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Spinning with the dinosaurs: the fossil record of spiders

When most people hear the word 'fossil' they tend to conjure up images of giant dinosaurs such as *Tyrannosaurus rex* or shelled marine invertebrates. Prior to the Hollywood blockbuster movie *Jurassic Park*, which was based on recreating dinosaurs through extracting their DNA from fossil mosquitoes preserved in amber, few non-palaeontologists would entertain the notion that small, soft-bodied organisms such as insects occur in the fossil record. However, insects and spiders are common as fossils in amber, where they are often preserved with life-like fidelity, and they also occur to a lesser degree in carbonate rocks.

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Spiders are familiar to us all as a result of their high global species biodiversity and their ubiquitous and often synanthropic (i.e. living alongside humans) habitat preferences. Most people have stopped, at one time or another, to marvel at the magnificent feat of engineering that is a freshly woven spider's web. Others have arachnophobia to such a degree that they cannot even bear to hear the word 'spider'. However, love them or loathe them, most people are unaware that spiders were among the first animals to conquer the land. They existed long before dinosaurs had evolved and they survived the mass extinction 65 Ma ago that eliminated the dinosaurs and many other groups. Palaeontological data exist to confirm the above, and many other interesting observations about the successful evolutionary history of spiders. Here we present an introduction to the fossil record of spiders and what it can tell us about this extremely diverse group of organisms.

What are spiders and how do they fit into the grand scheme of things?

Spiders (order Araneae) are arachnids not insects. They differ in having eight legs rather than six, no wings or antennae, only two parts to the body, and they possess silk spinning organs called spinnerets. Spiders have been familiar organisms to human cultures globally, at least since Man first recorded his observations of the natural world, as evidenced by drawings of spiders on the walls of caves. Spiders crop up in the mythology of many human societies, commonly as symbols of danger or of clever handiwork. With the exception of Antarctica, they abound in every terrestrial ecosystem (and in some aquatic ones). After the five largest insect orders (Coleoptera, Hemiptera, Diptera, Hymenoptera, Lepidoptera) and mites, spiders are the most abundant and diverse animals in terms of described species, in modern terrestrial ecosystems, with 39 882 extant species in 3676 genera and 108 families. In contrast to the aforementioned groups, each of which employs numerous feeding strategies, all spiders prey on other animals, i.e., they are all obligate predators. Thus, their ecological and evolutionary success is quite unique. This may be due to a combination of their antiquity (the oldest spider fossil known is Devonian, 390 Ma ago, so they were among the first recorded wave of terrestrialization by animals in the mid-Palaeozoic era), and their ability to produce and utilize silk in many more ways than any other animal. They are the primary predators of insects and possess a venom system to assist in prey capture. Many different modes of life have developed within the Araneae, to enable them to pursue their insect prey into all ecological niches. These include crypsis, mimics, orb-, sheet- and other web weavers, sit-and-wait predators, cursorial hunters, jumping spiders, burrowers, and even aquatic spiders. Dispersal by silken threads means that spiders may be found among the aerial plankton.

Spider fossils in amber and carbonate rocks

Most fossil spiders belong in extant families, although a number of strictly fossil families are recognized. However, many of these are based on poorly preserved or juvenile specimens (spider taxonomy is usually based in large part on adult genitalia) and so warrant reassessment. By far the commonest source of fossilized spiders is as inclusions in amber (Fig. 1). Amber has properties similar to amorphous polymeric glass and is the fossilized form of tree resin. It preserves fossil inclusions through a process similar to mummification by a combination of rapid and thorough fixation, dehydration and the antibiotic properties of the resin. The oldest amber that contains fossil arthropods (including spiders) is from the Lower Cretaceous (130 Ma old) of Lebanon (and Jordan), and various deposits (including sub-fossil resin, commonly termed copal) from around the world fill in the gaps from then until the present. Spiders are abundant in Tertiary ambers from the Baltic region, the Dominican Republic, Mexico and Paris, and in Cretaceous ambers from New Jersey, Myanmar, Siberia, Canada, Lebanon and Europe.

Syninclusions (two or more fossils in the same piece of amber) often preserve interactions between organisms in the form of behaviours frozen in time. In spiders, the following behaviours have been preserved in the fossil record: mating, predation, myrmecomorphy (mimicking ants), parasitism, phoresy (one organism being transported by another), silk production, and a possible case of maternal care. Egg sacs are sometimes encountered and even delicate spider webs are occasionally preserved, sometimes with prey attached. Amber may also preserve the death throes of the entombed arthropods as they struggled to escape the sticky exudates, for example, in the form of disarticulation of body parts. Recently, fossilized spider blood was reported exuding from joints where the resin had caused the legs to autospasize (detach as a result of an external force) from the body (Fig. 2).

Such observations as those listed above are rarely, if ever, encountered in the non-amber fossil record because of the different taphonomic processes that control the preservation of organisms in carbonate rocks and amber. That is not to say that non-amber fossils are any less important, particularly when one considers that from the Jurassic and earlier these form our only sources of fossil spiders. There are nearly as many different preservational styles as there are spider-yielding Lagerstätten. A number of Mesozoic occurrences are in Plattenkalk (lithographic limestone); thinly bedded, fine-grained limestones usually deposited in still water by settling of calcium carbonate grains. The best-known example in the fossil record is Solnhofen, Bavaria, but this deposit is marine in origin and includes no spiders. The early Cretaceous Plattenkalk from Crato, Brazil preserves spiders (and other organisms) by replacement with goethite (iron hydroxide) within the limestone. This is unusual, however, and in most lagoonal and lacustrine limestones the organisms are preserved as organic fragments. Examples of Lagerstätten with spiders preserved as organic matter in fluvial, lagoonal or lacustrine settings include Quaternary

Fig. 1. Pholcidae in lowermost Eocene amber from the Paris Basin, France (body length 1.5 mm).

Fig. 2. Filistatidae in Miocene amber from the Dominican Republic (arrows point to fossilized blood droplets; body length 2 mm).
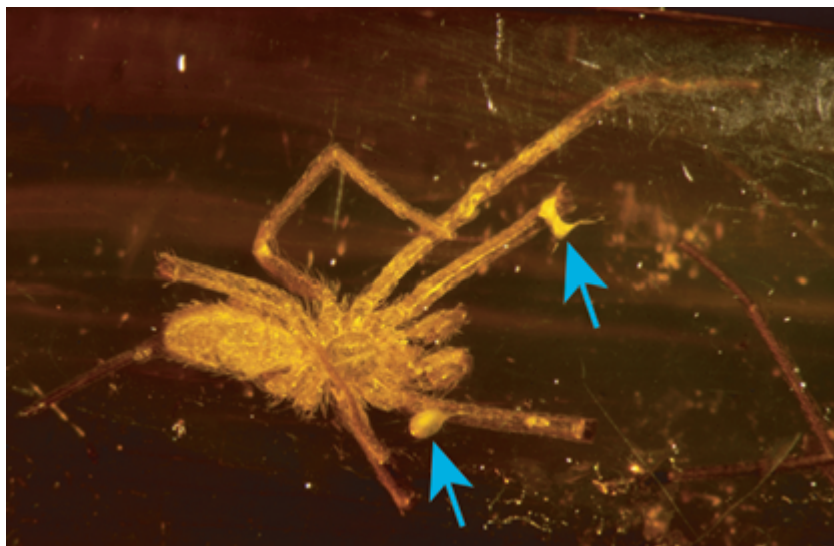
diatomite of Italy, the Miocene of Germany, Miocene of Switzerland, Miocene of Shanwang, China, Oligocene of Florissant, Colorado, USA, the early Cretaceous of Montsech and Las Hoyas, Spain, early Cretaceous of Siberia and Mongolia, early Cretaceous of South Gippsland, Victoria, Australia, early Cretaceous of Mexico, Jurassic and Cretaceous of north-east China, the Jurassic of Transbaikalia and Kazakhstan, the Triassic Grès à Voltzia, France, the Permian of the Ural Mountains, Russia, the late Carboniferous Molteno Formation of South Africa, and the late Devonian of Gilboa, New York, which yielded the oldest fossil spider, *Attercopus fimbriunguis*.

More unusual types of preservation include the following. The Bembridge Marls Insect Bed, Eocene of the Isle of Wight, England, in which the fossils occur as external moulds with calcite replacement of internal structures such as muscles and respiratory organs; a similar preservation is found in the Eocene of Aix en Provence. Fossil spiders from Carboniferous Coal Measures of Europe and North America are generally preserved as external moulds, sometimes infilled with kaolinite, in clay ironstone concretions, for example at Mazon Creek, Illinois. A most peculiar preservation—replacement by silica within calcareous nodules—occurs in the Miocene lacustrine Barstow Formation of California, USA. Some Czech Coal Measures spiders, e.g. *Pyritaranea tubifera*, are poorly preserved as pyrite replacement in organic black shale, and in the Triassic Solite deposits of Virginia, USA, the spiders are preserved as silver flakes in a black matrix. Often the preservation of these fossils is considerably poorer than those in amber, making their interpretation considerably more difficult, but sometimes, the fine detail of external and internal structures can be preserved. For example, preserved respiratory structures, including tracheal tubules, book lungs and a spiracle have been identified in Eocene spiders from the Isle of Wight. More recently, the description of funnel-web spiders (Dipluridae) (Fig. 3) from the Cretaceous Crato Formation of Brazil highlights the remarkable degree of preservation of fossils from this locality. Occasionally, problems of interpretation mean that fossils are mistakenly described as spiders, when in fact they actually belong to other orders. *Megarachne* was described from the Permo-Carboniferous of Argentina, and with a body length of 339 mm would have been the largest known spider ever to have lived on Earth. However, recently its true identity was revealed as being a eurypterid, an extinct order of giant sea scorpions.

The fossil record in general is notoriously incomplete. Amber and non-amber deposits preserve different samples of limited aspects of the spider communities and their ecologies. In general, larger

Fig. 3. Dipluridae from the Cretaceous Crato Formation, Brazil (body length 11 mm excluding spinnerets).

spiders are found preserved in sediments. The different forms of preservation provide complementary datasets which can be combined to give a better view of the fossil record than could be gleaned from either type of fossilization process alone. This is fine in qualitative assessments of palaeodiversity, but care should be taken in combining such data in quantitative palaeobiological investigations because of their incompatability in terms of 'sampling' methodology.

Spiders do not fossilize as readily as vertebrates because of their soft-bodied nature and lack of mineralized tissues. Therefore, the presence of spiders in a fossil locality signifies an example of a Konservat-Lagerstätte: an occurrence of exceptional preservation. These often permit detailed morphological comparisons with living relatives and this is particularly true of amber inclusions, which are particularly important from a phylogenetic perspective and can be used to investigate micro- as well as macroevolutionary processes. Despite the remarkable preservation of fossils in amber, many neontologists still tend to omit (or even worse, ignore) them in their analyses of extant faunas, claiming that they are taxonomically subequal to living forms. However, the novel application of existing technologies, such as Very High Resolution X-ray Computed Tomography (VHR-CT), to palaeontological specimens is providing remarkable results and demonstrates a high degree of phylogenetic inference from even very tiny amber fossils (Fig. 4).
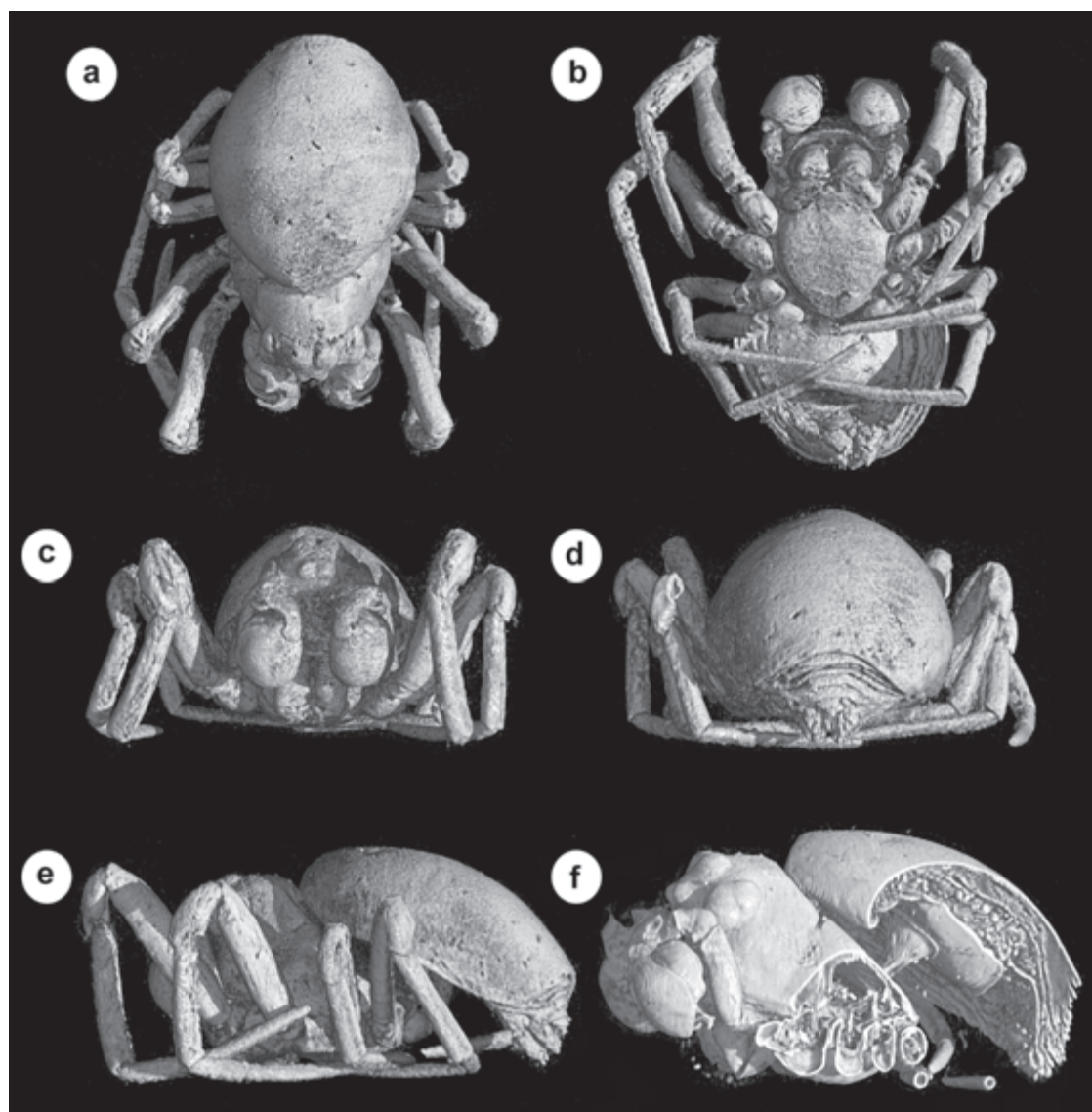
Fig. 4. X-Ray Computed Tomography scan of a male Micropholcommatidae in lowermost Eocene amber from the Paris Basin, France (body length 1 mm); **a.** dorsal; **b.** ventral; **c.** anterior; **d.** posterior; **e.** lateral; **f.** lateral (sectioned).

Age, radiations and extinction events

The evolutionary tree of spiders (Fig. 5) clearly illustrates the geological longevity and the early major radiations of this group and demonstrates that most extant families have been documented in the fossil record. Spiders existed long before the dinosaurs evolved and many of the spider families familiar to us today existed alongside them. Qualitative observations of all fossil spiders in conjunction with a quantitative analysis of spiders preserved only in amber have demonstrated that spider families passed through the extinction event that eliminated the dinosaurs relatively unaffected. The combination of their high global diversity, generalist predatory nature and their ability to enter a state of metabolic torpor in times of low food availability probably facilitated their survival.

The Early Cretaceous saw the origin of flowering plants (angiosperms) and an explosive radiation of modern insect groups concurrently. The major radiations of obligate anthophilous (flower loving) insects probably occurred during the late Early to Late Cretaceous, because this period is consistent with the appearance of entomolophilous (insect attracting) syndromes in Cretaceous flowers. Although not all spiders weave webs, silk use for prey capture is unique to spiders and there is a great deal of variation in how they employ this strategy, which in turn helps explain their high diversity and ubiquitous nature today. The orb-web typifies spiders to scientists and laypersons alike and this architecturally complicated and highly efficient prey capture strategy was already being employed by spiders in the Early Cretaceous. Spiders probably evolved the ability to weave orb-webs in the Jurassic or earlier, thus allowing them to
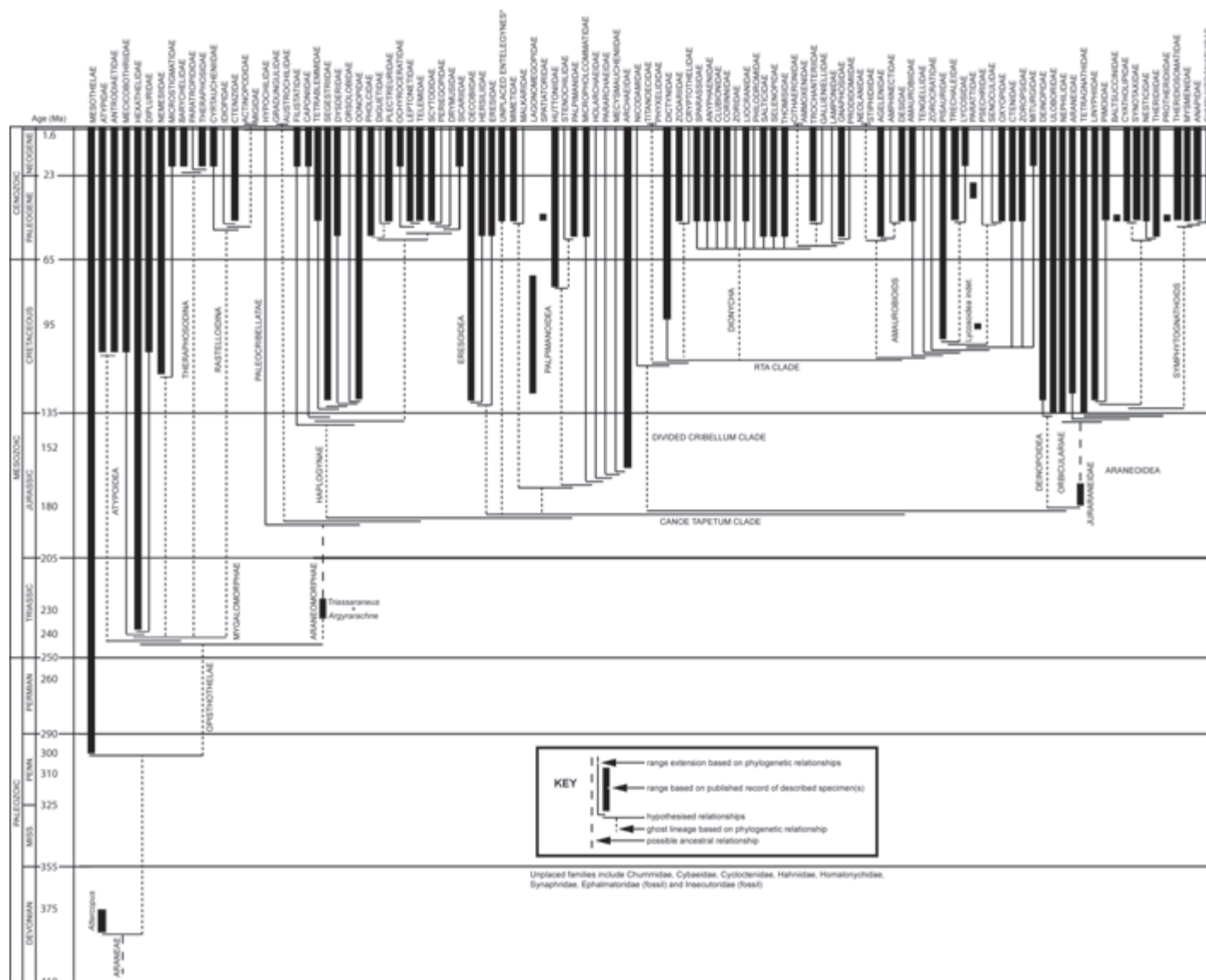
co-radiate alongside their insect prey without the need for a catch-up lag phase.

Comparing amber spider faunas

Despite almost 200 identified inclusion-bearing amber deposits, few have had inclusions described in sufficient numbers to provide datasets suitable for quantitative analysis. The further one goes back in geological time, the greater is the proportion of extinct groups, which can make such comparisons problematic if this is not factored into the analysis. The only two amber sources that are consistently producing identifiable inclusions in large numbers and which have many species already described, are those from the Tertiary deposits of the Baltic region and the Dominican Republic. Baltic amber is more

than twice as old (44–49 Ma) as Dominican amber (16 Ma) and accordingly contains considerably more extinct supraspecific taxa. For example, five strictly fossil spider families are known from Baltic amber, whereas none are present in Dominican amber. Both these amber deposits have been the focus of extensive palaeontological research and have thousands of described species representing most arthropod groups, and spiders alone account for approximately 500 species in Baltic amber and 150+ species in Dominican amber.

In order to justify ecological faunistic comparisons based on the inclusions preserved in these two different ambers, which differ botanically, geographically and by age, it is necessary to determine whether or not the resins sampled in a uniform manner, i.e., did they act as traps in the same

way? Using a pluralistic approach, analysing size distributions of 671 fossilized spider species from different behavioural guilds, a recent paper in *Biology Letters* demonstrated that ecological information about the communities of these two well-studied ambers is retained in the fossil record. Several lines of evidence showed that the greater structural complexity of Baltic compared to Dominican amber-producing trees explained the presence of larger web weavers in the Baltic amber fauna, whereas no size differences occurred in active hunters that did not weave webs. Web building is an energetically costly exercise, thus web site selection is a particularly important issue for spiders. Web weavers that live in higher strata, such as trees seek optimal sites for web attachment and in this niche the architectural features of the vegetation are important factors. Effects arise not only from variations in the availability of supports for web anchorage and space for the web capture area, but also from the provision of retreats, microclimate and prey availability. Experimental investigations of living spiders have demonstrated that the body size of arboreal web-weaving spiders is larger in more structurally complex habitats, as seen in the Baltic amber forest. Were the size differences related to the trapping mechanism of the resin then similar differences would be expected for the non-web-weaving spiders but there were no statistical differences. Consequently, it was demonstrated for the first time that resins were trapping spiders uniformly and that comparisons of amber palaeoecosystem structure across deep time are indeed possible in some instances.

What can fossil spiders tell us about global climate change?

Today, spider assemblages (and specific 'indicator taxa') are particularly good indicators of different climatic regimes. The study of fossils can provide important information on past changes in biogeographical distributions, which in turn can be correlated with changes in palaeoclimatological factors resulting from geomorphic and tectonic processes, which are still ongoing. In addition, anthropogenic factors such as the burning of fossil fuels and deforestation contribute additional factors with important consequences for climate change.

Again, a comparison of Baltic and Dominican ambers serves to highlight the above. The Baltic amber forest existed in a climate of early Tertiary equability, i.e., low temperature seasonality, very different to the temperate, climatic regime of high seasonality in the region at present. As a result, the fossil and extant spider assemblages from this region are very different. This is not true for the fossil and extant Hispaniolan faunas. Dominican amber was formed in a tropical climate similar to that in the region today. Therefore, the fossil and recent faunas are directly comparable ecologically and indeed, there is a high degree of similarity between the two spider faunas and also, in general, for other groups. As a result of repeated transgressions, subsidence, the end-Cretaceous Chicxulub bolide impact (that eliminated the dinosaurs) and associated mega-tsunamis, all Hispaniolan on-island lineages (including the amber inclusions) are relatively young. Comparative analyses of the amber and living faunas can provide valuable insights into the historical biogeography of the Caribbean region, which is considered a complex and currently unresolved problem with regard to competing hypotheses of dispersal, vicariance and sub-aerial landspans connecting the emergent Greater Antilles with northern South America.

Clearly, there is great potential here. Analyses of the palaeontological evidence from the fossil record, considered in relation to past climatic changes over deep time, should help us predict the potential consequences of the current episode.

Concluding remarks

Numerous descriptions of Tertiary fossil spiders from both amber and sedimentary deposits date back to the nineteenth century. However, it is only within the last two decades that the dearth of our knowledge with regard to Mesozoic fossil spiders has been addressed. The antiquity of many extant spider families and their high diversity in both fossil and Recent ecosystems provide large comparative datasets for addressing important, large scale macroevolutionary questions, such as global change over deep time, predator–prey co-evolutionary relationships and the effects of mass extinctions on terrestrial invertebrate faunas, to name but a few. It is evident from numerous amber inclusion assemblages that they represent the remains of extinct tropical rain forests. The climate and soil type of similar present day ecosystems provide poor opportunities for fossilization, yet they contain more than half of the terrestrial species in the world. When one considers the current rate of demise of these forests through anthropogenic factors, the value of these amber inclusions for predicting the consequences of these changes is immediately apparent. An invited, extensive review of the entire spider fossil record will be submitted shortly to the journal *Biological Reviews*.

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Suggestions for further reading

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