

RESISTANCE OF SPIDERS TO CRETACEOUS–TERTIARY EXTINCTION EVENTS

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Abstract.—Throughout Earth history a small number of global catastrophic events leading to biotic crises have caused mass extinctions. Here, using a technique that combines taxonomic and numerical data, we consider the effects of the Cenomanian–Turonian and Cretaceous–Tertiary mass extinctions on the terrestrial spider fauna in the light of new fossil data. We provide the first evidence that spiders suffered no decline at the family level during these mass extinction events. On the contrary, we show that they increased in relative numbers through the Cretaceous and beyond the Cretaceous–Tertiary extinction event.

Key words.—Araneae, Cenomanian–Turonian, fossil, mass extinctions, Mesozoic.

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A number of mass extinction events have been recognized throughout the history of life on Earth. They vary from major catastrophes such as the end-Permian event that wiped out perhaps 82% of marine genera (Erwin 1998), to less significant perturbations to the background extinction rate. The cause of some can be attributed to asteroid impacts or massive volcanic eruptions producing so-called nuclear winters that led to global environmental stress and extinction (Sharpton and Ward 1990). Regardless of the causes, it is likely that mass extinctions have accounted for the demise of less than 5% of all extinct species (Erwin 2001). Nevertheless, they created evolutionary opportunities for the survivors that have had major effects on the history of life (Erwin 2001). The Cretaceous–Tertiary (K/T) extinction event of 65 million years ago (mya) is the best studied, and the catastrophic nature of this event is generally accepted.

Within the last two decades there has been a plethora of publications regarding the causes of the K/T event and there is still no universally accepted consensus. In one scenario, the discovery of large concentrations of iridium associated with the K/T transition, led Alvarez et al. (1980) to propose an instantaneous event resulting from a bolide impact (see also Alvarez and Asaro 1990). However, Officer and Drake (1985) argued that because iridium and other associated elements were not deposited instantaneously in all regions across the globe at K/T time this pattern was difficult to explain by a single impact event. They questioned whether the observed geochemical signatures were of terrestrial or extraterrestrial origin. They concluded that the concentrations of the associated arsenic and antimony and clay mineralogy suggested a mantle source rather than a meteoritic one, but that the iridium and high-pressure lamellar quartz could result from either a mantle or meteoritic source (Officer and Drake 1985). In addition, the considerable chemical heterogeneity, including the calcophile elements, of the boundary clay at different localities was considered inconsistent with the clay settling from a globally dispersed dust cloud. Officer and Drake (1985) favored the mantle origin and proposed that the major environmental event at the K/T was an intense period of volcanic events, which occurred simultaneously at several localities across the globe.

The original Alvarez hypothesis was criticized by paleontologists because the dust cloud scenario was unlikely to account for the marked selectivity (see later) of the end-Cretaceous extinctions, with many terrestrial and marine groups surviving with little or no change, and because many important extinctions took place before the iridium event (Hallam 1987). Some authors (e.g. Briggs 1991) argued that the K/T extinctions were neither sudden nor catastrophic and that the current rate of global anthropogenic habitat destruction is far faster and greater than events of 65 mya. Briggs (1991) suggested that the species changes observed at the K/T were caused by a regression of sea level through the divergence of continents and the development and enlargement of mid-oceanic ridges. The subsequent decrease in primary productivity on the continental shelf, the increased volcanism associated with tectonic activity, the increased elevation of the continents and climatic fluctuations were all considered as contributing factors to the extinctions (Briggs 1991). The discovery of the massive Chicxulub crater (approximately 200 km diameter) in the submarine Yucatan region in the early 1990s (e.g. Ward 1995; Pope et al. 1998) and the geology of the Upper Cretaceous clastic deposits lining the Gulf of Mexico, have strengthened the case for a large bolide impact to the point where only a few researchers now reject that this was an important event at the end of the Cretaceous.

The selectivity of the extinctions, that is, what lived and what died, must provide a useful clue to the underlying cause because this is partly related to chance, but must also be ascribed to effects and killing mechanism of the event itself (Ward 1995). In a review of the K/T biostratigraphical record for most major fossil clades, MacLeod et al. (1997) found that many passed through the crisis with only minor changes in taxonomic richness. They proposed that ostracodes, bryozoans, ammonite cephalopods, bivalves, and archosaurs were in decline throughout the Maastrichtian, whereas diatoms, radiolarians, benthic foraminiferans, brachiopods, gastropods, fish, amphibians, lepidosaurs, and terrestrial plants passed through the K/T event relatively unaffected. Calcareous nannoplankton, dinoflagellates, and planktonic foraminiferans (see also Keller et al. 2002) experienced a turnover

of varying magnitudes in the latest Maastrichtian–earliest Danian, but most of these began in the latest Maastrichtian (MacLeod et al. 1997). These authors concluded that global events at the K/T boundary occurred over a longer period of time than that suggested by its catastrophic nature, causing sustained biotic change that affected different taxa at different rates. This manifested itself as a progressive reduction in biotic diversity throughout the Maastrichtian. A shorter-term global biotic event close to the K/T boundary affected some groups that were relatively untouched by the long-term Maastrichtian decline (MacLeod et al. 1997).

Insect family diversity was not drastically affected by the end-Cretaceous extinction (Labandeira and Sepkoski 1993; Briggs 1995; Ross et al. 2000). Labandeira et al. (2002) investigated a megafloreal sequence across the K/T boundary in the Williston Basin of southwestern North Dakota, which is associated with dinosaur extinctions and the loss of approximately 80% of megafloreal species. They recorded the amount of insect damage to the fossil plants on either side of the K/T boundary. They found that specialized associations between many monophagous, and some oligophagous, insects and plants that were present in the latest Cretaceous disappeared at the boundary and failed to reappear afterwards (Labandeira et al. 2002). They proposed this as evidence for a major, rapid extinction event at the boundary; however, they also observed that all generalized polyphagous insect–plant interactions traversed the boundary and were thus unable to provide direct evidence for insect extinction at family level.

In contrast, the Cenomanian–Turonian (C/T) mass extinction episode (93.5 mya) has been classed as a modest event that extinguished only 8% of families, 26% of genera, and 33–53% of species in the marine realm (Harries and Little 1999). Gale et al. (2000) even doubted that this was a mass extinction at all, and suggested that the observed faunal change is primarily an artifact due to immigration and emigration resulting from major, but quite normal, oceanographic change.

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 predator groups on land today. Much of their success is due to the co-radiation of spiders with their principal prey, the insects. The Tertiary fossil record of spiders is rich and nearly all families and many genera recorded from these deposits are extant (see Figs. 1 and 2). This suggests that the family diversity of the Tertiary spider fauna may have been of an order of magnitude similar to what it is today. However, the Mesozoic fossil record of spiders is sparse; the discovery of one new fossil can have a significant effect on known ranges and range extensions in the phylogenetic tree (Figs. 1 and 2; Selden 1996a). Advances in paleoentomology have produced detailed biodiversity data for insects through geological time (e.g. Labandeira and Sepkoski 1993; Ross et al. 2000). Fluctuating fortunes of food plants and their insect herbivores have been documented (examples in Labandeira 1998; Labandeira et al. 2002), particularly in the Mesozoic era. However, a more complete picture of Mesozoic terrestrial paleoecology cannot yet be assembled until information on one of the main predators of insects, the spiders, is included.

In this study we examine independently the taxic diversity

of all fossil spiders, and actual numbers relative to other arthropods, of spiders preserved in amber through and beyond the Cretaceous. These are discussed with special reference to the effects of the major (C/T and K/T) postulated extinction events.

METHODS

Spiders are rarely preserved as non-amber fossils because of their soft-bodied, fragile nature. In non-amber fossil Lagerstätten where these fossils do exist, they are usually allochthonous, that is, they are preserved out of the context of the environment in which they originally lived. This has a great bearing on the interpretation of these assemblages of fossils as once living communities. This is not true for amber inclusions, many of which lived in close association with one another, which makes the interpretation of this fossil assemblage easier and more reliable from an arachnological viewpoint. These two different datasets can be complementary and combined, as we do in our taxic diversity analysis. However, they are not directly comparable quantitatively. Amber fossils provide a more accurate picture of fossil terrestrial spider diversity, so only these are considered in the relative abundance analysis.

Taxic Diversity

Paleontological and neontological data can be combined in the form of an evolutionary or phylogenetic tree. These trees are constructed by superimposing well-supported and accepted cladograms of hypothesized phylogenetic relationships, derived from work on extant taxa, over stratigraphic data from the fossil record (Smith 1994). Three assumptions are made when constructing these trees: (1) the cladogram is robust and 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 (the extra stratigraphic range added to the observed range of a taxon to make the evolutionary tree concordant with the phylogenetic hypotheses) of sister taxa and ghost lineages (a branch of an evolutionary tree with no fossil data, but which needs to be hypothesized after combining cladistic and biostratigraphic data) and proposed ancestral lineages (which result from the addition of fossil metataxa) show the evolutionary history of a group over geological time. This technique, fully explained by Smith (1994), provides minimum dates for the hypothesized phylogenetic (sister taxa) dichotomies and provides a graphical representation of the fate, in terms of extinction, origination, and divergence events, of taxa through geological time. We investigated the evolutionary history of spiders (Figs. 1 and 2) using the cladograms of Coddington and Levi (1991) with amendments; for example, Griswold (1993), Scharff and Coddington (1997), and Griswold et al. (1998, 1999). The basic phylogeny of Coddington and Levi (1991) is considered robust. This has been repeatedly demonstrated in the subsequent studies listed, which have increased the resolution of the cladogram by incorporating additional families within the clades, rather than making radical changes to the overall structure. Schütt

TABLE 1. Amber spider inclusion data used in the relative abundance analysis.

Data point	Locality (age)	Number of inclusions	Number of spiders (%)	Reference
1	Àlava, Spain (upper Aptian–middle Albian)	600	15 (2.5)	Alonso et al. 2000
2	Eastern Taimyr, Siberia (Albian–Cenomanian)	31	1 (3.2)	Eskov and Wunderlich 1994
3	Burma (Albian–Cenomanian)	1198	36 (3.0)	Rasnitsyn and Ross 2000
4	Azerbaijan, Caucasus (early Cenomanian)	103	3 (2.9)	Eskov and Wunderlich 1994
5	Northwestern France (early Cenomanian)	71	2 (2.8)	Eskov and Wunderlich 1994
6	Western Taimyr, Siberia (late Cenomanian)	669	7 (1.0)	Eskov and Wunderlich 1994
7	New Jersey (Turonian)	1637	42 (2.6)	D. Grimaldi, pers. comm. 2000
8	Yakutia, Siberia (Turonian)	48	0 (0.0)	Eskov and Wunderlich 1994
9	Eastern Taimyr, Siberia (Coniacian)	197	6 (3.0)	Eskov and Wunderlich 1994
10	Eastern Taimyr, Siberia (Santonian)	2635	101 (3.8)	Eskov and Wunderlich 1994
11	Eastern Taimyr, Siberia (late Santonian)	220	9 (4.0)	Eskov and Wunderlich 1994
12	Manitoba, Canada (Campanian)	461	22 (4.8)	McAlpine and Martin 1969
13	Eastern Taimyr, Siberia (Danian)	947	56 (5.9)	Eskov and Wunderlich 1994
14	Baltic (middle Eocene)	640	27 (4.2)	Eskov and Wunderlich 1994
15	Baltic (middle Eocene)	7635	503 (6.6)	Larsson 1978

(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 figure legends for references).

Relative Abundance

The possibility of a linear relationship through the Cretaceous between percentage of amber spider quota and age of amber was analyzed using regression analysis. Data obtained from a variety of sources (Table 1) were examined to obtain the following variables: total number of inclusions, percentage of spider inclusions, and geological age of the amber. Since each datapoint derived from collections with differing sample sizes, the analysis employed a weighted least-squares regression, with the number of inclusions being used to weight the samples. Examination of residuals identified no obvious trend that would invalidate the analysis. The Tertiary Baltic amber datasets were included to incorporate the K/T extinction event.

RESULTS

Taxic Diversity

Figures 1 and 2 depict the evolutionary history of spiders and graphically demonstrate that extant spider families survived the C/T and K/T mass extinctions. The earliest spider is Devonian and major radiations occur throughout the Mesozoic and Cenozoic. The majority of Cretaceous fossil spiders can be placed in extant families. It is primarily within the last decade (e.g. Eskov and Zonshtein 1990; Selden 1990, 1996a,b, 2002; Selden and Gall 1992; Selden et al. 2002; Penney 2002a, 2003, in press; Penney and Selden 2002; Selden and Penney 2003) that new descriptions of Cretaceous fossil spiders have provided substantial range extensions for extant spider families to the period in geological history before the K/T mass extinction event. These fossils also predict the presence of many other extant spider families at the same point in time (Figs. 1 and 2), suggesting a higher spider biodiversity during the Cretaceous than can be observed from

fossils alone. Of the 109 extant spider families, 33% (15 observed, 21 predicted) existed before the K/T extinction event (Figs. 1 and 2).

Relative Abundance

The weighted regression analysis (Fig. 3) shows a steady increase (of about 0.07 per million years) throughout the Cretaceous and over the K/T boundary, in the relative number of spiders captured in resin (ANOVA, $F_{1,13} = 81.131$, $P < 0.001$).

DISCUSSION

The Tertiary fossil record of spiders is rich because of their frequent occurrence in Dominican Republic (Wunderlich 1988; Penney 2001; Penney and Perez-Gelabert 2002) and Baltic (Petrunkevitch 1958) ambers. Nearly all families and many genera recorded from these deposits are extant (Figs. 1 and 2). The cladograms used, which are considered the most complete for the Araneae, only allow the phylogenetic placement of 92 of the currently recognized 109 families. Of these, 79% (61 known, 25 predicted) were present in the Miocene, suggesting a spider fauna, at family level, as diverse then as now. The Mesozoic fossil record of spiders is still so sparse that the discovery of one new fossil can have significant effects on many of the proposed minimum ages of the phylogenetic (sister taxa) dichotomies shown in Figs. 1 and 2 (e.g. Selden 1996a). For example, recent descriptions of new Dysderoidea (Oonopidae and Segestriidae), Dictynoidea (Dictynidae), Eresoidea (Oecobiidae), Araneoidea (Araneidae), and the higher araneoids (Linyphiidae [also described from Upper Neocomian–basal Lower Aptian Lebanese amber; Penney and Selden 2002]) in Cretaceous (Turonian) New Jersey amber (Penney 2002a, in press) extended the ranges of these superfamilies by approximately 50 mya (Fig. 2). Previously, only four superfamilies of araneomorph spiders (Palpimanoidea [Eskov 1987; Eskov and Wunderlich 1994], Lycosoidea [Rayner and Dippenaar-Schoeman 1995], Deinopoidea [Selden 1990], and Araneoidea [Eskov 1984; Selden 1990]) were known from fossils in strata older than Cenozoic (Fig. 2). Similarly, the description of the extant

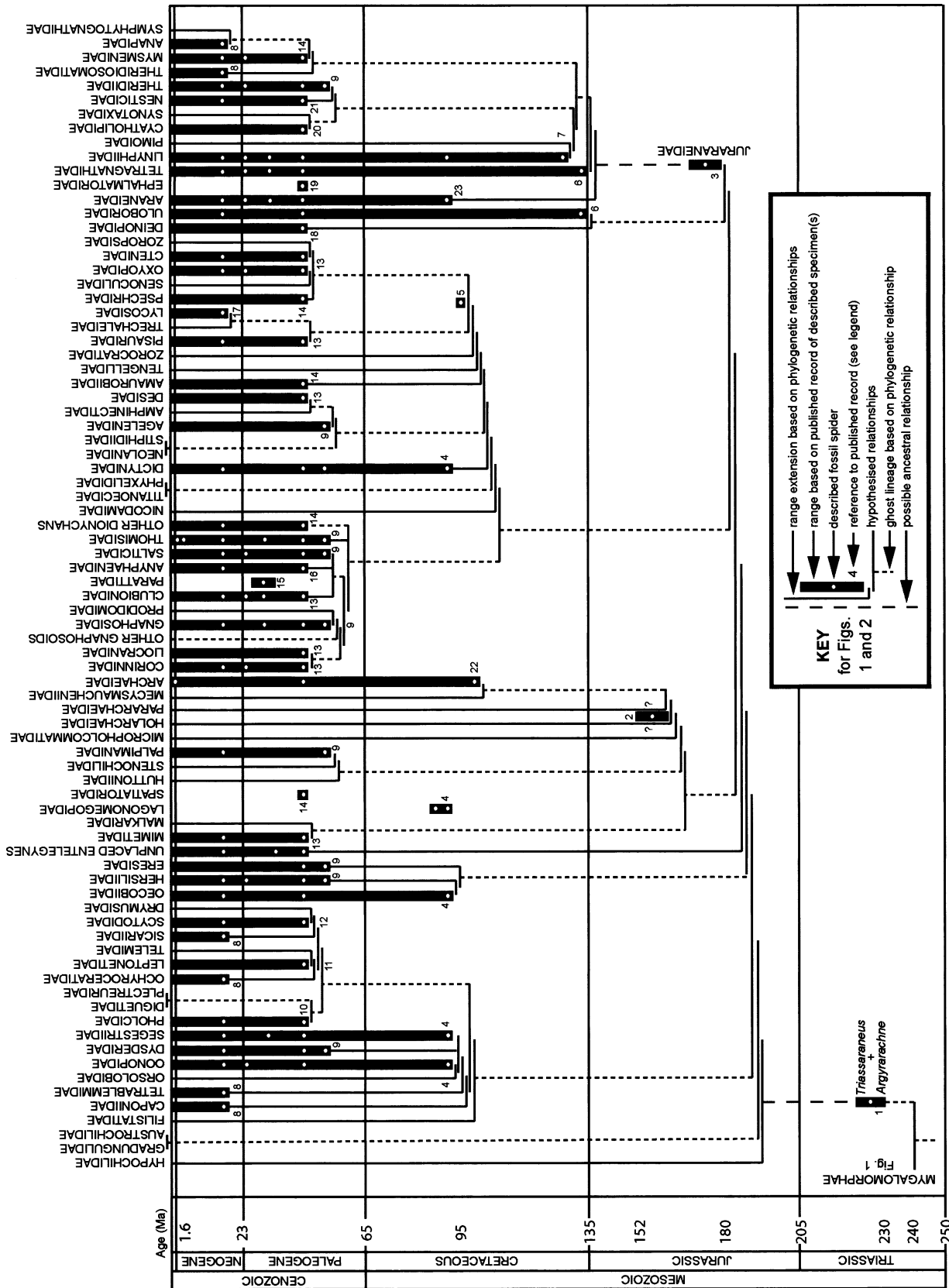


FIG. 2. Evolutionary tree of the spider suborder Araneomorphae. Other gnaphosoids include: Gallieniellidae, Ammoxenidae, Cithaerionidae, Trochanteriidae, and Lamponidae; other dionychans include: Zoridae, Selenopidae, Sparassidae, and Philodromidae (see Coddington and Levi 1991); unplaced entelegynes include: Cryptothelidae, Cybaeidae, Cycloctenidae, Hahniidae, Halidae, Homalonychidae, Miturgidae, and Zodariidae (see Griswold et al. 1999) and Chummiidae (Jocqué 2001). References: 1, Selden et al. 1999; 2, Eskov 1987; 3, Eskov 1984; 4, Penney 2002a; 5, Rayner and Dippenaar-Schoeman 1995; 6, Selden 1990, Selden and Penney 2003; 7, Penney and 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 and Marusik 1992; 22, Penney 2003; 23, Penney, in press.

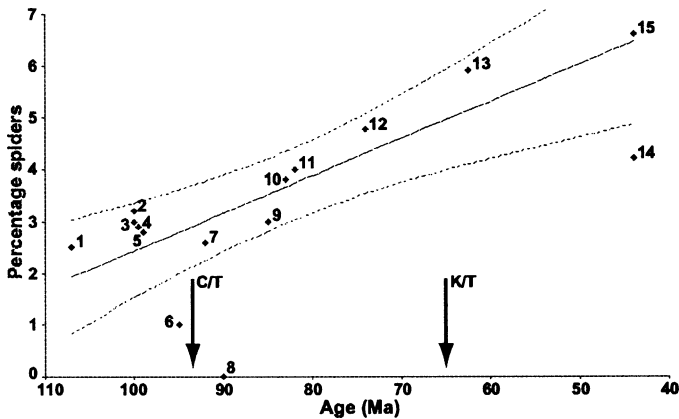


FIG. 3. Weighted least-squares regression, weighted by weights of percentage spider quota against age of amber: $y = 9.621 + 0.07183x$, adjusted $R^2 = 0.851$. Datapoints as in Table 1; dashed lines represent 95% confidence intervals.

As we demonstrate here, this is not the case for spiders. Therefore, although the overall increase in family diversity for both insects and spiders appears to follow a similar pattern, the similarities do not hold up under closer inspection.

We suggest that the observed extinction resistance of spiders is due to the majority of spiders being generalist predators. Those feeding predominantly on plant-specific herbivores that became extinct could easily have switched to a new primary food source, such as many of the nonherbivorous insects or polyphagous herbivores, which appear to have been little affected by the K/T extinction (Labandeira and Sepkoski 1993; Labandeira et al. 2002). Thus, the event probably had little effect on the Araneae (e.g. Selden 1996b) at least at family level. It is not currently possible to determine whether there were effects on subfamilial taxa, such as genera and species, because there is not enough data at the degree of taxonomic resolution currently available in the Mesozoic spider fossil record. Our hypothesis that spider families were little affected by the K/T extinction is supported by evidence from Cretaceous Burmese (Penney 2003), New Jersey (Penney 2002a, in press), Lebanese (Penney and Selden 2002), and Isle of Wight (Selden 2002) ambers and non-amber fossil spiders from other localities, because they extend the known geological range of extant spider families and their sister taxa to before the end-Cretaceous extinction event (Figs. 1 and 2). Indeed, a picture is emerging of great longevity of many spider families (Selden and Penney 2001; Penney 2002a; Penney and Selden 2002).

There appears to have been no notable decline in terrestrial faunas following the Cretaceous C/T extinction episode (Briggs 1995). However, a decline in the spider fauna over this boundary, based on the percentage spider quota of 11 fossil resins, was proposed by Eskov and Wunderlich (1994). Two of their datasets consisted of fewer than 50 samples: one spider in 31 inclusions (3.2%); zero spiders in 48 inclusions. The latter datapoint was estimated from a hand-drawn curve to predict a spider quotient of 1.5% (Eskov and Wunderlich 1994; in our examination it is included at its actual value, i.e. 0%). For small sample sizes, large increases in

percentage quota result from small increases in the number of inclusions identified as spiders.

The major outlier in our analysis (Fig. 3: datapoint 8) was used by Eskov and Wunderlich (1994) to support a decline for spiders early in the late Cretaceous. Our results show no such decline, but rather a steady increase (of about 0.07 per million years) throughout the Cretaceous in the relative number of spiders captured in resin (ANOVA, $F_{1,13} = 81.131$, $P < 0.001$; Fig. 3). The remaining points that fall outside the confidence intervals are mainly those below the line. With these sorts of data we might expect (especially for small samples like those between 100 and 90 mya) that new spider finds would have the effect of moving these points up. The inclusion of the Baltic amber data lowers the slope from the Cretaceous trend only very slightly (by 0.016) but still retains the significant trend of increase. The average of the two Baltic amber datapoints (i.e. 5.4%) would fall within the 95% confidence intervals of the Cretaceous trend predicted without the Baltic amber data.

The observed increase in the frequency of spiders preserved as amber inclusions may reflect a change in the predation strategy of spiders during the Cretaceous. This was an intense period of angiosperm and insect pollinator/herbivore co-radiation (Grimaldi 1999). Spiders may also have undergone a diversification during this time, from a predominantly ground-dwelling mode of life to fill the new arboreal niche and take advantage of the richly evolving insect communities. It has been established, at least for Dominican Republic amber, that the spider inclusions are closely related to Recent trunk-dwelling faunas and far removed from ground-dwelling faunas (Penney 2002b). The observed increase over time, coupled with the lack of major extinction, helps account for the high present-day diversity of Araneae, which 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.

In this paper, we have concentrated on the effect of the C/T and K/T mass extinctions on spiders. Our results show that these events had little effect on the geological ranges of spider families. Our quantitative results demonstrate that the relative numbers of spiders in amber increased over the time in question (Aptian-Albian to mid-Eocene). It would be interesting to investigate whether this trend of increase in the frequency of spiders preserved in amber continues throughout the Tertiary. There are a number of other Tertiary amber deposits that contain spider inclusions (for a list, see Penney 2002c) but few of these have sufficient data available for inclusion in such an analysis, and in some cases the dating constraint of these deposits is weak (e.g. Bitterfeld amber, dates range from 20–50 million years). One source of amber for which sufficient data are available for extending the range of our analysis is the relatively young, 15–20 million-year-old (Ituralde-Vinent and MacPhee 1996) Dominican Republic amber (e.g. Poinar and Poinar 1999: 2919 arthropod inclusions, 88 spiders; D. Grimaldi pers. comm.: 11,814 inclusions, 482 spiders; G. Bechly pers. comm.: 5687 inclusions, 523 spiders). Extending the analysis to include Dominican Republic amber data flattens the slope of the line so that no significant trend is observed (ANOVA, $F_{1,16} = 2.660$, $P > 0.05$). The

reason for this deviation from the observed Cretaceous trend is, we suggest, the extremely high number of ant inclusions in Dominican amber.

Ants form only a tiny proportion of inclusions in Cretaceous ambers (Grimaldi and Agosti 2000; Grimaldi et al. 2002) and the group remained rare, primitive, and of low diversity until the Eocene (Grimaldi and Agosti 2000). It was not until this time that modern genera that formed very large colonies first appeared in the fossil record (Grimaldi and Agosti 2000). Later, in Miocene times when the bulk of the Dominican Republic amber was being formed, ants became very diverse and abundant, especially in tropical ecosystems. It is well established that Dominican Republic amber was formed under tropical conditions similar to those in the region today (e.g. Poinar and Poinar 1999). All other ambers used in our analysis were formed in different climates as follows: Burma, humid, warm-temperate (Cruickshank and Ko 2003); New Jersey, Taimyr, and Canada, warm-temperate (Grimaldi et al. 2000); France, subtropical-tropical (Néraudeau et al. 2002); Spain, subtropical or warm-temperate (Alonso et al. 2000); Baltic, temperate-subtropical (Poinar 1992). There is general agreement that there was a very substantial rise in global biodiversity through the Cenozoic and especially the Neogene (i.e. the last 23 million years; Crame and Rosen 2002). This was a time of crucial plate tectonic movement that led to climate change and essentially gave the tropics their modern form (Crame and Rosen 2002). For the above reasons, ants are disproportionately abundant in Dominican Republic amber. For example, in a random sample of 2919 Dominican Republic amber animal inclusions listed by Poinar and Poinar (1999), ants represented 26.8% of the total, and in the collections of the American Museum of Natural History they represent 23.9% (D. Grimaldi pers. comm.), whereas total Hymenoptera (including ants) account for less than nine percent in Cretaceous Burmese amber (Grimaldi et al. 2002) and ants account for only 0.002%, 0.001%, and 0.05% of all insects in Cretaceous Canadian, Russian, and New Jersey ambers respectively (Grimaldi and Agosti 2000). This is not surprising, because in Recent ecosystems ants increase in biomass and diversity the closer one moves to the tropics. For example, Wilson (1987) found 43 species of ants in 26 genera (approximately equal to the entire ant fauna of the British Isles) from a single leguminous tree in a Peruvian rain forest. He estimated that ants may account for 10 percent of the biomass of all animals in the Amazonian rainforest. Such an overabundance of ants in the Miocene Dominican Republic amber disproportionately lowers the percentage spider quotient value of this fossil resin, such that this amber is not directly comparable with the others used in our analysis.

Ideally, we would like to run the analysis for all the ambers excluding ant inclusions for each fossil resin, but these data are not available. In many cases the only data available are from Eskov and Wunderlich (1994) and consist of percentage of spiders and percentage of "others." An alternative approach would be to consider the ant inclusions in the Cretaceous resins negligible when compared to the Dominican Republic amber and to run the analysis with the ants subtracted from the Dominican Republic amber. In this case, there is a significant regression for the rate of increase for

spiders over time (ANOVA, $F_{1,16} = 7.812$, $P < 0.05$) and the slope of the line is not significantly different from that using the Cretaceous and Baltic amber data ($t = 0.7507$, $df = 29$, $P > 0.1$). This suggests that the original model is robust bearing in mind the tropical nature of the amber and the extension in time past the extinction events. The lack of a significant model when ants are included is probably due to the expansion of ants during the Tertiary, especially in tropical environments. More data between the Baltic and Dominican Republic amber datapoints and data from nontropical ambers in the Miocene (not available) would be an interesting addition to these analyses.

Our approach combines independent quantitative and qualitative data that support one another. The quantitative analysis considers numerical data (relative numbers of specimens, because these are the only data available), and these conclusions are supported qualitatively by the taxonomic data. The model will be tested, refined, and extended over a longer time scale as the taxonomy of the amber inclusions becomes resolved, and with additional data from future discoveries of fossil spiders.

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