Silk and venom: The geological history of spiders

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In this talk I first introduce the spiders. What kind of animals are they, and who are their relatives? Spiders belong to the arthropod subphylum Chelicerata. These are characterized by the first pair of appendages being pincers (chelicerae). Other chelicerates include the horseshoe crabs, harvestmen, scorpions, and the too-familiar mites and ticks, among others. Then I discuss why spiders are important in the general scheme of Nature. Far and away the most abundant and diverse animals on land are the insects (mainly beetles), but next in abundance are the arachnids: spiders and mites in particular. There are some 42,000 species of spider known to be alive today (and probably many more yet to be discovered). They are the most abundant predators on land and keep the insect hordes at bay.

What principally separates spiders from their arachnid relatives can be conveniently boiled down to venom and silk. While many arthropods produce silk, none do so from glands in their rear end (opisthosoma) nor manipulate it so successfully into the myriad uses that spiders do. Similarly, while venom is widespread in the animal kingdom, no other arachnid makes use of it through glands in the fore-part of the body (prosoma), which discharge through the cheliceral fangs. There are three main groups of spiders; the most primitive Mesothelae are found today in trapdoor burrows in south-east Asia and also as fossils in Carboniferous rocks. All other spiders belong to Opisthothelae which has two subgroups: the Mygalomorphae, are the funnel-web, trapdoor and tarantula spiders, and the Araneomorphae, which are by far the commonest, often called the true spiders.

All spiders produce silk, and there are many different kinds of glands which produce silk for different purposes. For example, all spiders lay a dragline wherever they go. This is useful as a belay rope for spiders maneuvering through vegetation or for finding their way back home. Some spiders make silken sleeping bags, and most wrap their eggs in silk. Webs are the most conspicuous silken structures made by spiders, and these vary tremendously in form and function. Orb webs are the most familiar, especially when covered in dew on a cold morning (dew collects on silk because it is hygroscopic, and the spider uses this effect as a means of drinking). The commonest orbs are made by araneoid spiders, whose webs have a spiral of sticky silk covered in glue droplets which catch insects. Another group of spiders, the cribellates, make a woolly kind of silk which traps insect hairs like burrs on a sweater, and they use no glue. Numerous lines of evidence indicate that cribellate orbs were invented first, and one group of orbweavers then developed the glue which proved more effective. Among both cribellate and araneoid orbweavers there are lineages which have modified or reduced the orb web to horizon-

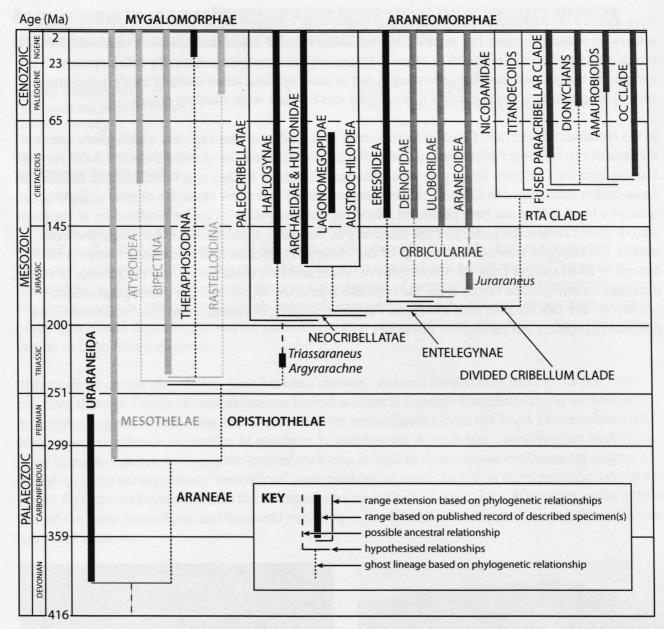


Figure 1. Phylogenetic tree of spiders. Shades indicate major predation modes. Light grey = mainly burrowers. Medium grey = weavers of orb webs and their derivatives (araneoid and cribellate). Dark grey = free-living hunters, including jumping spiders. Black = others, including some sheet-web weavers and unknown (fossils). Modified from Vollrath, F. & Selden, P. A. 2007. The role of behavior in the evolution of spiders, silks, and webs. **Annual Review of Ecology, Evolution, and Systematics 38**, 819–846.

tal sheets or even single lines. Some spiders do not use webs and hunt in other ways, but all use silk in one way or another.

Spiders fossilize poorly. They are relatively soft bodied, and live on land well away from any normal environment where sediment is deposited. An exception to this is amber. This is fossilized resin from

trees, and is a very effective entombment and preserving medium. More than 90 percent of all fossil spiders are found in amber, but since amber inclusions do not occur in rocks older than early Cretaceous, older specimens are found in other sedimentary environments, especially lake deposits. In order the eke the greatest possible information out of fossil spiders, some exciting modern techniques, such as synchrotron x-ray computer tomography can be used, with startling results.

In the remainder of the talk, I look at a number of case studies of fossil spiders which give a taste of the kind of extraordinary preservation and information which can be gleaned from the fossil record. Starting with the Cenozoic Era, I give some examples of amber spiders and webs, and one instance of a non-amber occurrence in Canada. In the Mesozoic Era, I first show examples of how a single occurrence of a fossil spider can have profound effects on our knowledge of spider biodiversity in the fossil record. Then I review the history of the discovery of Mesozoic spiders, before showing a few case studies. For example, how our knowledge of the history of cribellate and araneoid orb webs is enhanced by fossil spiders from the Cretaceous of Spain; and new fossil finds from the Jurassic of China, including an unexpected family from the opposite side of the world, and the oldest giant golden orbweaver. The talk finishes with a study of Paleozoic spiders, or rather, some fossil which were first described as spiders but turned out not to be!