Shifts in hexapod diversification and what Haldane could have said

Peter J. Mayhew

Department of Biology, University of York, PO Box 373, York YO10 5YW, UK (pjm19@york.ac.uk)

Data on species richness and taxon age are assembled for the extant hexapod orders (insects and their six-legged relatives). Coupled with estimates of phylogenetic relatedness, and simple statistical null models, these data are used to locate where, on the hexapod tree, significant changes in the rate of cladogenesis (speciation-minus-extinction rate) have occurred. Significant differences are found between many successive pairs of sister taxa near the base of the hexapod tree, all of which are attributable to a shift in diversification rate after the origin of the Neoptera (insects with wing flexion) and before the origin of the Holometabola (insects with complete metamorphosis). No other shifts are identifiable amongst supraordinal taxa. Whilst the Coleoptera have probably diversified faster than either of their putative sister lineages, they do not stand out relative to other closely related clades. These results suggest that any Creator had a fondness for a much more inclusive clade than the Coleoptera, definitely as large as the Eumetabola (Holometabola plus bugs and their relatives), and possibly as large as the entire Neoptera. Simultaneous, hence probable causative events are discussed, of which the origin of wing flexion has been the focus of much attention.

Keywords: adaptive radiation; extinction; Insecta; macroevolution; speciation; tree balance

1. INTRODUCTION

In a famous, yet possibly apocryphal event, the biologist J. B. S. Haldane remarked on the Creator's 'inordinate fondness for beetles' (Hutchinson 1959; Williamson 1992). In a macroevolutionary context, Haldane's remark implies that the hexapod order Coleoptera contains an unexpectedly large number of species. The biological literature is replete with such cherished statements describing taxa, or their characteristics, that are reputed to have filled more than their fair share of our planet's biodiversity (Heard & Hauser 1995). In recent years, the molecular and cladistic revolutions, coupled with improved techniques for extracting information from phylogenetic trees (Mooers & Heard 1997), have made it possible to re-examine such macroevolutionary hypotheses (Purvis 1996; Barraclough *et al.* 1999). I examine the hypotheses relating to the diversification of hexapods, probably the most species-rich class of organisms.

The causes of macroevolutionary diversity may be environmental, or they may be novel characteristics of taxa (key innovations) (Stanley 1979; Heard & Hauser 1995). Two general approaches allow them to be identified. The first is to search for characteristics that have arisen repeatedly in different taxa, and to ask if taxa sharing the feature are more diverse than their sister clades, which do not. However, the events that have promoted diversification may also be unique, and for these a second approach is required. Taxa that have unusual rates of diversification must first be correctly identified. Following this, characteristics or events associated with the origins of those taxa must be examined to determine which is the most plausible culprit.

The hexapods, particularly the insects, have been a focus of speculation and research into macroevolution for many decades. In recent years, several studies have addressed the role of repeatedly evolved characteristics.

These have shown that the origin of novel oviposition substrates (Zeh *et al.* 1989), of phytophagy (Mitter *et al.* 1988) and associations with angiosperms (Farrell 1998), and the opportunity for sexual conflict (Arnqvist *et al.* 2000) have promoted diversification, whilst carnivorous parasitism (Wiegmann *et al.* 1993) and the leaf mining habit (Connor & Taverner 1997) have not. Unique events have not been investigated with the same earnestness, but several such events are commonly implicated as major contributors to hexapod diversification. In addition to Haldane's famous statement about Coleoptera, the origin of four taxa and their associated unique characteristics are commonly implicated (figure 1): (i) the Insecta, possessing a suite of novel characteristics often described as the insect body ground plan, (ii) the Pterygota, possessing wings, (iii) the Neoptera, possessing wing flexion, and (iv) the Holometabola, possessing complete metamorphosis (Evans 1984; Carpenter & Burnham 1985; Carpenter 1992; Gullan & Cranston 2000). I use data on species richness, taxon age and phylogenetic relatedness of the extant hexapod orders, combined with simple statistical null models to ask which, if any, of these taxa have diversified more rapidly than expected given their phylogenetic position. I then discuss what this may imply about the causes of hexapod diversification.

2. MATERIAL AND METHODS

(a) *Species richness*

The data on species richness for each hexapod order were taken mostly from Parker (1982), which is the most recently completed concurrent inventory of all major living taxa. The data are on number of described species only, and were compiled by summing the estimates for each individual family comprising the order. In a few instances, family-level estimates were not given but an estimate of the order as a whole was, in which case the latter was taken. For the Diptera, a precise estimate was

Proc. R. Soc. Lond. B (2002) **269**, 969–974
DOI 10.1098/rspb.2002.1957
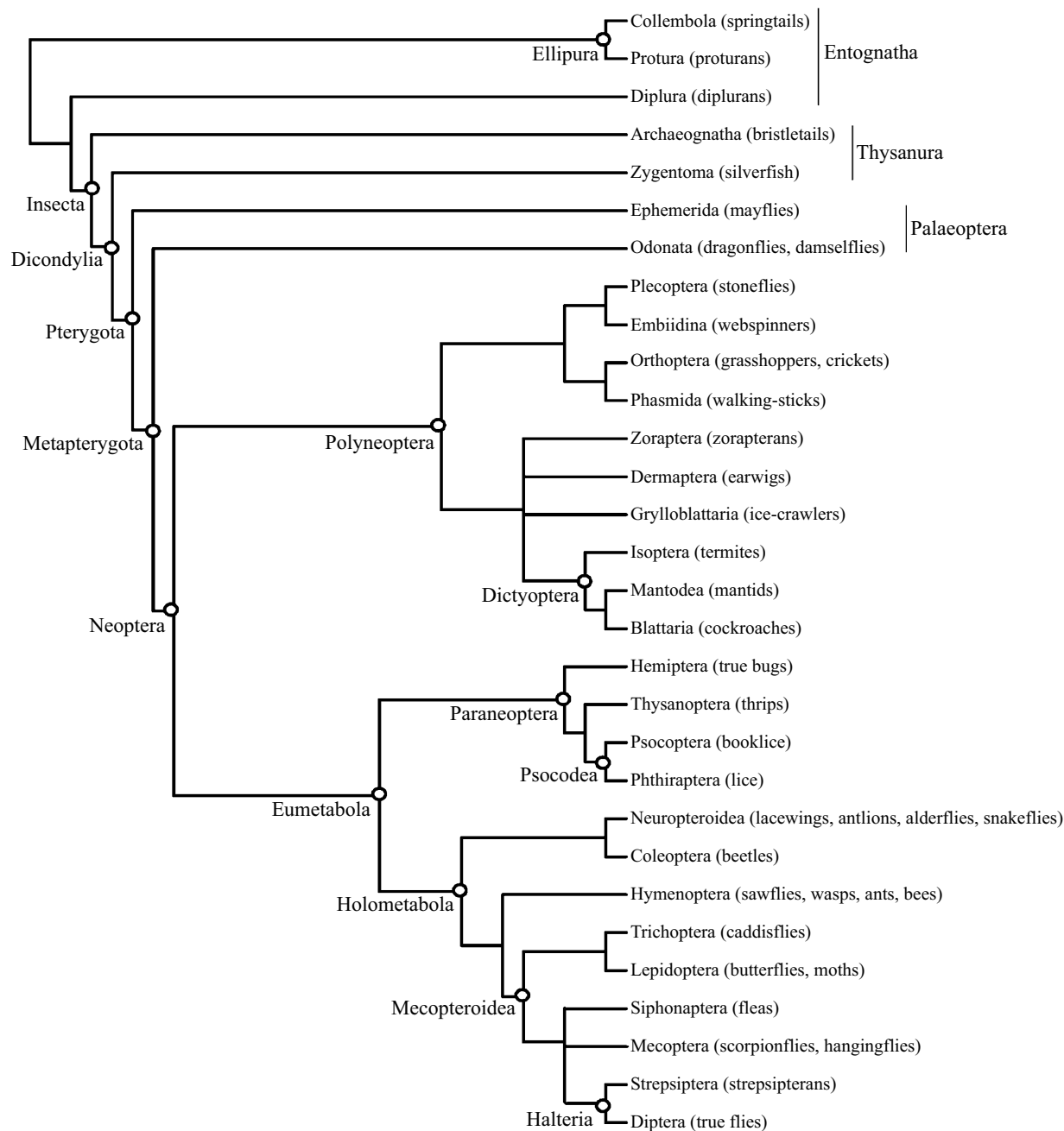
969

© 2002 The Royal Society

Figure 1. One putative set of relationships between extant hexapod orders, showing higher taxa mentioned in the text. Fig. 20 in Wheeler *et al.* (2001), on which the initial analyses here were based, differs only in assuming a monophyletic Entognatha. Monophyly of the Thysanura, paraphyly of the Polyneoptera, and a sister grouping of Coleoptera and Strepsiptera are major alternatives also considered.

not given for one species-rich family, and the ordinal richness given was also very imprecise (100 000–150 000). For this group, other concurrent texts (e.g. Richards & Davies 1978) gave estimates slightly below the lower estimate in Parker (1982), whilst those family-level estimates given in Parker summed close to the lower ordinal level estimate given. I thus used 100 000 as the estimate for this order. Estimates were not given for the Odonata, nor for the non-insect hexapod groups, for which I used other well known and, where possible, contemporaneous sources (Richards & Davies 1978; Davies & Tobin 1985; Hopkin 1997). Whilst ignorance of the total (i.e. described + undescribed) species richness of each order is frustrating, extrapolating beyond the present data introduces unacceptable error (Hawksworth & Kalin-Arrayo 1995), and

conclusions must be restricted to the data that described species present, with all appropriate caution.

(b) *Taxon age*

Data on the age of each extant order, and appropriate higher taxa, were estimated by first compiling the age of the oldest fossil definitely attributable to the taxon, from Ross & Jarzembowski (1993), using the midpoint of the age span of the stratum concerned. Ignoring earlier but more doubtful fossils is conservative because it may underestimate taxon age and thus make significant differences more difficult to detect (see § 2(d), below).

I modified the estimates of taxon age by making a further logical step based on phylogenetic relationships. Sister taxa are, by definition, the same age. Therefore, if the estimated age of two

sister taxa using oldest fossils differed, both were assigned the age of the oldest of the pair. This assumes that any inconsistency in the age of the earliest fossils arises from the incompleteness of the fossil record (e.g. Carpenter & Burnham 1985) rather than through paraphyly. The latter occurs when fossil stem groups arising prior to a node are mistakenly identified as having arisen after it (i.e. are not recognized as stem groups): in which case, one of the taxa arising at the node is paraphyletic but is treated as monophyletic, and the age of the node is overestimated. A special effort has been made to avoid this problem in recent palaeoentomological taxonomy (Hennig 1981). The assumption is most probably not supported amongst the polyneopterous orders, particularly Blattaria and Mecoptera: fossils assigned to both may represent stem forms of Neoptera and Holometabola, respectively, and were abundant in the early fossil history of those taxa (Hennig 1981; Carpenter 1992). However, this would only reduce the ages of related orders, and would not affect any of the main conclusions below.

Age estimates were initially based on fig. 20 of Wheeler *et al.* (2001), and for alternative phylogenetic hypotheses for the appropriate alternative pairings of sister taxa (figure 1). For the latter, I report only the ages of taxa not considered in the initial analysis. As the sister group of the hexapods has not been positively identified (Blaxter 2001), I assumed the age of the root to be the earliest hexapod fossil (Whalley & Jarzembowski 1981). The resulting estimates agree well with molecular clock data (Burmester *et al.* 1998), and those for supraordinal taxa directly reflect the fossil data.

(c) *Phylogenetic topology*

The most recent survey of the phylogeny of the hexapod orders is that of Wheeler *et al.* (2001). Because that analysis may not be definitive in the long term, I explored several putative sets of relationships, and correspondingly derived estimates of taxon age (figure 1). I considered the possibility of a monophyletic Entognatha, Diplura as the sister group of the Insecta, a monophyletic Thysanura and the Zygentoma as the sister group of the Pterygota. The Polyneoptera are supported as monophyletic on morphological grounds, although some molecular analyses show them as paraphyletic to the Eumetabola, a possibility I considered. Relationships between the neuropteroid orders, and between the Siphonaptera, Mecoptera (possibly a paraphyletic order) and Halteria are poorly resolved, and I refrained from comparisons amongst them. The Strepsiptera may be the sister group of the Diptera, the Coleoptera, or part of the Coleoptera itself, with the former more recently supported. The Psocoptera are generally considered paraphyletic to the Phthiraptera, and I treated them as a single inclusive taxon, the Psocodea. I assumed all other orders to be monophyletic.

(d) *Analysis*

I performed two kinds of analysis based on simple null models of cladogenesis. The first compares the species richness of sister clades. If two sister taxa radiate at equal (but not necessarily constant) rates through time (Nee *et al.* 1994), all possible partitions of N species into the two clades are equi-probable (Farris 1976). The (two-tailed) probability of an equal or greater magnitude of split under the null model is given by $2[N_{small}/(N_{small} + N_{large} - 1)]$. Caution is required before attributing a significant result to a shift in diversification at that node: shifts occurring only amongst derived taxa will automatically raise the species richness of higher clades to which they belong. It is therefore essential to examine the components of species-rich

taxa to see if even the most primitive members of that group are also species rich. If not, it is probable that the actual shift occurred at some more derived node (see Sanderson & Donaghue 1994). I did this by observing if any further significant results occur within the most species-rich taxon and, if so, repeating the test excluding those taxa. Whilst the total number of comparisons across the tree is necessarily large, raising the spectre of a type 1 error somewhere in the results, I have not corrected significance for multiple comparisons because each test addresses a completely separate null hypothesis. The more general null hypothesis, that there has been no shift in diversification within the hexapods, would require such correction.

The second test uses information on taxon age and allows comparison of non-sister taxa. By treating clade growth as a pure birth process (Nee 2001), the mean radiation rate of a clade can be estimated from the clade's current age (t) and current species richness (N). The maximum-likelihood estimate of mean radiation rate (speciation minus extinction) is simply $\ln(N)/t$. A 95% confidence interval can be placed on the estimate to allow comparison between different clades. The intervals are $-\ln(1 - 0.975^{1/N})/t$ and $-\ln(1 - 0.025^{1/N})/t$ (Purvis 1996). Thus, confidence intervals are greater for young taxa. Note that because of their different assumptions and use of data, hypotheses rejected by one test may not always be rejected by the other. More powerful tests are available to identify significant radiations (e.g. Purvis *et al.* 1995). However, they require more phylogenetic information than is presently available for hexapods.

3. RESULTS

Many sister taxon comparisons near the base of the tree show significant departures from the null model (table 1, comparisons 1–8). However, in comparisons 1–7 the significant results are all attributable to more recent shifts in diversification higher up the tree and therefore do not, in themselves, represent shifts in diversification (tables 1 and 2) (see § 2(d)). For example, whilst the comparisons between insects and their putative sister groups (table 1, comparisons 1 and 3) suggest that insects have radiated faster, the primitive insect lineages have not, in fact, radiated significantly faster than their non-insect relatives (e.g. table 1, comparison 12). The same conclusions apply to comparisons representing the origin of the Pterygota (table 1, comparison 10), and all the other above comparisons below the Metapterygota, even considering the most imbalanced of phylogenetic relationships (table 1, comparisons 9–12).

There is no evidence that the origin of the Holometabola and Paraneoptera represents a shift in diversification. Neither sister-taxon comparisons nor estimated rates of cladogenesis are statistically unexpected (table 1, comparison 17; table 2). The comparison between the Polyneoptera and Eumetabola is also not significant (table 1). This suggests that the high species richness of the Neoptera (table 1, comparison 8) is a more general property of that group and not just a few derived clades, and thus represents a true shift in diversification. A paraphyletic Polyneoptera would imply a number of impoverished primitive neopterous lineages, such as the Dictyoptera and Plecoptera + Embiidina (Wheeler *et al.* 2001), and a later rather than earlier balancing of the tree (table 1, comparisons 14–16), but definitely before the origin of the Eumetabola.

Table 1. Sister-taxon comparisons between putative hexapod lineages and associated probabilities under the null model of equal (but not necessarily constant) rates of speciation and extinction in the two lineages (smaller and larger taxon).

comparison	smaller taxon	species	larger taxon	species	p (two-tailed)
1	Entognatha	7 500	Insecta	852 871	0.017
2	Ellipura	6 700	Insecta + Diplura	853 671	0.016
3	Diplura	800	Insecta	852 871	0.002
4	Archaeognatha	280	Dicondylia	852 591	0.001
5	Thysanura	614	Pterygota	852 257	0.001
6	Zygentoma	334	Pterygota	852 257	0.001
7	Ephemerida	2 148	Metapterygota	850 109	0.005
8	Odonata	4 875	Neoptera	845 234	0.011
9	Ephemerida	2 148	Odonata	4 875	0.612
10	Zygentoma	334	Pterygota excluding Neoptera	7 023	0.091
11	Archaeognatha	280	Dicondylia excluding Neoptera	7 357	0.073
12	Diplura	800	Insecta excluding Neoptera	7 637	0.190
13	Polyneoptera	32 320	Eumetabola	812 914	0.076
14	Dictyoptera	7 473	other Neoptera	837 761	0.018
15	Plecoptera + Embiidina	2 164	Eumetabola + Orthoptera + Phasmida	834 058	0.005
16	Orthoptera + Phasmida	21 144	Eumetabola	812 914	0.051
17	Paraneoptera	90 657	Holometabola	722 257	0.223
18	Coleoptera + Neuropteroidea	341 503	Hymenoptera + Mecopteroidea	380 754	0.946
19	Neuropteroidea	4 610	Coleoptera	336 893	0.027
20	Hymenoptera	130 000	Mecopteroidea	250 754	0.683
21	Strepsiptera	363	Diptera	100 000	0.007

This demonstrates that imbalance amongst higher, more inclusive taxa originates at, or after, the origin of the Neoptera, but before the origin of the Holometabola, and this region of the hexapod tree therefore represents the most important shift in diversification.

Two further, ordinal comparisons indicate that shifts in rates of cladogenesis have occurred: the Coleoptera have probably diversified more rapidly than the Neuropteroidea (table 1, comparison 19; although the difference in table 2 is marginally non-significant), as are the Diptera versus the Strepsiptera (table 1, comparison 21; table 2). However, only the Strepsiptera have diversified at rates significantly different from the Holometabola as a whole (table 2), whilst the Coleoptera have not diversified significantly faster than most holometabolan orders (table 2). If the Strepsiptera are the sister group of the Coleoptera, both the above results would be even more notable; the Strepsiptera would be older and the sister group of a more diverse clade, whilst the Coleoptera would be the sister group of a less diverse one. If the Coleoptera are paraphyletic with respect to Strepsiptera, the Strepsiptera might not have unexpected rates of cladogenesis, but the comparison between Coleoptera and Neuropteroidea is still relevant.

4. DISCUSSION

The results provide no evidence that either the origin of the Insecta, Pterygota, or Holometabola represent significant shifts in diversification. The results do, however, suggest that a significant radiation occurred shortly after the origin of the Neoptera, although the precise timing of the radiation, and taxa involved, depend on phylogenetic assumptions about Polyneoptera. This study also presents the first statistical test of J. B. S. Haldane's famous statement about the Creator's 'inordinate fondness for beetles'. The Coleoptera have probably diversified more rapidly

than either of their putative sister groups, but are not outstanding compared with other Holometabola. Thus, paraphrasing Haldane, we can only demonstrate a 'probable preference for beetles over their sister group', rather than an inordinate fondness for beetles *per se*, and a 'fondness for Neoptera or Eumetabola' more accurately reflects the results. This is the message about the diversification of higher hexapod taxa transmitted by current data and methods.

The values of mean radiation rate, $\ln(N)/t$, were estimated at *ca.* 0.01–0.06 Myr^{-1}. These are low compared with previous estimates for many taxa, including some holometabolan families, but are comparable with estimates for marine bivalves and gastropods (Stanley 1979). This is surprising given the apparent modern diversity of insects, but shows that species-rich clades need not necessarily have high average rates of diversification as long as they are ancient.

Demonstrating the timing and magnitude of shifts in diversification is only the first step to understanding the processes of diversification. Ultimately, it is desirable to know what has caused the observed shifts. Below, I discuss the candidate explanations and the extent to which conclusions can be drawn.

When the events that affect diversification have occurred repeatedly, associations between the trait and species richness can be demonstrated statistically. With unique events, statistical associations cannot be made, and we must revert to logical tests (Purvis 1996). Such tests, although not always straightforward, are nonetheless vital if a complete understanding of diversification is to be achieved. We are easily able to rule out some candidate explanations; for example, events occurring after the shift in diversification cannot be responsible. This rules out complete metamorphosis as a reason for the major shift seen here. Events prior to the shift may have contributed, but cannot have been sufficient: the insect body plan and

Table 2. Number of described species, taxon age and estimated rates of cladogenesis ($\pm$ 95% confidence interval (CI)) for the major hexapod taxa. Taxon age is estimated by equalizing the ages of sister taxa using the oldest fossil of the pair. Rates of cladogenesis are calculated by assuming a pure birth process.

taxon	species	earliest fossil stratum (system)	stratum age (Myr)	taxon age (Myr)	$\ln(N)/t$ (Myr^{-1})	+95% CI (Myr^{-1})	−95% CI (Myr^{-1})
Collembola	6 500	Pragian (Devonian)	393.3	393.3	0.0223	0.0317	0.0190
Protura	200	no fossil record	—	393.3	0.0135	0.0228	0.0102
Diplura	800	Moscovian (Carboniferous)	307.1	393.3	0.0170	0.0263	0.0137
Archaeognatha	280	Maastrichtian (Cretaceous)	69.5	327.8	0.0172	0.0284	0.0132
Zygentoma	334	Maastrichtian (Cretaceous)	69.5	327.8	0.0177	0.0289	0.0138
Ephemerida	2 148	Moscovian (Carboniferous)	307.1	327.8	0.0234	0.0346	0.0194
Odonata	4 875	Rhaetian (Triassic)	208.8	327.8	0.0259	0.0371	0.0219
Plecoptera	1 964	Kungurian (Permian)	257.9	257.9	0.0294	0.0437	0.0243
Embiidina	200	Priabonian (Tertiary)	37.0	257.9	0.0205	0.0348	0.0155
Orthoptera	18 644	Gzelian (Carboniferous)	292.5	292.5	0.0336	0.0462	0.0292
Phasmida	2 500	Sinemurian (Jurassic)	199.0	292.5	0.0267	0.0393	0.0223
Zoraptera	20	Chattian (Tertiary)	26.3	317.0	0.0095	0.0210	0.0056
Dermaptera	1 506	Sinemurian (Jurassic)	199.0	317.0	0.0231	0.0347	0.0190
Grylloblattaria	13	Tatarian (Permian)	247.5	317.0	0.0081	0.0197	0.0044
Isoptera	1 989	Berriasian (Cretaceous)	143.1	317.0	0.0240	0.0356	0.0198
Mantodea	1 800	Albian (Cretaceous)	104.5	317.0	0.0236	0.0352	0.0195
Blattaria	3 684	Bashkirian (Carboniferous)	317.0	317.0	0.0259	0.0375	0.0218
Hemiptera	79 977	Kungurian (Permian)	257.9	257.9	0.0438	0.0580	0.0387
Thysanoptera	5 000	Portlandian (Jurassic)	148.9	148.9	0.0572	0.0819	0.0484
Psocodea	5 680	Aptian (Cretaceous)	118.2	148.9	0.0581	0.0827	0.0493
Neuropteroidea	4 610	Tatarian (Permian)	247.5	247.5	0.0341	0.0489	0.0288
Coleoptera	336 893	Ladinian (Triassic)	237.2	247.5	0.0514	0.0663	0.0462
Hymenoptera	130 000	Rhaetian (Triassic)	208.8	285.8	0.0412	0.0541	0.0366
Trichoptera	6 411	Artkinsian (Permian)	264.2	264.2	0.0332	0.0471	0.0282
Lepidoptera	141 764	Sinemurian (Jurassic)	199.0	264.2	0.0449	0.0588	0.0400
Siphonaptera	1 740	Aptian (Cretaceous)	118.2	247.5	0.0301	0.0450	0.0249
Mecoptera	476	Asselian (Permian)	285.8	285.8	0.0216	0.0344	0.0170
Strepsiptera	363	Priabonian (Tertiary)	37.0	247.5	0.0238	0.0387	0.0186
Diptera	100 000	Tatarian (Permian)	247.5	247.5	0.0465	0.0614	0.0412
Hexapoda	860 371	Pragian (Devonian)	393.3	393.3	0.0347	0.0441	0.0314
Entognatha	7 500	Pragian (Devonian)	393.3	393.3	0.0227	0.0320	0.0194
Thysanura	614	Gzelian (Carboniferous)	292.5	327.8	0.0196	0.0308	0.0156
Ellipura	6 700	Pragian (Devonian)	393.3	393.3	0.0224	0.0317	0.0191
Insecta + Diplura	853 671	Serpukhovian (Carboniferous)	327.8	327.8	0.0417	0.0529	0.0377
Insecta	852 871	Serpukhovian (Carboniferous)	327.8	393.3	0.0348	0.0441	0.0315
Dicondylia	852 591	Serpukhovian (Carboniferous)	327.8	327.8	0.0417	0.0529	0.0377
Pterygota	852 257	Serpukhovian (Carboniferous)	327.8	327.8	0.0417	0.0529	0.0377
Metapterygota	850 109	Bashkirian (Carboniferous)	317.0	327.8	0.0417	0.0529	0.0377
Neoptera	845 234	Serpukhovian (Carboniferous)	327.8	327.8	0.0416	0.0528	0.0377
Polyneoptera	32 320	Bashkirian (Carboniferous)	317.0	317.0	0.0328	0.0444	0.0286
Paraneoptera	90 657	Kungurian (Permian)	257.9	285.8	0.0399	0.0528	0.0354
Eumetabola	812 914	Asselian (Permian)	285.8	317.0	0.0429	0.0545	0.0388
Holometabola	722 257	Asselian (Permian)	285.8	285.8	0.0472	0.0601	0.0426
Mecopteroidea	250 754	Asselian (Permian)	285.8	285.8	0.0435	0.0564	0.0389

wings are examples in the present case. One or more events coinciding exactly with the shift (including synapomorphies of the diverse clade) must have provided the initial stimulus and were therefore necessary, although they may not have been sufficient or have been countered by subsequent events in derived clades. Evaluating simultaneous events requires a plausible mechanism by which the candidates can affect speciation and/or extinction rates.

The major shift in diversification shown here occurred either at the origin of the Neoptera, the Eumetabola, or somewhere in between. Any characteristics acquired then are candidate influences. Wheeler *et al.* (2001) list ten morphological synapomorphies of the Neoptera, and some

molecular ones. Of these, wing flexion has commonly been described as a key innovation by allowing winged insects to radiate into concealed and architecturally complex microhabitats. A cautionary note is that wing flexion was independently acquired by a now extinct order, the Diaphanopterodea (Carpenter & Burnham 1985). Nonetheless, the functional link between architectural niche complexity and species richness is plain in modern hexapod communities (e.g. Lawton 1983). The ovipositor has also been modified in the Neoptera, and changes to this organ have been implicated in hexapod diversification (Zeh *et al.* 1989). Again this is linked with the ability to exploit novel niches. The Eumetabola have at least four morphological synapomorphies (Wheeler *et al.* 2001),

including modifications to the wings and leg articulation, but none of them have been previously discussed as potential key innovations.

What of the Coleoptera? They have probably radiated faster than their sister group, whatever that proves to be. Farrell (1998) has shown that a higher rate of diversification of coleopteran subtaxa is linked to associations with angiosperms. Interestingly, neither of the candidate sister taxa for the Coleoptera are phytophagous, suggesting that this difference may also explain the current trend at order level. However, the work of Farrell (1998) suggests that even if we were to accept the order Coleoptera as unusually diverse, this is more appropriately viewed as diversity of a few beetle lineages than the order as a whole.

What, in general, is the relationship between the results shown here and the previous finding that associations with plants affects insect diversity (Mitter *et al.* 1988)?

The important points are that (i) the most diverse clades do include phytophagous taxa, (ii) the most diverse clades are also the most derived but, (iii) not all derived clades are species rich. It therefore seems likely that neither phytophagy nor synapomorphies of Neoptera or Eumetabola are solely responsible for species richness, but some interaction of the two. In particular, it seems probable that one or more synapomorphies of Neoptera or Eumetabola have promoted phytophagy or have helped make phytophagy a more diversifying strategy.

There are several opportunities for further work. Phylogenetic consideration of the Polyneoptera would help locate the timing of the shift more precisely, and further functional studies could then help evaluate the effect of events at that time. However, in the longer term, a more precise evaluation of the questions raised here will require alpha taxonomy, in quantity, new fossil and molecular data to resolve conflicts in taxon-age estimates, and increasingly refined estimates of phylogeny.

REFERENCES

Arnqvist, G., Edvardsson, M., Friberg, U. & Nilsson, T. 2000 Sexual conflict promotes speciation in insects. *Proc. Natl Acad. Sci. USA* **97**, 10 460–10 464.

Barraclough, T. G., Vogler, A. P. & Harvey, P. H. 1999 Revealing the factors that promote speciation. In *Evolution of biological diversity* (ed. A. E. Magurran & R. M. May), pp. 202–219. New York: Oxford University Press.

Blaxter, M. 2001 Sum of the arthropod parts. *Nature* **413**, 121–122.

Burmester, T., Massey, H. C., Zakharkin, S. O. & Benes, H. 1998 The evolution of hexamerins and the phylogeny of insects. *J. Mol. Evol.* **47**, 93–108.

Carpenter, F. M. 1992 *Treatise on invertebrate paleontology*. Part R. *Arthropoda, superclass Hexapoda*. Boulder, CO: Geological Society of America; and Lawrence, KS: University of Kansas.

Carpenter, F. M. & Burnham, L. 1985 The geological record of insects. *A. Rev. Earth Planet. Sci.* **13**, 297–314.

Connor, E. F. & Taverner, M. P. 1997 The evolution and adaptive significance of the leaf-mining habit. *Oikos* **79**, 6–25.

Davies, D. A. L. & Tobin, P. 1985 The dragonflies of the world: a systematic list of extant species of Odonata. 2. Anisoptera. *Soc. Int. Odonatol. Rapid Commun. (Suppl.)* 51–151.

Evans, H. E. 1984 *Insect biology*. Reading, MA: Addison-Wesley.

Farrell, B. D. 1998 'Inordinate fondness' explained: why are there so many beetles? *Science* **281**, 555–559.

Farris, J. S. 1976 Expected asymmetry of evolutionary rates. *Syst. Zool.* **25**, 196–198.

Gullan, P. J. & Cranston, P. S. 2000 *The insects: an outline of entomology*, 2nd edn. Oxford: Blackwell Scientific.

Hawksworth, D. L. & Kalin-Arrayo, M. T. 1995 Magnitude and distribution of biodiversity. In *Global biodiversity assessment* (ed. V. H. Heywood), pp. 107–191. Cambridge University Press.

Heard, S. B. & Hauser, D. L. 1995 Key evolutionary innovations and their ecological mechanisms. *Hist. Biol.* **10**, 151–173.

Hennig, W. 1981 *Insect phylogeny*. Chichester, UK: Wiley.

Hopkin, S. P. 1997 *Biology of the springtails (Insecta: Collembola)*. New York: Oxford University Press.

Hutchinson, G. E. 1959 Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* **93**, 145–159.

Lawton, J. H. 1983 Plant architechture and the diversity of phytophagous insects. *A. Rev. Entomol.* **28**, 23–39.

Mitter, C., Farrell, B. & Weigmann, B. 1988 The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? *Am. Nat.* **132**, 107–128.

Mooers, A. Ø. & Heard, S. B. 1997 Inferring evolutionary process from phylogenetic tree shape. *Q. Rev. Biol.* **72**, 31–54.

Nee, S. 2001 Inferring speciation rates from phylogenies. *Evolution* **55**, 661–668.

Nee, S., May, R. M. & Harvey, P. H. 1994 The reconstructed evolutionary process. *Phil. Trans. R. Soc. Lond.* B **344**, 305–311.

Parker, S. P. (ed) 1982 *Synopsis and classification of living organisms*. New York: McGraw–Hill.

Purvis, A. 1996 Using interspecies phylogenies to test macroevolutionary hypotheses. In *New uses for new phylogenies* (ed. P. H. Harvey, A. J. Leigh Brown, J. Maynard Smith & S. Nee), pp. 153–168. New York: Oxford University Press.

Purvis, A., Nee, S. & Harvey, P. H. 1995 Macroevolutionary inferences from primate phylogeny. *Proc. R. Soc. Lond.* B **260**, 329–333.

Richards, O. W. & Davies, R. G. 1978 *Imms general text book of entomology*, 10th edn. London: Chapman & Hall.

Ross, A. J. & Jarzembowski, E. A. 1993 Arthropoda (Hexapoda; Insecta). In *The fossil record 2* (ed. M. J. Benton), pp. 363–426. London: Chapman & Hall.

Sanderson, M. J. & Donaghue, M. J. 1994 Shifts in diversification rate with the origin of the angiosperms. *Science* **264**, 1590–1593.

Stanley, S. M. 1979 *Macroevolution: pattern and process*. San Fransisco, CA: Freeman.

Whalley, P. & Jarzembowski, E. A. 1981 A new assessment of *Rhyniella*, the earliest known insect, from the Devonian of Rhynie, Scotland. *Nature* **291**, 317.

Wheeler, W. C., Whiting, M., Wheeler, Q. D. & Carpenter, J. M. 2001 The phylogeny of the extant hexapod orders. *Cladistics* **17**, 113–169.

Wiegmann, B. M., Mitter, C. & Farrell, B. D. 1993 Diversification of carnivorous parasitism: extraordinary radiation or specialized dead-end? *Am. Nat.* **142**, 737–754.

Williamson, M. 1992 Haldane's special preference. *The Linnean* **8**, 12–15.

Zeh, D. W., Zeh, J. A. & Smith, R. L. 1989 Ovipositors, amnions, and eggshell architecture in the diversification of terrestrial arthropods. *Q. Rev. Biol.* **64**, 147–168.