Fossil History of the Arachnids

by Paul A. Selden

Among terrestrial animal groups, the arachnids are second only to the insects in abundance and diversity. Although numerous on Earth today, arachnids fossilise poorly, so new finds of fossils generally cause momentous changes to the arachnid fossil record. During the last year, a number of reports in the literature have both considerably extended the fossil record of arachnids and so enriched it that a new pattern of arachnid evolution is beginning to emerge (Fig. 1).

The vast majority of fossil arachnids are preserved in exceptional circumstances. Such extraordinary occurrences of rarely preserved organisms are known as Fossil Lagerstätten (though circular reasoning dictates that because arachnids are generally rare as fossils, beds containing them are *ipso facto* Lagerstätten). The earliest demonstrably terrestrial animals are the arachnids found in the celebrated Rhynie Chert of Aberdeenshire, of Lower Devonian age. Other important Devonian faunas with arachnids are the Alken-an-der-Mosel in Germany (Lower Devonian), and the Gilboa mudstones in New York (Middle Devonian). The next youngest cluster of arachnid records is in the Upper Carboniferous: Coal Measures sites in Europe and North America. These include Mazon Creek in Illinois, Coseley in the English West Midlands, and Nýřany in Czechoslovakia. Mesozoic arachnids are particularly rare, and Cenozoic occurrences are mainly of modern-aspect forms in amber.

In 1989, the earliest fossil evidence of orb-web weaving spiders, from the Lower Cretaceous of north-east Spain, was reported (Selden, 1989). Both groups of orb-web weavers, araneoids and deinopoids, occur in this deposit, which thus places the common origin of the orb-web weaving groups in the Jurassic at least. One of these specimens was illustrated in Newsletter **57,** p. 6, and a full description appeared in Selden (1990). Among the three new species described in that paper is one (*Macryphantes cowdeni*) named in remembrance of Doug Cowden (see obituary in Newsletter **55,** p. 4).

Later in 1989, the earliest evidence of spider spinnerets, from Devonian rocks of Gilboa, was reported (Shear *et al.*, 1989). The occurrence of a spinneret implies the ability to spin silk (though not necessarily the weaving of an aerial web for prey capture), and the find is the earliest evidence of silk use by any animal. Such spinnerets are known only from spiders, and so this is the most convincing evidence for the presence of spiders as early as the Devonian. Other Devonian specimens previously assigned to the Araneae are insufficiently preserved (they lack spinnerets) for their identity to be certain. The same Gilboa locality has also yielded the oldest known pseudoscorpion, reported in Shear, Schawaller & Bonamo (1989): at one stroke, the fossil record of pseudoscorpions was increased tenfold, their previous earliest record being in Palaeogene amber. Earlier this year, book-lungs were reported from a Lower Carboniferous scorpion (Jeram, 1990). Early scorpions were aquatic, and this record suggests that the first scorpions to make the transition to land by converting their book-gills into air-breathing organs, had done so by Lower Carboniferous times.

This deluge of new records of fossil arachnids provides an opportunity to update our knowledge of the arachnid fossil record and, in particular, to view the record in the light of current ideas of arachnid phylogeny based on phylogenetic analysis of the living animals.

Figure 1 shows the fossil record of arachnids. Anthracomarti, Trigonotarbi, and Phalangiotarbi are known only as fossils; these groups probably never crossed the Permo-Triassic boundary. Of these extinct forms, only the Trigonotarbi are well-studied; they are the oldest known terrestrial animals, and are closely related to spiders (Shear *et al.*, 1987). Palpigrades and schizomids are minute and, whilst this attribute has not prevented the discovery of fossil mites, the detection of fossil palpigrades and schizomids is less likely than that of larger and commoner forms. Schizomids are included within the Uropygi by many workers, and most regard them as miniaturised representatives of this group. Cenozoic palpigrades have been described (Rowland & Sissom, 1980), and there is a questionable record from the Jurassic. All other groups are now known to originate in the Carboniferous or earlier. It is tempting to view the record in Figure 1 as representing a late Silurian origin and radiation of terrestrial arachnids, which culminated in a rich diversity in the late Carboniferous, with some groups failing to survive the Permo-Trassic extinction event. It is also notable that no arachnid order became extinct across the Cretaceous-Cenozoic boundary (the time the dinosaurs died out), though the record of this time is sparse.

The most recent cladistic treatment of arachnid phylogeny, by Shultz (1989), was based on features of leg jointing and musculature (Fig. 2a). Shultz's phylogenetic hypothesis bears some similarity with that of van der Hammen (1989) (Fig. 2b), in placing Scorpiones in

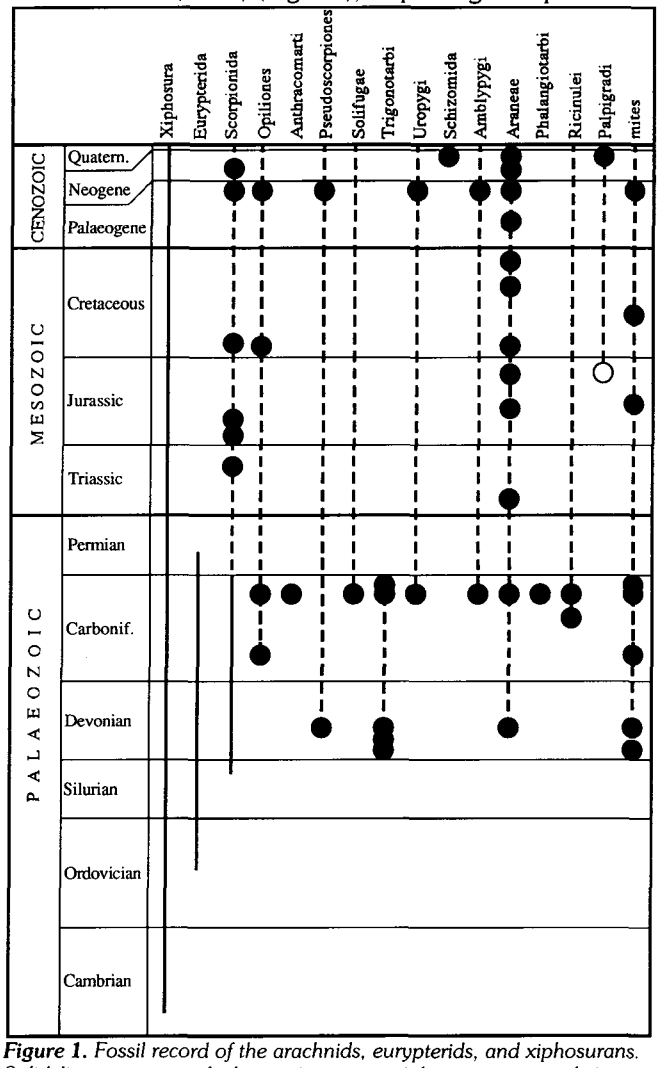
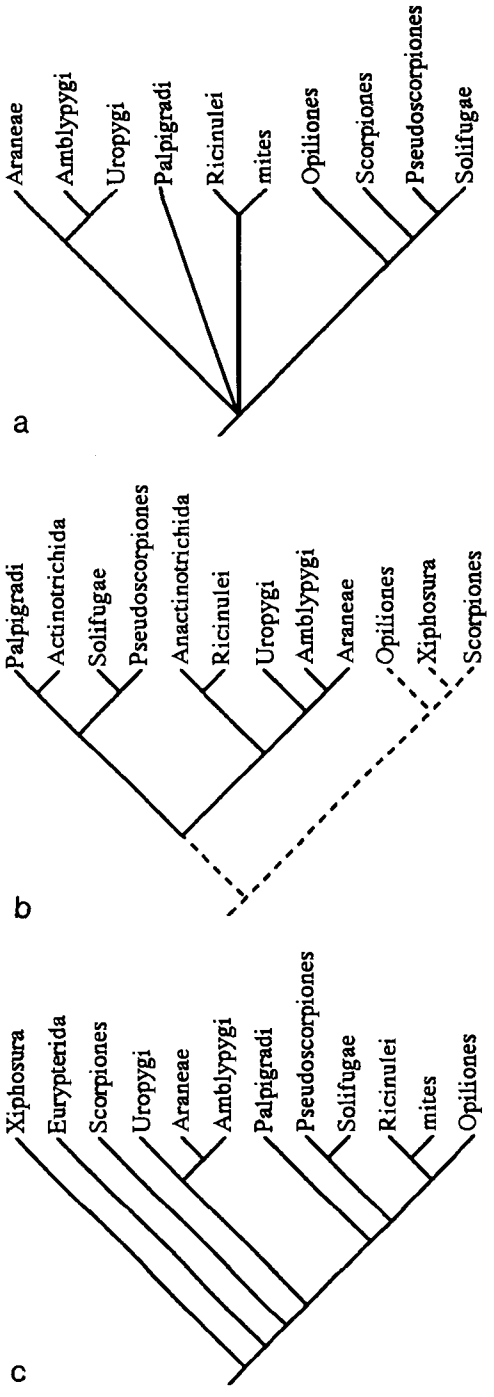


Figure 1. *Fossil record of the arachnids, eurypterids, and xiphosurans. Solid lines represent fairly continuous, mainly aquatic record; interrupted lines connect isolated occurrences which are shown as filled circles; open circle is a doubtful record. Based on published and unpublished data.*

Figure 2. Cladograms of relationships among the arachnid groups. **a,** *Shultz (1989), Xiphosura are taken as the out-group, the main groups are unresolved at the base.* **b,** *Van der Hammen (1989), interrupted lines indicate uncertainty: the mites are viewed as two groups, Actinotrichida and Anactinotrichida.* **c,** *Weygoldt & Paulus (1979).*



a more derived position than Opiliones. Both of these schemes differ from traditional views, and from the exhaustive cladistic study of Weygoldt & Paulus (1979), in which Opiliones were placed in a derived position among arachnids, and scorpions as sister-group to all other arachnids (Fig. 2c). Successive dichotomies in clades must occur in ascending chronological order; thus a cladogram reflecting evolutionary events should concur with a complete fossil record in the sequence of events. How well do the conflicting hypotheses in Figure 2 accord with the known fossil record?

Comparison of the cladogram of Weygoldt & Paulus (Fig. 2c) with Figure 1 reveals that the only dichotomy which is markedly asynchronous with the fossil record is that linking Palpigradi with its apomorphic sister-clade. Their hypothesis predicts that palpigrades should occur in strata at least as old as Lower Devonian because the more derived mites and pseudoscorpions occur at Gilboa. In fact, all three cladograms predict this for the palpigrades, and in addition, that either Ricinulei are derived from mites or they were present in pre-Devonian times. If van der Hammen's scheme (Fig. 2b) is correct then an arachnid group recognisable as Opiliones was present in the Cambrian. Shultz's cladogram (Fig. 2a) predicts that Opiliones occurred in pre-late Silurian times, and Pseudoscorpiones + Solifugae were also present then or are derived from scorpions. Silurian scorpions are thought to have been aquatic (Selden & Jeram, 1989), so Shultz's scheme implies either that Opiliones were aquatic in the Silurian or scorpions became aquatic in late Silurian times, and then terrestrial again.

The major discrepancy, therefore, between the fossil record and the hypotheses of van der Hammen and Shultz, lies in their placings of Opiliones and Scorpiones relative to other arachnids. Van der Hammen (1989) linked Opiliones, Scorpiones, and Xiphosura (horseshoe crabs) together in a group he called Myliosomata, on the basis of their shared utilisation of movable coxae during feeding. However, he was unable to determine the relationships between the groups of Myliosomata, and the arrangement shown in Figure 2b is therefore only tentative. Shultz (1989) placed Opiliones, Scorpiones, Pseudoscorpiones, and Solifugae together on the presence of a femoropatellar extensor muscle. Extensors are rare at arachnid leg joints, a condition considered by some to be an advanced feature, but by others (including Shultz) to represent the primitive condition. Shultz suggested that the femoropatellar extensor was homologous not only among these arachnids but also with a flexor muscle (present in other arachnids and the more primitive Xiphosura) which had moved dorsal to the articulation axis at the femur-patella joint. The lack of the extensor in Solifugae was explained as a secondary loss.

Shultz's cladogram must be read with care. Apart from a smattering of well-defined apomorphies, it is based almost entirely on appendicular characters. The specialised, marine burrower *Limulus* was used as the out-group even though the well-known, though extinct, eurypterids are considered by most workers (including Shultz) to be the sister-group of the arachnids. In Shultz's scheme, compound eyes must have been reduced to simple eyes at least three times; the pre-anal tail (metasoma) of scorpions and eurypterids and homologues of the scorpion pectines, eurypterid and xiphosuran gill-covers must have been lost more than once; the opilionid tube-tracheae must have developed directly from book-gills or from book-lungs separately developed from those of scorpions, pseudoscorpions and solifuges, and other arachnids.

An exhaustive phylogenetic analysis cannot be attempted here, but it is apparent that a study incorporating all available characters, and including information from the now very well known extinct eurypterids, trigonotarbids, and aquatic scorpions, would be fascinating. Meanwhile, the search for Silurian and older fossil arachnids, especially Opiliones, continues.

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Arachne

The spider left her muddy hole
Among the forests of the coal
To suck the prey that crept across
Her limy lines among the moss.

She spun her webs, concealed from view,
In shrewd geometries of dew.

A hundred million years went by
Before the first unwitting fly,
Unheeding, took the air and met
Disaster in the subtle net,
And perished in the lacy maze.

It took you but a hundred days.

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NOTES AND COMMENTS

Dr Peter Merrett adds the following information to Deborah Procter's article on *Robertus insignis* in Newsletter **47:** Wunderlich (1976, *Senckenberg. biol.* **57:** 97-112) recorded one male and three females of the species from Estonia.

The Daily Telegraph continues to be a source of interesting arachnological anecdotes. A short article on miniature ladders providing an escape-route for spiders trapped in baths gave rise to a spate of correspondence, including a letter from an arachnophobe Group-Captain. Another arachnophobe was reported as having spent an afternoon with his leg stuck in a lavatory after trying to stamp on a spider crawling along the seat. He was extracted by firemen. Firemen were also involved in giving 'the kiss of life' to a 'tarantula spider' overcome by fumes in a bungalow blaze at Rye in Sussex. 'We revived it by putting a breathing mask over it. When it came to, we stayed clear'.

Mr A. E. R. Gaulty of Tarporley, in a letter to a local newspaper (exact source unrecorded) recollects a sentence from the columns of the Anglesey *Y Cloriannydd* ('The Balancer'): *'O'i wiw wy i'w we e a'*. This translates as 'he goes from his own egg into his own web', and was in an article about the *cop bach* (little spider) — *cop* being one of the Welsh words for spider, which survives in English in the combination 'cobweb'.

Tegenaria Features in Legal Case

by Charles Dondale

Most scientists, if given the choice, would probably stay out of court, even if their appearance was only to give evidence. Their views tend to be misunderstood, and they tend to speak from a base of probabilities and inferences rather than certain truth. The scientist who takes a bible in hand and swears to 'tell the truth, the whole truth, and nothing but the truth, so help him God' should be prepared to face a certain amount of controversy.

These were some of the thoughts that ran through my mind one day early last spring with the arrival of a court subpoena by post. 'Whereas' the letter ran, 'a certain farmer on the Canadian prairies did unlawfully attempt to defraud an insurance company of money in an amount exceeding $1000.00, and whereas it has been made to appear that you are likely to give evidence for the prosecution, therefore you are commanded to attend before the Presiding Judge at the Court of Queen's bench in Portage la Prairie, Manitoba on Monday, April 3 at 9.30 a.m. to give evidence concerning the said charge.'

The farmer in question had reported the emptying by thieves of two large steel granaries, one holding 5,000 bushels of wheat and the other 4,500 bushels of flax. He had filed an insurance claim to recover his loss.

The insurance company, as was its custom in such cases, sent the Royal Canadian Mounted Police to investigate. On entering the granaries the Constable became suspicious and requisitioned video films of the interiors. The walls of both granaries were draped with large dusty webs of the kind made by *Tegenaria* spp. The species was presumed to be *domestica*, though the R.C.M.P. did not collect any of the spiders.

The films were sent to me in Ottawa. Having viewed them I supplied a written statement to the Police to the effect that in my professional opinion the granaries must have been empty for a much longer period than that inferred from the farmer's claim. My reasons were that (1) air temperatures, as estimated from weather data taken at a location some 12 km to the north, were too low for web building, the month being November when night lows were all below 0°C and highs during the day at most 8.5°C; (2) the spiders would be in diapause at that season, regardless of prevailing temperatures, with little or no inclination either to spin or to feed; and (3) the webs could not have been made prior to the date of the alleged theft if, as claimed, the granaries had been full of grain until that time. With my report I included a request that the Police try to find a similar granary from which the grain really had been removed about a week previously, predicting that such a granary would show no webs or dust. As it turned out, a granary of that description was found and filmed and, as expected, the walls were shiny clean.

At the trial a dozen witnesses, including some