in articulate brachiopod
581 morphology before and after the Permian mass extinction event: do
582 developmental constraints limit morphological innovation? *Evolution and*
583 *Development* 6:260 – 274.

584 Colless, D. H. 1995. Relative Symmetry of Cladograms and Phenograms: An
585 Experimental Study. *Systematic Biology* 44:102-108.

586 Congreve, C. R., A. Z. Krug, and M. E. Patzkowsky. 2015. Phylogenetic revision
587 of the Strophomenida, a diverse and ecologically important Palaeozoic
588 brachiopod order. *Palaeontology* 58:743–758.

589 Congreve, C. R., M. E. Patzkowsky, and P. J. Wagner. 2021. An Early Burst in
590 brachiopod evolution corresponding with significant climatic shifts during

- 591 the Great Ordovician Biodiversification Event. *Proceedings of the Royal*
592 *Society B: Biological Sciences* 477:20211450.
- 593 Didier, G., M. Fau, and M. Laurin. 2017. Likelihood of tree topologies with fossils
594 and diversification rate estimation. *Systematic Biology* 66:964–987.
- 595 Drummond, A. J., S. Y. W. Ho, M. J. Phillips, and A. Rambaut. 2006. Relaxed
596 phylogenetics and dating with confidence. *PLoS Biol* 4:e88.
- 597 Eldredge, N. 1971. The allopatric model and phylogeny in Paleozoic invertebrates.
598 *Evolution* 25:156 – 167.
- 599 Eldredge, N., and S. J. Gould. 1972. Punctuated equilibria: an alternative to
600 phyletic gradualism. p. 82 – 115 *in* T. J. M. Schopf, ed. *Models in*
601 *paleobiology*. Freeman, San Francisco.
- 602 Foote, M. 1994. Morphological disparity in Ordovician – Devonian crinoids and
603 the early saturation of morphological space. *Paleobiology* 20:320 – 344.
- 604 ————. 1996a. On the probability of ancestors in the fossil record.
605 *Paleobiology* 22:141 – 151.
- 606 ————. 1996b. Models of morphologic diversification. p. 62 – 86 *in*
607 D. Jablonski, D. H. Erwin and J. H. Lipps, eds. *Evolutionary paleobiology:*
608 *essays in honor of James W. Valentine*. University of Chicago Press,
609 Chicago.
- 610 ————. 2023. Diversity-dependent diversification in the history of
611 marine animals. *The American Naturalist*
- 612 Foote, M., R. A. Cooper, J. S. Crampton, and P. M. Sadler. 2018. Diversity–
613 dependent evolutionary rates in early Palaeozoic zooplankton. *Proceedings*
614 *of the Royal Society B: Biological Sciences* 285:20180122.
- 615 Foote, M., S. M. Edie, and D. Jablonski. 2024. Ecological structure of diversity-
616 dependent diversification in Phanerozoic marine bivalves. *Biology Letters*
617 20:20230475.
- 618 Foote, M., J. P. Hunter, C. M. Janis, and J. J. Sepkoski, Jr. 1999. Evolutionary and
619 preservational constraints on origins of biologic groups: divergence times of
620 eutherian mammals. *Science* 283:1310 – 1314.
- 621 Gingerich, P. D. 1979. The stratophenetic approach to phylogeny reconstruction in
622 vertebrate paleontology. p. 41 – 77 *in* J. Cracraft and N. Eldredge, eds.
623 *Phylogenetic analysis and paleontology*. Columbia University Press, New
624 York.
- 625 Gradstein, F. M., J. G. Ogg, M. D. Schmitz, and G. M. Ogg (eds.). 2020. *Geologic*
626 *Time Scale 2020*. Elsevier, Amsterdam.
- 627 Guex, J., and E. Davaud. 1984. Unitary associations method: use of graph theory
628 and computer algorithm. *Computers & Geosciences* 10:69-96.

- 629 Harrison, L., and H. C. E. Larsson. 2015. Among-character rate variation
630 distributions in phylogenetic analysis of discrete morphological characters.
631 *Systematic Biology* 64:307 – 324.
- 632 Heath, T. A., J. P. Huelsenbeck, and T. Stadler. 2014. The fossilized birth–death
633 process for coherent calibration of divergence–time estimates. *Proceedings*
634 *of the National Academy of Sciences* 111:E2957–E2966.
- 635 Höhna, S., M. J. Landis, T. A. Heath, B. Boussau, N. Lartillot, B. R. Moore, J. P.
636 Huelsenbeck, and F. Ronquist. 2016. RevBayes: Bayesian phylogenetic
637 inference using Graphical Models and an interactive model–specification
638 language. *Systematic Biology* 65:726–736.
- 639 Huelsenbeck, J. P., and M. Kirkpatrick. 1996. Do phylogenetic methods produce
640 trees with biased shapes? *Evolution* 50:1418 – 1424.
- 641 Hunt, G. 2013. Testing the link between phenotypic evolution and speciation: an
642 integrated paleontological and phylogenetic analysis. *Methods in Ecology*
643 *and Evolution* 4:714–723.
- 644 Hunt, G., M. J. Hopkins, and S. Lidgard. 2015. Simple versus complex models of
645 trait evolution and stasis as a response to environmental change. *Proceedings*
646 *of the National Academy of Sciences* 112:4885–4890.
- 647 Kass, R. E., and A. E. Raftery. 1995. Bayes factors. *Journal of the American*
648 *Statistical Association* 90:773–795.
- 649 Krug, A. Z., and D. Jablonski. 2012. Long-term origination rates are reset only at
650 mass extinctions. *Geology* 40:731–734.
- 651 Lande, R. 1976. Natural selection and random genetic drift in phenotypic
652 evolution. *Evolution* 30:314 – 334.
- 653 Lewis, P. O. 2001. A likelihood approach to estimating phylogeny from discrete
654 morphological character data. *Systematic Biology* 50:913 – 925.
- 655 Lowery, C. M., and A. J. Fraass. 2019. Morphospace expansion paces taxonomic
656 diversification after end Cretaceous mass extinction. *Nature Ecology &*
657 *Evolution* 3:900 – 904.
- 658 McShea, D. W. 1994. Mechanisms of large-scale evolutionary trends. *Evolution*
659 48:1747 – 1763.
- 660 Nylander, J. A. A., F. Ronquist, J. P. Huelsenbeck, and J. L. Nieves–Aldrey. 2004.
661 Bayesian phylogenetic analysis of combined data. *Systematic Biology* 53:47
662 – 67.
- 663 Polly, P. D. 1997. Ancestry and species definition in paleontology: a stratocladistic
664 analysis of Paleocene–Eocene Viverravidae (Mammali, Carnivora) from
665 Wyoming. *Contributions from the Museum of Paleontology, the University*
666 *of Michigan* 30:1 – 53.

- 667 R Core Team. 2018. R: A language and environment for statistical computing.
668 program distributed by the R Foundation for Statistical Computing. Vienna,
669 Austria.
- 670 Sadler, P. M., W. G. Kemple, and M. A. Kooser. 2003. CONOP9 programs for
671 solving the stratigraphic correlation and seriation problems as constrained
672 optimization. p. 461 – 462 *in* P. Harries, ed. High-Resolution Stratigraphic
673 Approaches in Paleontology. Plenum Press, New York.
- 674 Sanderson, M. J. 1997. A nonparametric approach to estimating divergence times
675 in the absence of rate consistency. *Molecular Biology and Evolution* 14:1218
676 – 1231.
- 677 Servais, T., A. W. Owen, D. A. T. Harper, B. Kröger, and A. Munnecke. 2010. The
678 Great Ordovician Biodiversification Event (GOBE): The palaeoecological
679 dimension. *Palaeogeography, Palaeoclimatology, Palaeoecology* 294:99–
680 119.
- 681 Sheldon, P. R. 1996. Plus ça change – a model for stasis and evolution in different
682 environments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127:209
683 – 227.
- 684 Stadler, T. 2010. Sampling-through-time in birth–death trees. *Journal of*
685 *Theoretical Biology* 267:396–404.
- 686 ————. 2011. Mammalian phylogeny reveals recent diversification
687 rate shifts. *Proceedings of the National Academy of Sciences* 108:6187 –
688 6192.
- 689 Stadler, T., D. Kühnert, S. Bonhoeffer, and A. J. Drummond. 2013. Birth–death
690 skyline plot reveals temporal changes of epidemic spread in HIV and
691 hepatitis C virus (HCV). *Proceedings of the National Academy of Sciences*
692 110:228–233.
- 693 Stanley, S. M. 1975. A theory of evolution above the species level. *Proceedings of*
694 *the National Academy of Sciences, USA* 72:56 – 76.
- 695 Stigall, A. L. 2018. How is biodiversity produced? Examining speciation processes
696 during the GOBE. *Lethaia* 51:165–172.
- 697 Thomas, S., C. M. Borja, and A. T. H. David. 2021. The Great Ordovician
698 Biodiversification Event (GOBE) is Not a Single Event. *Paleontological*
699 *Research* 25:315–328.
- 700 Valentine, J. W. 1969. Patterns of taxonomic and ecological structure of the shelf
701 benthos during Phanerozoic time. *Palaeontology* 12:684 – 709.
- 702 ————. 1980. Determinants of diversity in higher taxonomic
703 categories. *Paleobiology* 6:444 – 450.
- 704 Wagner, G. P., and G. B. Müller. 2002. Evolutionary innovations overcome
705 ancestral constraints: a re–examination of character evolution in male sepsid
706 flies. *Evolution & Development* 4:1–6.

- 707 Wagner, P. J. 1995a. Stratigraphic tests of cladistic hypotheses. *Paleobiology*
708 21:153 – 178.
- 709 _____ . 1995b. Testing evolutionary constraint hypotheses with early
710 Paleozoic gastropods. *Paleobiology* 21:248 – 272.
- 711 _____ . 2000. The quality of the fossil record and the accuracy of
712 phylogenetic inferences about sampling and diversity. *Systematic Biology*
713 49:65 – 86.
- 714 _____ . 2019. On the probabilities of branch durations and
715 stratigraphic gaps in phylogenies of fossil taxa when rates of diversification
716 and sampling vary over time. *Paleobiology* 28:30 – 55.
- 717 Wagner, P. J., and D. H. Erwin. 1995. Phylogenetic patterns as tests of speciation
718 models. p. 87 – 122 *in* D. H. Erwin and R. L. Anstey, eds. *New approaches*
719 *to studying speciation in the fossil record*. Columbia University Press, New
720 York.
- 721 Wagner, P. J., and J. D. Marcot. 2010. Probabilistic phylogenetic inference in the
722 fossil record: current and future applications. p. 195 – 217 *in* J. Alroy and G.
723 Hunt, eds. *Quantitative methods in paleobiology*. Paleontological Society,
724 New Haven, Connecticut.
- 725 Warnock, R. C. M., T. A. Heath, and T. Stadler. 2020. Assessing the impact of
726 incomplete species sampling on estimates of speciation and extinction rates.
727 *Paleobiology* 46:137–157.
- 728 Warnock, R. C. M., and A. M. Wright. 2020. Understanding the Tripartite
729 Approach to Bayesian Divergence Time Estimation. *Elements of*
730 *Paleontology* 2:in press.
- 731 Wright, A. M. 2019. A systematist’s guide to estimating Bayesian phylogenies
732 from morphological data. *Insect Systematics and Diversity* 3:1 – 14.
- 733 Wright, A. M., D. W. Bapst, J. Barido-Sottani, and R. C. M. Warnock. 2022.
734 Integrating Fossil Observations Into Phylogenetics Using the Fossilized
735 Birth–Death Model. *Annual Review of Ecology, Evolution, and Systematics*
736 53:251-273.
- 737 Wright, A. M., and G. T. Lloyd. 2021. Bayesian analyses in phylogenetic
738 palaeontology: interpreting the posterior sample. *Palaeontology* 64:in press.
- 739 Wright, A. M., G. T. Lloyd, and D. M. Hillis. 2016. Modeling character change
740 heterogeneity in phylogenetic analyses of morphology through the use of
741 priors. *Systematic Biology* 65:602 – 611.
- 742 Wright, A. M., P. J. Wagner, and D. F. Wright. 2021. Testing character-evolution
743 models in phylogenetic paleobiology: a case study with Cambrian
744 echinoderms. *Elements in Paleobiology* 2:1 – 42.

745 Yang, Z. 1994. Maximum likelihood phylogenetic estimation from DNA sequences
746 with variable rates over sites: approximate methods. *Journal of Molecular*
747 *Evolution* 39:306 – 314.
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750 Supplementary Information.

751

752 I. Traces of Continuous-Time and Punctuated Models.

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