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Fossil and phylogenetic analyses reveal recurrent periods of diversification and extinction in dictyopteran insects

Fabien L. Condamine, André Nel, Philippe Grandcolas, Frédéric Legendre

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1 **Title**

2 **Fossil and phylogenetic analyses reveal recurrent periods of diversification**
3 **and extinction in dictyopteran insects**

4

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22

23 **Short running title**

24 Extinction events in cockroaches and allies

25 *Abstract*

26 Variations of speciation and extinction rates determine the fate of clades through time.
27 Periods of high diversification and extinction (possibly mass extinction events) can punctuate
28 the evolutionary history of various clades, but they remain loosely defined for many
29 biological groups, especially non-marine invertebrates like insects. Here, we examine
30 whether the cockroaches, mantises and termites (altogether included in Dictyoptera) have
31 experienced episodic pulses of speciation or extinction and how these pulses may be
32 associated with environmental fluctuations or mass extinctions. We relied on molecular
33 phylogeny and fossil data to shed light on the times and rates at which dictyopterans
34 diversified. The diversification of Dictyoptera has alternated between (1) periods of high
35 diversification in the Late Carboniferous, Early-Middle Triassic, Early Cretaceous, and
36 middle Paleogene, and (2) periods of high extinction rates particularly at the Permian-Triassic
37 boundary, but not necessarily correlated with the major global biodiversity crises as in the
38 mid-Cretaceous. This study advocates on the importance of analyzing, when possible, both
39 molecular phylogeny and fossil data to unveil diversification and extinction periods for a
40 given group. The causes and consequences of extinction must be studied beyond mass
41 extinction events alone to gain a broader understanding of how clades wax and wane.

42

43	Table of contents
44	
45	Introduction
46	
47	Materials and Methods
48	<i>Time-calibrated phylogeny and fossil data for Dictyoptera</i>
49	<i>Bayesian analyses of the fossil record</i>
50	<i>Episodic process of phylogeny-based diversification</i>
51	
52	Results
53	<i>Origin and extinction of major dictyopteran lineages</i>
54	<i>Fossil-based diversification dynamics</i>
55	<i>Phylogeny-based analyses</i>
56	
57	Discussion
58	<i>Diversification and extinction events in Dictyoptera history</i>
59	<i>Fossil record, phylogeny and the study of extinction</i>
60	<i>Conclusion</i>
61	
62	Acknowledgements
63	
64	References
65	

66 **Introduction**

67 The death of species, also known as species extinction, is a natural process, but today human-
68 driven decline of global biodiversity is dramatic and is eventually leading us to the sixth mass
69 extinction (Barnosky et al., 2011; Pimm et al., 2014; Ceballos et al., 2017). Yet, how lineages
70 face extinction and recover from it or not remains elusive. Mass extinction events draw much
71 attention because they resulted in dramatic species losses over very short times (Raup and
72 Sepkoski, 1982). Nevertheless, if more than 99% of all species that ever lived are now extinct
73 (Raup, 1992), these losses cannot be related to mass extinctions (Jablonski, 2002). Beyond
74 astronomic or anthropogenic events responsible for these biological crises, species extinction
75 is more commonly driven by interspecific competition, environmental changes, and
76 stochastic factors (Benton, 2009). These account for ‘background’ extinction, but we also
77 need to look at contrasts between mass extinctions to understand better the dynamics of
78 species extinction (Blois and Hadly, 2009; Harnik et al., 2012; Condamine et al., 2013).

79 Mass extinctions have punctuated the history of life, eliminating whole groups of
80 organisms while fostering the subsequent diversification of others (Raup and Sepkoski, 1982;
81 Alroy, 2010). These events caused, in less than one million years (Myrs), more than 75%
82 species loss (Raup and Sepkoski, 1982; Barnosky et al., 2011; Culshaw et al., 2019). Five
83 mass extinction events over the past 542 Myrs, often referred to as the ‘Big Five’, have been
84 identified (Raup and Sepkoski, 1982; Alroy, 2010): the Ordovician–Silurian extinction event
85 (~443 Myrs ago, ~86% species loss), the Late Devonian extinction event (~376-359 Myrs
86 ago, ~75% species loss), the Permian–Triassic (P-T) extinction event (~252 Myrs ago, ~96%
87 species loss), the Triassic–Jurassic (T-J) extinction event (~201 Myrs ago, ~80% species loss)
88 and the Cretaceous–Paleogene (K-Pg) extinction event (~66 Myrs ago, ~76% species loss).
89 However, those percentages of species lost are to be taken with caution because they do not
90 include some of the most diverse clades since the Late Carboniferous, and in particular

91 insects (Nel et al., 2010). For instance the T-J extinction event does not correspond to any
92 visible mass extinction among this already hyper-diverse clade.

93 Insects have undergone multiple and contemporary ecological and evolutionary
94 radiations as well as extinction events (Engel, 2015; Foottit and Adler, 2018), resulting in at
95 least one million species worldwide (Stork, 2018) and in a rich fossil record extending back
96 to more than ~410 Myrs ago (Grimaldi and Engel, 2005; Garrouste et al., 2012). During their
97 history, they have survived the most severe mass extinctions and evolved against the
98 backdrop of radical alterations in terrestrial floras, continental rearrangements, and changes
99 in key environmental parameters such as average global temperatures (Labandeira and
100 Sepkoski, 1993; Mayhew, 2007; Rainford et al., 2014; Condamine et al., 2016). Yet, today,
101 insect diversity tumbles: for example, between 1989 and 2016 in Germany, flying insect
102 biomass has dropped in average by 76% (Hallmann et al., 2017). There is a consensus that
103 insect diversity is strongly affected in many ecosystems (Sánchez-Bayo and Wyckhuys,
104 2019; Seibold et al., 2019; Simmons et al., 2019) and those population declines bring the
105 question of how insects coped with preceding extinction events like mass extinctions.

106 Insects are thought to be resilient to mass extinctions. Except for the P-T event, the
107 history of insect diversification reveals no clear evidence of mass extinction (Labandeira and
108 Sepkoski, 1993; Condamine et al., 2016). At best, evidence is conflicting or equivocal. For
109 instance, most fossil-based studies discovered a drop in diversity during the P-T mass
110 extinction, but phylogenetic studies did not (Labandeira and Sepkoski, 1993; Condamine et
111 al., 2016). The impact of other mass extinctions, such as the T-J or the K-Pg events, is even
112 less obvious or not detectable at the family-level or above. Similarly, other clues, such as
113 those drawn from morphological changes, also failed to identify an impact of the main
114 biodiversity crises on insects (Nel et al., 2010; Rainford et al., 2016; Nel et al., 2018). To
115 refine these results, different lines of evidence like phylogenies and fossils should be studied

116 together (Mayhew, 2007; Ksepka et al., 2014; Condamine et al., 2016). They provide two
117 complementary windows for understanding the temporal variations in biodiversity and
118 investigating what lies behind the dynamics of insect diversification.

119 Among insects, the Dictyoptera (mantises, cockroaches and termites; **Fig. 1**) is an
120 ideal group to contrast background and mass extinction. The current knowledge on
121 Dictyoptera allows investigating extinction, the most critical and controversial component of
122 net diversification rates, for two main reasons (Rabosky, 2010; Beaulieu and O'Meara, 2015;
123 Hagen et al., 2018). First, dictyopteran fossils and molecular phylogenies indicate these
124 insects originated during the earliest Late Carboniferous (~310 Myrs ago, Zhang et al., 2013;
125 Legendre et al., 2015), suggesting they experienced at least three known mass extinctions (i.e.
126 252, 201 and 66 Myrs ago) without disappearing, but the extent of the clades' extinction
127 remains unknown. In other words, studying Dictyoptera allows investigating multiple mass
128 extinction events to contrast with background extinction. Second, although not devoid of
129 gaps and taxonomic issues (Nel et al., 2018), a large fossil record of dictyopterans is
130 available (Grimaldi and Engel, 2005; Bechly, 2007). This should allow inferring a global
131 diversification pattern across the evolutionary history of Dictyoptera. Finally, phylogenetic-
132 based and fossil-based analyses can be confronted to identify their limits and
133 complementarities (Sanmartín and Meseguer, 2016), as it has been done for insects as a
134 whole (Condamine et al., 2016).

135 In this study we asked how extinction events influenced the diversification of
136 Dictyoptera. Did dictyopteran insects suffer declines of diversity during periods of dramatic
137 environmental changes or instead experienced pulses of speciation, for instance when other
138 clades disappeared or new niches opened? To investigate these diversification dynamics, we
139 relied on a molecular phylogeny to shed light on the time and rate at which modern
140 dictyopterans attained their diversity. Molecular phylogenetic analyses of Dictyoptera have

141 resulted in a taxonomically well-sampled time-calibrated tree suited for examining their
142 diversification dynamics until the early Cenozoic (Legendre et al., 2015). Time-calibrated
143 trees inform us on historical extinction rates as they retain signatures of shifts in
144 diversification (Nee et al., 1994; Harvey et al., 1994). Teasing apart speciation and extinction
145 from phylogenies remains, however, challenging (Rabosky, 2010, 2016; but see Morlon et al.,
146 2011; Beaulieu and O’Meara, 2015). To address this caveat, we also relied on the
147 dictyopteran fossil record. We studied both types of data with Bayesian and maximum-
148 likelihood birth-death models to estimate the past dynamics of speciation and extinction rates.
149 We aimed at proposing a scenario for the macroevolutionary history of dictyopterans by
150 examining whether the clade has experienced episodic pulses of speciation or extinction and
151 how these pulses may be associated with environmental fluctuations or mass extinctions.

152

153 **Materials and Methods**

154 *Time-calibrated phylogeny and fossil data for Dictyoptera*

155 We used a recently published time-calibrated phylogeny of Dictyoptera including 762 extant
156 species of the ~10,000 living dictyopteran species (Legendre et al., 2015; Stork, 2018). This
157 phylogeny is built based on a molecular dataset comprising four mitochondrial genes (12S
158 rRNA, 16S rRNA, and cytochrome c oxidase subunits I and II) and two nuclear markers (18S
159 rRNA and 28S rRNA). Divergence times were estimated using a relaxed-clock approach,
160 with the penalized likelihood method, coupled with 17 fossils, which were used as minimum
161 age constraints on different nodes and a maximum age for the tree root (Legendre et al.,
162 2015).

163 We studied the fossil record of dictyopterans using the data available in *Paleobiology*
164 *Database* via the *FossilWorks* application (accessed on February 24, 2017; Clapham et al.,
165 2016) and supplemented the matrix with recent fossil findings (e.g. Schubnel and Nel, 2019;

166 Zhao et al., 2019). We checked for fossil occurrences using the name ‘Dictyoptera’, and we
167 specified the taxonomic criteria to look for family and genus names. Relying only on family
168 names would be fraught with danger because some extinct families, supposedly related to
169 Dictyoptera, are ill-defined and need to be investigated further. At the species level, the fossil
170 record is equivocal because of a poor spatio-temporal distribution of fossil species and of
171 numerous Paleozoic species unclearly described and/or based on very incomplete fossils.
172 Combining family and genus level analyses limit these issues. We also used the geological
173 stages and epochs as time unit.

174 Because phylogenetic affinities with stem Dictyoptera have been disputed (Prokop et
175 al., 2014; Guan et al., 2016; Aristov, 2017a,b), we generated an additional dataset including
176 Dictyoptera fossil occurrences as described above and the fossil occurrences of the putative
177 sister lineage Paoliida. However, we did not include the previously thought sister lineage,
178 Eoblattida, because *Eoblatta*, the type genus of the family Eoblattidae and the superorder
179 Eoblattida, is considered as an Archaeorthoptera without any affinity to Dictyoptera
180 (Schubnel et al., 2019). The fossil dataset is available in Appendix S1.

181

182 ***Bayesian analyses of the fossil record***

183 We analyzed the dictyopteran fossil record using a Bayesian model to simultaneously infer
184 (1) the times of speciation and of extinction for each taxon in the dataset, (2) the temporal
185 dynamics of origination and extinction rates, and (3) the preservation of fossil taxa as
186 implemented in PyRate (Silvestro et al., 2014). The preservation process infers the individual
187 origination and extinction times of each taxon based on all fossil occurrences and on an
188 estimated preservation rate, denoted q , and expressed as expected occurrences per taxon per
189 Myrs. This approach uses as input data all fossil occurrences that can be assigned to a taxon,
190 in our case fossil genera and families.

191 We followed the PyRate approach as developed in Silvestro et al. (2015) to study the
192 long evolutionary history of vascular plants. This approach includes several modifications
193 appropriate for the type of data and the aims of our study, which is mainly focused on
194 variation in origination and extinction on a global scale and large temporal ranges. We used a
195 homogeneous Poisson process (*-mHPP* option) of preservation (Silvestro et al., 2014). We
196 also accounted for varying preservation rates across taxa using the Gamma model (*-mG*
197 option), that is, with gamma-distributed rate heterogeneity (Silvestro et al., 2014). Because of
198 the large number of occurrences analyzed and of the vast timescale considered, we used eight
199 rate categories to discretize the gamma distribution (*-ncat 8* option) and accommodate the
200 potential for more variability of preservation rates across taxa.

201 Furthermore, we dissected the birth–death process into time intervals (*-fixShift* option),
202 which are defined either by the geological periods of the stratigraphic timescale (Gradstein et
203 al., 2012) resulting in 18 time intervals, or by 10-Myrs bins resulting in 32 time intervals. We
204 estimated origination and extinction rates within these intervals (*-A 0* option). We adopted
205 this solution as an alternative to the algorithms implemented in the original PyRate that
206 jointly estimates the number of rate shifts and the times at which origination and extinction
207 undergo a shift (*-A 2* option, Silvestro et al., 2014). The estimation of origination and
208 extinction rates within fixed time intervals improved the mixing of the MCMC and allowed
209 us to obtain an overview of the general trends of rate variation throughout a long timescale
210 (Silvestro et al., 2015). Both the preservation and the birth–death processes are modeled in
211 continuous time and are not based on boundary crossings. Thus, the origination and
212 extinction rates are measured as the expected number of origination and extinction events per
213 lineage per Myrs. One potential problem in fixing *a priori* the number of rate shifts is over-
214 parameterization. We overcame this issue by assuming that the rates of origination and

215 extinction are part of two families of parameters following a common prior distribution, with
216 parameters estimated from the data using hyper-priors (Gelman, 2004).

217 We ran PyRate for 10 million MCMC generations on 10 randomly replicated datasets
218 using the *extract.ages* function, which resamples the age of fossil occurrences randomly
219 within their respective temporal ranges (Silvestro et al., 2014; e.g. a fossil from the
220 Sinemurian stage would have an age fixed randomly between 190.8 and 199.3 Myrs for each
221 replicate). After excluding the first 10% of the samples as a burn-in period, we combined the
222 posterior estimates of the origination and extinction rates across all replicates to generate
223 rates-through-time plots. Rates of two adjacent intervals were considered significantly
224 different when the mean of one lay outside of the 95% highest posterior density (HPD) of the
225 other, and conversely. We looked at the marginal posterior distributions of origination and
226 extinction rates through the largest extinction events documented in geological history. In
227 particular, we examined the diversification dynamics at three of the Big Five events: the P-T,
228 the T-J, and the K-Pg boundaries (*sensu* Raup and Sepkoski, 1982). We focused on the
229 magnitude of rate changes, their statistical significance and the uncertainty around those
230 estimates.

231

232 ***Episodic process of phylogeny-based diversification***

233 We investigated whether diversification dynamics correlate with dramatic changes in tectonic
234 or climatic settings (e.g. Pangea break-up) or environmental changes (e.g. the Cretaceous rise
235 of Angiosperms) or rapid mass extinction events (e.g. the Cretaceous-Paleogene event) using
236 episodic birth-death models implemented in the R-packages *TreePar* 3.3 (Stadler, 2011) and
237 *TESS* 2.1 (CoMET model, Höhna et al., 2016b; May et al., 2016). These methods relax the
238 assumption of constant rates and can detect discrete changes in speciation (denoted as λ) and
239 extinction (denoted as μ) rates concurrently affecting all lineages in a tree. Both approaches

240 estimate changes in diversification rates at discrete points in time, but can also infer mass
241 extinction events, defined as sampling events in the past in which the diversity is reduced to a
242 percentage of the pre-extinction diversity. Speciation and extinction rates can change at those
243 points but remain constant within time intervals. The underlying likelihood function is
244 identical in the two methods (Stadler, 2011; Höhna, 2015), but TreePar and TESS differ in
245 the inference framework (maximum likelihood vs. Bayesian) and the method used for model
246 comparison (corrected Akaike information criterion [AICc] vs. Bayes factors [BF]). In
247 addition, TESS uses independent compound Poisson prior (CPP) to simultaneously detect
248 mass extinction events and discrete changes in speciation and extinction rates, while TreePar
249 estimates the magnitude and timing of speciation and extinction changes independently to the
250 occurrence of mass extinctions (i.e. the three parameters cannot be estimated simultaneously
251 due to parameter identifiability issues; Stadler, 2011).

252 TreePar analyses were performed using the '*bd.shifts.optim*' function that allows for
253 estimating discrete changes in speciation and extinction rates and extinction events in under-
254 sampled phylogenies (Stadler, 2011). Going backward in time, it estimates the maximum
255 likelihood speciation and extinction rates together with the rate shift times $t = (t_1, t_2, \dots, t_n)$ in a
256 phylogeny. At each time t , the rates are allowed to change and the phylogeny may undergo a
257 sudden extinction event (when the option mass extinction [ME] is set to TRUE). TreePar
258 analyses were run with the following settings: *start* set to 60 Myrs ago (to include the K-Pg
259 event), *end* set to the group's crown age estimated by the dating analyses, *grid* set to 1 Myrs
260 (evaluating a possible shift every Myrs), and *posdiv* set to FALSE to allow the diversification
261 rate to be negative (i.e. allows for periods of declining diversity).

262 Contrary to studies that examined the diversification rates of groups from their origin
263 to the present, we focused our study on investigating macroevolutionary rates from the clade
264 origin to a given point in time following Meredith et al. (2011) and Kergoat et al. (2014).

265 Potential biases in diversification rate analyses are known for incomplete phylogenies (e.g.
266 Cusimano and Renner, 2010; Brock et al., 2011), therefore our aim is to reveal a global
267 diversification pattern and its dynamic over deep timescales, where we assume the tree is
268 fully sampled and all the higher-level lineages are included in the tree (Legendre et al., 2015).
269 Indeed the tree lacks most of the extant diversity of the group, and we thus have preferred to
270 not study the Cenozoic diversification (pending more complete phylogenetic trees for
271 Dictyoptera). Here we studied the whole diversification history of the Dictyoptera from the
272 origin of the clade (*ca.* 325 Myrs ago) to 60 Myrs ago. Hence, we did not use a correction for
273 incomplete sampling since it is virtually impossible to know how many lineages were alive
274 60 Ma.

275 We fitted the constant-rate birth-death model as the reference for further model
276 comparison. We also applied five different diversification scenarios (containing one to five
277 shift times) to the consensus time-calibrated tree and computed the log-likelihood (logL), the
278 corrected Akaike information criterion (AICc) and Akaike weights (AIC ω) corresponding to
279 each scenario. We performed a model selection based on the lowest AICc and highest AIC ω ,
280 but also using the likelihood ratio test (LRT, at $P < 0.05$) since TreePar models are nested. If
281 the model with lowest/highest AICc/AIC ω was supported by LRT, it was considered the best.
282 If it was not supported by LRT, the simpler model — with fewer parameters — was
283 considered the best. Given the maximum likelihood estimates of the net diversification rate
284 ($r = \lambda - \mu$) and turnover rate ($\epsilon = \frac{\mu}{\lambda}$), we can infer the speciation and extinction rates. We
285 investigate the robustness of our results to the effect of phylogenetic and dating uncertainties
286 by fitting the TreePar models over 100 time-calibrated trees (Legendre et al., 2015).

287 CoMET uses a reversible jump Markov Chain Monte Carlo (MCMC) algorithm to
288 test the probability of rate shifts in speciation and extinction through time, comparing the
289 probability of temporal rate shifts to no rate shifts using BF (May et al., 2016). We specified

290 initial speciation and extinction rates and estimated the number of rate changes and extinction
291 events empirically as in TreePar. Contrary to TreePar, CoMET cannot be applied over a
292 specific temporal range, and we thus fitted CoMET throughout the dictyopteran tree. We set
293 a correction for incomplete sampling ($\rho=0.1$) but we only interpreted the results prior to 60
294 Ma. The initial rate shift prior and number of extinction rates prior were drawn from a CPP,
295 and the new rates drawn from a lognormal distribution with the mean and standard deviation
296 of the distribution based on empirically estimated hyperpriors. Hyperpriors were estimated
297 based on initial MCMC runs under constant-rate models to center the priors of the rate shift
298 parameters with those means and standard deviations. The number of expected rate changes
299 and mass extinction events were drawn from a CPP with a mean of $\log(2)$ to constrain the
300 complexity of the model and avoid inferring overly complex scenarios, and expected mass-
301 extinction time set to 3, corresponding to the P-T boundary, T-J boundary and the K-Pg
302 boundary. We condition on the survival of the lineage to the present. We set the initial
303 extinction probability to 0.5, and the β distributed prior on survival probability had shape
304 values of 2 and 10, which put most of the prior distribution over low values of survival
305 (~ 0.15) while being wide enough to allow for less strict probabilities (up to 0.70).
306 Independent MCMC analyses were run using a minimum effective sample size (ESS) of 200
307 as the stopping criterion. We used the diagnostics tools to assess the convergence of MCMC
308 using Gelman-Rubin statistics.

309 To compare inferences between CoMET and TreePar, we performed another series of
310 TreePar analyses allowing for mass extinction events (argument ME=TRUE, everything else
311 being equal to the TreePar analyses above). We compared models with 0, 1 or 2 rate mass-
312 extinction events in TreePar using the AICc, while BF comparisons were used to assess
313 model fit between models with varying number and time of changes in speciation/extinction
314 rates and mass extinctions in TESS.

315

316 **Results**

317 *Origin and extinction of major dictyopteran lineages*

318 For Dictyoptera *sensu stricto*, we assembled a fossil dataset at the family level comprising
319 2277 occurrences and a genus-level dataset including 2458 occurrences (more occurrences
320 because several genera are not assigned to a family). The family dataset contains 45 extinct
321 dictyopteran families and 16 extant families, while the genus dataset comprises 513 genera of
322 which 442 are extinct and 71 are extant. With the fossil occurrences of the putative extinct
323 sister lineage Paoliida, the family-level dataset includes 2450 occurrences for 16 extant and
324 71 extinct families, while the genus-level dataset comprises 2631 occurrences for 71 extant
325 and 497 extinct genera.

326 The PyRate analyses on the family-level dataset estimate the origin of Dictyoptera in
327 the Late Carboniferous (median = 324.02 Myrs ago, 95% HPD: 321.94 – 329.71 Myrs ago).
328 Overall, the fossil record shows four main periods of clades' origins: in the Late
329 Carboniferous, in the Early-Middle Triassic, in the Early Cretaceous, and in the middle
330 Paleogene (**Fig. 2**). The PyRate analyses also bring insights into the origin of extant families,
331 for instance Blaberidae at 94.77 Myrs ago (95% HPD 90.02 – 104.93 Myrs ago), Blattidae at
332 183.32 Myrs ago (95% HPD 175.66 – 197.43 Myrs ago), Ectobiidae at 127.98 Myrs ago
333 (95% HPD 125.52 – 131.09 Myrs ago), Mantidae at 59.79 Myrs ago (95% HPD 56.01 –
334 79.52 Myrs ago), Mantoididae at 56.27 Myrs ago (95% HPD 48.24 – 80.42 Myrs ago),
335 Mastotermitidae at 132.28 Myrs ago (95% HPD 129.54 – 137.16 Myrs ago), and Termitidae
336 at 53.84 Myrs ago (95% HPD 49.26 – 56.80 Myrs ago). Based on the posterior samples of the
337 ages of origin derived from all replicates, we computed the estimated parameter values
338 (offset, scale and shape), which may be directly used for other studies as calibrations to date
339 molecular phylogenetic trees using relaxed molecular clock models. The estimated

340 parameters and offset values are given following the parameterization used in BEAST or
341 MrBayes (see **Table 1** for families, and Appendix S2 for genera), two popular programs for
342 molecular dating. It is important to note that these ages predate those of the oldest fossil
343 occurrences for each group because they reflect the use of all available occurrence data to
344 model the preservation process while incorporating the uncertainties around the fossil ages.
345 To our knowledge, we are not aware of any study using such parameters and offset values to
346 estimate divergence times, however they can be useful for future dictyopteran phylogenetic
347 studies.

348 The fossil record shows three main periods for the extinction of clades: in the
349 Carboniferous-Permian boundary, at the Permian-Triassic boundary, and in the mid-Late
350 Cretaceous (**Fig. 3**). Fourth and fifth, albeit lesser, extinction periods are recovered in the
351 middle Permian and at the Jurassic-Cretaceous boundary. The Cenozoic witnessed the
352 extinction of only three families.

353

354 *Fossil-based diversification dynamics*

355 Regardless of the time intervals (10-Myr-bins or geological epochs) used for the birth-death
356 analyses of PyRate, a dynamic diversification pattern is inferred along the evolutionary
357 history of Dictyoptera (**Fig. 4**; Appendix S3). The analyses based on the 10-Myr-bins bring
358 more insights into the effect of mass extinctions. Dictyoptera had an early burst of speciation
359 in the Late Carboniferous, followed by a sharp four-fold decrease of speciation in the
360 Permian. The Permian period is characterized by high extinction rates, except in the mid-
361 Permian, until the mass extinction 252 Myrs ago. The decrease of speciation associated with
362 the increase of extinction results in a negative net diversification in the Permian, recovered at
363 both taxonomic levels in all analyses (**Fig. 4**; Appendix S3).

364 The recovery after the mass extinction in the Early and Middle Triassic is
365 characterized by a two-fold increase of speciation, with a decrease of extinction in the Middle
366 Triassic at both the family and genus levels (rates of diversification became positive). The
367 speciation rate significantly dropped to almost zero in the Late Triassic resulting in negative
368 net diversification rate while approaching the Triassic-Jurassic extinction at the family level
369 but not for genera (**Fig. 4**). The Early Jurassic has equal speciation and extinction rates
370 resulting in a null net diversification (high turnover). While the PyRate analyses show a
371 concomitant increase of speciation and decrease of extinction in the Middle Jurassic turning
372 the net diversification to positive, the analyses further show a concomitant decrease of
373 speciation and increase of extinction in the Late Jurassic indicating a negative diversification
374 rate at the end of the Jurassic, a result supported by all analyses (**Fig. 4**; Appendix S3).

375 The Cretaceous period is divided in two contrasted speciation trends with the Early
376 Cretaceous having speciation rates twice as high as the speciation during the Late Cretaceous;
377 the latter potentially due to a lack of post-Cenomanian localities. Interestingly the extinction
378 rate is low in the earliest and latest Cretaceous epochs but is very high in the mid-Cretaceous
379 (**Fig. 4**; Appendix S3). Nonetheless, we find a difference between the analyses with 10-Myr-
380 bins and geological epochs. The 10-Myrs-bins analyses reveal an important extinction period
381 at the end of the Early Cretaceous (Albian-Aptian, 100 – 120 Myrs ago, **Fig. 4**), explained by
382 a nearly null speciation rate and the highest extinction rate inferred thus resulting in negative
383 net diversification (mean = -0.045, 95% HPD: -0.01 to -0.08). In contrast, with the analyses
384 based on the geological epochs, net diversification rates were positive in the Early Cretaceous
385 and became negative in the Late Cretaceous while approaching the K-Pg boundary
386 (Appendix S3). Such discrepancy might be due to the fact that the Cretaceous (~80 Myrs
387 long) is only divided into two epochs, and we unveil clear temporal variations of
388 diversification rates within each epoch with the analyses using 10-Myrs-bins intervals.

389 Alternatively, the mid-Cretaceous represents an important turnover period for the
390 entomofauna, but is not perceived in the marine invertebrate fossil record, probably because
391 the data were only analyzed for the two Cretaceous epochs and not through eight time
392 intervals as in our 10-Myrs-bins analyses.

393 A boom of origination in the Paleocene and Eocene with high net diversification rates
394 characterized the Cenozoic dictyopteran diversification, but the Oligocene was a turnover
395 period with null net diversification. We do not find substantial shifts in origination and
396 extinction rates in the Neogene: net diversification rates are estimated to be close to zero (**Fig.**
397 **4**; Appendix S3).

398 The PyRate analyses allow inferring the times of origin and times of extinction (if the
399 taxon is extinct) of each taxon in the fossil dataset. Summing the times of origin and times of
400 extinction through time permits the estimation of the number of genus / family lineages
401 through time (paleodiversity) for the group (**Fig. 5**; Appendix S4). The paleodiversity of the
402 group has substantially fluctuated at both taxonomic levels: it shows the Late Carboniferous,
403 the Middle Triassic, the Early Cretaceous, and the Paleogene as the main periods of
404 taxonomic origination, and shows the Carboniferous-Permian boundary, the Permian-Triassic
405 boundary, the Late Jurassic, and the middle Cretaceous as periods of clade extinction.

406 Including the fossil occurrences belonging to Paoliida does not alter the global
407 diversification pattern of Dictyoptera. We estimate the same major periods of diversification
408 and extinction and also a similar magnitude in the evolutionary rates (Appendix S5).

409

410 *Phylogeny-based analyses*

411 The episodic birth-death model of TreePar (with mass extinction disallowed) finds that a
412 model with a single shift time best explains the diversification dynamics of the dictyopteran
413 groups (**Table 2**). Applied to 100 dated trees, the analyses indicate that most of the trees

414 (81%) had a negative shift of diversification in the Maastrichtian (the last stage of the Late
415 Cretaceous) or even at the K-Pg boundary (median age = 65.3 Myrs ago, **Fig. 6a**). The
416 TreePar analyses do not find support for a diversification shift in deeper times (i.e. models
417 with more shifts are not supported), although models with multiple shifts inferred
418 diversification changes around periods of mass extinction (e.g. 248 Ma with the model
419 including five shifts; **Table 2**).

420 We further find that this shift of diversification is not due to a mass extinction because
421 the episodic birth-death model of TreePar (with mass extinction allowed) indicates that a
422 model without mass extinction best fits to the diversification dynamics of Dictyoptera:
423 $\Delta\text{AICc} = 6.06$ between a constant-rate model and a model including one mass extinction
424 event, and $\Delta\text{AICc} = 12.17$ against a model with two mass extinction events. Applied to 100
425 dated trees, the analyses reflect the uncertainty around the estimate of a mass extinction,
426 which could have occurred in three periods: the mid-Permian, the mid-Cretaceous, and the
427 Maastrichtian, but with most trees suggesting an extinction event in the mid-Cretaceous
428 (median age = 117.5 Myrs ago, **Fig. 6b**).

429 The TESS analyses (Appendix S6) show that diversification increased throughout the
430 Paleozoic, and since the P-T boundary (highest net diversification) the dictyopteran
431 diversification has slowed down drastically until the mid-Cretaceous (lowest net
432 diversification). After the mid-Cretaceous, the diversification increased again, until it
433 dropped abruptly to negative values in the Eocene-Oligocene (~35 Myrs ago). A high
434 turnover is inferred all along the dictyopteran history with a peak in the mid-Cretaceous and
435 the Eocene-Oligocene. Applying the CoMET model, a single possible mass extinction is
436 detected in the mid-Permian but with Bayes factors < 6 (Appendix S7).

437

438 **Discussion**

439 *Diversification and extinction events in Dictyoptera history*

440 Estimated to date back to the Late Carboniferous or even before (Legendre et al., 2015;
441 Evangelista et al., 2019), stem- and crown-Dictyoptera have faced three massive extinction
442 events. How these events have affected their diversification dynamics has however rarely
443 been investigated. It has even been questioned as to whether insects were impacted by mass
444 extinctions (Labandeira and Sepkoski 1993; Mayhew, 2007; Condamine et al., 2016). Here
445 we found that, like for many other organisms, the diversification dynamics of Dictyoptera has
446 alternated between periods of high and low diversification, but these changes are not
447 necessarily correlated with mass extinction events. Far from their misleading stereotypical
448 image of invulnerable insects (Laurentiaux, 1959; Garfield, 1990; Appel, 1995), Dictyoptera
449 have experienced periods of high extinction rates, sometimes resulting in negative net
450 diversification and thus declines in diversity; a result supported by our phylogeny- and fossil-
451 based approaches.

452 On the basis of the available data, we identified three main periods of diversification
453 for Dictyoptera (i.e. Early Triassic, Early Cretaceous and Paleogene) and three main periods
454 of extinction (i.e. early Permian, late Permian and mid-Cretaceous). The Early Cretaceous
455 diversification seems to have concerned the insects as a whole (Schachat et al., 2019).
456 Phylogeny-based inferences with TESS indicated a possible fourth extinction period in the
457 Eocene-Oligocene, which we will not discuss because it might be due to a methodological
458 artifact given the low sampling of extant species. These diversification and extinction periods
459 conceal different situations that we were able to delineate analyzing phylogeny- and fossil-
460 based results. We discuss below the most remarkable of those patterns and their putative
461 underlying processes.

462 Dictyoptera diversified greatly during the Early Triassic, which is an epoch with a
463 poor fossil record with only one important Anisian deposit (ca. 247 Myrs ago, Papier et al,

1994, 1996; Papier and Grauvogel-Stamm, 1995; Vršanský, 2010), while the Middle Triassic counts several deposits. This timing also corresponds to the rise of many modern lineages of other insects such as Acercaria and Holometabola (especially beetles, flies and wasps, Papier et al., 2005; Misof et al., 2014; Rainford et al., 2014; Condamine et al., 2016; Montagna et al., 2019). Likewise, during the Cretaceous, the high origination rates of Dictyoptera parallel the rise of most of the modern insect families, currently well-known through recent discoveries in early Cenomanian Burmese amber (Grimaldi and Engel, 2005; Rainford et al., 2014; Ross, 2019), while the high extinction rates match the fall of roachoid fossils, which are not related to crown-Blattodea (Schubnel, 2018). With high origination and extinction rates, the Cretaceous is a period of major turnover in dictyopteran lineages. Interestingly, the Cretaceous underwent drastic environmental changes including the shift in ecological dominance of terrestrial plants with the Angiosperm Revolution (Labandeira and Currano, 2013) and the Cretaceous Terrestrial Revolution (Lloyd et al., 2008). Rather than a mass extinction event, these environmental changes and their aftermath on biotic interactions might explain this period of high turnover in Dictyoptera.

We found a boom-then-bust pattern (boosts of origination followed by boosts of extinction) at the Carboniferous-Permian and P-T boundaries but also in the middle Cretaceous, three periods when diversification rates shifted from positive to negative, hence from expanding to declining diversity (**Fig. 5**). Among these declines, only the P-T boundary corresponds to a known mass extinction, which has been found in the insect fossil record as a whole (Labandeira and Sepkoski, 1993; Condamine et al., 2016) but not recovered in beetles (Smith and Marcot, 2015). The Carboniferous-Permian pattern matches the diversification of the mesophytic flora during the late Carboniferous – early Permian (Cleal and Cascales-Minana, 2014; Servais et al., 2019). It could also reflect the peak of the Late Paleozoic Ice Age that extended throughout the Carboniferous and early Permian (Qie et al., 2019), causing

489 changes in the entomofaunas. Alternatively, it could be artefactual and merely illustrate the
490 effect of the push of the past, which posits that ancient clades that survived during a long
491 time are more likely to have a slowdown of diversification. Indeed, a high rate of early
492 diversification is a necessary condition for most clades to survive a substantial length of time
493 (Budd and Mann, 2018). Dating back to the Late Carboniferous, a high rate for Dictyoptera is
494 thus expected at this epoch.

495 Finally, Dictyoptera underwent an extinction event at the end of the Early Cretaceous
496 at the boundary of the Aptian and Albian (~115 Myrs ago), which does not correspond to a
497 mass extinction event. Strikingly, both phylogeny- and fossil-based analyses recovered the
498 signal of this extinction event. A high extinction rate during the Aptian and Albian stages has
499 already been observed in insects (Labandeira, 2005). Different underlying reasons have been
500 postulated, the most convincing being a change and increase in angiosperm food resources as
501 a trigger of clade extinction through competition (Labandeira, 2005). During the Aptian-
502 Albian, the angiosperms (aquatic and strictly terrestrial) began to be quite frequent in
503 sedimentary deposits with numerous fossils with exceptional preservation, and a high
504 diversity in many clades (i.e. konservat lagerstätten) like the Crato Formation in Brazil
505 (Martill et al., 2007). In beetles, families of Polyphaga thrived during this period, while non-
506 Polyphaga families experienced high extinction rates and diversity declines (Smith and
507 Marcot, 2015). Beyond the causes that our study cannot decipher, our results confirm that this
508 period has been critical for several insect groups, be they detritivorous like most Blattodea or
509 carnivorous like Mantodea that underwent an important diversification at that time (Delclòs
510 et al., 2016). The Aptian-Albian is also the period of the first known diversification of the
511 eusocial ‘lower’ termites (mastotermitid- and hodotermitid-like taxa, and Kalotermitidae,
512 Engel et al., 2009; Zhao et al., 2019).

513 Although these results must be considered in light of the heterogeneity of the fossil
514 record (see below), they suggest that Dictyoptera, and likely other insects, have not been
515 impacted as heavily as other organisms by mass extinction events (Labandeira and Sepkoski,
516 1993; Condamine et al., 2016). This agrees with, for instance, both a steady diversification of
517 insect mouthparts (diets) for which no massive extinction events have been revealed (Nel et
518 al., 2018), and with the origin of major innovations (e.g. diets, wings, metamorphosis) that
519 did not parallel main era or period transitions (Rainford and Mayhew, 2015). A noticeable
520 exception for Dictyoptera is the K-Pg transition. This crisis matches the main shift of
521 diversification in Dictyoptera (**Fig. 6a**), with the rise of the first eusocial Dictyoptera, the
522 termites, that were already quite diverse during the Cretaceous (Engel et al., 2009; Legendre
523 and Condamine, 2018). However, there could be a bias around the K-Pg crisis because the
524 insect fossil record for the Maastrichtian remains poorly studied, hence potentially leading to
525 some uncertainty in the timing of these changes. But, apart from this exception, mass
526 extinctions in insects seem to have played a lesser role than biotic interactions, which
527 deserves further studies (Labandeira and Currano, 2013).

528

529 *Fossil record, phylogeny and the study of extinction*

530 Estimating extinction rates is a major hurdle to the study of the clades' diversification
531 dynamics, especially from molecular phylogenies of extant species (Rabosky, 2010; Quental
532 and Marshall, 2010; Morlon et al., 2011; Beaulieu and O'Meara, 2015; Rabosky, 2016;
533 Hagen et al., 2018). To overcome this difficulty, fossils have a key role (Quental and
534 Marshall, 2010; Fritz et al., 2013). Indeed, fossils are direct evidence of the diversification
535 processes and they contribute to improve our estimates and understanding of the role of
536 extinction during life history (Wagner and Lyons, 2010). However, two general issues may
537 influence any diversification analysis: (i) the fossil record is biased and incomplete (Kidwell

538 and Holland, 2012), and (ii) the taxonomic ranks used to perform diversification studies may
539 impact the outcomes of the analyses.

540 Notorious gaps in insect fossil records exist (Nel et al., 2018). The main Lagerstätten
541 for insects are not spread homogeneously over geological time (e.g. Smith and Marcot, 2015;
542 Clapham et al., 2016). A major “Hexapod gap” is known from the Early Carboniferous,
543 which hinders our understanding of the first winged insects (Nel et al., 2013), whose origin
544 remains unclear (e.g. decrease of atmospheric oxygen level, rarity, or preservation artifacts –
545 Retallack, 2011; Schachat et al., 2018). The lack of a rich fossil record in the late Permian,
546 Early Triassic, Early Jurassic, and latest Cretaceous (Nel et al., 2018) might blur the
547 diversification dynamics of Dictyoptera. Conversely, the rich fossil record in the Paleogene,
548 mostly due to Eocene Baltic ambers, might lead us to overestimate origination rates at this
549 time. Rich Paleocene outcrops like Menat (60 Myrs ago, France) remain to be studied.
550 However, in the case of PyRate, simulations confirm the absence of consistent biases due to
551 the incompleteness of the data in the fossil record (Silvestro et al., 2014). Incomplete taxon
552 sampling appears to have fewer problematic effects on the estimation of speciation and
553 extinction rates because, in contrast to molecular phylogenies (e.g. Cusimano and Renner,
554 2010; Brock et al., 2011), removing a random set of taxa does not affect the observed
555 occurrences of other lineages (Silvestro et al., 2014; 2019). We estimated a substantial
556 extinction effect of the P-T event in the fossil-based analyses, a result not found with
557 phylogeny-based analyses. Although filling gaps in the fossil record is a primary objective to
558 better understand insect evolution, we identified changes in the diversification dynamics of
559 Dictyoptera with this incomplete fossil record, changes we were unable to measure with the
560 phylogeny-based analyses of this study. In parallel, molecular phylogenies of Dictyoptera are
561 now in their genomic era (Evangelista et al., 2019), with termites (Bourguignon et al., 2017)
562 and cockroaches (Bourguignon et al., 2018) being more and more sampled and sequenced,

563 resulting in unprecedented topological resolutions. Applying phylogeny-based diversification
564 models to future dated dictyopteran phylogenies would allow revising our results.

565 We also found that family-, genus- or species-level diversification analyses of the
566 fossil record differ in their advantages and drawbacks. A species-level analysis of the fossil
567 record would seem the most appropriate, but because of biases in the insect fossil record and
568 the few specimens per species (most fossil species are known from singletons), we risk
569 deriving wrong conclusions. Genus- and family-level analyses are less prone to these issues.
570 They have commonly been used to estimate insect diversification (Labandeira and Sepkoski,
571 1993; Clapham et al., 2016; Condamine et al., 2016), but have other limitations. For
572 Dictyoptera, family-level analyses are questionable because several families were not defined
573 according to accurate synapomorphies and are most likely para- or polyphyletic (e.g.
574 Mesoblattinidae, Blattulidae). All of the Paleozoic dictyopteran families have never been
575 revised under a phylogenetic perspective and are mainly based on unpolarized wing venation
576 characters subject to important intraspecific variations (see Schneider, 1983, 1984). Counting
577 non-monophyletic entities is dubious for deriving any evolutionary conclusion. This problem
578 is, however, less significant at the genus level. Here, the importance of this effect was
579 downplayed by running analyses at both the family and genus levels.

580 Despite unavoidable limitations inherent to infer diversification dynamics with
581 phylogenies or fossils, we are confident that the recent methodological developments (e.g. the
582 birth-death chronospecies (BDC) model in Silvestro et al., 2018) will continue improving the
583 estimation of speciation and extinction rates thanks to joint analyses of fossils and
584 phylogenetic data.

585

586 **Conclusion**

587 In this study, using both the fossil record and molecular phylogeny coupled with state-of-the-
588 art diversification models, we show that Dictyoptera have experienced alternative periods of
589 high and low diversification, but instead of massive extinction events (except at the end of
590 the Permian), other factors might have played key roles. We thus deemphasize the
591 importance of mass extinction events in the diversification dynamics of dictyopteran insects.
592 We rather underline that the causes and consequences of extinction must be studied beyond
593 mass extinction events alone to gain a broader understanding of how clades wax and wane.
594 With the current biodiversity crisis where thousands of species face extinction (Régnier et al.,
595 2015; Ceballos et al., 2017; Sánchez-Bayo and Wyckhuys, 2019; Simmons et al., 2019;
596 Seibold et al., 2019), such general knowledge is urgent and critical.

597

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615

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- 889

890 **Figure legends**

891 **Figure 1.** Images of extant and extinct species of praying mantises, cockroaches and termites.

892 (a) An unidentified fossil mantis from Cretaceous amber of Myanmar (© Wikimedia
893 commons). (b) *Paratithrone royi* Lombardo, 1996 (© S. Hugel). (c) †*Etoblattina klebsi*
894 Meunier, 1921 (© G. Doitteau – type specimen MNHN.F.R51484). (d) *Notolampra punctata*
895 (Saussure, 1873) (© S. Hugel). (e) Fossil termite †*Meiatermes bertrani* Lacasa Ruiz and
896 Martínez-Delclòs 1986 from Cretaceous of Spain (© Wikimedia commons). (f) A
897 physogastrous queen with a worker of an unidentified termite species (© F. Legendre).

898

899 **Figure 2. Estimated times of origin (crown ages) for dictyopteran families.** Bold names
900 are extant families. The four main periods of origination are in shaded grey in the background.

901 The distributions were obtained from modeling the preservation process in PyRate and after
902 combining 10 replicated analyses to incorporate the uncertainties around the ages of the fossil
903 occurrences. The time of origin of Dictyoptera (not shown here) was 324.02 Myrs ago (95%
904 HPD: 321.94 – 329.71 Myrs ago). These distributions (Table 1) can be directly implemented
905 as calibration priors for dating the phylogenies of these clades using Bayesian relaxed
906 molecular clocks. The parameterization provided here follows that implemented in popular
907 molecular dating approaches. Asterisks indicate the illustrated families with pictures of
908 *Parastylotermes krishnai*, *Lithoblatta lithophila*, and *Parvifuzia peregrina* from ©
909 Wikimedia commons. Abbreviations: Ng = Neogene.

910

911 **Figure 3. Estimated times of extinction for dictyopteran families.** Bold names are extant
912 families. The three main periods of extinction are in shaded grey in the background. The
913 distributions were obtained from modeling the preservation process in PyRate and after
914 combining 10 replicated analyses to incorporate the uncertainties around the ages of the fossil

915 occurrences. Asterisks indicate the illustrated families with pictures of *Parastylotermes*
916 *krishnai*, *Lithoblatta lithophila*, and *Parvifuzia peregrina* from © Wikimedia commons.
917 Abbreviations: Ng = Neogene.

918

919 **Figure 4. Fossil-based diversification analysis of dictyopteran families (a) and genera (b).**

920 Origination (blue), extinction (red), and net diversification (grey) rates were estimated using
921 the Bayesian approach implemented in PyRate with time shifts defined every 10 million
922 years (results with time shifts defined by epochs of the geologic timescale are shown in
923 Appendix S3). Solid lines indicate mean posterior rates, whereas the shaded areas show 95%
924 credibility intervals. The vertical dashed lines indicate the major mass extinction events: at
925 the Permian–Triassic (P-Tr), Triassic–Jurassic (Tr-J), and Cretaceous–Paleogene (K-Pg)
926 boundaries. C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg,
927 Paleogene; Ng, Neogene.

928

929 **Figure 5. The paleodiversity trajectories of dictyopteran families (a) and genera (b).**

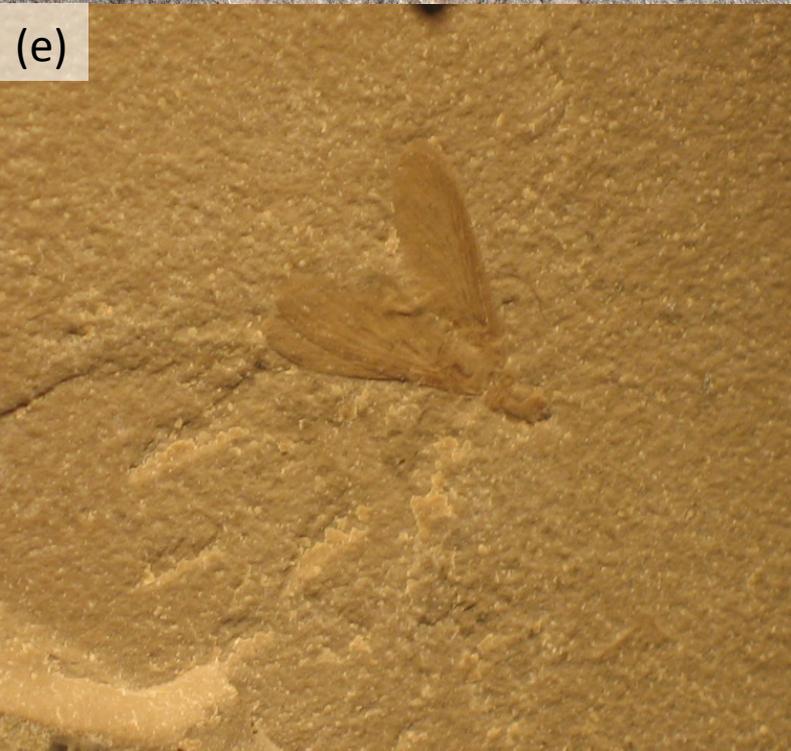
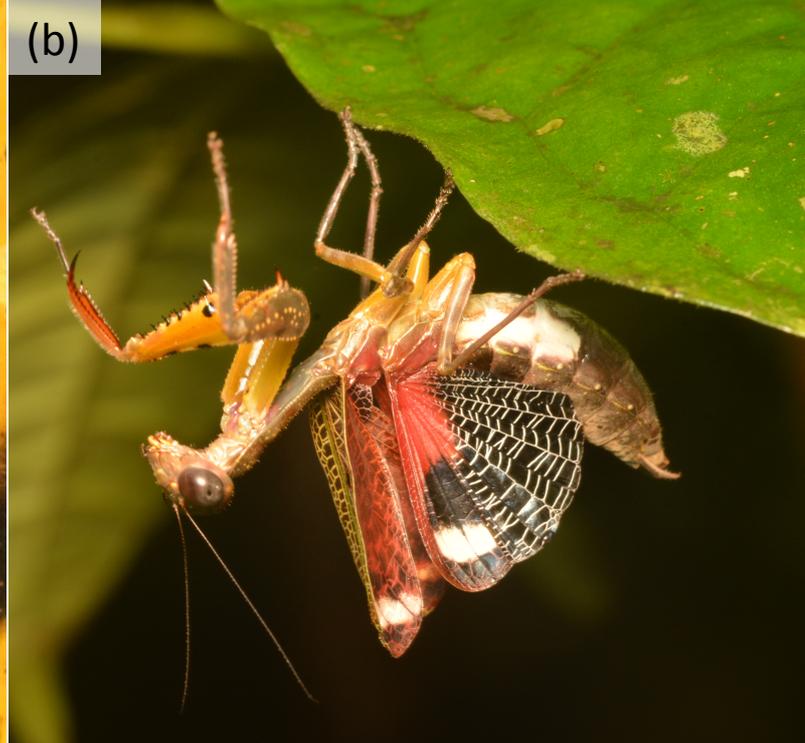
930 Reconstructions of diversity trajectories are based on times of origin and times of extinction
931 of each taxon, and are replicated 10 times to incorporate uncertainties around the age of the
932 fossil occurrences (results with time shifts defined by epochs of the geologic timescale are
933 shown in Appendix S4). The vertical dashed lines indicate the major mass extinction events:
934 at the Permian–Triassic (P-T), Triassic–Jurassic (T-J), and Cretaceous–Paleogene (K-Pg)
935 boundaries.

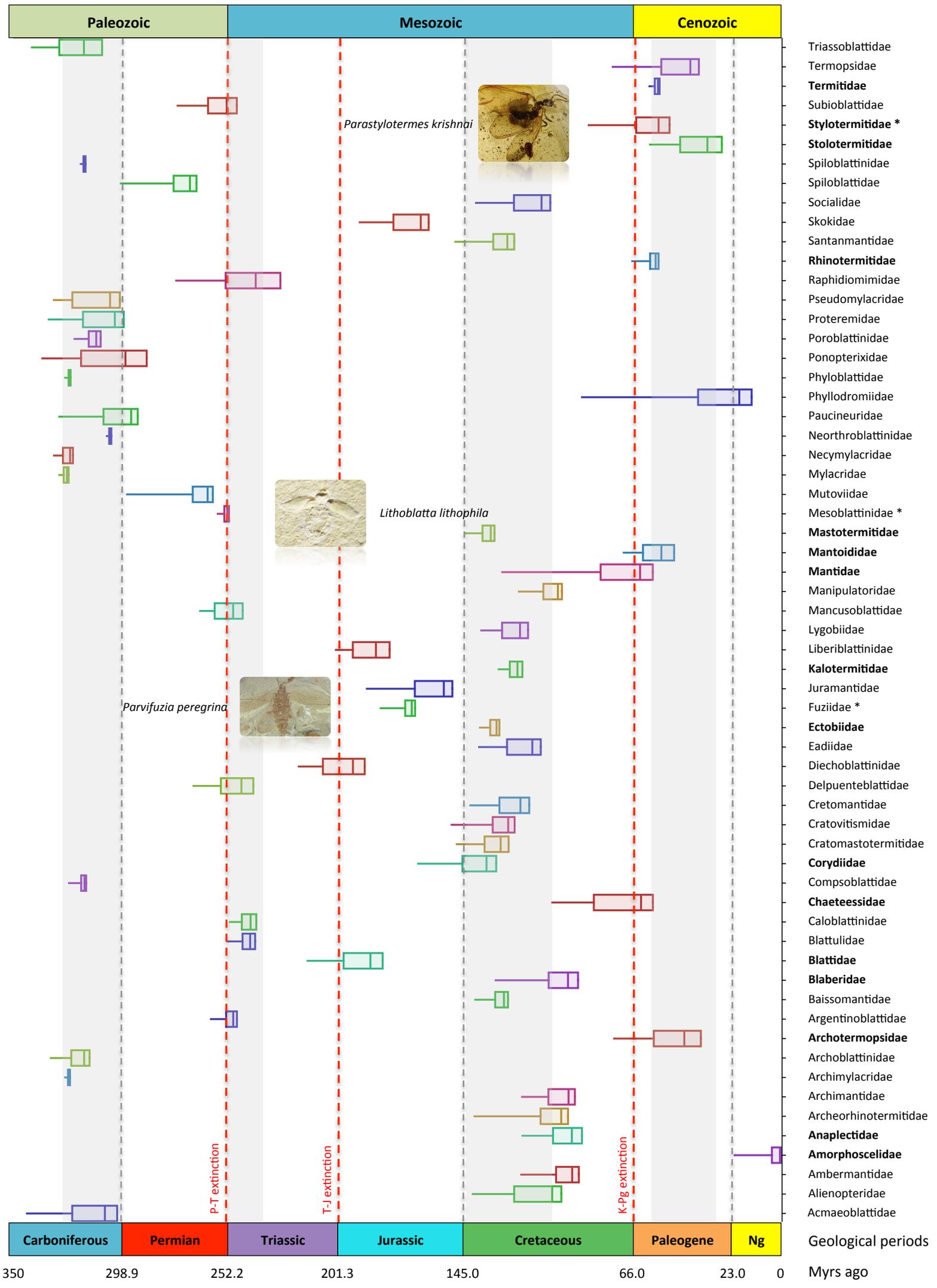
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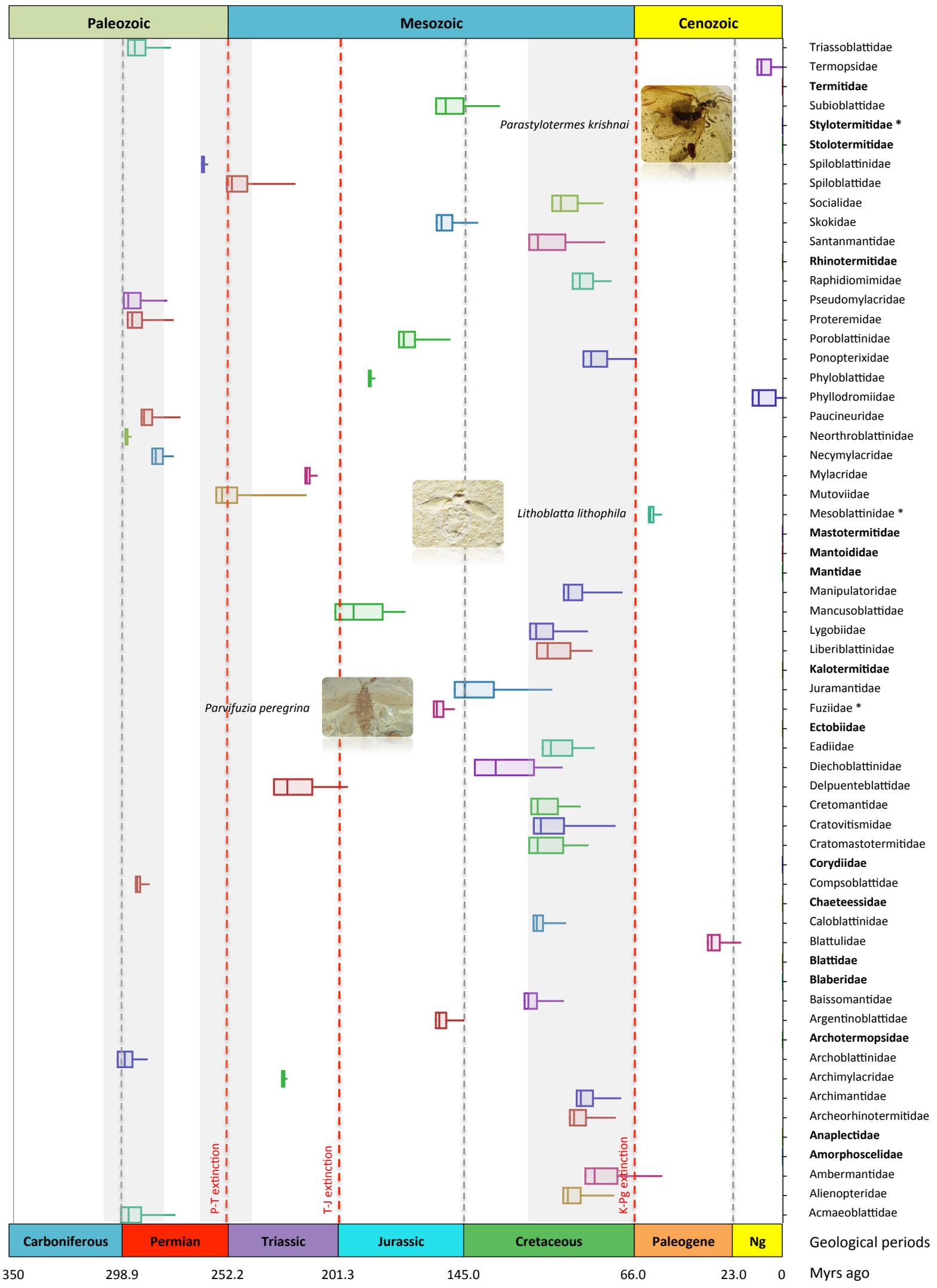
937 **Figure 6. Phylogenetic diversification dynamics of Dictyoptera inferred with time-**

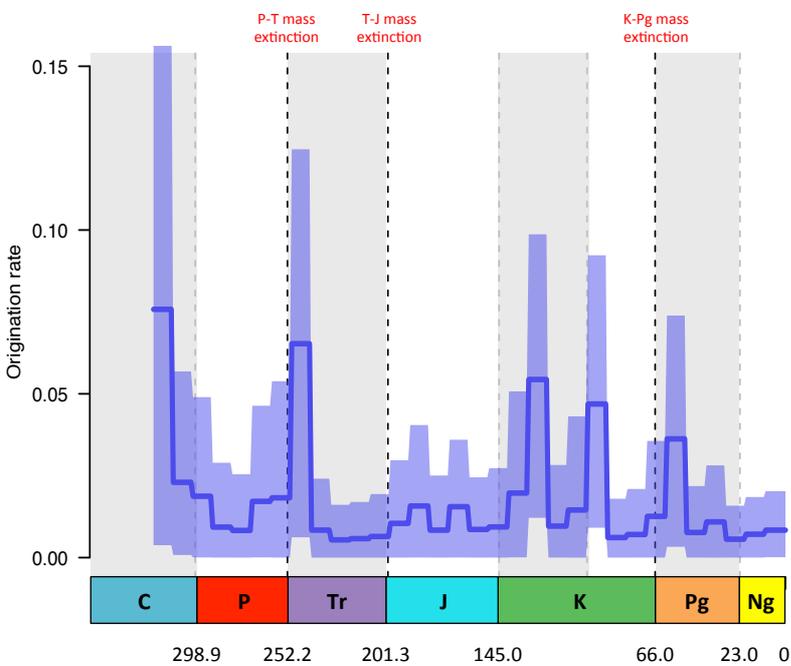
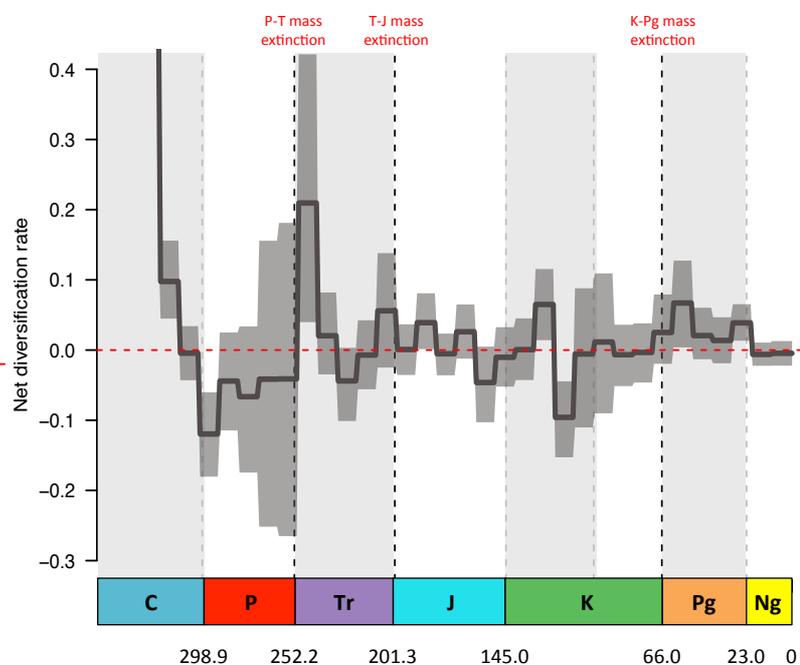
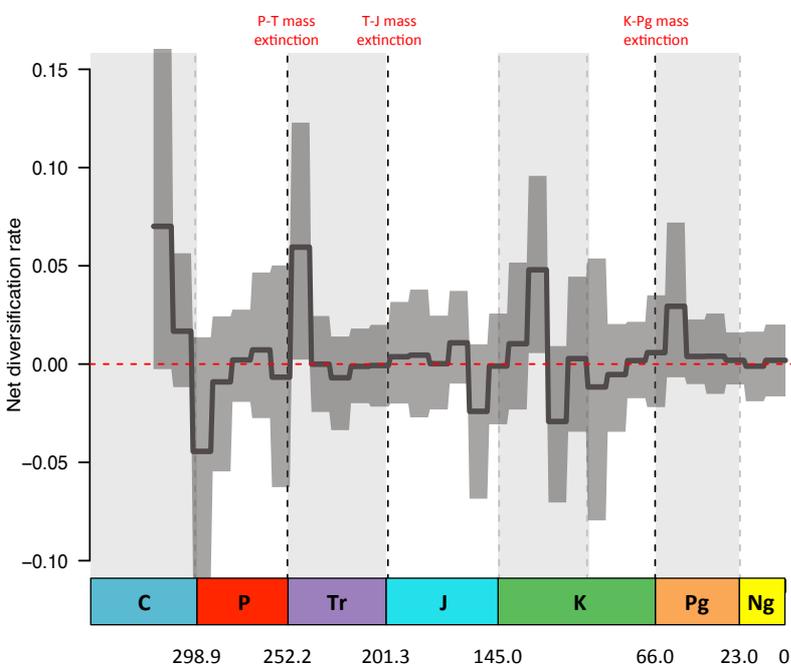
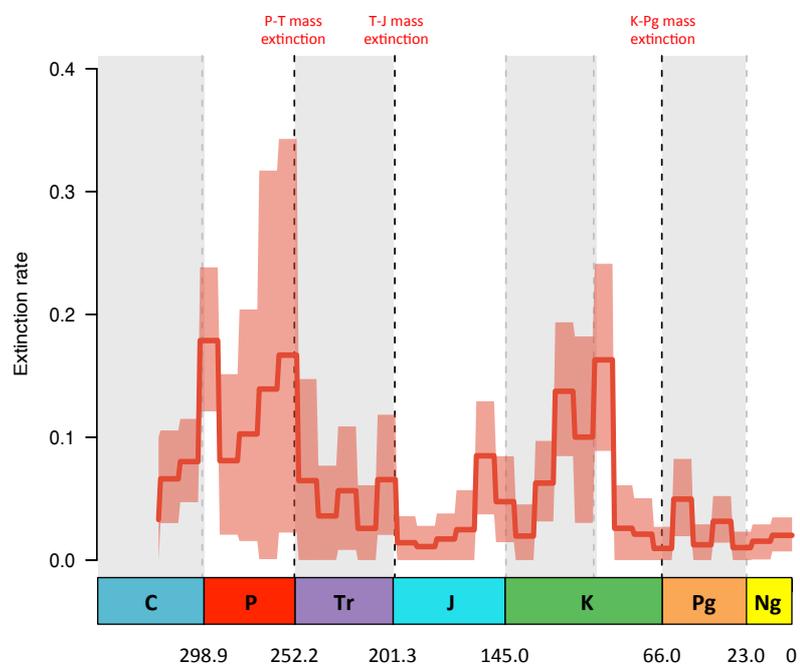
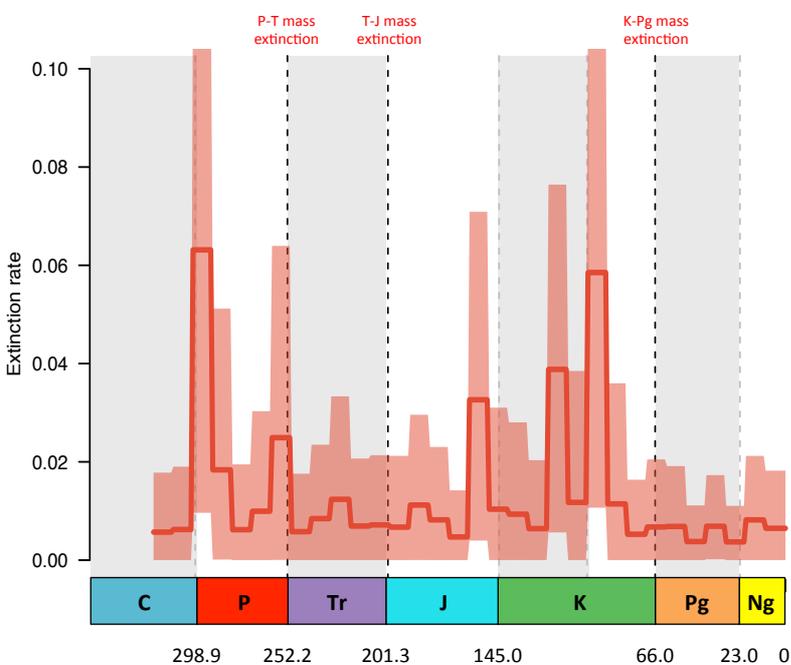
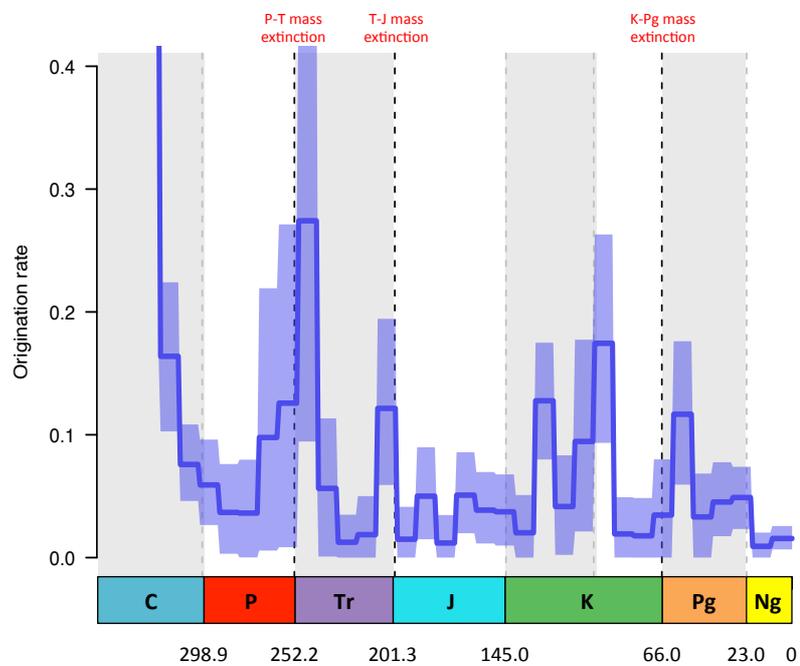
938 **dependent models.** (a) Episodic birth-death models in TreePar identified a significant
939 negative shift of diversification at the K-Pg boundary. The TreePar model estimated a

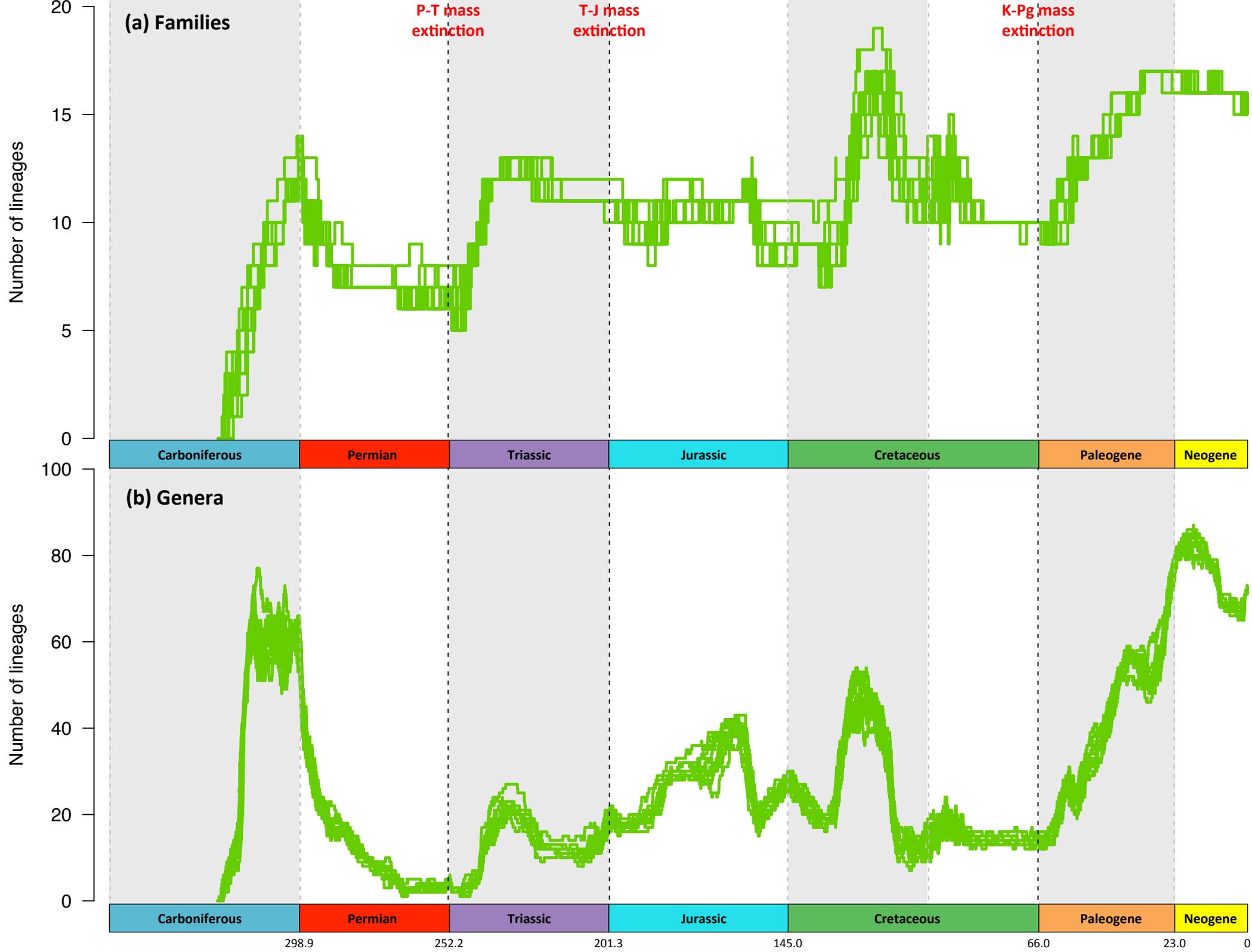
940 decrease in diversification after the K-Pg (Table 2). (b) Mass extinction models in TreePar
941 recovered a possible (not significant) mass extinction event in the mid-Cretaceous (similar
942 results obtained with CoMET, Appendix S7). The histograms show the uncertainty around
943 the timing of the shift time (a) and mass extinction event (b) based on the estimates over 100
944 trees with TreePar (the red lines show the median age of shift and mass extinction). C,
945 Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; Ng,
946 Neogene.
947



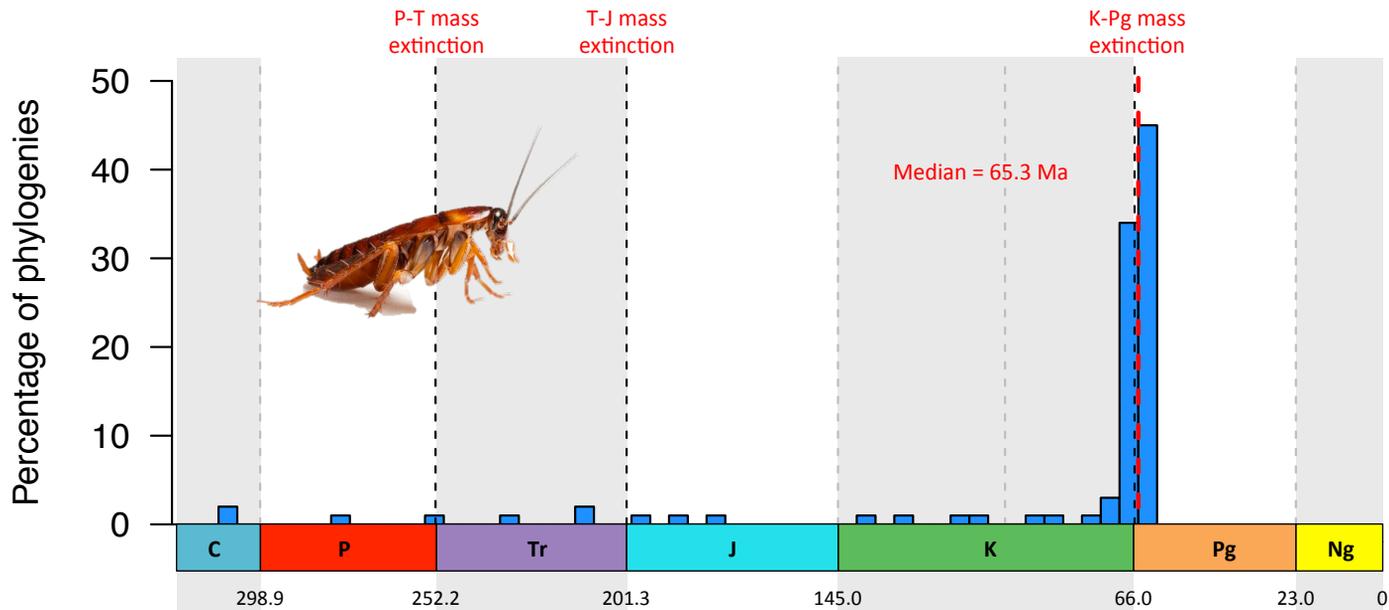




(a) Diversification dynamics of dictyopteran families**(b) Diversification dynamics of dictyopteran genera**



(a) TreePar analyses estimating whether **shifts in diversification occurred**



(b) TreePar analyses estimating whether a **mass extinction occurred**

