

Does the fossil record of spiders track that of their principal prey, the insects?

David Penney

ABSTRACT: The currently accepted cladogram of spider phylogeny and palaeontological data are used to evaluate spider family richness through geological time. A significantly more diverse spider fossil record is predicted than observed. The predicted rate of spider family diversification is considered more accurate because of its close similarity at 0 Ma to the number of extant families. Predicted spider family palaeodiversity is compared with insect family palaeodiversity to investigate whether spiders track insects through geological time. At the family level, the insects, and observed and predicted spider fossil records show an exponential increase over time, the pattern typical of a radiating group. No significant differences are observed in the rates of change in the slopes, and hence rate of diversification of spiders and insects over time. This suggests that spiders probably co-radiated alongside the insects, with the major radiations of both groups occurring at least 100 Ma before the origin of angiosperms.

KEY WORDS: Arachnids, Araneae, evolutionary history, palaeoarachnology, palaeoentomology, phylogenetic tree

Arachnids were among the first terrestrial animals (Late Silurian) (Jeram *et al.* 1990) and are among the most diverse and abundant predators on land today. Advances in palaeoentomology have produced detailed biodiversity data for insects through geological time (Labandeira & Sepkoski 1993; Jarzembowski & Ross 1996; Ross *et al.* 2000; Grimaldi 2001). Fluctuating fortunes of plants and their insect herbivores have been documented, particularly in the Mesozoic Era (Labandeira & Sepkoski 1993; Labandeira *et al.* 2002). However, a complete picture of Mesozoic terrestrial palaeoecology has not yet been assembled because information on the main predators of insects, the spiders, was missing. In the light of available fossil data, the present paper investigates whether there are any correlations in evolutionary diversification between spiders and insects through geological time, and in particular, whether the fossil record of spiders tracks that of their principal prey, the insects.

1. The insect and spider fossil records

The insect fossil record stems predominantly from lacustrine and fluvial sediments, but is supplemented in the Cretaceous and Tertiary by their remarkable preservation in amber (Ross *et al.* 2000). The oldest fossil hexapod is Early Devonian, although the first flying insects did not appear in the known fossil record until the Mid-Carboniferous (Jarzembowski & Ross 1996). After the first 60 million years of their history, for which few fossils are known (Labandeira & Sepkoski 1993), the record is relatively rich when compared to other major terrestrial animal taxa. It is not restricted to a few, easily preserved higher taxa, but consists of a wide range of extant and extinct orders. However, investigations of palaeodiversity and taxonomic richness of this most diverse class on Earth are notably few (Labandeira & Sepkoski 1993). The main reason for this is the lack of a suitable fossil species database, the last was published in 1908 by Handlirsch (1906–1908). A new palaeoentomological database is in preparation, but will not be complete enough to be useful for many years (Ross *et al.* 2000). Therefore, we must rely on family data to investigate changes in insect diversity over time. The use of family-level data for

investigations of insect palaeodiversity by Labandeira & Sepkoski (1993) was justified on the following grounds: (1) This taxonomic rank appeared to correlate well with underlying species diversity in other studies of fossil diversity. (2) Families are less prone to irregular and biased sampling than are fossil species and genera, thus maintaining a better evolutionary signal at that level. (3) Extant insect families are reasonably well established through consensus among taxonomists, but this is often untrue for fossil species and genera, which are more idiosyncratically defined. (4) Insect families possess discrete, often highly stereotyped life habits, which can be informative in numerous palaeontological investigations. In this paper, the present author makes the assumption that these observations of Labandeira & Sepkoski (1993) are reliable and that they also hold true for spiders.

Examination of insect family data in the fossil record demonstrates diversity peaks in the Late Permian, Early Cretaceous and Mio–Pliocene, with peaks showing progressively less turnover, and origination greatly exceeding extinction by the Tertiary (Jarzembowski & Ross 1996). Distinct troughs in diversity occur in the Early Triassic and Palaeocene, with a shallower trough in the Middle Jurassic; origination peaks appear in the Late Carboniferous, Lower Jurassic, Lower Cretaceous and Eocene (Jarzembowski & Ross 1996). The fossil record for all of the 30 commonly recognised extant insect orders was depicted using spindle diagrams of insect family richness superimposed over geological time by Labandeira & Sepkoski (1993, fig. 2). All but the Lepidoptera showed a similar Tertiary family richness to the extant fauna; this was attributed to a negative taphonomic bias of the Lagerstätten in relation to butterflies and moths. Insect family richness increased steadily after the Permian–Triassic until Mid-Tertiary times, when it increased sharply, almost certainly because of their common occurrence in amber and compression Lagerstätten. This steady increase appears to be caused not by high origination rates, but by low extinction rates (Labandeira & Sepkoski 1993; Jarzembowski & Ross 1996).

Jarzembowski & Ross (1996) reviewed insect orders, families and genera over geological time, providing graphs showing origination, extinction and overall richness. These



demonstrated the basic diversity patterns over time, but no quantitative analyses were employed within or between groups, and their conclusions merely addressed the limitations of their data, without actually addressing the main concept of their paper. Ross *et al.* (2000) used the same technique to investigate the Cretaceous and Cenozoic insect fossil record with respect to global change. Insect family diversity was not drastically affected by the end-Cretaceous extinction (Briggs 1995; Labandeira & Sepkoski 1993; Ross *et al.* 2000). Labandeira *et al.* (2002) studied a megafloral sequence across the K/T boundary in the Williston Basin of southwestern North Dakota, USA, associated with dinosaur extinctions and the loss of approximately 80% of megafloal species. They recorded the amount of insect damage observed in the fossil plants on either side of the K/T boundary. Specialised associations between many monophagous, and some oligophagous insects and plants present in the latest Cretaceous disappeared at the boundary and failed to reappear afterwards (Labandeira *et al.* 2002). This was proposed as evidence for a major, rapid extinction event at the boundary. However, they also observed that all generalised polyphagous insect–plant interactions traversed the boundary, and thus, were unable to provide direct evidence for insect extinction at family level. There is no evidence to suggest that spiders were significantly affected by the K/T extinction (Penney *et al.* 2003). For a brief review of palaeontologists and their work over the last century, see Grimaldi (2001).

Labandeira & Sepkoski (1993) stated that the appearance and radiation of angiosperms had no effect on insect family diversification, but may have had an effect at the subfamilial level (see also Grimaldi 1999). However, when origination and extinction data are considered separately, there appears to have been a high turnover of insect families during the Early Cretaceous (Ross *et al.* 2000). No evidence exists to suggest the same is true for spiders. Arthropod–primitive land plant interactions, inferred from the study of coprolites, date back to the Late Silurian to Mid-Devonian (Labandeira 2000). However, the first evidence of insect–plant interactions does not occur until the interval spanning the Early Carboniferous to Late Permian, when primitive ancestral insect taxa consumed spores, prepollen and pollen from ferns and seed plants (Labandeira 2000). The early phase of the modern insect fauna and its association with non-angiosperm seed plants stems from the Early Triassic to the Mid-Cretaceous, during which time there is a relatively rapid change towards a dominance of modern insect taxa and angiosperm plants (Labandeira 2000). Fossil evidence exists for the presence of pollinating insects during the Late Jurassic, their mutualisms may have been subsequently fine-tuned by the angiosperms (Labandeira 2000). However, the major radiations of the obligate anthophilic insects probably occurred during the Late Lower to Upper Cretaceous, because this period is consistent with the appearance of entomophilous syndromes in Cretaceous flowers (Grimaldi 1999). In fact, based upon the palaeo-chronology of angiosperm reproductive features, most of which are associated with entomophily, insect anthophily appears to have been present in the Aptian/Albian, well established by the Cenomanian and fully intact by the Turonian (Grimaldi 1999). However, 65–88% of the modern insect mouthpart classes were present by the Middle Jurassic (Labandeira & Sepkoski 1993). Therefore, the great radiation of insects began at least 100 Ma before the radiation of the angiosperms (Labandeira & Sepkoski 1993).

No such palaeodiversity studies or data sets currently exist for spiders. Selden (1993) listed fossil spiders known at this time and the same author (1996a) provided a brief review of the geological history of spiders. In the latter publication, he

listed the spider families known from fossils; however, a number of taxonomic and systematic changes in the arachnological literature had been omitted (e.g. Wunderlich 1984, 1986). Spiders first appeared in some of the earliest terrestrial ecosystems (Mid-Devonian; Selden *et al.* 1991), and are one of the most diverse and abundant predatory arthropod groups on land today. The Tertiary fossil record of spiders is rich because of their common occurrence in Dominican (e.g. Penney & Pérez-Gelabert 2002) and Baltic (e.g. Petrunkevitch 1958) ambers. It is evident from Figure 1 that the majority of fossil spiders belong to extant families and that currently only four strictly fossil families are known. Many of the Mesozoic fossils are known from singletons or only a few individuals; however, many of these are identifiable to species that can be placed in extant genera (e.g. Penney 2002, 2003, 2004). The Tertiary spider fossil record consists of many thousands of identifiable spider specimens primarily from Baltic and Dominican ambers. A greater percentage of these can be placed in extant genera compared to those of the Mesozoic. In excess of 330 fossil spider species from 41 families (two extinct) have been described from Baltic amber. Approximately 70% of the 130+ recorded genera are extinct (literature-derived data). In the slightly younger Dominican Republic amber, 145 species in 87 genera (25 fossil) are recorded from 44 extant families (Penney & Pérez-Gelabert 2002). All spider species described from fossils are currently considered extinct. All three extant spider suborders (i.e. the Mesothelae, Mygalomorphae and Araneomorphae) were present in the Triassic (Selden *et al.* 1999). Furthermore, the most evolved of these groups, the Araneomorphae, is represented by fossil taxa which are considered more derived than many extant taxa, suggesting that a reasonable degree of radiation had occurred within the Araneae before the Late Triassic (Selden *et al.* 1991). Both cribellate and ecribellate orb-weavers were already well defined by the Early Cretaceous (Selden 1989). In this paper, the author provides graphically, and in a phylogenetic context, the current state of knowledge of the longevity of fossil and extant spider families. From this, spider palaeodiversity data are obtained for comparison with existing insect palaeodiversity data.

2. Material and methods

Palaeontological and neontological data for spiders were combined in the form of an evolutionary or phylogenetic tree. These trees are constructed by superimposing cladograms (assuming all trees are congruent) of hypothesised phylogenetic relationships, derived from work on extant taxa, over stratigraphic data from the fossil record (Smith 1994). Three assumptions are made: (1) the cladogram provides the best available evidence for phylogenetic relationships of the taxa; (2) demonstrably monophyletic taxa have not given rise to other taxa; and (3) stratigraphic range extensions should be kept to a minimum. The known ranges provided by the fossil taxa, and the subsequent range extensions of sister taxa, ghost lineages and proposed ancestral lineages, show the evolutionary history of a group over geological time. A range extension is the extra stratigraphic range added to the observed range of a taxon to make the evolutionary tree concordant with the phylogenetic hypotheses. A ghost lineage is a branch of an evolutionary tree with no fossil data, but which needs to be hypothesised after combining cladistic and biostratigraphic data. Ancestral lineages result from the addition of fossil metataxa. This technique, fully explained by Smith (1994), provides minimum dates for the hypothesised phylogenetic (sister taxa) dichotomies, and provides a graphical representation of origination, extinction and divergence events of taxa

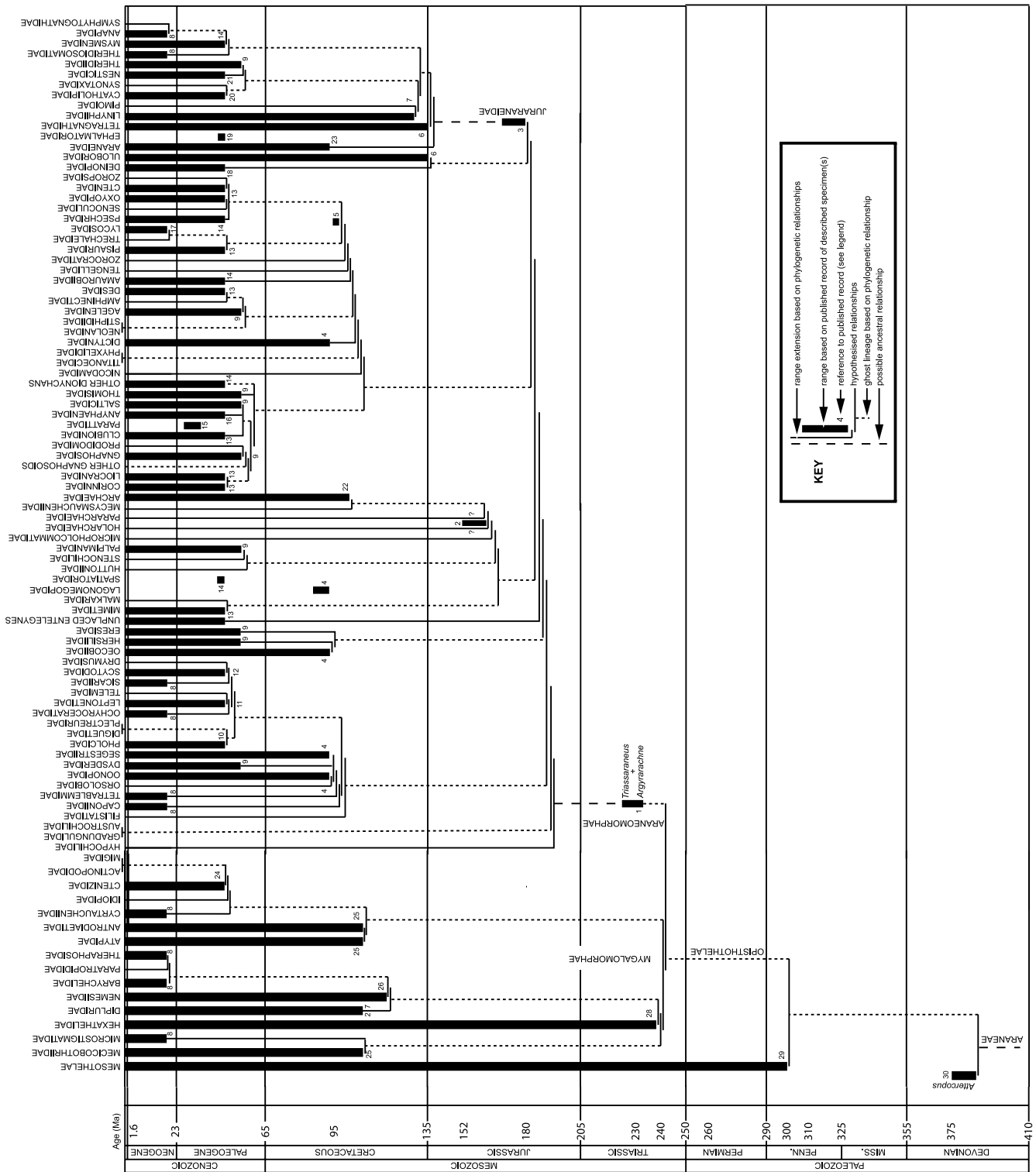
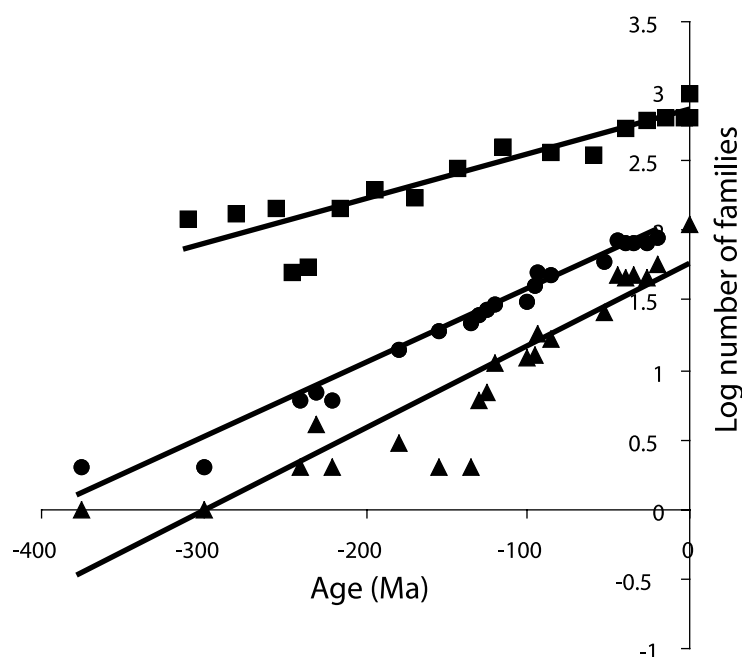


Figure 1 Evolutionary tree of the Araneae. Other gnaphosoids include: Gallieniellidae, Ammoxenidae, Cithaeronidae, Trochanteriidae and Lamponidae; other dionychnans include: Zoridae, Selenopidae, Sparassidae and Philodromidae (see Coddington & Levi 1991); unplaced entelegynes include: Cryptothelidae, Cybaeidae, Cycloctenidae, Hahniidae, Halidae, Homalonychidae, Miturgidae and Zadariidae (see Griswold *et al.* 1999), and Chummidae (Jocqué 2001). References: (1) Selden *et al.* (1999); (2) Eskov (1987); (3) Eskov (1984); (4) Penney (2002); (5) Rayner & Dippenaar-Schoeman (1995); (6) Selden & Penney (2003) and Selden (1990); (7) Penney & Selden (2002); (8) Wunderlich (1988); (9) Gourret (1888); (10) Menge (1869); (11) Wunderlich (1991); (12) Wunderlich (1993a); (13) Petrunkevitch (1958); (14) Petrunkevitch (1942); (15) Petrunkevitch (1922); (16) Petrunkevitch (1946); (17) Penney (2001); (18) Wunderlich (1986); (19) Petrunkevitch (1950); (20) Wunderlich (1993b) (see also Griswold 2001); (21) Eskov & Marusik (1992); (22) Penney (2003); (23) Penney (2004); (24) Wunderlich (2000); (25) Eskov & Zonshteyn (1990); (26) Selden (2002); (27) Selden *et al.* (2002); (28) Selden & Gall (1992); (29) Selden (1996b); and (30) Selden *et al.* (1991). A complete review of the spider fossil record is in preparation.

Table 1 Spider family palaeodiversity data derived from the evolutionary tree and insect family palaeodiversity data from Ross (pers. comm.); graph published in Ross (1998): (Ma) age in millions of years; (Obs) observed; and (Pre) predicted

Spiders																						
Ma	375	300	240	230	220	180	154	135	130	125	120	101	95	94	86	53	44	40	35	27	20	0
Obs	1	1	2	4	2	3	3	5	6	7	11	12	13	18	17	26	48	46	47	46	58	110
Pre	2	2	6	7	6	14	19	22	25	27	30	31	40	50	49	61	84	82	83	82	88	—

Insects																					
Ma	310	280	255	245	235	215	195	170	143.5	116	86	59	39	27	15	3.3	0.8	0			
Obs	122	130	143	50	55	142	198	176	280	401	369	347	543	624	640	641	644	967			

**Figure 2** Linear regressions on the log number of observed and predicted spider family and observed insect palaeodiversity over geological time: (●) predicted spider, $y=0.0054x+2.0947$, $R^2=0.9753$; (▲) observed spider, $y=0.0059x+1.7327$, $R^2=0.8415$; and (■) observed insect, $y=0.0032x+2.8492$, $R^2=0.8293$.

through geological time. The phylogenetic tree of spiders was derived from the cladograms of Coddington & Levi (1991), with amendments, (e.g. Griswold 1993; Scharff & Coddington 1997; Griswold *et al.* 1998, 1999). Schütt (2000) suggested a number of changes to this phylogeny, based on a small number of morphological characters from seven families, but did not undertake a new cladistic analysis; her changes are not included here. The known ranges for the extant families are based on the oldest described fossil for each spider family (see the legend to Fig. 1 for references). By combining both amber and non-amber fossil spider data in this way, the possibility of taphonomic bias is less than it would be if, for example, analyses of amber fossils alone were considered. In addition, inclusion-bearing amber deposits only occur back to the Lower Cretaceous and biodiversity data for these older deposits, many of which have only recently been discovered, are inadequate for any form of quantitative analysis. The first extant spider family from Cretaceous amber was described by Penney (2002).

From the tree, observed spider family palaeodiversity over time was obtained by counting the number of known taxon ranges, derived from described fossils. A dataset of predicted family palaeodiversity was obtained by counting the presence of range extensions and ghost lineages, in addition to the known, observed ranges. These data were compared against

the linear phase of the observed insect family palaeodiversity from Jarzembowski & Ross (1996) and Ross *et al.* (2000). Linear regressions were compared using analysis of covariance (ANCOVA).

3. Results and discussion

Figure 1 illustrates the current knowledge of the evolutionary history of spiders. The observed and predicted spider family palaeodiversity counts, derived from this tree, along with the insect family palaeodiversity data from Jarzembowski & Ross (1996) and Ross *et al.* (2000), are given in Table 1. Figure 2 shows the observed and predicted spider and observed insect family palaeodiversities through geological time.

The increase of a taxon's diversity over time is essentially a Markovian process, i.e. the newly evolved taxa are dependent on the presence of the ancestral taxa. Thus, the number of new taxa at any time is dependent, in part, upon the number of existing taxa. Therefore, the null model for the diversification process of a radiating group is a sigmoid curve with exponential increase, and the logarithm of its diversity plot during the incremental phase will form a straight-line regression function of geological time (Sepkoski 1979). This is seen in both observed and expected spider family palaeodiversities (Fig. 2).

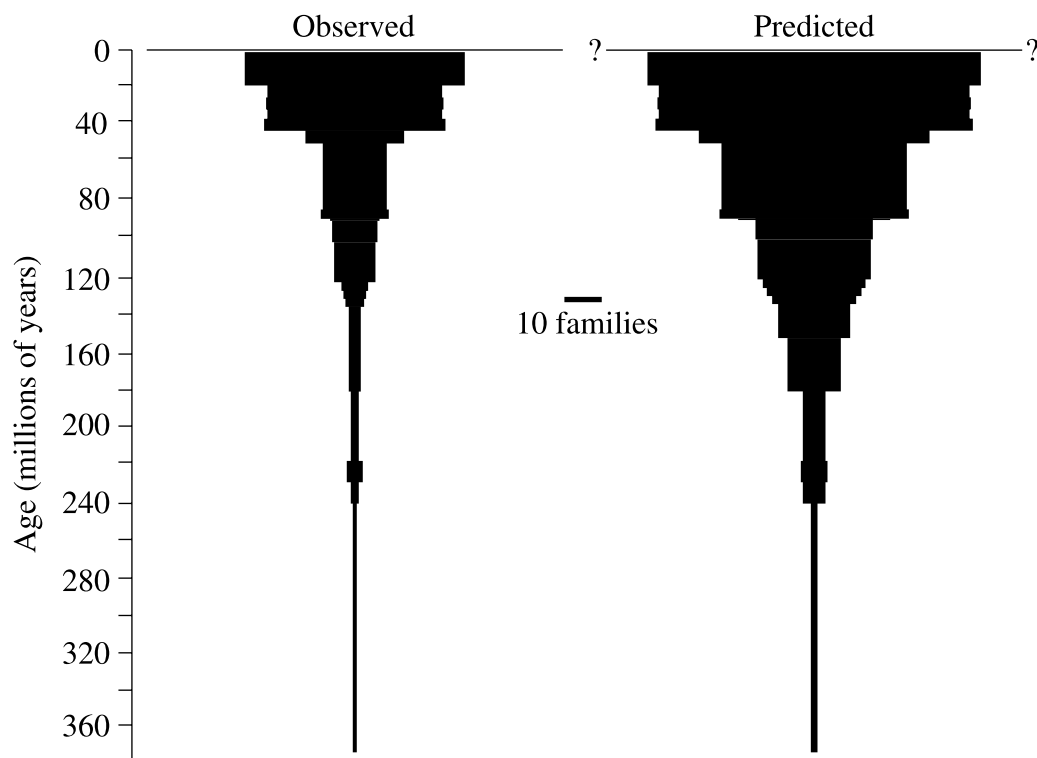


Figure 3 Spindle diagrams of observed and predicted spider family palaeodiversity over time. Data derived from the phylogenetic tree (Fig. 1) and presented in Table 1.

In fact, ANCOVA shows barely any difference between the two slopes ($t = -0.8942$, $d.f. = 39$, $p > 0.1$), and therefore, the rate of exponential increase is similar in both observed and predicted spider family palaeodiversities over time. However, there is a highly significant difference between the heights of the lines ($t = -7.4469$, $d.f. = 40$, $p < 0.0001$). If the y -intercepts are compared (observed = 1.7327; expected = 2.0947) and the logs of these values are inverted, a predicted value for the number of extant spider families, i.e. at 0 Ma, is obtained. The observed line predicts the presence of approximately 54 families, whereas the expected predicts 124 families. Clearly, the predicted value is much closer to the actual value ($n = 110$) (e.g. Platnick 2002; see Marusik & Lehtinen 2003 for an additional family) than the observed one. It is entirely feasible that 10 or so families remain to be discovered or newly erected, which would more closely approximate to the predicted value. However, this value was obtained by extending the exponential regression line from 20 Ma (the most Recent data point; Dominican Republic amber) to the present. This pattern of diversification, if left unconstrained, would tend towards infinity (Sepkoski 1979), which is clearly absurd and this line can be expected to plateau off once the maximum spider family diversity sustainable by the constraints of the ecosystem has been reached.

The observed insect family palaeodiversity and the predicted spider family palaeodiversity (Fig. 2) show a significant difference between the heights of the lines ($t = 10.5809$, $d.f. = 37$, $p < 0.0001$), but not between the two slopes ($t = -0.9522$, $d.f. = 36$, $p > 0.1$); examination of residuals demonstrated no discernible patterns. Thus, the rate of exponential increase is the same for both groups.

The order Araneae ranks seventh in terms of numbers of described extant terrestrial species, after the Acari and the five largest insect orders: Coleoptera, Hemiptera, Hymenoptera, Diptera and Lepidoptera. If the data in Table 1 are used to construct spindle diagrams for observed and predicted spider

family palaeodiversities (Fig. 3) and these are compared with the spindle diagrams of Labandeira & Sepkoski (1993, fig. 2) for the above insect orders, then the observed spider fossils resemble that of the Lepidoptera, and the expected spider diversity resembles those of the remaining orders. It was mentioned earlier that the diagram for the Lepidoptera is an underestimation of their true palaeodiversity because of the negative taphonomic bias of Lagerstätten towards butterflies and moths (Labandeira & Sepkoski 1993). It is expected that this order should follow a similar pattern to the other major insect orders (Labandeira & Sepkoski 1993). There have been considerably fewer palaeoarachnologists, living and dead, than there are living palaeoentomologists, and fewer palaeoarachnological publications. The present author considers these important factors in the deficit of the observed, i.e. the known and described, spider fossils when compared to those of insects. Therefore, the predicted spider family palaeodiversity is a better representation of spider fossil history, within the constraints of our current palaeoarachnological knowledge. This is supported by the similar value for extant spider family richness (i.e. at 0 Ma) (Fig. 2) determined by the regression analysis on the predicted data, when compared to that observed today.

Coevolution can be defined as reciprocally induced evolutionary change between two or more species or populations (Thompson 1989; Price 1996). Therefore, coevolution *sensu stricto* may be considerably narrower in scope than typical coverage in the literature might imply. For example, the following are often cited as involving coevolution: competition, the fossil record, pollinating and seed dispersal systems and predator-prey interactions to name but a few. However, genetically based, reciprocally induced relationships are rarely present in such cases. The occurrence of coevolution is more likely where two species interact directly with one another and where at least one is dependent on the other; for example, in host-parasite interactions (Price 1996). Evidence for

plant–pollinator (Feinsinger 1983) and plant–herbivore (Craig *et al.* 1988) coevolution in natural systems is usually inconclusive, although recent studies have demonstrated that it may exist in some cases (e.g. Farrell & Mitter 1998; Pellmyr & Lebens-Mack 1999). Some authors refer to evolutionary changes in other species which are produced by evolutionary change in a given species as coevolutionary responses, regardless of whether there is reciprocal coevolution *per se* (Abrams 1991). The three-trophic-level system of spider–insect–plant encompasses far in excess of half of all known extant terrestrial species. Innumerable microevolutionary processes, and not coevolution *per se*, have occurred to produce the Recent biodiversity and the macroevolutionary patterns observable in the fossil record. The majority of spiders are generalist predators, and therefore coevolution *sensu stricto* with their insect prey is unlikely. Most predators, if confronted with a well-protected prey, would switch to one that is more vulnerable. In addition, the predator may also form prey in the diet of other predators, and therefore selective factors which favour its own survival, rather than its ability to obtain food, should predominate (Conway Morris 1995). Possible cases where there may be consistent trends indicating reciprocal coevolution are when the prey can occasionally maim or kill the attacker, or when the predator feeds on a very limited number of closely related species, or a single prey species. Therefore, the term co-radiation, with the accompanying potential for coevolution, is more appropriate when considering the combined evolutionary histories of spiders with their main prey, the insects.

It is not unreasonable to expect a predator–prey co-radiation between spiders and insects, given their present day interactions. The similarity in the slopes of spider and insect family palaeodiversities supports this idea. The major radiation of the insects took place 100 Ma before the ascendancy of the angiosperms (Labandeira & Sepkoski 1993), and there was a sufficiently diverse basal stock of Araneae present at this time (Fig. 1) to radiate concurrently with the insects. By the time the angiosperms appeared in the Cretaceous, allowing for further insect diversification, the co-radiation of spiders and insects was probably already well established, allowing the Araneae to thrive and diversify alongside the angiosperm–insect co-radiation.

The idea that insect and spider diversity may be linked is both plausible and old. What is presented here is the first quantitative evidence in support of this idea. However, these data do not provide unequivocal evidence that co-radiation occurred between these two groups. Maybe both increased in diversity at similar rates, but for different reasons, and the observed similarity in rate of increase is pure coincidence. In fact, even if the slopes differed, it would be hard to argue against co-radiation. The observed trends may be the result of the relative paucity of older fossils or of taphonomic bias. The preservation potential of spiders and insects in amber is presumably similar; however, amber inclusions do not occur before the Cretaceous. In sedimentary rocks, the preservation potential of spiders is considerably lower compared to that of insects, primarily because of their terrestrial habits. Demonstrating or differentiating between co-radiation and other causes for the similarity in observed trends in these two large groups is a complicated issue. It is hoped that the present paper will form a first step in the right direction for addressing this problem. A number of new Lagerstätten have been identified recently and the author is currently involved in a project documenting Mesozoic amber spiders. This research should hopefully shed further light on the interwoven evolutionary relationships of spiders and their prey.

4. Acknowledgements

I thank P. A. Selden (University of Manchester) for his comments on the first draft of the manuscript, A. Roland Ennos (University of Manchester) and C. Philip Wheeler (Manchester Metropolitan University) for statistical advice. I also thank A. Ross (Natural History Museum) for insect palaeodiversity data and the reviewers for their comments, and acknowledge funding from the Leverhulme Trust.

5. References

- Abrams, P. A. 1991. The effects of interacting species on predator–prey coevolution. *Theoretical Population Biology* **39**, 241–62.
- Briggs, J. C. 1995. *Global biogeography*. Amsterdam: Elsevier.
- Coddington, J. A. & Levi, H. W. 1991. Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics* **22**, 565–92.
- Conway Morris, S. 1995. Coevolution. In Briggs, D. E. G. & Crowther, P. R. (eds) *Palaeobiology, a synthesis*, 136–8. Oxford: Blackwell Science.
- Craig, T. P., Price, P. W., Clancy, K. M., Waring, G. L. & Sacchi, C. F. 1988. Three-trophic-level system: willow, a gall-forming herbivore, and parasitoid. In Spencer, K. C. (ed.) *Chemical mediation of coevolution*, 57–80. San Diego: Academic Press.
- Eskov, K. 1984. A new fossil spider family from the Jurassic of Transbaikalia (Araneae, Chelicerata). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1984**, 645–53.
- Eskov, K. 1987. A new archaetid spider (Chelicerata, Araneae) from the Jurassic of Kazakhstan, with notes on the so-called ‘Gondwanan’ ranges of Recent taxa. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **175**, 81–106.
- Eskov, K. & Marusik, Y. M. 1992. Fossil spiders of the family Nesticidae (Chelicerata, Araneida). *Palaeontologicheskii Zhurnal* **2**, 87–95.
- Eskov, K. & Zonshtein, S. L. 1990. First Mesozoic mygalomorph spiders from the Lower Cretaceous of Siberia and Mongolia, with notes on the system and evolution of the infraorder Mygalomorphae (Chelicerata, Araneae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **178**, 325–68.
- Farrell, B. D. & Mitter, C. 1998. The timing of insect/plant diversification: might *Tetraopes* (Coleoptera: Cerambycidae) and *Asclepias* (Asclepiadaceae) have co-evolved. *Biological Journal of the Linnean Society* **63**, 553–77.
- Feinsinger, P. 1983. Coevolution and pollination. In Futuyma, D. J. & Slatkin, M. (eds) *Coevolution*, 282–310. Sunderland, MA: Sinauer.
- Gourret, M. P. 1888. Recherches sur les arachnides Tertiaires d’Aix en Provence. *Recueil Zoologique Suisse* **1888**, 431–96.
- Grimaldi, D. 1999. The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Annals of the Missouri Botanical Garden* **86**, 373–406.
- Grimaldi, D. 2001. Insect evolutionary history from Handlirsch to Hennig, and beyond. *Journal of Paleontology* **75**, 1152–60.
- Griswold, C. E. 1993. Investigations into the phylogeny of the lycosoid spiders and their kin (Arachnida, Araneae, Lycosoidea). *Smithsonian Contributions to Zoology* **539**, 1–39.
- Griswold, C. E. 2001. A monograph of the living world genera and afro-tropical species of cyatholipid spiders (Araneae, Orbicularia, Araneioidea, Cyatholipidae). *Memoirs of the Californian Academy of Sciences* **26**, 1–251.
- Griswold, C. E., Coddington, J. A., Hormiga, G. & Scharff, N. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbicularia: Deinopoidea, Araneioidea). *Zoological Journal of the Linnean Society* **123**, 1–99.
- Griswold, C. E., Coddington, J. A., Platnick, N. I. & Forster, R. R. 1999. Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). *Journal of Arachnology* **27**, 53–63.
- Handlirsch, A. 1906–1908. *Die fossilen Insekten und die Phylogenie der rezenten Formen: Ein Handbuch für Paläontologen und Zoologen*. Leipzig: Engelmann.
- Jarzewowski, E. A. & Ross, A. J. 1996. Insect origination and extinction in the Phanerozoic. In Hart, M. B. (ed.) *Biotic recovery from mass extinction events*, 65–78. Geological Society, London, Special Publication, **102**.
- Jeram, A. J., Selden, P. A. & Edwards, D. 1990. Land animals in the Silurian: arachnids and myriapods from Shropshire, England. *Science* **205**, 658–66.

- Jocqué, R. 2001. Chummididae, a new spider family (Arachnida: Araneae) from South Africa. *Journal of Zoology: London* **254**, 481–93.
- Labandeira, C. C. 2000. The paleobiology of pollination and its precursors. Phanerozoic terrestrial ecosystems. *Paleontological Society Papers* **6**, 233–69.
- Labandeira, C. C. & Sepkoski, J. J. Jr. 1993. Insect diversity in the fossil record. *Science* **261**, 310–5.
- Labandeira, C. C., Johnson, K. C. & Wilf, P. 2002. Impact of the terminal Cretaceous event on plant insect associations. *Proceedings of the National Academy of Sciences, USA* **99**, 2061–6.
- Marusik, Y. M. & Lehtinen, P. T. 2003. Synaphridae Wunderlich 1986 (Aranei, Araneioidea), a new family status, with a description of a new species from Turkmenistan. *Arthropoda Selecta* **11**, 159–65.
- Menge, A. 1869. Über einen Scorpion und zwei Spinnen im Bernstein. *Schriften der Naturforschenden Gesellschaft zu Danzig* **2**, 2–9.
- Pellmyr, O. & Lebens-Mack, J. 1999. Forty million years of mutualism: evidence for Eocene origin of the yucca-yucca moth association. *Proceedings of the National Academy of Sciences, USA* **96**, 9178–83.
- Penney, D. 2001. Advances in the taxonomy of spiders in Miocene amber from the Dominican Republic. *Palaentology* **44**, 987–1009.
- Penney, D. 2002. Spiders in Upper Cretaceous amber from New Jersey (Arthropoda: Araneae). *Palaentology* **45**, 709–24.
- Penney, D. 2003. *Afrarchaea grimaldii*, a new species of Archaeidae (Araneae) in Cretaceous Burmese amber. *Journal of Arachnology* **31**, 122–30.
- Penney, D. 2004. New spiders in Upper Cretaceous amber from New Jersey in the American Museum of Natural History (Arthropoda, Araneae). *Palaentology* **47**, 367–75.
- Penney, D., Wheeler, C. P. & Selden, P. A. 2003. Resistance of spiders of Cretaceous–Tertiary extinction events. *Evolution* **57**, 2599–607.
- Penney, D. & Selden, P. A. 2002. The oldest linyphiid spider, in Lower Cretaceous Lebanese amber (Araneae, Linyphiidae, Linyphiinae). *Journal of Arachnology* **30**, 487–93.
- Penney, D. & Pérez-Gelabert, D. E. 2002. Comparison of the Recent and Miocene Hispaniolan spider faunas. *Revista Ibérica de Aracnología* **6**, 203–23.
- Petrunkevitch, A. 1922. Tertiary spiders and opilionids of North America. *Transactions of the Connecticut Academy of Arts and Science* **25**, 211–79.
- Petrunkevitch, A. 1942. A study of amber spiders. *Transactions of the Connecticut Academy of Arts and Science* **34**, 119–464.
- Petrunkevitch, A. 1946. Fossil spiders in the collection of the American Museum of Natural History. *American Museum Novitates* **1328**, 1–36.
- Petrunkevitch, A. 1950. Baltic amber spiders in the Museum of Comparative Zoology. *Bulletin of the Museum of Comparative Zoology* **103**, 259–337.
- Petrunkevitch, A. 1958. Amber spiders in European collections. *Transactions of the Connecticut Academy of Arts and Science* **41**, 97–400.
- Platnick, N. I. 2002. *The world spider catalog, version 3.0*. American Museum of Natural History. [www.document.] URL <http://research.amnh.org/entomology/spiders/catalog81-87/index.html>
- Price, P. W. 1996. *Biological evolution*. Fort Worth, Texas: Saunders College Publication.
- Rayner, R. J. & Dippenaar-Schoeman, A. S. 1995. A fossil spider (superfamily Lycosoidea) from the Cretaceous of Botswana. *South African Journal of Science* **91**, 98–100.
- Ross, A. J. 1998. *Amber, the natural time capsule*. London: The Natural History Museum.
- Ross, A. J., Jarzembowski, E. A. & Brooks, S. J. 2000. The Cretaceous and Cenozoic record of insects (Hexapoda) with regard to global change. In Culver, S. J. & Rawson, P. F. (eds) *Biotic response to global change: the last 145 million years*, 288–302. Cambridge: Cambridge University Press.
- Scharff, N. & Coddington, J. A. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). *Zoological Journal of the Linnean Society* **120**, 355–434.
- Schütt, K. 2000. The limits of the Araneioidea (Arachnida: Araneae). *Australian Journal of Zoology* **48**, 135–53.
- Selden, P. A. 1989. Orb-web weaving spiders in the early Cretaceous. *Nature* **340**, 711–13.
- Selden, P. A. 1990. Lower Cretaceous spiders from the Sierra del Montsech, north-east Spain. *Palaentology* **33**, 257–85.
- Selden, P. A. 1993. Arthropoda (Aglaspida, Pycnogonida and Chelicerata). In Benton, M. J. (ed.) *The fossil record 2*, 297–320. London: Chapman and Hall.
- Selden, P. A. 1996a. The geological history of spiders (Araneae). *Boletín de la SEA* **16** (Palaeontologia), 105–12.
- Selden, P. A. 1996b. First fossil mesothelid spider, from the Carboniferous of France. *Revue Suisse de Zoologie* **2**, 585–96.
- Selden, P. A. 2002. First British Mesozoic spider, from Cretaceous amber of the Isle of Wight. *Palaentology* **45**, 973–83.
- Selden, P. A., Shear, W. A. & Bonamo, P. M. 1991. A spider and other arachnids from the Devonian of New York, and reinterpretations of Devonian Araneae. *Palaentology* **34**, 241–81.
- Selden, P. A., Anderson, H. M., Anderson, J. M. & Fraser, N. C. 1999. The oldest araneomorph spiders, from the Triassic of South Africa and Virginia. *Journal of Arachnology* **27**, 401–14.
- Selden, P. A., Casado, F. da C. & Mesquita, M. V. 2002. Funnel-web spiders (Araneae: Dipluridae) from the Lower Cretaceous of Brazil. *Boletim do 6 Simpósio sobre o Cretácico do Brasil/2 Simpósio sobre el Cretácico de América del Sur* **2002**, 89–91.
- Selden, P. A. & Gall, J.-C. 1992. A Triassic mygalomorph spider from the northern Vosges, France. *Palaentology* **35**, 211–35.
- Selden, P. A. & Penney, D. 2003. Lower Cretaceous spiders (Arthropoda: Arachnida: Araneae) from Spain. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **2003**, 175–92.
- Sepkoski, J. J., Jr 1979. A kinetic model of Phanerozoic taxonomic diversity II. Early Phanerozoic families and multiple equilibria. *Paleobiology* **5**, 222–51.
- Smith, A. B. 1994. *Systematics and the fossil record: documenting evolutionary patterns*. Oxford: Blackwell Science.
- Thompson, J. N. 1989. Concepts of coevolution. *Trends in Ecology and Evolution* **4**, 179–83.
- Wunderlich, J. 1984. Die bisher von Baltischem und Dominikanischem Bernstein bekannten Familien und Unterfamilien fossiler Spinnen, mit Anmerkungen zu zwei Schriften von W. Schawaller (Arachnida: Araneae). *Entomologische Zeitschrift* **94**, 87–92.
- Wunderlich, J. 1986. *Spinnenfauna gestern und heute. Fossile Spinnen in Bernstein und ihre heute lebenden Verwandten*. Wiesbaden: Erich Bauer Verlag bei Quelle und Meyer.
- Wunderlich, J. 1988. Die fossilen Spinnen im Dominikanischen Bernstein. *Beiträge zur Araneologie* **2**, 1–378.
- Wunderlich, J. 1991. Beschreibung der ersten fossilen Spinne der Familie Leptonetidae: *Eoleptoneta kutscheri* n. gen., n. sp. in Sächsischem Bernstein (Arachnida, Araneae). *Entomologische Zeitschrift* **101**, 21–5.
- Wunderlich, J. 1993a. Die ersten fossilen Becherspinnen (Fam. Cyatholipidae) in Baltischem und Bitterfelder Bernstein (Arachnida, Araneae). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* **75**, 231–41.
- Wunderlich, J. 1993b. Die ersten fossilen Speispinnen (Fam. Scytodidae) im Baltischen Bernstein (Arachnida, Araneae). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* **75**, 243–7.
- Wunderlich, J. 2000. Zwei neue Arten der Familie Falltürspinnen (Araneae: Ctenizidae) aus dem Baltischen Bernstein. *Entomologische Zeitschrift* **110**, 345–8.

DAVID PENNEY, Department of Earth Sciences, University of Manchester, M13 9PL, UK.
e-mail: david.penney@man.ac.uk

MS received 9 May 2003. Accepted for publication 3 October 2003.