

This is a repository copy of *Fossil evidence for key innovations in the evolution of insect diversity*.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/90947/>

Version: Submitted Version

---

**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>

---

**Reuse**

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

**Takedown**

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing [eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk) including the URL of the record and the reason for the withdrawal request.

## **Fossil evidence for key innovations in the evolution of insect diversity: Electronic Supplementary Material**

**David B. Nicholson, Andrew J. Ross & Peter J. Mayhew**

### **Supplementary methods.**

#### **Literature search**

The starting point for the dataset was that of Ross & Jarzembowski [1] and a subsequent update [2]. Taxonomic and range changes were then modified using information in published literature derived from AJR's reprint and PDF collection, comprehensive order-by-order searches of Web of Knowledge, Google Scholar and the International Palaeontological Society library page, from cited works in the reference lists of relevant papers and requests of PDFs from authors. The data were then checked against the EDNA fossil insect database (<http://edna.palass-hosting.org/>). The completed dataset [3] draws on nearly 3,000 published works, around 2,500 of which were published between 1996 and end-2009.

#### **Geological time scale and deposit dates**

Both Benton [4] and Labandeira [5] used the geological time scale of Harland et al. [6]. For the current data, the stage names and dates of Ogg et al.'s [7] International Stratigraphic Chart were used, as refinements in dating and correlation of regional stratigraphy make this the international standard to which most Earth scientists now adhere, making the dataset more comparable with the work of other researchers. Ranges of families were often only given to epoch (or even period, in the case of some Carboniferous and Permian families) in Ross and Jarzembowski [1]. This is partly to do with the restricted stratigraphic knowledge of the time but also from using Carpenter's hexapod volumes of the *Treatise on Invertebrate Paleontology* [8] as a starting point for the data-set, itself fairly vague on fossil dates. The result of this is that, in some cases, only a single "e.g." specimen from one deposit is mentioned as the start/end of the range, where in fact there are more deposits within this period/epoch (but not in the same stage) containing the family in question. Thus, some families appear as single-interval taxa and would be left out of diversity curves using only "cross-over" taxa (aka boundary crossers) and rate metrics, such as those used here, which similarly ignore single interval taxa.

More recent stratigraphic work has improved resolution so that family ranges within periods and epochs can be shown to stage level, particularly in the Carboniferous and Permian of

Europe and America. An example from the insects is for the Mischopteridae (Megasecoptera), listed in Jarzembowski and Ross [2] as “e.g. *Mischoptera douglassi*, Mazon Creek C2” but, in fact, specimens have long been known from Commeny (France), giving the family a range of Moskovian–Kasimovian. By lumping the data from different time intervals together, apparent diversity can be greatly exaggerated. However, occasionally the reverse can be true. For example, the megasecopteran family Brodiopteridae is listed in Jarzembowski and Ross [2] as ranging from Namurian B (*Brodioptera stricklani* from the Manning Canyon Shale Formation, Utah, USA) to Westphalian A (*Brodioptera cumberlandensis* from Joggins coalfield, Nova Scotia, Canada [erroneously cited as coming from the United States]). Both of these regional stages fall within the Carboniferous Bashkirian stage (lowermost Pennsylvanian), rendering these families, which were previously boundary-crossers, single-interval taxa on this scale. On balance, the consistency afforded by use of the ICS scale along with improved resolution of many other family ranges more than makes up for these very occasional losses in range data.

Despite improvements in recent years, not all deposits have been easy to date. Chinese terrestrial Mesozoic strata remain difficult and the dating of the Yixian Formation has proved to be particularly contentious. Stratigraphers had long argued over whether the deposits were Jurassic or Lower Cretaceous. This proves to be particularly significant as some of the earliest occurrences of angiosperm macrofossils and several other important groups occur in these deposits. Radiometric dates have since confirmed a Lower Cretaceous (Barremian–Aptian) age (see [9,10]). Also of particular difficulty are amber deposits, which are most often dated indirectly by the sediments in which they are found. This provides only a minimum age as amber is frequently redeposited. The Burmese (Myanmar) amber provides a striking example of this. Previously assumed to be Oligocene in age, it is now accepted as mid-Cretaceous. Ross and York [11] and Ross et al. [12] gave an Albian age, which was used in this dataset, however more recently it has been re-dated as Cenomanian [13]. Either way, it extends the range of some families in earlier datasets back from the Cenozoic. Where uncertainties still exist over the dating of a deposit, a consensus view was adopted or the youngest of the possible stages was used by convention and a note of this made in the dataset. This only occurred in a small number of cases and has mostly involved choosing a later stage when a deposit has been dated to a stage boundary (e.g. the Langhian aged Shanwang Formation in China).

## **Taxonomic system**

The traditional Class system, as set out by Carpenter [8] and adopted in Jarzembowski & Ross [2], contains non-cladistic groupings at higher taxonomic levels, in particular the ‘Apterygota’, used to group the primitively wingless insects of the orders Archaeognatha, Monura (now considered to nest within Archaeognatha) and Zygentoma, along with the non-insect hexapod orders Protura, Diplura and Collembola. In modern classification schemes, the ‘Apterygota’ is considered to be a paraphyletic grouping. Even within modern classification schemes there are different schools of thought regarding the extinct orders of fossil insects. These can be (very) crudely characterised as the Russian scheme, outlined in Rasnitsyn and Quicke [14], and the Eur-American scheme, as shown in Grimaldi and Engel [15]. Both of these texts are authoritative and widely referenced but, in the interests of consistency, the scheme used in Grimaldi and Engel ([15]; pp. 111, 147) has been followed here, as it has gained dominance in recent years, with minor changes adopted from more recent taxonomic revisions to reflect a modern phylogenetic scheme. The focus on families over genera or species is partly to do with greater taxonomic stability between workers [16]. There is not always total agreement and in these cases a consensus view was taken, or that of a particular senior authority, and a note of it made in the database.

The issue of paraphyly in the fossil record was not directly addressed during data collection, as the purpose was to collate knowledge of the fossil record as presented in the literature rather than to critique the current state of fossil insect phylogenetics. It is our opinion that the large majority of extant families are probably monophyletic, with well defined synapomorphies, and molecular phylogenetics is currently weeding out any exceptions. The greater risk is for extinct taxa with a patchy fossil record, particularly if they are likely to be concentrated in any particular clade rather than randomly distributed throughout the Hexapoda, as this could inflate the apparent extinction rate through pseudoextinctions. This seems most likely in the Palaeoptera and Polyneoptera, which dominated insect diversity in the Palaeozoic with largely archaic forms not present in the modern fauna. This could affect the finding of increased rates of extinction in Palaeoptera compared to Apterygota, although the degree of paraphyly would have to be very large amongst extinct Palaeoptera; probably not realistically so. Furthermore, the finding that Holometabola have lower rates of extinction than Paraneoptera is unaffected by this issue.

## **Pull of the Recent**

To make the collation of data feasible within a reasonable timeframe, the last occurrence of all extant families was recorded as Recent, in line with previous datasets on the group [1,5]. This raises the issue of the Pull of the Recent (the tendency for the ranges of fossil taxa to be pulled forwards towards the present, inflating apparent richness in range-through datasets) [17]. Since we do not have the last known fossil occurrence of all extant families in our dataset, an alternative is to examine the richness of only extinct taxa through time.

The percentage of families within each stage which remain extant today (also known as Lyellian survival) was plotted alongside the raw counts of extant and extinct families in each stage through time (figure S3). Times when extant families comprise a substantial proportion of the total mark the potential for a strong Pull-of-the-Recent effect.

The proportion of extinct and extant taxa through time shows that elements of the modern fauna began to appear in the Late Permian just before 250 Ma and increased in the Late Jurassic (~153–148 Ma). The number of presently extinct taxa in each stage declines steadily after the Barremian (127.5 Ma, Early Cretaceous) and forms an insignificant portion of the fauna before the end of the Cretaceous at 65.5 Ma. This suggests that the broad trajectory of richness seen in the dataset may be unduly affected by the Pull of the Recent from around the mid-Cretaceous onwards.

Looking only at extinct taxa in each clade (figure S4), however, shows that some of the patterns observed in the total dataset (rapid diversification in Holometabola, with a higher asymptote in Holometabola than Paraneoptera) were well-established in the early part of the record and are not an artefact of the way the data were collected. Since the main focus of the analyses presented here is in the comparison between the trajectories of different taxa, questions over the broad trajectory of overall richness is probably of less import.

## **Analysis**

Adjacent geological stages were aggregated to form time bins of approximately equal length (mean, SD 9.87±3.1 Myr) while maintaining Period-level boundaries, namely Bashkirian+Moscovian, Kasimovian+Gzhelian, Asselian+Sakmarian, Artinskian+Kungurian, Roadian+Wordian+Capitanian, Wuchiapingian+Changhsingian, Induan+Olenekian, Anisian, Ladinian, Carnian, Norian+Rhaetian, Hettangian+Sinemurian, Pliensbachian, Toarcian+Aalenian, Bajocian+Bathonian+Callovian, Oxfordian+Kimmeridgian, Tithonian,

Berriasian+Valanginian, Hauterivian+Barremian, Aptian, Albian, Cenomanian, Turonian+Coniacian+Santonian, Campanian, Turonian+Coniacian+Santonian, Campanian, Maastrichtian, Danian+Selandian+Thanetian, Ypresian+Lutetian, Bartonian+Priabonian, Rupelian+Chattian, Aquitanian+Burdigalian, Langhian+Serravallian, Tortonian+Messinian+Zanclean+Piacenzian. Richness was estimated by assuming that all families were present between their first and last occurrence in the dataset. Per capita origination and extinction rates were estimated using Foote's [18] 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 sensitive to variation in sampling intensity. As the rates time series are highly right skewed and repeated measures (figure 2, main text), they were compared across taxonomic groups using non-parametric Friedman tests using the function `friedman.test` in R [19]. Because the time series began at different intervals for different groups, tests were implemented pairwise, and to limit Type 1 errors, comparisons were restricted to the core hypotheses.

Nonlinear least-squares regressions were used to investigate diversification models. Preferred model choice was identified using the Akaike Information Criterion, with a correction for finite sample sizes (AICc) values [20,21]. The AICc is a measure of the goodness of fit of a statistical model, describing the trade-off between model accuracy and model complexity, designed to discourage over-fitting. Relatively lower AICc values represent a favourable trade-off (better accuracy for a given complexity).

Associations between short term patterns in the time series were explored by Pearson correlation on the first differences, using both unlagged data, and datasets in which the first differences of one variable were compared with first differences of the other one time step later. Significance was estimated by bootstrapping of the data to create confidence intervals around the model coefficients using the function `boot` in R [19]. Rows of data (x, y pairs in a correlation) are sampled with replacement from the true data to create a new pseudo-dataset of the same size as the original. The statistical test is applied and test statistic stored. This process is repeated many times, typically 10,000, to produce a distribution of the coefficient that illustrates the way the coefficient may change with changing the sample, within the observed limits of the data. This distribution can then be used to calculate confidence intervals on the coefficient. We used the bias corrected and accelerated (BCa) technique [22]

for calculating confidence limits, which corrects for the bias (difference between the observed mean and bootstrap mean) and asymmetry of the bootstrap distribution.

## References

1. Ross, A. J. & Jarzembowski, E. A. 1993 Arthropoda (Hexapoda; Insecta). In *The Fossil Record 2* (ed M. J. Benton), pp. 363–426. London: Chapman and Hall.
2. Jarzembowski, E. A. & Ross, A. J. 1996 Insect origination and extinction in the Phanerozoic. *Geol. Soc. London, Spec. Publ.* **102**, 65–78. (doi:10.1144/GSL.SP.1996.001.01.05)
3. Nicholson, D. B. 2012 *Fossil perspectives on the evolution of insect diversity*. PhD Thesis, University of York, 1–421.
4. Benton, M. J., editor 1993 *The Fossil Record 2*. Chapman & Hall, London.
5. Labandeira, C. C. 1994 A compendium of fossil insect families. *Milwaukee Public Museum Contrib. Biol. Geol.* **88**, 1–71.
6. Harland, W. B., Armstrong, R. L., Cox, A. V., Craig, L. E., Smith, A. G. & Smith, D. G. 1990 *A geologic time scale*. Cambridge University Press.
7. Ogg, J. G., Ogg, G. & Gradstein, F. M. 2008 *The Concise Geologic Time Scale*. Cambridge University Press. (doi:10.1017/S0016756809006207)
8. Carpenter, F. M. 1992 Superclass Hexapoda. In *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4 (3&4)*, pp. xxi + 655. Boulder, C. O. and Lawrence, K. A.: Geological Society of America and University of Kansas Press.
9. Zhou, Z., Barrett, P. M. & Hilton, J. 2003 An exceptionally preserved Lower Cretaceous ecosystem. *Nature* **421**, 807–814. (doi:10.1038/nature01420)
10. Zhang, H.-C., Wang, B. & Fang, Y. 2010 Evolution of insect diversity in the Jehol Biota. *Sci. China Earth Sci.* **53**, 1908–1917. (doi:10.1007/s11430-010-4098-5)
11. Ross, A. J. & York, P. V. 2004 The Lower Cretaceous (Albian) arthropod fauna of Burmese amber, Myanmar: Forward. *J. Syst. Palaeontol.* **2**, 95–100. (doi:10.1017/S1477201904001130)
12. Ross, A. J., Mellish, C., York, P. & Crighton, B. 2010 Burmese Amber. In *Biodiversity of fossils in amber from the major world deposits* (ed D. Penney), pp. 208–235. Siri Scientific Press.
13. Shi, G., Grimaldi, D. A., Harlow, G. E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q. & Li, X. 2012 Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretac. Res.* **37**, 155–163. (doi:10.1016/j.cretres.2012.03.014)

14. Rasnitsyn, A. P. & Quicke, D. L. J., editors 2002 *History of Insects*. Springer.
15. Grimaldi, D. A. & Engel, M. S. 2005 *Evolution of the Insects*. Cambridge University Press.
16. Labandeira, C. C. & Sepkoski, Jr., J. J. 1993 Insect diversity in the fossil record. *Science* **261**, 310–315. (doi:10.1126/science.11536548)
17. Alroy, J. 2010 Fair sampling of taxonomic richness and unbiased estimation of origination and extinction rates. *Paleontol. Soc. Pap.* **16**, 55–80.
18. Foote, M. 2000 Origination and extinction components of taxonomic diversity: general problems. *Paleobiology* **26**, 74–102. (doi:10.1666/0094-8373(2000)26[74:OAECOT]2.0.CO;2)
19. R Core Team 2014 R: A Language and Environment for Statistical Computing. *Vienna Austria R Found. Stat. Comput.*
20. Akaike, H. 1974 A new look at the statistical model identification. *IEEE Trans. Automat. Contr.* **19**, 716–723.
21. Burnham, K. P. & Anderson, D. R. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. Second. Springer.
22. Efron, B. 1987 Better bootstrap confidence intervals. *J. Am. Stat. Assoc.* **82**, 171–185. (doi:10.2307/2289144)



Supplementary figure legends

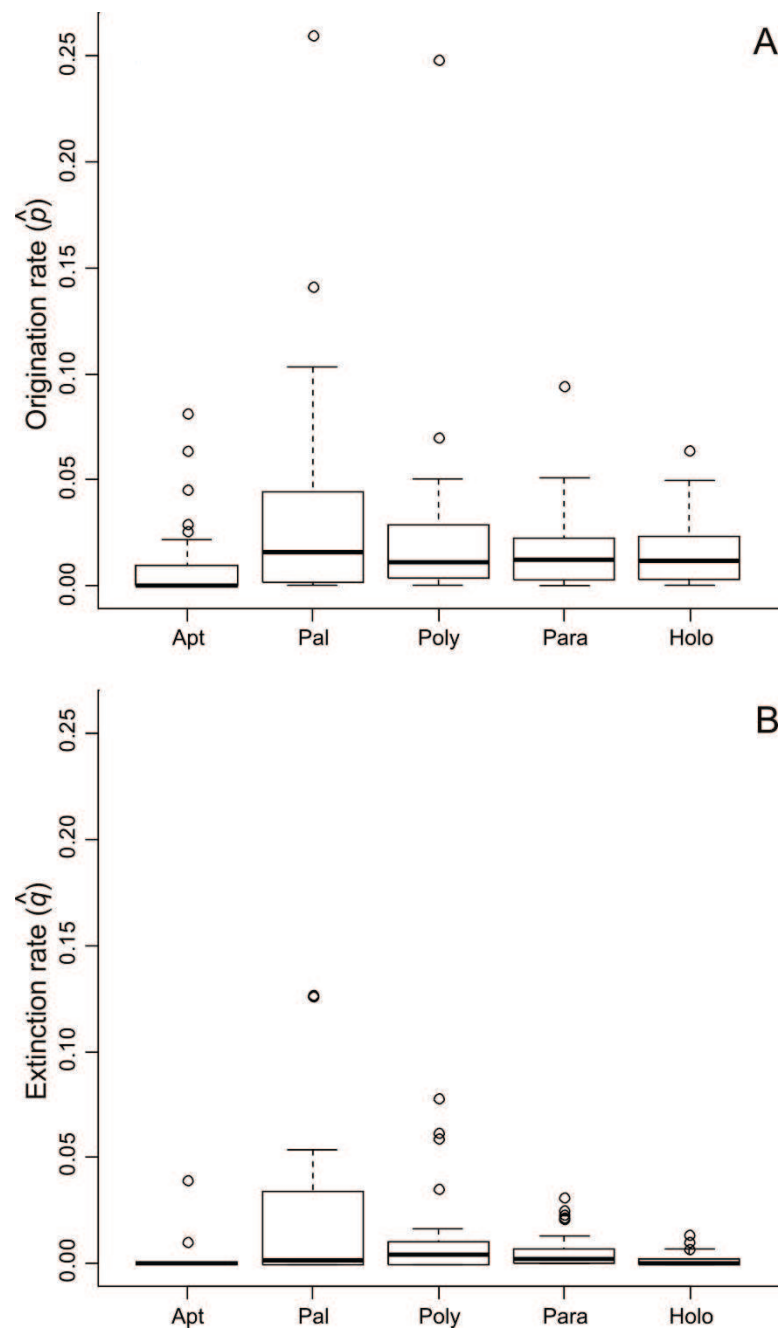
**Figure S1 Distribution of rates of origination ( $\hat{p}$ ) and extinction ( $\hat{q}$ ) in the five major groups of hexapods.** Boxplots: base of box = lower quartile (Q1); top of box = upper quartile (Q3); bold line = median (Q2); lower tail is the lowest point within 1.5× the interquartile range (Q1 to Q3) below Q1; upper tail is the highest point within 1.5× the interquartile range above Q3; and open circles are outliers.

**Figure S2 Cumulative hexapod richness by major taxonomic group.** Family richness of each group is represented by the area between lines. **Apt** = ‘Apterygota’, **Pal** = Palaeoptera, **Poly** = Polyneoptera, **Para** = Paraneoptera, **Holo** = Holometabola.

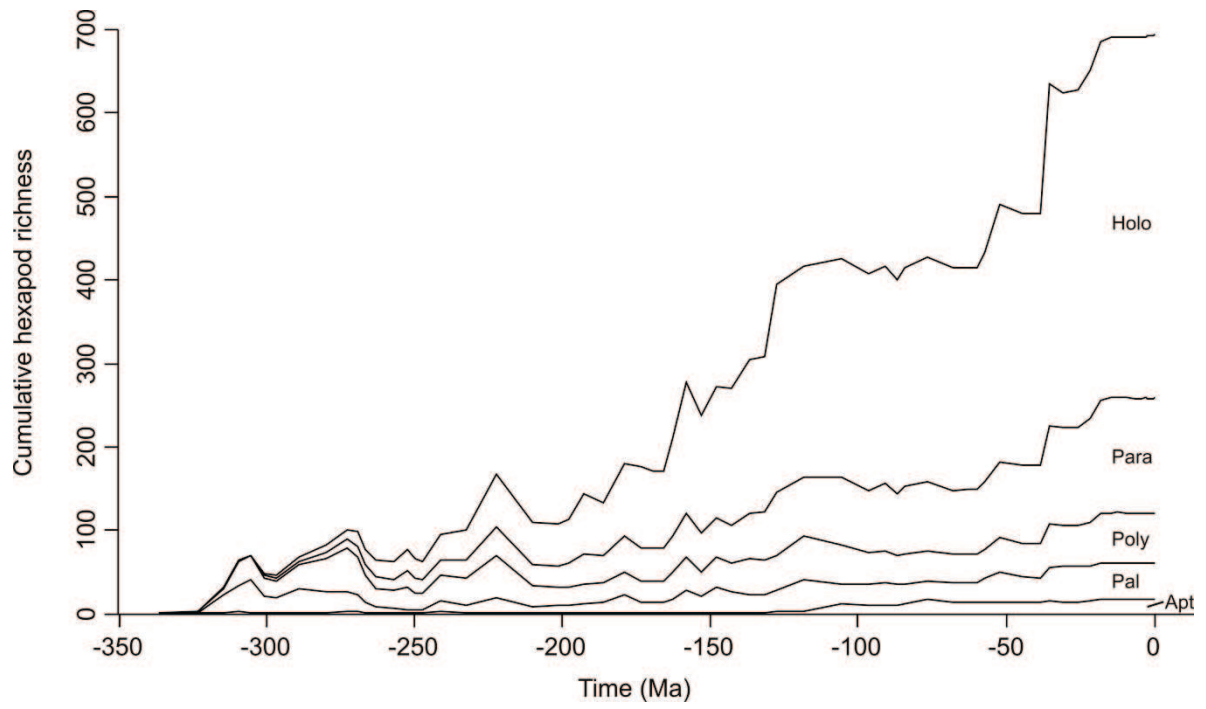
**Figure S3 Lyellian survivorship curve** showing the proportion of taxa in each stage which remain extant today (left y-axis) and numbers of hexapod families in the fossil record per stage which are now extinct or extant (right y-axis).

**Figure S4 Family richness of presently extinct hexapods per stage by clade.** Circles = ‘Apterygota’, Xs = Palaeoptera, squares = Polyneoptera, triangles = Paraneoptera, +s = Holometabola.

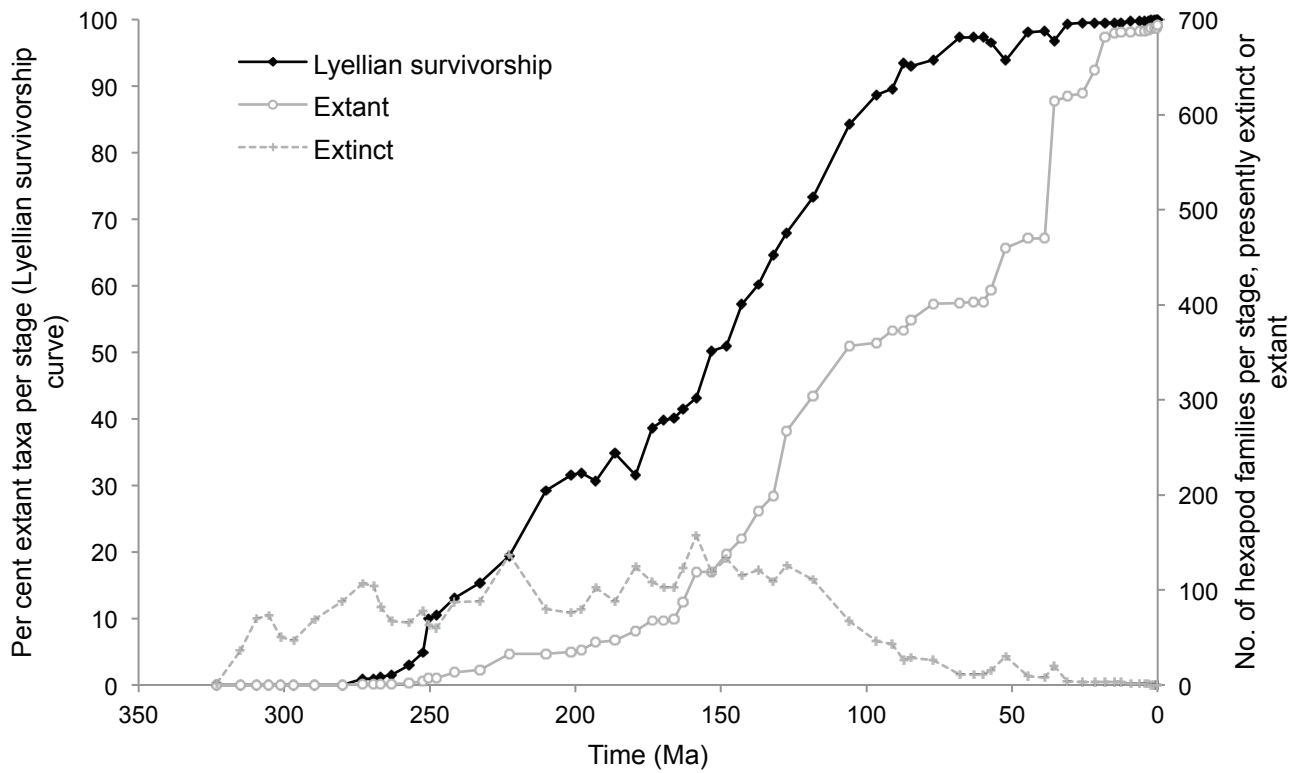
Figure S1



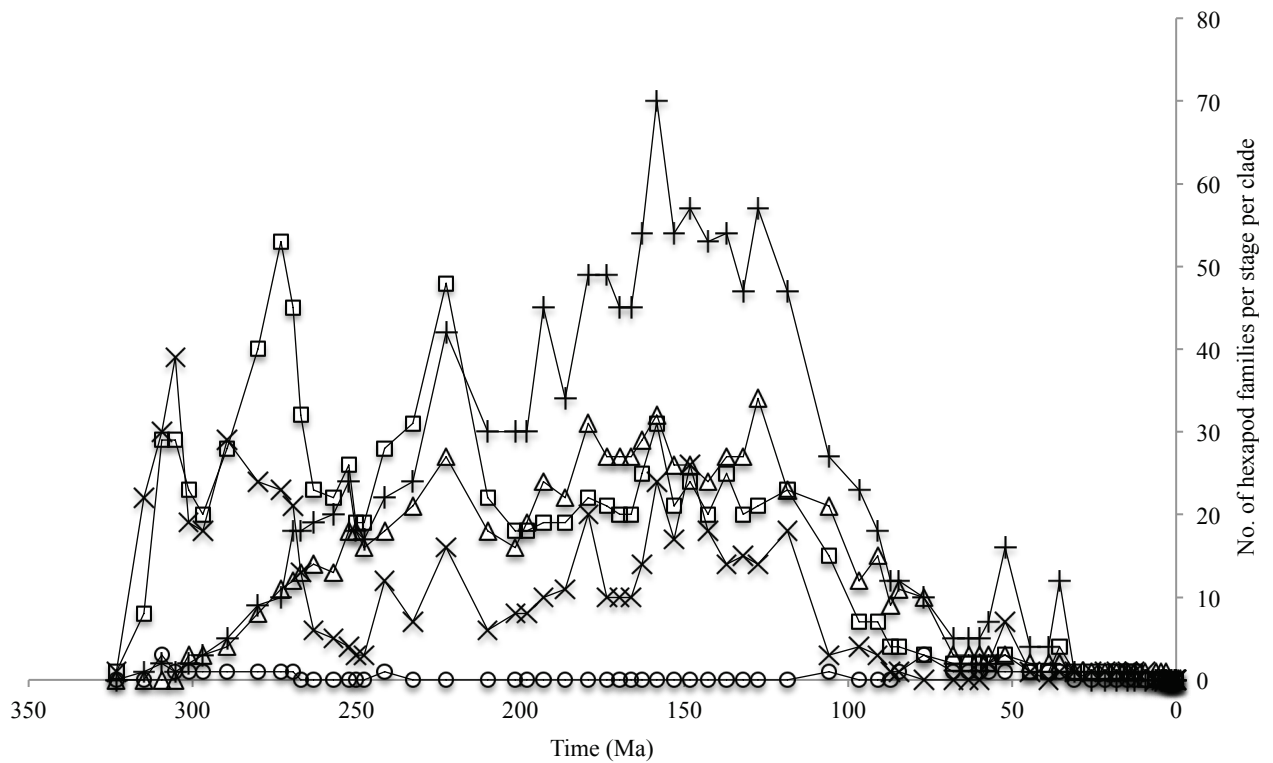
**Figure S2**



**Figure S3**



**Figure S4**



**Table S1 Comparison of rates of origination and extinction within groups.** Significant  $p$ -value from Friedman test indicates strong separation in the distribution of rates, while the reported median indicates which distribution is greater. The distribution of origination rates for apterygotes is higher than extinction (significantly so), despite medians of zero for both.

Group	Median $\hat{p}$	Median $\hat{q}$	$p$ -value
'Apterygota'	0.00000	0.00000	0.0196*
Palaeoptera	0.01568	0.00250	0.0330*
Polyneoptera	0.01088	0.00519	0.0499*
Paraneoptera	0.01219	0.00197	0.0143*
Holometabola	0.01144	0.00095	<0.0001**

**Table S2 Tests for the effects of key innovations: rates of origination and extinction (Myr<sup>-1</sup>) between groups.** Significant *p* value from Friedman test indicates strong separation in the distribution of rates, while the reported median indicates which distribution is greater.

Group 1	Group 2	Key Innovation	Group 1 median	Group 2 median	<i>p</i> -value
<b><math>\hat{p}</math> (origination)</b>					
Entognatha	Apterygote	Insect <i>bauplan</i>	0	0	0.180
	Ectognatha				
‘Apterygota’	Palaeoptera	Wings	0	0.0157	0.0004**
Palaeoptera	Polyneoptera	Wing folding	0.0157	0.0109	0.0588
Paraneoptera	Holometabola	Complete metamorphosis	0.0122	0.0114	0.144
<b><math>\hat{q}</math> (extinction)</b>					
Entognatha	Apterygote	Insect <i>bauplan</i>	0	0	0.317
	Ectognatha				
‘Apterygota’	Palaeoptera	Wings	0	0.00250	0.0002**
Palaeoptera	Polyneoptera	Wing folding	0.00250	0.00519	0.414
Paraneoptera	Holometabola	Complete metamorphosis	0.00197	0.000953	0.0412*
<b><math>\hat{p} - \hat{q}</math></b>					
‘Apterygota’	Palaeoptera	Wings	0	0.00167	0.841
Palaeoptera	Polyneoptera	Wing folding	0.00167	0.00540	1
Paraneoptera	Holometabola	Complete metamorphosis	0.00823	0.00834	0.465
‘Apterygota’	Holometabola	NA	0	0.00834	0.0195*