The Role of Behavior in the Evolution of Spiders, Silks, and Webs

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Abstract

Spiders' silks and webs have made it possible for this diverse taxon to occupy a unique niche as the main predator for another, even more diverse taxon, the insects. Indeed, it might well be that the spiders, which are older, were a major force driving the insects into their diversity in a coevolutionary arms race. The spiders' weapons were their silks and here we explore the evidence for the evolution of silk production and web building as traits in spider phylogeny.

INTRODUCTION

Spiders cover a large variety of morphological forms (Bristowe 1958, Comstock 1948, Foelix 1996) ranging from the huge, hairy mygalomorphs to pin-size, bald oonopids, from eight-eyed to two-eyed, from using lung to using trachea (or both or neither) to breathe, from having very long to very short legs. A spider's morphology (Bristowe 1958), anatomy (Snodgrass 1952), and nervous system (Barth 1985, 2002) typically reflect its general ecology (Main 1976, Nentwig 1986, Wise 1993) and behavior (Robinson 1975, Vollrath 1992). Most importantly, all spiders make and use silk throughout their lives, however diverse their morphology, ecology, and behavior. Thus, spider silk is not only an interesting material in its own right (Craig 1997, 2003; Vollrath & Knight 2001, Vollrath & Porter 2006), but it is an integral part of the behavior of all spiders, whether an individual uses it simply as a trailing safety line or integrates it into the often complex structures of the famous, and characteristic, spider's web (Shear 1986, Tilquin 1942, Witt et al. 1968).

Spiders tend to employ their different silks rather specifically. Hence, both silk type and silk deployment tend to be good indicators for a spider's specific lifestyle. Applied to spiders' webs, the character traits of web engineering and silk use are typically correlated with specific morphological and anatomical traits of the animal's body plan (Coddington 1986, Eberhard 1990, Shear 1986, Vollrath & Knight 2005, Witt et al. 1968). In addition, web geometry is a representation also of the spider's movements and thread manipulations (Vollrath 2000), which together comprise the spider's web-building behavior. Thus, the structure of the web represents an intimate interaction between morphology and behavior. Indeed, the web provides a rare example where a behavior pattern can be used analytically to provide quantitative character traits for large-scale cladistic analysis (Coddington & Levi 1991, Eberhard 1990, Griswold et al. 1998). It follows that a spider's web provides insights into not only spider taxonomy but also spider phylogeny by the analysis of present-day character traits, such as details of extant web architecture (Coddington & Levi 1991, Eberhard 1990, Griswold et al. 1998, Opell 2002), extant silk properties (Garb et al. 2006, Gatesy et al. 2001, Opell 2002, Opell & Bond 2001, Vollrath & Edmonds 1989; Vollrath & Knight 2003), and extant silk production systems (Coddington 1989; Glatz 1972, 1973; Shultz 1987; Vollrath & Knight 2001, 2005).

Of the tremendous diversity of spider web types (**Figure 1**), the orbicular webs of the araneid orb weavers are the most accessible analytically (Vollrath 1992; Zschokke & Vollrath 1995a,b) and to date these kinds of webs have provided the most important data sets for structure-function analysis. After all, two-dimensional geometries hanging freely in the air are more easily observed, drawn, photographed and filmed than three-dimensional structures that are often fully integrated into the vegetation. Still, both two-dimensional and three-dimensional web architectures are the outcome of dedicated building behavior patterns (Benjamin & Zschokke 2003; Eberhard 1986; Krink & Vollrath 1997, 1998; Opell 1996; Robinson & Lubin 1979; Zschokke & Vollrath 1995a,b), providing a wide range of traits for classification (Coddington & Levi 1991; Eberhard 1982, 1987, 1990; Gotts & Vollrath 1992; Griswold et al. 1998; Opell 2002).

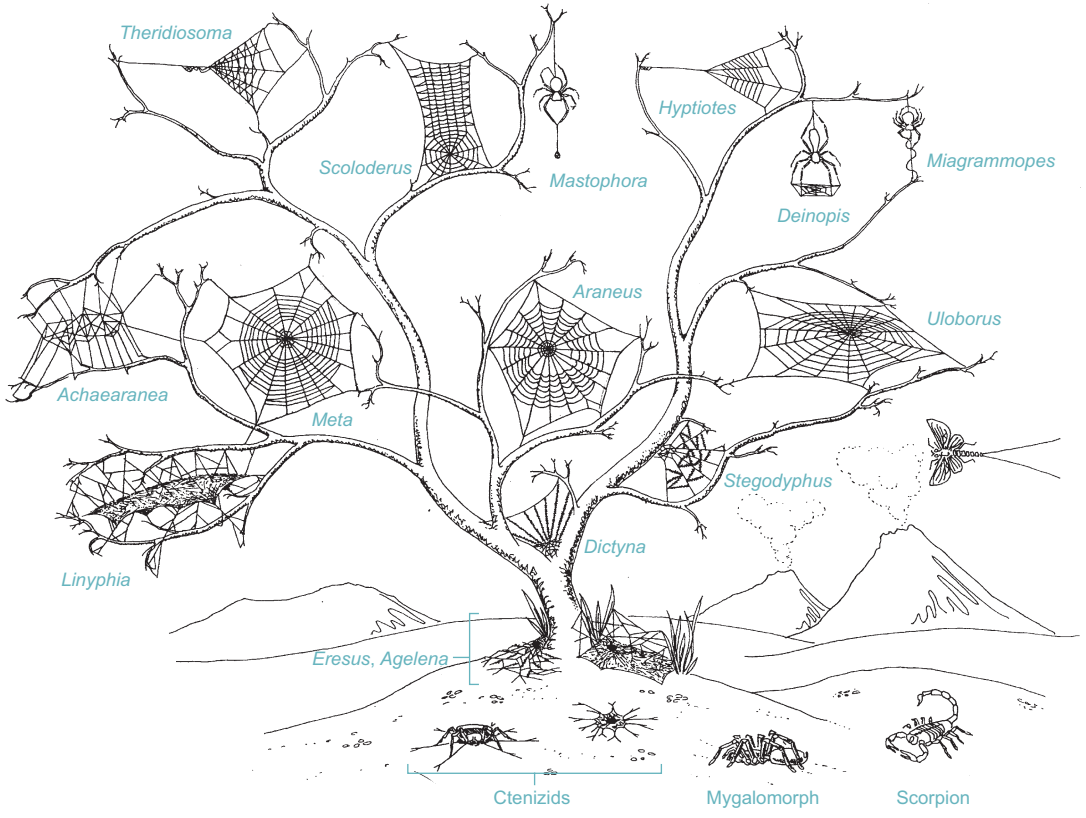

Figure 1

Schema of spider web evolution. A selection of orb web on a tree to demonstrate the various web types—this is certainly not a phylogenetic tree. Distant ancestors such as scorpions and more close ones such as mygalomorphs and ctenizids roam the ground, already using silk to line burrows and construct trip-lines. Further ancestral relatives (e.g., *Eresus* and *Agelena*) build their webs on the base of vegetation; a *Dictyna* web spans the fork of the tree. The right-hand branch contains (in order from its base) the webs of *Stegodyphus*, *Uloborus*, *Hypotiotes*, *Deinopis*, and *Miagrammopes*. The center branch holds a two-dimensional araneid orb web by *Araneus*. The left-hand branch holds a two-dimensional tetragnathid orb web by *Meta*. This branch also supports (*upper left to right*) derived orb webs by *Theridiosoma* and *Scoloderus*, and the minimalist *Mastophora* glue-drop web as well as (*below on the extreme left*) the highly derived three-dimensional webs by *Achaearanea* and *Linyphia* (adapted from Vollrath 1988).

Web and behavior are so closely linked that it is possible to deconstruct the web structure not only to provide a continuous record of the visible steps taken by the spider but also to infer from this visible record the underlying and hidden rules that are guiding these steps (Eberhard 1969; Gotts & Vollrath 1992; Krink & Vollrath 1997, 1998, 1999). A prerequisite for a successful behavioral dissection is a very good understanding of both, web engineering and spider activity (Eberhard 1981, 1986, 1988a,b; Heiling & Herberstein 1998; Herberstein & Heiling 1999; Vollrath 1987,

1988, 1992a; Vollrath et al. 1997). Fortunately, the modern techniques of filming and movement analysis are making this increasingly easy (Benjamin & Zschokke 2002, 2003; Zschokke & Vollrath 1995a) and accessible to modern simulation and modeling tools (Gotts & Vollrath 1992; Krink & Vollrath 1997, 1998, 1999, 2000). Integrating the analysis of thread manipulation and limb movements with the track of the spider's body, and using these data in combination with simulation and modeling of movement/track patterns, is thus beginning to elucidate the decision rules (algorithms) that govern the spider's web-building behavior. These kinds of analytical studies are taking Hans Peter's (1937), Bill Eberhard's (1969), Peter Witt's (1971) and Mike Robinson's (1975) seminal studies into the next phase of integrated modeling analysis (Gotts & Vollrath 1992; Krink & Vollrath 1997, 1999).

In summary, it appears that a detailed analysis of spider web structure gives access to a wide range of behavior patterns. One key to their analysis lies in the taxonomic position of the animals as well as specific morphological and anatomical characteristics.

Here we examine the question of whether (and how well) we can use a spider's morphology and anatomy (by studying overall body shape as well as specific organs) to deduce the animal's behavior (and specifically its use of silk) in the phylogenetic context. By this we hope to gain novel insights into the ecology and evolution of more ancestral spiders. Clearly, we are unlikely to find good evidence for many of the traits of interest in the fossils themselves. Hence we will have to infer ancestral traits from extant spiders and present-day web architecture and modern web-building characteristics.

LINKING MORPHOLOGY AND BEHAVIOR

Fossil spiders carry a surprising amount of detailed morphological and anatomical information. Such well-preserved structural data often allow us to infer specific behavior patterns. After all, the extant spiders provide many excellent examples of clear links between body structure and behavior. Thus, always considering likely differences in the ecological environment at the time of study, we can use preserved morphology to infer invisible behavior. In effect, we can use our understanding of the anatomical phenotype in combination with taxonomic status to deduce the architectural phenotype of a web—if a web was part of the extinct spider's hunting behavior. This should be possible because in spiders the trait "web-building behavior," i.e., its various constituent "fixed action" components, is a genetic trait not all that different from anatomical and morphological traits.

The evidence is strong that the web-building decision rules are inherited (Reed et al. 1970), although there is, of course, a large component of temporally adapted structural details that emerge from the composite action of these rules (Eberhard 1981, Krink & Vollrath 1998). Furthermore, there is also strong evidence that, in order to perform appropriately, the spider's actions and activites require very specific morphological adaptations in the body shape and leg dimensions (Bond & Opell 1998, Opell 1984, Vollrath 1987) and the spinning glands and spigots (Kovoor 1977, 1987; Opell 1989; Tillinghast & Townley 1987, 1994; Townley et al. 1993), as well as the sensory organs (Barth 1985, 2002; Vollrath 1995), and finally the claws, from which its

walking type (whether on ground or in web, Comstock 1948) can be inferred. Many of these traits tend to be visible also in palaeontological specimen (Selden 1990). In this review, we will examine the evidence of web evolution by combining morphological and ecological insights from extant species with palaeontological data on extinct spiders and their main prey, insects.

Why would it be interesting to infer extinct webs from the morphology of extinct spiders? And why might such an exercise be important beyond its relevance for spider evolution? All evidence suggests that spiders got where they are today because of their silk and the way they use silk to make webs (**Figure 2**). Because those webs are the

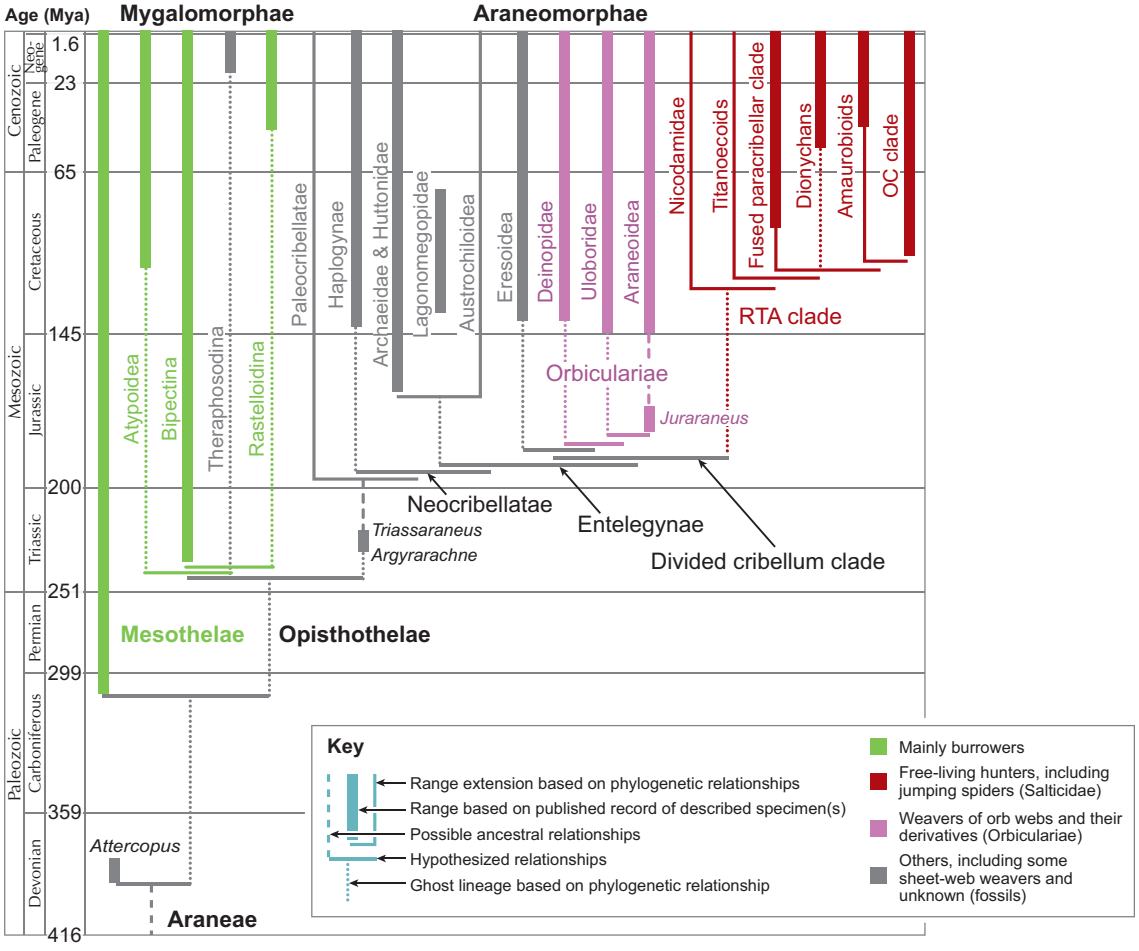

Figure 2

Phylogenetic tree of spiders. Data from the cladogram of Griswold et al. (2005) and published records of fossil spiders are combined to provide a view of spider evolution over geological time. Colors indicate major predation modes.

essence of spider behavior, we have in this entire group an excellent example where we can study the coevolution of behavior and morphology with implications far beyond the coevolution of spiders and insects.

After all, behavior is notoriously bad at being fossilized—except in the case of trace fossils (see below and Seilacher 1967). Having good evidence to infer behavior from morphology gives us a chance to study the evolution of a behavior pattern in the context of the overall climatic conditions at the time, which in turn could allow us to make inferences about the wider ecosystem that those animals inhabited (Robinson 1975). Being able to access the evolution of a complex behavior pattern by interpreting body morphology is of wider interest because typically it is behavior and not morphology that drives evolution, although it tends to be assumed otherwise both implicitly and explicitly. Behavior, with its great flexibility, allows the animal to take advantage of novel opportunities as they arise far quicker than morphology could. Highly variable circumstances as well as specific conditions that persist briefly provide behavior (with its rapid ability to adapt and habituate, even learn) with prospects far beyond the ability of morphology (with its long, averaging time frames) to exploit. Being able to take optimum advantage of environmental conditions has obvious rewards in terms of fitness, both physical and genetic. Thus behavior typically would lead the way in biasing reproductive success in the population. Morphological adaptations will follow as the paybacks of the changed behavior patterns accrue in genetic fitness.

Inferring fleeting behavior from morphological traits tends to be far from easy at the best of times; and it is rather tricky when the behavior is multifaceted. Spider's webs are a rare example to this rule of thumb, as discussed earlier. They provide a window into the evolution of a complex behavior because the extant species already provide an enormous variety of records (web types) with an ecological as well as structural diversity that can be firmly coupled to detailed insights into web-building behavior as well as foraging specialization (prey capture). Thus spiders allow us, virtually throughout their full range of ecotypes and without excessive effort yet with great detail, to study the structure-function relationship between an animal's body morphology and its behavior and ecology.

In summary, the evolution of the web, and especially the emergence of the orb web (and its occasional abandonment), has the potential to be a telling example for the evolution of behavior, if only we can begin to unravel the forces that drove the rise (and fall, if we want to call it that) of the orb-web spider tribe. Orb weavers are an important arachnid guild, with most of the extant species making orb webs or having evolved from orb-web builders. The guild of web makers per se is even bigger, of course, with a significant proportion of all spiders building a prey-capture web of some sort (Foelix 1996). Indeed, there is strong evidence that two important groups, the lycosid and pisaurid "wolf" spiders, derive from the builders of prey-capture webs, as do the salticid jumping spiders (Foelix 1996). In any case, with or without a web, spiders are among the most prominent of terrestrial predators. Indeed, the arachnids are the only major animal order that consists solely of predators. There is not a herbivore or detritivore among them, although the juveniles of some orb weavers seem to require air-borne pollen to get them through the first instars (Smith & Mommsen 1984).

This review touches on recent developments relevant to our core question: How might web-building behavior have affected the evolution of the spiders? Here we do not provide extended surveys of the literature on spider evolution and ecology, or on silk function or web-building behavior, because these topics have been superbly reviewed fairly recently by Coddington & Levi (1991) on spider evolution, Wise (1993) on spider ecology, Eberhard (1990) on web function and phylogeny, Craig (1997, 2003) on silk and silk evolution, Coddington (1989) on spinneret morphology, and Eberhard (1982) and Vollrath (1992) on behavior. However, a number of recent research studies have added significantly to our understanding of spider web evolution and these studies will form the focus of our review. More importantly however, we will use our vision of the evolution of the spider's web as an example to state the overriding importance of behavior in the evolution also of nonbehavior traits. Generally taxonomists and systematists ignore or underplay the role of behavior in the evolution of morphological traits because behavior can neither be easily measured nor genetically classified. Spiders and their webs are a rare, perhaps the only, exception to this generalization because a web structure can be analyzed just like a body morphology.

WHAT IS A WEB AND WHEN DID IT ORIGINATE?

A web can represent two types of character states. Web architecture is principally static with a semipermanent geometry, although its functional engineering is dynamic (Lin et al. 1995). However, web architecture is the outcome of web building, which is highly flexible, fleeting behavior. Thus, in analogy, web architecture compares with anatomy/morphology, while building behavior compares with embryology. Webs range from simple lines (laid down as the spider moves along) to complex structures (specifically assembled by the animal often over a considerable time span). If we include all spider structures made of silk then we must add to the tally the shroud of the prey-wrap, the tent or burrow of the retreat, and finally the cradle of the egg sac as well as the para-gliders of the ballooning spiderlings (Bell et al. 2005).

How did it all start? Sometime in the early Devonian (Selden et al. 1991, Shear et al. 1989) the first semiterrestrial spider-like arachnid—probably also carnivorous like all of today's spiders—shifted its prey-hunting behavior or its predator-escape behavior from the water to the land (**Figure 2**). This exposure to novel atmospheric conditions would have had grave implications not only for locomotion and reproduction but for breathing physiology (Selden & Edwards 1989) and (ecologically a tipping point) silk production mechanisms. Whatever the reasons for the first steps from water through intertidal (Churchill & Raven 1989, McQueen & McLay 1983) or freshwater swamps (Rovner 1987, 1989) to dry land, the spiders, once out of the water, quickly evolved silk producing organs that were fully functional (Rovner 1987). Silk is a biopolymer that, on the whole, functions best dry (Vollrath & Knight 2005), and we must assume that any underwater preadaptations for silk (Decae 1984, Rovner 1987) were released by this step onto land. This move thus quickly became a key step that allowed the adaptive radiation of the spiders into the taxon that is defined by its silk, both morphologically and ecologically.

There are two scenarios for the beginning of silk evolution. In one, the animal's eggs were at first covered by proteinaceous exudates from the coxal glands of the abdominal legs, which then evolved into a fibrous and sticky covering—perhaps to form a more effective glue or shield for deposited eggs as protection against the elements and predators (Shultz 1987). Scenario two assumes a protein mucus membrane to cover the whole abdomen, perhaps to shield and moisten the gills before they had time to evolve into the book lungs of the modern spiders (Damen et al. 2002, Strazny & Perry 1984). Either the membrane or the exudates could have evolved into a network of thin, individual thin filaments. Such a mesh would have been more effective as both a water-retaining sac when the land fell dry or an air-sac when the land was submerged. In either case, such a structure would have acted as a physical bubble or plastron lung (Messner & Adis 1995) allowing gas exchange between the inner and outer medium (be it air or water in- or outside). The presence of such a hypothetical silken lung would certainly have allowed the early spiders to invade drying-out flood-plains. Moreover, it would have given them an opportunity to explore their new environment while responding to its novel conditions by evolving their book lungs (which in effect are inverted gills housed inside a body cavity). Indeed, the highly derived *Argyroneta aquatica* today uses her silk to construct a diving-bell plastron lung allowing her to live fully underwater while other spiders, such as the sheet weaver *Desis marina* (Lamoral 1968a,b; McQueen & McLay 1983; Powell 1878) or the trapdoor spider *Idioctis* (Churchill & Raven 1989) and other purely terrestrial spiders living in areas prone to flooding (Rovner 1987), can survive extended periods of submersion in their silken sleeping sacs or cellars. The question of how the spiders first evolved (and used) silk is so far unresolved for lack of fossil data. Indeed, perhaps both selection pressures on proto-silk (to shield eggs as well as to provide a plastron) acted together. After all, *Argyroneta*'s air bubble not only prevents her eggs from drowning but the tough membraneous silk net also protects the eggs from predators.

Although the principal selective advantages leading to the evolution of silk fibers are still hypothetical, we have fairly good evidence on the morphological origin of the material. It is quite clear that spinnerets evolved from legs (Damen et al. 2002, Popadic et al. 1998) but the origin of silk glands remains somewhat shrouded. One hypothesis has it that they may be modified coxal glands (Bristowe 1958, Gertsch 1979, Kaston 1964, Marples 1967) assuming that silk evolved from an excretory product. However, while coxal glands are mesodermal in origin, silk glands are ectodermal (Craig 1997).

PRE-ADAPTATIONS FOR WEB BUILDING

Ancestral spiders, most likely, were freely roaming hunters that, after they had moved onto dry land, needed to seek shelter from the sun's rays or from tidal flooding for part of the day. As argued, silk initially may have evolved in response to the need to protect the animal's body as well as its eggs and young. After the uncoupling of silk production from reproduction and protection, single silk threads might have been extended beyond the shelter to provide guide lines for the spider as well as signal lines to detect nearby prey (Shear 1986). Eventually such single threads were interwoven to provide ever more efficient and effective traps that evolved to stop and retain potential prey.

However, building a trap requires not only the appropriate complement of silk producing organs but also the appropriate behavior patterns. In addition, constructing a silken trap, typically many times larger than the builder, requires spatial orientation. The evidence is strong that even the most ancestral spiders already had this capacity, as we outline now in a brief overview of the physiological ecology of extant spiders.

The Primitive *Liphistius* and the Mygalomorphs

Most of these spiders live in burrows, some rather complex with side chambers and several entrances (Main 1976) and many featuring concealed trap-door burrows. Some have silken lines radiating out from the opening to act as sensory trip-wires and/or home-finding devices on excursions. We know surprisingly little about the orientation mechanisms and survival mechanisms in the key taxon *Liphistius* (Foelix 1996, Main 1993), although recent work is beginning to provide new insights (Haupt 2003).

Hunting Spiders

Hunting spiders generally have good (and clear) vision in the principal eyes used for binocular, focal vision while the remaining eyes are for peripheral vision and movement detection (Barth 2002). The principal eyes may be used to identify prey or a mate, and may also help inform orientation. Some wolf spiders living at the edge of ponds can run away over the water; they return to firm ground by using visible landmarks or, if these are absent, astronomical cues such as the polarization pattern of the sky corrected by an internal clock (Barth 2002). In addition to such long-range orientation (employing direct landmarks) and navigation (with more indirect cues) hunting spiders also find their way much more locally (Vollrath 1992). For example, a hunting spider chased away from a prey or robbed of an egg sac tends to return in a straight line, even if the outward journey was along a circuitous route, indicating that the spider not only knows the direction of the shortcut but also its length (Görner & Claas 1985, Seyfarth et al. 1982). It seems that in these cases the spiders do not use any external cues but instead use an internal guidance system, often referred to as idiothetic memory (Barth 2002). The kinesthetic cues necessary for such a system may be provided by the lyriform slit sense organs in the cuticula of particular legs, as their immobilization affects the spider's performance (Barth 2002). As we shall see, orb weavers also seem to be able to use idiothetic orientation, perhaps also controlled by the lyriform organs. In any case, the anatomies of the eyes and of specific sensory organs on the legs and the chephalothorax are morphological features relevant to the spider's behavior.

Sheet-Web Spiders

The web of agelenid funnel spiders consists of a densely packed sheet of silk, often triangular and on ground level connected to a long, silken tube-retreat in one corner (Bristowe 1958). Prey falls onto the sheet and is grabbed in a dash by the spider

running from its retreat on top of the sheet. Typically the prey is consumed inside the retreat after a return dash that is always straight in a bee-line, even if the outward journey was circuitous. It seems that the spider uses information about its outward path to constantly calculate the vector pointing homeward. Such navigation by path integration (Mittelstaedt 1985) could be done by using information about leg and body turns gathered with kinesthetic senses (Barth 2002) and stored in some form of idiothetic memory (Görner & Claas 1985, Seyfarth et al. 1982). Thus guided into the vicinity of the retreat (for such systems are inherently inaccurate), the spider then locates the mouth of its retreat using a variety of different mechanisms such as the shape and spatial position of the sheet as well as thread tensions and web elasticity, perhaps even smell (Barth 2002, Seyfarth et al. 1982). In addition the animal may use light or the polarization pattern of the sky to provide further reference cues (Barth 2002). Whether the necessary information is collected internally or externally, on site or enroute, the behavior of the funnel-web spiders clearly shows that they use a variety of cues and mechanisms to orient and navigate. The sensory organs on the legs and the claws as well as the spinnerets are relevant behavioral features.

Space-Web Spiders

The web of the linyphiid spiders consists of a bowl-shaped fabric in a three-dimensional network of tangled threads well integrated into vegetation. The bowl collects prey falling in from above, and the spider moves on the underside of the bowl, typically waiting at the lowest point to attack from below using web tensions to orient (Suter 1984). Conformation of the spinnerets is a key trait for use of silk. In addition, the theridiid spiders [which most probably are derived orb weavers (Griswold et al. 1998) although they exclusively build three-dimensional space webs] have little combs on their legs that are a key feature of this group and are probably connected to the way they have of throwing sticky silk at prey. Moreover, many theridiids, like some other spider groups (Witt & Rovner 1982), also have specific stridulation organs. These are used by theridiids to vibrate threads (or the surface, in the case of the lyosids) during courtship, and thus provide another trait closely linked to behavior and webs, albeit they have little to do with the predatory behavior mostly associated with webs and web building.

Orb-Web Spiders

The typical orb web consists of a flat wheel of stiff radial threads overlaid by a spiral of elastic and sticky threads suspended freely in vegetation from a few guy lines. Radials and spiral often show distinct asymmetries in shape and spacing typically associated with a vertical orientation of the web and constituting a fine-tuning to maximize prey capture (Vollrath et al. 1997). In order to orient in the web, the spider uses vibrations but also the direction of illumination, which, together with gravity provides a general compass direction (Vollrath 1992). In addition to hand-railing along existing threads and orienting by a set of rather simple decision rules (Krink & Vollrath 1999), some orb weavers also navigate using idiothetic path integration (Vollrath et al. 2000).

Orb-web construction thus requires the use of local as well as global cues. Because theridiid spiders derived from orb spiders (Griswold et al. 1998), it is not surprising that they share common orientation mechanisms (Benjamin & Zschokke 2002, 2003). These groups also share many silk related traits, which can be seen in the details of the spinnerets (Coddington 1989) as well as relevant sensory organs on the legs and body (Barth 1985, 2002, Hergenröder & Barth 1983).

Jumping Spiders

Modern jumping spiders are highly visual, webless hunters although the evidence is strong that they have evolved from web-based spiders (Jackson et al. 2001). The jumping spider's hunt consists of three stages: approach, stalk, and jump. Jumps are only over relatively short distances, whereas the spider can see prey over long distances. In a three-dimensional habitat this means that the prey insect may often have to be approached via a detour, which indeed is done by some jumping spiders with great skill, suggesting that an excellent sense of spatial orientation is coupled with a memory of the maze (Hill 1979, Tarsitano & Jackson 1997). Clearly, the spider acquires specific knowledge about its surroundings visually and it appears that the animal is thus able to calculate accurately the fly's position relative to its own from a combination of visual and idiothetic memory. In this group the main trait that links morphology to behavior is the highly specialist eyes (Land 1985).

SUMMARY

In summary, spiders employ a wide variety of sensory modes and orientation/navigation aides, which they use to either hunt without a web or locate a site for a web and inform its construction as well as find their way about in the web. Silk and the use of a retreat would have been one of the first apomorph traits setting all modern spiders aside from their sister groups such as scorpions, mites, and the only primarily aquatic chelicerate, the horseshoe crab *Limulus*. Behavior would have already been important for the first use of silk in wall papering a burrow, as outlined earlier, but the rules of laying down the silk must have been refined rapidly when silk started to be used for prey capture. Many of the behavioral traits have good morphological correlates, whereas others are more difficult to identify, often because of lack of data and insights.

FOSSIL EVIDENCE

Fossil evidence for spider silk and the use of silk in webs comes from a wide number of sources. In some cases there are not only excellent morphological data but also information on silk production or even fossil webs that provide indirect or even direct evidence for ancestral behavior patterns. However, most of our insights to date originate from analyzing the morphology of fossilized spiders and comparing it with that of modern spiders where we have good information on their silks and webs. Here we consider mainly the evidence for silk use inferred from spider morphology, although spider trace fossils, rare as they are, can illuminate important aspects of the behavior of the ancestors (Seilacher 1967). However, there are also a few

examples of trace fossils produced by spiders, such as silk strands and bits of web (Bachofen-Echt 1949, Peñalver et al. 2006, Zschokke 2003), as well as traces of locomotion (Repichnia) (Braddy 1995, Sadler 1993) and dwellings (Domichnia) (Gregory et al. 2006).

Locomotion traces recorded from the Permian Coconino Sandstone (275 million years old) of Arizona and New Mexico (Braddy 1995) were attributed to spiders by comparing the modern desert ecosystem of the southwest United States (in which large mygalomorph spiders are a common element of the fauna) with the Permian ichnofaunal association of these desert sandstones. A particular locomotion trackway, known as *Octopodichnus*, suggests that the behavior of that particular Permian spider walking across desert substrates was similar to the movement pattern of present-day descendants like Aphonopelma chalcodes or Brachypelma spp. (Sadler 1993).

It is rare that the maker of a trace fossil can be identified with certainty, but Pickford (2000) described fossils of the characteristic buck-spoor spider *Seothyra* from Miocene aeolianites from the ancient Namib Desert. *Seothyra* is widespread and common across southern African desert regions (Dippenaar-Schoeman 1990). It constructs a vertical burrow that opens out at the sand surface into a wide dish containing the horizontal web covered with sand; a pair of pits on either side of the web gives the impression at the desert surface of the footprint of a small antelope (Lubin & Henschel 1990). The Namib is an ancient desert in an area of south West Africa that may have experienced an arid or semiarid climate for some 80 million years (Cretaceous), whereas the dunes sands of the Kalahari Sequence date back 65 million years to the start of the Cenozoic era (Schneider 2004).

Evidence from mammalian fossils indicates that the distinctive Namib habitat dates back to at least the mid-Miocene (Pickford & Senut 1999). All in all, this particular and distinctive trace fossil is good evidence for the antiquity of the genus *Seothyra*, its behavior, and (indeed) its habitat.

Given the abundance of today's spider burrows in environments that are prone to flooding (and hence preservation in the fossil record) it is surprising that fossilized spider burrows are rather rarely recorded. Perhaps this is a collection or rather identification artifact and they have been misidentified as being produced by other burowing arthropods such as Hymenoptera (Gregory et al. 2006).

Real fossil silks and webs, however, are not all that rare if we examine amber occurrences such as the Bachofen-Echt Cretaceous silk described by Zschokke (2003), or other samples from Canadian Cretaceous (P.A. Selden, unpublished observations). There are even records of flies caught in an amber web (Peñalver et al. 2006).

Before considering the body–fossil record of spiders, it is important to discuss ideas about the atmospheric composition of the mid-Palaeozoic Earth and whether this had any relevance to spider evolution and behavior at that time. For many years, it was assumed that the concentration of oxygen in the atmosphere in the mid-Palaeozoic was much lower than the present atmospheric level of 20% (Selden & Edwards 1989). Such a low level of oxygen would be insufficient to form an ozone layer to block lethal UV-B radiation and thus allow life to exist out of water. More recent work has shown that not only were today's oxygen levels finally reached in the Silurian period but that a possible drop in the level of atmospheric oxygen could explain a paucity of

terrestrial fossils in early Carboniferous times, known as Romer's Gap (Ward et al. 2006). By the late Carboniferous, oxygen levels were somewhat higher than today, which could explain the greater incidence of charcoal (resulting from wildfires) in the fossil record (Scott & Glasspool 2006). Thus, atmospheric and climatic effects would have had major effects on the total terrestrial ecosystem at the time.

Atmospheric oxygen concentration could have had a more direct effect on spider behavior. Lowered oxygen concentration could have rendered respiratory systems ineffective (Ward et al. 2006), resulting in migration to different habitats or extinction as well as the evolution of a more efficient breathing apparatus such as the combination of book-lungs with trachea (Bromhall 1987a,b). UV-B radiation would have been a major problem for any organism moving from water (which effectively blocks this radiation) onto land, whenever this might have been (and some researchers have advocated, on biochemical rather than palaeontological evidence, that complex terrestrial organisms existed even as early as the Precambrian). Ways to avoid harmful UV-B radiation would be to venture onto land at night, and to retreat behind a barrier during the daytime: under a stone, in a burrow, under water, or perhaps beneath a silken canopy. Some spider silks are highly UV reflective (Craig 2003), and so would have been very useful to the earliest spiders were they around when UV-B radiation was still at a high level.

Devonian

The oldest known spider is *Attercopus fimbriunguis* (Shearet al. 1987) from the Middle Devonian of Brown Mountain, Gilboa, New York (Selden et al. 1991), first described by Shear et al. (1987) as a possible trigonotarbid (an extinct group of Palaeozoic arachnids related to spiders). However, compelling evidence of spider-like spinnerets in the sample (Shear et al. 1989) suggests that *Attercopus* was a real spider showing for many characters more plesiomorphic states than were found in the most primitive genera of all known extant spiders, i.e., *Liphistius* spp. Accordingly, *Attercopus* was placed within the Araneae as sister group to all other spiders (Selden et al. 1991). The animal material itself consists of small cuticle fragments recovered from the siltstone matrix by maceration with hydrofluoric acid (HF), which is a process that can yield astonishing results. For example, Selden et al. (1991) managed to isolate a specimen of *Attercopus* cuticle bearing 19–20 spigots. Each spigot consists of a bell-shaped base, about twice as long as wide at the base, supporting a narrow shaft about three times as long as the base and comparable to the simplest spigots of some extant spiders (**Figure 3**).

The mesothele spider *Liphistius* is typically considered a living fossil because of its segmented abdomen (opistosoma) (Bristowe 1975), but we recall that the single-articled median spinnerets of *Liphistius* typically bear only one spigot (or none), while its more complex lateral spinnerets are pseudosegmented (Haupt 2003). Curiously, the *Attercopus* spigot consists of a single, fusiform spinneret and thus has more in common with the median spinnerets of the more derived mygalomorph spiders, which are single-articled and bear many spigots. Hence, the Devonian spinneret seemed to be more comparable to mygalomorph spinnerets, at least in its superficial morphology, than to the bulk of mesothele spinning organs. It must be noted here

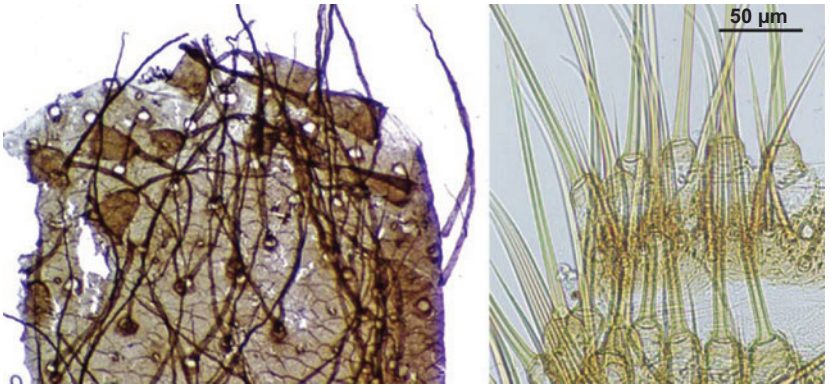

Figure 3

Macerated preparations of spigots of *Attercopus fimbriunguis* of Devonian (390 Mya) age, New York; and *Heptathela kimurai*, Recent (0 Mya), Japan.

that recent studies (Shear & Selden 2001) suggest that the original specimen is not a fusiform spinneret-like tube but a single sheet of cuticle folded over twice with the spigots arranged in two rows along one edge of the sheet. Other specimens also show spigots arranged in a double row along the edge of a piece of cuticle, while yet others could be pieces of spinnerets very much resembling flattened cylinders.

Thus, spiders were present among the earliest known terrestrial faunas and from the beginning were producing silk from fully formed spigots whether they were placed on spinnerets or directly on the body. Other arthropod fauna present in the *Attercopus* ecosystems included: scorpions, trigonotarbids, amblypygids, pseudoscorpions, mites, diplopods, chilopods, arthropleurids, and collembolans (Shear & Selden 2001). Many of these, e.g., collembolans, mites, and myriapods, would have been prey for *Attercopus* and other spiders, while other arachnids as well as chilopods would have been competitors for the diverse prey as well as predators on the early spiders. In any case, we may presume that the construction of a burrow (perhaps even with a trap door) would have been equally as beneficial to Devonian spiders as it is to burrowing spiders today.

Finally, we note that at that stage insects must have been in the infancy of their adaptive radiation. The only unequivocal evidence for true insects in the Devonian is a pair of jaws called *Rhyniognatha hirsti* from the Rhynie Chert of Scotland. These were first reported by Hirst & Maulik (1926); Tillyard (1928) described them and suggested that they were insect-like. The specimen was studied by many experts over the years, until Engel & Grimaldi (2004) confirmed that it belonged to a true insect. The next youngest insect is *Delitzschala bitterfeldensis* from the early Carboniferous of Germany (Brauckmann & Schneider 1996). There were certainly no flying animals at this time, which is important for any discussion of spider silk and web evolution, as well as the theory that spiders drove the evolution of the insects (Eisner et al. 1964).

Carboniferous

By Upper Carboniferous times the true Mesothelae had apparently become well established. However, although about 30 specimens of Carboniferous spiders have been

reported, many are incorrectly identified as such, e.g., *Megarachne* (Selden et al. 2005). Nevertheless, one true mesothele has been identified: *Palaeothele montceauensis* from the Upper Carboniferous of France (Selden 1996a,b, 2000). In addition to the characteristic plesiomorphies of Mesothelae (dorsal opisthosomal tergites, two book-lung opercula, orthognath chelicerae, and fully-developed anterior median spinnerets), *Palaeothele* has a narrow sternum, which is an synapomorphy for mesothele spiders. At least five spinnerets can be seen in the holotype of *Palaeothele*: left anterior lateral (ALS), two anterior medians (AMS), and at least one posterior lateral (PLS). An additional spinneret adjacent to the PLS was interpreted as most likely to be the other PLS, implying absence of the posterior median spinneret (PMS) (Selden 1996a). A monograph on Carboniferous spiders is in preparation by P.A. Selden, but preliminary observations have already been published. Carboniferous spiders originally identified as araneomorphs (specifically the family Archaeometidae) are either not araneomorph spiders (e.g., *Archaeometa nephilina* (Selden et al. 1991) or *Eopholcus* (P.A. Selden, unpublished observations) or not even spiders at all (Penney & Selden 2006).

However, there were Carboniferous spiders families, e.g., the Arthrolycosidae and Arthromygalidae, that, as far as can be told from the specimens, were all Mesothelae (Penney & Selden 2006). By late Carboniferous times (c. 310 Mya) insects had become an important element of the predominantly forest fauna and insect flight had evolved (Grimaldi & Engel 2005). This was a critical time in the evolution of spider webs, but unfortunately direct evidence is lacking on the kinds of webs that spiders might have been producing at this time. Two scenarios could be envisioned: either that spider predation drove insects into the air with the spiders' webs coevolving with the insects wings or that insects took to the air for some other reason (such as dispersal or pollination) and that spiders followed them. At present, we have no fossil evidence for either scenario and cannot even say when spiders' webs first left the ground and ascended into the vegetation. Crucially, we have no good evidence that would allow us to pinpoint the timing of insect flight development. The abundant remains of the earliest true insects from the early Carboniferous of Germany (Brauckmann et al. 1985, 1996) show that a significant diversity of flying insect groups had already evolved by that time and in a later section we discuss in more detail the issue of insect radiation and flight (**Figure 4**).

In any case, we must consider that spiders were not the only Devonian predators of the early insects. For example, trigonotarbids were also sit-and-wait predators similar, and closely related, to spiders. But they, importantly, lacked both silk and venom, which we may assume to have been an ancestral (apomorph) trait for all spiders given that today only one spider taxon (Uloboridae) has secondarily lost venom glands. Nevertheless, the greater abundance in the late Palaeozoic of trigonotarbids compared with spiders would have meant that at that time trigonotarbids may have exerted a greater influence on insect evolutionary ecology. Other possible insect predators include other arachnids, such as scorpions, amblypygids and uropygids, and chilopods, as well as vertebrates, all of which (certainly the scorpions and vertebrates) would have left the water and become terrestrial by the late Carboniferous.

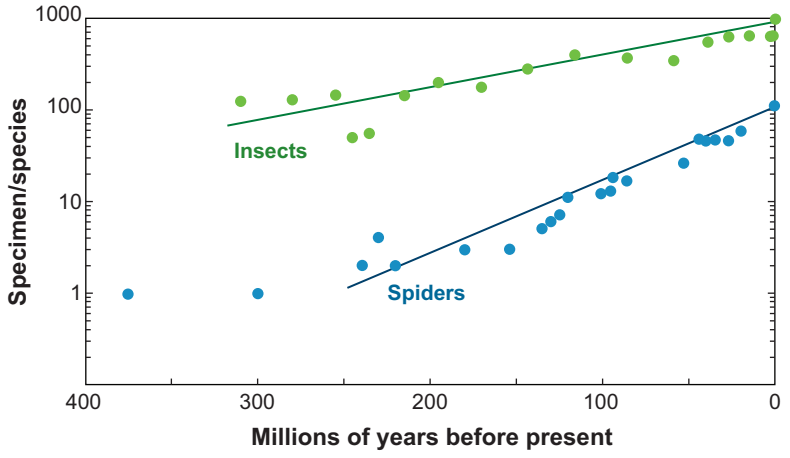

Figure 4

Graph showing relationship of spiders and insects over geological time. Note the similarity between the slopes of the two data sets. Further note the much greater age of the oldest specimen, the spider *Attercopus fimbriunguis*. Finally, note the logarithmic scale for the species distribution disguising the nonlinear increase in specimen of both taxa (data taken with permission from Penney 2004a).

Permian

Until recently, no arachnid fossils were known from the Permian period, in spite of abundant fossil insects from that period. The first Permian arachnid to be described was the trigonotarbid *Aphantomartus* (Rössler 1998); now we have the first spiders from this period, *Permarachne* and *Arthrolycosa* (Eskov & Selden 2005). *Permarachne*, especially, is an interesting specimen in that it is clearly a mesothele (showing plesiomorphies for spiders together with a narrow sternum—synapomorphic for mesotheles), but it also bears an elongate, flagelliform structure apparently emerging from the end of its abdomen. Eskov & Selden (2005) evaluated this flagelliform structure and considered it most likely to be an elongate spinneret. Elongate spinnerets are found in funnel-web spiders, such as the mygalomorph family Dipluridae and the araneomorph family Agelenidae, for example, but are not known in modern mesotheles. Hence, these researchers concluded that this was a new silk (and probably web) type for the Mesothelae. The argument went further (Eskov & Selden 2005), suggesting that there might have been a greater diversity of mesotheles in the late Palaeozoic than today. Finally, this kind of spinneret was considered to provide evidence for the late Palaeozoic development of a funnel web, which is primarily adapted to capture jumping insects.

If true, then the arms race between insects and spiders had begun in the Permian, i.e., c. 270 Mya (**Figure 4**). The hypothesis of a Permian period of rapid (co)adaptive radiation of both spiders and insects is intriguing. After all, this is a time with a rich fossil record of flying insects, at least from a few Fossil-Lagerstätten. Alas, this abundance of insects has yet to be matched by fossil spiders. As and when more

spiders come to light from this period, we would hope to see more evidence of morphological features that would suggest the building of aerial webs. However, the end of the Permian, and the end of the Palaeozoic era, was marked by the greatest extinction event Earth has ever experienced. Its causes are, as yet, poorly understood (Erwin 2006), but its effects were profound: some 82% of genera, and more than half of all marine families, disappeared at this event.

How it might have affected the spiders and insects is not clear. For the insects, Labandeira & Sepkoski (1993) considered the skewing effect of Lagerstätten on their data (rich Permian deposits in Russia and Kansas but few in the Triassic), but concluded that the apparent drop in diversity at family level was real and due to the Permian-Triassic extinction. The effect on the spiders of the time is presently impossible to assess owing to lack of fossils.

Triassic

An extinction event is typically followed by a period of rapid adaptive radiation. Accordingly, among the insects there was a change at the end of the Palaeozoic as a large group of pterygote Palaeoptera, the Archaeoptera or palaeodictyopteroids, became extinct and were replaced by the pterygote Neoptera. The Palaeoptera were unable to fold their wings, whereas the Neoptera could do so. Interestingly, two groups of Palaeoptera survived the extinction and continue to the present day: the Odonata (dragon- and damselflies) and the Ephemeroptera (mayflies).

For spiders, the Triassic period saw the first mygalomorphs, such as *Rosamygale grauvogeli* in the modern family Hexathelidae (Selden & Gall 1992), as well as the first araneomorphs, i.e., modern web spiders (Selden et al. 1999). The hexathelids, as their name suggests, bear six spinnerets (ALS, PLS, PMS), and the PLS are elongated for the weaving of a funnel web (the infamous Sydney Funnelweb spider, *Atrax*, belongs in this family). *Rosamygale* was about 5-cm large and apparently lived in a semiarid environment on a delta, living presumably in a burrow or retreat from which a funnel web extended to catch jumping prey. Insects are abundant in the Voges region of France where it occured, mostly those with aquatic connections, e.g., aquatic larvae. Mygalomorphs include the tarantulas, funnel-web and bird-eating spiders. The importance of finding a mygalomorph spider in Triassic strata is enhanced by also finding species belonging to the sister group of that infraorder, the araneomorphs (Selden et al. 1999). *Argyrarachne* from Virginia is a juvenile, but *Triassaraneus* from South Africa is more likely to be an adult. These early araneomorphs already closely resemble modern orb weavers in general habitus. *Triassaraneus* has long, slender legs, a leg formula (longest to shortest) of 1243, no scopulae, and sparse bristles, all features suggestive of Araneomorphae. Furthermore, leg shape and arrangement, the lack of leg spines, the small tarsal claws and lack of scopulae, the paucity and arrangement of bristles, and the possible metatarsal trichobothrium seen on one leg are all suggestive of this specimen belonging to the extant group of Araneoidea.

Araneoids are primarily weavers of orb webs although some families and genera weave webs secondarily derived from orbs (Coddington 1986). Consequently it is possible, indeed likely, that the orb web dates from as early as the Triassic, i.e., is

over 200 million years old. As we find during those times a great abundance of flying insects of modern aspect (neopteran pterygotes) that might have served as prey, we are beginning to see the predator-prey arms race in full swing.

Jurassic

The first Mesozoic spiders to be described date from the Jurassic period and are represented by modern-looking araneoids such as *Juraraneus rasnitsyni* (Eskov 1984) or even more contemporay araneomorphs such as *Jurarchaea zherikhini* (Eskov 1987). More recent finds of fossil spiders in the Jiulongshan Formation (Huang et al. 2006) include a wide range of mygalomorphs and araneoids as well as uloborids and palpimanoids (including arachaeid forms, see below) (P.A. Selden, D. Huang, D. Ren, in preparation). In conclusion, it appears that the Jurassic araneofauna contained a diversity of orb-web weavers (Orbiculariae), including both cribellate uloborids and ecribellate araneoids.

Because the orb web is considered to have originated among cribellate orbiculariens (Coddington 1986), the presence of ecribellate araneoids is evidence of the split of ecribellate from cribellate orbicularians in at least late Jurassic times, and possibly earlier. By Jurassic times, holometabolous insects had originated and radiated, so that nearly all modern orders were present (Jarzembowski & Ross 1996). The diversity of spiders was obviously much higher than that presented by fossil evidence alone [Mesothelae; Mygalomorphae; Hexathelidae; Araneomorphae; Araneoidea (Juraraneidae, probably Tetragnathidae); Palpimanoidea (Archaeidae and others); Uloboridae]. By that time we had not only burrow dwelling spiders, but also funnel webs and orb webs. Most interestingly, modern Archaeidae are specialist spider hunters (araneophages) and the similarity in the morphology (elongate chelicerae) between the Jurassic and the modern species suggests that this mode of foraging had already evolved then.

Cretaceous

From early cretaceous rocks in Spain we have records of tetragnathid (including nephilinid) and uloborid spiders (Selden 1989, 1990; Selden & Penney 2003) that show the distinctive tarsal claw pattern of moderen orb-web weavers. Like the early Cretaceous Chinese Yixian formation (Zhou et al. 2003) yielding araenoids and uloborids (P.A. Selden, unpublished data), the Spanish deposits also represent lacustrine environments, some with volcanic ash falls. Today's tetragnathids are rather common along lakeshores, where they feed in the evening on the abundant insect life. Spiders do not fall into lake waters quite so readily as insects do (fossil insects in lacustrine deposits outnumber spiders by about 1000 to 1). But volcanic ash falls would certainly help to cause webs to collapse or spiders to lose their purchase and fall into the water. It is thus possible that we are already seeing a typical modern lake-shore spider fauna as far back as the early Cretaceous or Jurassic. It is only within the past dozen years that spiders have been described from Mesozoic ambers. Eskov & Wunderlich (1994) described the enigmatic new family Lagonomegopidae from two

juvenile specimens in amber from Yantardakh, Taimyr, Siberia, and mentioned a further 50 undescribed specimens from the Upper Cretaceous of the region, some of which were placed in the superfamilies Araneoidea, Dysderoidea, and Thomisoidea. Eskov & Wunderlich also mentioned spiders from fossil resins from Azerbaijan and Armenia. The 47 amber spider specimens mentioned by Zherikhin & Sukatsheva (1973) from Yantardakh, Siberia may now be lost (Eskov & Wunderlich 1994). Other described Cretaceous amber spiders include the families Segestriidae, Oonopidae, Lagonomegopidae, Oecobiidae, Dictynidae, Araneidae, and Linyphiidae from New Jersey amber (Penney 2002, 2004b); Archaeidae, Pisauridae, Lagonomegopidae, and Ooniopidae in Burmese amber (Penney 2003a, 2004c, 2005, 2006); Linyphiidae and Deinopidae from Lebanese amber (Penney 2003b, Penney & Selden 2002); and Lagonomegopidae and Oonopidae from Canadian amber (Penney 2005, 2006).The first Mesozoic mygalomorphs were described by Eskov & Zonshtein (1990) from localities in the Lower Cretaceous of Siberia and Mongolia. These were placed in the modern families Mecicobothriidae, Antrodiaetidae, and Atypidae. The modern family Nemesiidae was reported from early Cretaceous amber from the Isle of Wight (Selden 2002), and Dipluridae from the early Cretaceous of Brazil (Selden et al. 2006).

Amber is an interesting fossil fixative as it not only conserves the spider but it also tends to preserve the silk and web. Hence amber spiders will take us closest to understanding the habits and habitat of fossil spiders (Zschokke 2003).

SUMMARY AND CONCLUSIONS

An analysis of spider and insect palaeontological data allowed Penney (2004a) to evaluate family richness through geological time. He concluded that both insect and spider fossil records show an exponential increase over time, which is the pattern typical of a radiating taxon. He further concluded that both taxa, insects and spiders, had comparable rates of diversification, which suggests that spiders and insects may have coradiated. The perceived main spurt of radiation would have happened at least 100 Mya before the origin of angiosperms (**Figure 4**). This suggests that insect evolution was driven less by flowering plants than by other factors, with spider predation being a strong possibility for a major selective force.

Present-day spiders, unlike their insect counterparts, are all carnivores, without exception (Foelix 1996). This suggests to us that the ancestral spiders were also carnivore insectivores. Alternatively, one would have to assume that an arachnid herbivore morphotype existed at some stage and perished without leaving a trace, fossil or otherwise. All evidence, from the mouthparts to the digestive tract and emzymes suggests specialist carnivory (Foelix 1996). Indeed, the whole body plan, including the silk glands and their position as well as the claws on the legs, suggests a deeply rooted predatory existence (Foelix 1996). A predatory life style would be greatly helped by the opportunistic flexibility offered by behavior patterns, which are exponentially increasing with increasing complexity of the rules as emergent properties add ever more flexibility of expression (Krink & Vollrath 1998). Such flexibility would be invaluable in an arms race between the predator and its prey. Here we must remember that spiders are not only predators but also prey; after all, the major predators of spiders

are other spiders (Wise 1993). However this may be, a predatory life style with silk as a primary tool has served spiders very well, looking at their ecological diversity and importance.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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