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**Article:**

Nicholson, David B, Ross, Andrew J and Mayhew, Peter J orcid.org/0000-0002-7346-6560 (2014) Fossil evidence for key innovations in the evolution of insect diversity. Proceedings of the Royal Society B: Biological Sciences. 20141823. ISSN: 1471-2954

<https://doi.org/10.1098/rspb.2014.1823>

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## Fossil evidence for key innovations in the evolution of insect diversity

|                               |   |
|-------------------------------|---|
| Journal:                      | <i>Proceedings B</i>  |
| Manuscript ID:                | RSPB-2014-1823.R1   |
| Article Type:                 | Research  |
| Date Submitted by the Author: | n/a   |
| Complete List of Authors:     | Nicholson, David; University of York, Biology; The Natural History Museum, Department of Earth Sciences; National Museums Scotland, Department of Natural Sciences<br>Ross, Andrew; National Museums Scotland, Department of Natural Sciences<br>Mayhew, Peter; University of York, Biology |
| Subject:                      | Palaeontology < BIOLOGY, Evolution < BIOLOGY, Ecology < BIOLOGY   |
| Keywords:                     | adaptive radiation, extinction, flight, Hexapoda, macroevolution, complete metamorphosis  |
| Proceedings B category:       | Evolutionary Biology  |
|                               |   |

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# **Fossil evidence for key innovations in the evolution of insect diversity**

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## Summary

Explaining the taxonomic richness of the insects, comprising over half of all described species, is a major challenge in evolutionary biology. Previously, several evolutionary novelties (key innovations) have been posited to contribute to that richness, including the insect *bauplan*, wings, wing folding, and complete metamorphosis, but evidence over their relative importance and modes of action is sparse and equivocal. Here, a new dataset on the first and last occurrences of fossil hexapod (insects and close relatives) families is used to show that basal families of winged insects (Palaeoptera e.g. dragonflies) show higher origination and extinction rates in the fossil record than basal wingless groups (Apterygota e.g. silverfish). Origination and extinction rates were maintained at levels similar to Palaeoptera in the more derived Polyneoptera (e.g. cockroaches) and Paraneoptera (e.g. true bugs), but extinction rates subsequently reduced in the very rich group of insects with complete metamorphosis (Holometabola e.g. beetles). Holometabola show evidence of a recent slow-down in their high net diversification rate, whilst other winged taxa continue to diversify at constant but low rates. These data suggest that wings and complete metamorphosis have had the most effect on family level insect macroevolution, and point to specific mechanisms by which they have influenced insect diversity through time.

**Keywords:** adaptive radiation, extinction, flight, Hexapoda, macroevolution, complete metamorphosis

## 22    **1. Introduction**

23    Why some groups of organism are very speciose, whilst others are species-poor, is a  
24    problem that has fascinated evolutionary biologists ever since Darwin [1–3]. The  
25    insects, with over half of all described species [4,5], have long stood out as a very  
26    speciose group whose richness requires explanation [6]. Of the many hypotheses  
27    proposed to explain this richness, some of the most prominent include the origin of  
28    novel phenotypic characters known as key innovations [7]. Here we use a new dataset  
29    on the fossil record of the hexapods (insects and their six-legged relatives such as  
30    springtails) to assess the relative importance of, and mechanisms underlying, several  
31    putative key innovations.

32    Macroevolutionary approaches to understanding current standing diversity require  
33    data on the past history of life, which comes from two complementary sources of  
34    information [8]. The neontological approach uses phylogenies of extant taxa to infer  
35    changes in past processes [9]. The palaeontological approach uses information from the  
36    fossil record [10]. Phylogenies of extant taxa allow one to study processes at the species  
37    level and in the absence of a fossil record, but inferences about speciation and extinction  
38    rates are problematic (e.g. [11]). Fossils, although often studied at taxonomic levels  
39    above the species, and though prone to sampling biases [12], provide direct evidence  
40    about the timing of changes in rate, as well as extinctions [13].

41    Ultimate causes of macroevolutionary change can include extrinsic factors such as  
42    environmental change [14,15], as well as intrinsic ones such as evolutionary novelties  
43    [16]. Key innovations are novel phenotypic characters such as morphologies,  
44    behaviours, or developmental strategies that enhance species richness [8,17], seen  
45    through an increase in net diversification rate. The underlying macroevolutionary

46 process could be an increase in speciation, decrease in extinction or some combination  
47 of changes in both. Three general ecological mechanisms have been proposed to explain  
48 the macroevolutionary effects of key innovations [8], corresponding to changes in three  
49 macroevolutionary parameters [7]: a) escape from competition into a new adaptive  
50 zone, thus changing the carrying capacity of taxa in the environment; b) decreasing the  
51 probability of extinction; and c) ecological or reproductive specialization, thus  
52 increasing the speciation rate. For neontological studies, explicit data supporting these  
53 macroevolutionary parameters may be lacking because they work with the net outcome  
54 rather than the underlying origination and extinction rates, making it hard to tease the  
55 different underlying parameters apart. In contrast, fossil studies are intrinsically better  
56 able to provide data on these different macroevolutionary parameters, thus aiding  
57 inference of the mechanism.

58 Four progressive evolutionary steps have traditionally been recognized in the  
59 evolutionary history of the hexapods, based on the sequence in which they appear in the  
60 fossil record [18,19] and phylogenies (e.g. [20]) (figure 1). These are the evolution of  
61 the insect *bauplan* in wingless insects, wings, wing folding, and complete  
62 metamorphosis (figure 1). Evidence that acquisition of these features increased net  
63 diversification rates, and are therefore key innovations, has largely come from sister-  
64 group species-richness comparisons across orders [21,22], suggesting that shifts in net  
65 diversification rate occurred at or after the origin of wings. However, the results of  
66 these studies are sensitive to phylogenetic uncertainties [22], give no indication of  
67 which macroevolutionary parameters may have changed [21], and may be biased by the  
68 low phylogenetic resolution and simple macroevolutionary models employed (e.g. [11]).  
69 Fossil studies have been rare, but Yang [23] used Lyellian survival analysis on family

level data [24] to suggest that extinction rates do not differ between Holometabola and Paraneoptera, and hence that differences in origination rates probably account for the larger increase in families in Holometabola. However, Yang only considered this single key innovation, and the dataset on which his study was based is now considerably dated. Since 1994 there have been major changes to insect taxonomy (e.g. [25]), the estimated ages of deposits (e.g. [26]), about 400 additional insect families are known from the fossil record [27] and 21% of the families in Labandeira [24] have since been synonymised.

Here we use a new compilation of the first and last occurrences of fossil hexapod families to test for the effects of potential key innovations, by seeking tell-tale significant differences in the rates of origination, extinction, and accumulation of taxa across major morphological groupings (figure 1). Specifically, we test for the effect of the insect *bauplan* by comparing non-insect Entognatha (e.g. springtails) with ectognathan Apterygota (e.g. silverfish); for the effect of wings by comparing primitively wingless hexapods (Apterygota) with the primitive winged Palaeoptera (e.g. dragonflies); for the effect of wing folding by comparing Palaeoptera (which cannot fold their wings) with Polyneoptera (e.g. cockroaches, which can); and we test for complete metamorphosis by comparing Holometabola (e.g. beetles, with metamorphosis) with their sister group Paraneoptera (e.g. true bugs, without metamorphosis) (figure 1). We examine the shape of the temporal accumulation of taxa across the different groups, and associations between richness and rates within and across taxa, to test for constraints on richness, and whether certain key innovations might have elevated diversification rates.

## 2. Methods.

### (a) Data collection

Starting with the dataset of Ross & Jarzembowski [28], searches were made of the published literature to the end of 2009 for the earliest and latest occurrence (stage resolution) of each fossil family of Hexapoda. Families were classified into higher taxa following the widely adopted Eur-American scheme [5], with some differences due to recent revisions (see Supplementary Material). Where there was disagreement over the taxonomic status of a specimen or family, a consensus approach was taken. The timescale of Ogg et al. [29] was adopted to date stages.

### **(b) Data analysis**

Adjacent geological stages were aggregated to form time bins of approximately equal length (mean, SD  $9.87 \pm 3.1$  Myr) (see Supplementary Material). Per capita origination and extinction rates were estimated using Foote's [30] metrics  $\hat{p}$  and  $\hat{q}$  which help control for variation in interval duration and sampling intensity because they are instantaneous rates and ignore single interval taxa which are more susceptible to sampling bias. As the rates time series are highly right skewed (figure S2) and log-transformation does not normalise their distribution, they were compared across taxonomic groups using non-parametric Friedman tests. Because the time series began at different intervals for different groups, tests were implemented pairwise so as not to discard data unnecessarily, and to reduce Type 1 errors (false positives), tests were limited to the most essential hypotheses. Because there are so few families of Apterygota, comparisons between Entognatha and Ectognatha lacked power and were not pursued beyond these initial basic analyses, which failed to show any significant differences between them (see Results).

Diversification models were investigated using nonlinear least-squares regressions on the clade richness data through time, with time coded relative to the present (i.e.



negative numbers becoming less negative through time). Linear, exponential, logistic and Gompertz models were fitted using the `nls()` function from the `nlrwr` package, and the preferred model for each clade identified by comparison of AICc values [31,32] using the `akaike.weight()` function in the `qpcR` package in R [33; supplementary information]. For Palaeoptera and Polyneoptera, logistic and Gompertz model runs failed to converge on a solution. Examination of terminated model runs showed selection for an ever-increasing (and unrealistically large) value of the richness asymptote. The fitted values resembled exponential or linear growth, with little sign of a richness asymptote in the data, whilst the AICc scores were relatively high, indicating that the assumption of a richness asymptote was inappropriate. For these cases, model runs were terminated after 500 iterations and output for illustrative purposes, noted where appropriate in Table 1.

Associations between richness, origination and extinction in the time series for different groups were investigated using bivariate correlation of the first differences. First differencing is a simple detrender that removes short-term autocorrelation, long term patterns and the spurious correlations that may derive from them, as well as removing random walk effects. Significance was assessed using bootstrapping of the test statistic to reduce the necessary underlying assumptions about the data.

### 3. Results

#### (a) Origination and extinction rates

Instantaneous per capita family origination and extinction rates [30] are mostly low but with occasional high values, mostly restricted to the early half of the record (figure 2). Unsurprisingly, origination rates are generally higher than extinction rates in all morphological groups (figure 2, table S1). Through time, however, there is

heterogeneity in the difference between these rates. There are intervals when extinction rates temporarily outweigh origination rates, most noticeably during the Permian (299–251Ma) in Palaeoptera and Polyneoptera, but not in Holometabola (figure 2), and Upper Triassic (229–200Ma) in Polyneoptera. Episodes when origination rates are much higher than extinction rates include the Pennsylvanian (318–299Ma), Lower Triassic (251–246Ma), Barremian (130–125Ma), and Eocene (56–34Ma) (figure 2 and Supplementary Data). Both rates are higher for Palaeoptera than Apterygota (Friedman tests,  $p < 0.0001$ ). However, origination rates do not differ significantly between Palaeoptera and Polyneoptera, or Paraneoptera and Holometabola (figure 2, table S2, figure S1). Extinction rates do not differ significantly between Palaeoptera and Polyneoptera (figure 2, table S2, figure S1), but are significantly lower in Holometabola than Paraneoptera (Friedman test,  $p = 0.041$ ). The median net diversification rate is highest in Holometabola and lowest in Apterygota, and differs significantly between them (Friedman test,  $p = 0.02$ ), but not between other groups (figure 2, table S2).

**(b) Rates of family accumulation and correlations amongst time series.**

The best-fit diversification model varies by clade: logistic for Apterygota, exponential for Palaeoptera and Polyneoptera, and Gompertz for Paraneoptera and Holometabola (figure 3), although for Paraneoptera the exponential and logistic models are only marginally worse, as is the linear model for Polyneoptera (see table 1). This indicates a decrease in the rate of accumulation of taxa in the more-derived and richer Paraneoptera and Holometabola (most strongly in the latter) towards the present, with the more-basal Palaeoptera and Polyneoptera showing no slow-down in diversification despite an overall slow rate of taxon accumulation (figure 3). There is also a strong

preference for a logistic growth model for Apterygota, indicating a low current rate of diversification.

The first differences in log richness were most highly correlated between Paraneoptera and Holometabola ( $r = 0.848$ ,  $n = 29$ ,  $p < 0.001$ ), and between Palaeoptera and Polyneoptera ( $r = 0.623$ ,  $n=29$ ,  $p < 0.01$ ), reflecting similar short-term richness trajectories in those pairs of taxa (figure 3). First differences in richness were negatively correlated with future (1 interval step) origination in Palaeoptera ( $r = -0.627$ ,  $n = 28$ ,  $p < 0.001$ ), Polyneoptera ( $r = -0.540$ ,  $n = 28$ ,  $p < 0.05$ ), Paraneoptera ( $r = -0.657$ ,  $n = 28$ ,  $p < 0.001$ ) and Holometabola ( $r = -0.548$ ,  $n = 28$ ,  $p < 0.001$ ). However, there was no significant relationship between the first differences in extinction rate and future origination rate except in Palaeoptera, where it was negative ( $r = -0.505$ ,  $n = 28$ ,  $p < 0.01$ ). There were significant positive relationships between (first differences in) Holometabola richness and Polyneoptera extinction ( $r = 0.651$ ,  $n = 29$ ,  $p < 0.001$ ) and Palaeoptera extinction ( $r = 0.556$ ,  $n = 29$ ,  $p < 0.05$ ), whilst first differences in Holometabola richness are also negatively correlated with future richness in Polyneoptera ( $r = -0.549$ ,  $n = 28$ ,  $p < 0.05$ ) and Palaeoptera ( $r = -0.569$ ,  $n = 28$ ,  $p < 0.01$ ).

#### 4. Discussion

Net rates of diversification vary across taxa [21] but are also highly heritable in the hexapods [34]. These facts, long casually observed, have suggested that key evolutionary changes have been responsible for generating much of the richness in this very diverse group, and four such evolutionary innovations have held centre stage [18,19]: the insect *bauplan* [35], wings [36], wing folding [21] and complete metamorphosis [23]. Here we have reported evidence that both fossil family origination and extinction rates increased in groups that have wings but not the other key

189 innovations, whilst insects with complete metamorphosis have lower extinction rates  
190 than their sister group without this innovation. There is evidence from the most derived  
191 groups that the rate at which described richness accumulates has slowed through their  
192 history, with taxonomic replacement evident between Palaeozoic and post-Palaeozoic  
193 faunas. These results suggest specific modes by which taxonomic richness has been  
194 generated by key innovations in the hexapods.

195 The contrast between the rates of origination and extinction in Palaeoptera and  
196 Apterygota, taken at face value, suggests that the origin of wings, in-of-itself, led to large  
197 macroevolutionary changes, a fact that has long been suspected [36], although the  
198 phylogenetic evidence for this is equivocal since the richness of Palaeopteran orders is  
199 not very much greater than that of some apterygote orders [21]. Previous authors have  
200 suggested that dispersal via wings could not only lower rates of extinction (e.g. [37]), for  
201 example via increased immigration rates within metapopulations, but also raise  
202 speciation rates via dispersal to isolated habitat patches [7]. Our data indicate that  
203 winged insects had both increased speciation and extinction rates. Many Paleozoic  
204 Palaeoptera families did not survive into the Mesozoic (figure 2), suggesting that the  
205 Permo-Triassic extinction is one reason for the high extinction rates in this group,  
206 although extinction rates also remained high after the P-T boundary (figure 2). *Prima*  
207 *facie*, this suggests that susceptibility to extinction has tempered the evolutionary  
208 potential of basal winged insects. It is debateable, on the strength of this evidence,  
209 whether wings should be regarded as a key innovation in of themselves, as the  
210 difference between the speciation and extinction rates is not significantly greater than  
211 Apterygota, and family richness, like species richness, is not particularly enhanced  
212 (figure 3).

The other potential key innovation highlighted by our results is complete metamorphosis. A decline in extinction in Holometabola was previously proposed by Ross et al. [38] who considered Holometabola less susceptible to mass extinction than other groups. However, another fossil analysis [23] suggested that origination rates have increased in Holometabola, and suggested that extinction rates are unchanged. Our results suggest that the difference between the origination and extinction rate has widened in more derived groups, despite origination rates generally declining. There are a number of differences between our analyses and Yang's [23] including the underlying data, the rate metrics used, and the analytical approaches. In all these characteristics we consider our analysis to be an improvement: the data take account of more recent discoveries (including 400 more families); we use more robust rate metrics (estimated per capita rates ignoring single-interval taxa); we use statistical approaches that take account of repeated measures; we assess origination and extinction directly and in ways that account for the whole of the time series available (as opposed to Lyellian survival analysis which mainly reflects the latter part of the time series). How extinction rates might be lowered by metamorphosis has been little discussed: metamorphosis might allow greater buffering from environmental variability in the protected pupal stage [38], faster development, higher population sizes, and reduced intraspecific competition between adult and offspring. All plausible and testable contributors [5].

The richness time series of the different taxa appear *prima facie* consistent with the macroevolutionary changes described above. Over the majority of the time series, richness is highest in the derived Holometabola, and lowest in the basal Apterygota (figure 2, figure S4). Palaeozoic richness was dominated by Palaeoptera and

237 Polyneoptera, which gave way to the more derived groups Paraneoptera and  
238 Holometabola (see also [39]), with lower extinction rates. This reflects a more general  
239 tendency in the fossil record for high turnover groups to dominate the earlier record  
240 [40]. The first differences in the time series confirm that these pairs of taxa (Palaeoptera  
241 and Polyneoptera; Paraneoptera and Holometabola) show very similar short-term  
242 trajectories. Only Holometabola and Apterygota show clear evidence of a slow-down in  
243 the rate of addition of taxa (figure 3, table 1), although with Apterygota it is difficult to  
244 say if this is simply due to the paucity of data from the fossil record. Palaeoptera and  
245 Polyneoptera best fit exponential or linear models of diversification, implying that limits  
246 to family richness, if there are any, have not yet been met by these groups. By contrast,  
247 the Holometabola only show signs of possible limits to richness after attaining  
248 considerably higher richness than the less derived Palaeoptera and Polyneoptera, limits  
249 that are apparently not yet fully attained. The Paraneoptera show signs of a slow-down  
250 with a preferred Gompertz growth model, but the evidence for this is not much better  
251 than that for an exponential model (table 1). These patterns of richness through time  
252 provide equivocal support for the idea of new adaptive zones [17]: Holometabola have  
253 attained richnesses far above those ever achieved by the other taxa, but there is not  
254 strong evidence that the richness has been constrained by carrying capacity limits in  
255 Paraneoptera, Palaeoptera, or Polyneoptera. The latter clades therefore conform to  
256 other terrestrial studies showing exponential clade growth [e.g. 41–44], whilst the  
257 others conform to a pattern that may be more common in marine taxa [but see 45].  
258 Whilst increases in richness tend to be associated with decreases in future origination,  
259 which in the marine record has been interpreted as density-dependent cladogenesis  
260 [13], in insects it likely simply reflects the episodic nature of origination in the record  
261 [5], an interpretation supported by the lack of a predicted positive relationship between

current extinction and future origination [13]. The associations between increases in Holometabola richness and current extinction and future reductions in richness in Polyneoptera and Palaeoptera may suggest that the latter faunas have been negatively affected by the rise of more derived faunas.

Our data provide no support for the idea that the basic or primitive insect *bauplan* is a key innovation, in common with previous phylogenetic tests [21,22]. Zeh et al. [35] made the case for modification to the egg and egg-laying apparatus in apterygote insects as a key innovation, though as with wings, the low diversity of basal groups with this innovation suggests that it is insufficient for generating high diversity, though perhaps necessary. There is also little support for wing folding, and in fact Polyneoptera show a marginally non-significant decline in origination rates relative to Palaeoptera (Table S2), as well as a quite similar richness. It is however likely that the diversity of Holometabola is in some way contingent [16] on this innovation given the richness of species, such as beetles, that depend on it.

Recently, analyses of fossil richness and rates have paid much attention to the effect of sampling bias through time as an explanation for patterns (e.g. [12,44–46]). Since our analyses focus on variability across groups rather than through time, and because it is doubtful that even standardized subsampling of occurrence data could eliminate the taphonomic biases that likely accrue across time intervals in hexapods, this issue is less important than an alternative one; that sampling may be biased due to uneven preservation potential of different taxa. However, Labandeira & Sepkoski [39] tested variation in preservation potential across orders by observing the correlation between the number of extant families per order and the number fossilized in the latest Tertiary. They found a very high correlation in which the only outlying order was Lepidoptera,

suggesting little support for such bias at the scale of this analysis. Standardized estimates of richness through time would likely depress the apparent growth of clades near the present [46], but are unlikely to affect the rank order of richness across the major taxa considered here.

Our analyses suggest a new model of insect macroevolution; that of a major up-shift in both family-level origination rates and extinction rates (but not net diversification rate) with the origin of wings, giving rise to a group of families vulnerable to extinction. This was followed by a decline in extinction rates in Holometabola, allowing richness to rise towards an apparent limit that has never been attained by the other groups. In this latter respect, Holometabola conform to the classical notion of an adaptive radiation [17]. The mechanism of change, through a reduction in sub-clade extinction rate [17], has also been suggested as an explanation for the radiation of the angiosperms [47]. In contrast, there is little evidence from the fossil record that wing folding or the insect *bauplan* were sufficient to alter insect family macroevolution, although they may have been necessary. The different extinction propensities of taxa shown here may also imply differing resistance to anthropogenic extinction, and hence contribute to debate on the vulnerability of extant insects to environmental change [7]. In the future, better-resolved phylogenetic studies may allow additional tests of the importance of metamorphosis and there is a need to elucidate the ecological or life history determinants of the proximate macroevolutionary forces suggested above.

**Acknowledgements.** We thank James Rainford, Gareth Monger (for the image of an aptergote in figs. 1 and 2), Matthew Nicholson, Matthew Carroll, Alistair McGowan, an



anonymous referee, and the many palaeoentomologists who sent us copies of their papers.

**Funding statement.** DBN was supported by a NERC studentship, National Museums Scotland, and The Natural History Museum, London.

**Data accessibility.** Data presented in this paper are available as an Electronic Data Supplement.

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Fig. 1 Four putative hexapod key innovations, together with the taxa defined by them [7].

Fig 2. Family level origination ( $\hat{p}$  - solid lines) and extinction rates ( $\hat{q}$  - dashed lines) through time in the five major groups of hexapods.

Fig 3. Accumulation of hexapod families through time in the major groups. The thick lines show the fitted values of different models. **Apt** (circles) = Apterygota (logistic model), **Pal** (Xs) = Palaeoptera (exponential model), **Poly** (squares) = Polyneoptera (exponential model), **Para** (triangles) = Paraneoptera (Gompertz model), **Holo** (+s) = Holometabola (Gompertz model). Relative support for these models can be seen in table 1.

**Table 1. Competing nonlinear least squares models for clade diversification, with AICc scores.** Parameters: Linear a, b; Logistic/Gompertz a, b and c; Exponential y0, b; NULL intercept only. Parameter significance levels: \* < 0.05; \*\* < 0.01; \*\*\* < 0.001. Note that significance may be inflated due to autocorrelation in the time series.

| Model                 | Par 1      | Par 2      | Par 3                  | AICc    | ΔAICc  | AICc weight | R <sup>2</sup> |
|-----------------------|------------|------------|------------------------|---------|--------|-------------|----------------|
| <b>Apterygota</b>     |            |            |                        |         |        |             |                |
| logistic              | 17.087***  | 5.757***   | 0.053***               | 143.64  | 0.00   | 0.74        | 0.9139         |
| Gompertz              | 17.363***  | 0.009      | 0.040***               | 145.70  | 2.06   | 0.26        | 0.9083         |
| exponential           | 22.111***  | 104.115*** | –                      | 157.41  | 13.77  | 0.00        | 0.8593         |
| linear                | 16.013***  | 0.057***   | –                      | 179.92  | 36.28  | 0.00        | 0.7217         |
| NULL                  | 7.000***   | –          | –                      | 219.86  | 76.22  | 0.00        | –              |
| <b>Palaeoptera</b>    |            |            |                        |         |        |             |                |
| exponential           | 40.277***  | 307.667*** | –                      | 255.23  | 0.00   | 0.69        | 0.3097         |
| linear <sup>§</sup>   | 35.998***  | 0.067**    | –                      | 257.78  | 2.55   | 0.19        | 0.2544         |
| Gompertz <sup>§</sup> | 22040      | 6.497      | 2.82×10 <sup>-4</sup>  | 260.26  | 5.02   | 0.06        | 0.2533         |
| logistic              | 1405       | -3.737     | 0.002                  | 260.40  | 5.17   | 0.05        | 0.2500         |
| NULL                  | 25.364***  | –          | –                      | 265.195 | 9.96   | 0.00        | –              |
| <b>Polyneoptera</b>   |            |            |                        |         |        |             |                |
| exponential           | 52.049***  | 496.706**  | –                      | 260.73  | 0.00   | 0.47        | 0.2817         |
| linear                | 50.136***  | 0.073**    | –                      | 261.38  | 0.64   | 0.34        | 0.2675         |
| logistic <sup>§</sup> | 169.5      | -0.880     | 0.002                  | 263.66  | 2.93   | 0.11        | 0.2707         |
| Gompertz <sup>§</sup> | 6414       | 4.903      | 2.882×10 <sup>-4</sup> | 264.20  | 3.46   | 0.08        | 0.2588         |
| NULL                  | 38.52***   | –          | –                      | 269.38  | 8.65   | 0.00        | –              |
| <b>Paraneoptera</b>   |            |            |                        |         |        |             |                |
| Gompertz              | 1210.72    | 2.147      | 0.997***               | 221.82  | 0.00   | 0.60        | 0.9647         |
| exponential           | 149.643*** | 133.714*** | –                      | 223.93  | 2.10   | 0.21        | 0.9591         |
| logistic              | 331.46     | 29.69      | 103.58***              | 224.06  | 2.24   | 0.19        | 0.9620         |
| linear                | 124.714*** | 0.434***   | –                      | 236.49  | 14.67  | 0.00        | 0.9386         |
| NULL                  | 60.097***  | –          | –                      | 320.72  | 98.90  | 0.00        | –              |
| <b>Holometabola</b>   |            |            |                        |         |        |             |                |
| Gompertz              | 745.8***   | 0.522**    | 0.993***               | 301.46  | 0.00   | 0.95        | 0.9739         |
| logistic              | 519.148*** | -95.47***  | 59.354***              | 307.41  | 5.95   | 0.05        | 0.9686         |
| linear                | 411.201*** | 1.525***   | –                      | 324.40  | 22.93  | 0.00        | 0.9423         |
| exponential           | 508.75***  | 116.8***   | –                      | 324.73  | 23.27  | 0.00        | 0.9417         |
| NULL                  | 176.44***  | –          | –                      | 413.68  | 112.22 | 0.00        | –              |

<sup>§</sup>Model run terminated and output after 500 iterations due to non-convergence (see Methods for explanation).







