FOSSIL SPIDERS

Presidential address to the Manchester Geological Association
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by PAUL SELDEN

"If you wish to live and thrive, let the spider run alive!" as my aged aunt used to say (and probably still does). There are many legends and old wives' tales about spiders. They are creatures which we admire rather than despise, for their exquisite handiwork and general good manners in helping to rid our habitations of pestering flies. One age-old story is told by the Navajo Indians of the south-western USA, who are accomplished weavers. In Canyon de Chelly is a tall, inaccessible pinnacle of dune-bedded Permian de Chelly Sandstone called Spider Rock. The story goes that a young girl disappeared one day, and when she reappeared had learned the art of weaving which she taught to the rest of the tribe. The squaw had been captured by the Spider Woman who lives on the top of the pinnacle. To this day, genuine Navajo weavings have a hole in the pattern - the spider's lair - in recognition of the origin of their craft.

Myths abound too, where spiders are concerned. It is true that the male spider must approach the female with care in order not to be mistaken for prey, and often a morsel of food is proffered to occupy her while mating occurs. If a swift exit is not made afterwards, the female may attack the lingering male, but by now his job is done, and it makes ecological and evolutionary sense to recycle biomass within the species! The so-called bird-eating spiders do not really eat birds, although some large tree-dwelling species have been recorded taking baby hummingbirds!

Even our common or garden spiders can reveal some astounding facts and figures. W S. Bristowe, author of the excellent book *The World of Spiders* (Collins New Naturalist, now sadly out of print), estimated that the British spider population consumes insects equivalent to the weight of the entire human population of these islands each year A single acre of summer meadow in the south of England may provide homes for $2^1/_4$ million spiders, and the typical house probably has 2,000!

All spiders are carnivorous, some are catholic in their diet, while others are specialized. A handsome British spider is *Dysdera*, which has huge jaws (chelicerae) with long fangs for getting between the body segments of woodlice, its main food source. All spiders have a pair of chelicerae at the front of the body, followed by a pair of palps (modified in the male for sperm transfer), and then four pairs of legs. Spiders have two parts to the body· the front part which bears the appendages is called the prosoma, and the rear part which bears spinnerets at

its end is the abdomen. Poisonous fangs and silk-producing spinnerets are unique features of spiders.

Not all spiders weave webs, however. Silk is used in many different ways. The wandering wolf spiders capture prey by running after it; they use silk principally to wrap their eggs, and females can be seen carrying the sacs attached to their abdomens on warm June days. Female spiders appear to show maternal instincts: the wolf spider mother continues to carry her young on her back even when hatched, and many stay with their eggs and young, warding off predators until they leave the nest. Crab spiders catch insects by waiting motionless for one to alight on a flower head or leaf, when they grab the hapless creature with outstretched forelegs. Their similarity to crabs lies in their habit of walking backwards and sideways as well as forwards, but their unusual ability is to be camouflaged by taking on the colour of the flower petals upon which they lie in wait. Jumping spiders, as their name suggests, can be seen on warm walls in the summer, leaping on flies which alight nearby They have an enormous pair of eyes at the front of the prosoma which permit effective binocular vision for their accurate jumps.

The most outstanding achievement of spiders, to human eyes, is their ability to weave geometric orb webs. The common garden spider, *Araneus diadematus*, weaves the familiar structure with its radial lines which hold up a spiral of sticky silk. Building an orb web may take hours, and spiders are meticulous in its construction, each species producing a slightly different version; the web of the garden spider has 15° angles between the radii, for example. The true function of the web is not to act like a fishing net to tangle prey, but rather it is the sticky spiral of silk to which the insect adheres. Important too, is the tension of the web so that the spider can detect the correct vibrations which alert it to the presence of a prey item rather than, say, a predator.

Construction of an orb web is a delight to behold. First, the spider lets out a line of silk which any slight breeze will carry across the space to be filled later by the web. Once this tightrope is established, the spider walks across it, then halfway back again. Now in the middle, she drops down and thus establishes a triangle of silk with the future centre of the orb at its apex. Sides and a bottom line are laid down and the spider continues by adding radii, at the angles distinctive for the species. Once the radii are down, the spider begins to lay down a spiral starting from the centre and working outwards, being sure to tension each thread as she goes. That finished, the final stage is to remove the spiral just laid, from the outside in to the centre, and at the same time to lay down a new, sticky prey-capturing spiral. All this may seem like a great deal of hard work, as indeed it is (especially since she will take it down again the next evening to construct a new one), but then the whole survival of the animal depends on it.

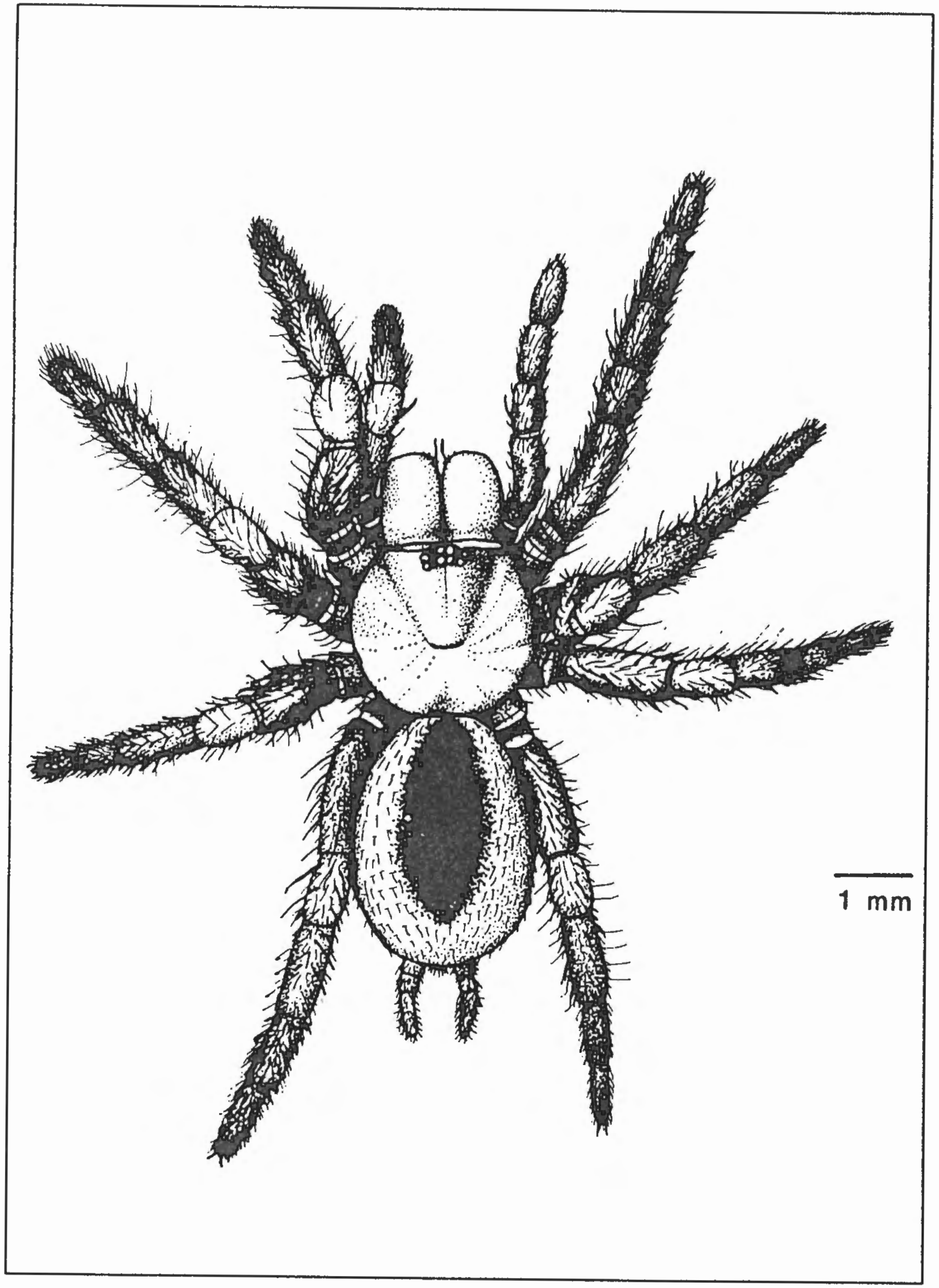

Figure 1 A reconstruction of *Rosamygale* - the oldest mygalomorph spider from the Triassic of the Vosges, France. (Selden and Gall 1992).

A major question which has taxed the minds of arachnologists over the years has been: is the orb web the pinnacle of spiders' achievements, or is it, on the contrary, a rather simple structure from which webs with different architectures have been derived? The reason for this puzzle is that there are a great many modified orb webs. Some have a zig-zag band of bright silk running across the centre in a line, or the web may have a cross woven into it (the St. Andrews cross spider from Australia, for example). Such a device, called a stabilimentum, may function to draw attention to the web and thus prevent large flying creatures such as birds from crashing through the web and destroying it. Some orb webs are elongated in one direction, forming a ladder web. Others are horizontal, rather than the more familiar vertical ones, and have a complex arrangement of scaffolding above or below Such webs may use the scaffolding as a baffle which small flying insects hit and fall onto the orb-sheet, while others have stick droplets on threads hanging below the horizontal orb to trap insects walking underneath. All these web types could be considered specializations developed from the basic orb plan. Specialization may require reducing the orb; in some species it has been cut down to a mere triangle, and perhaps the ultimate in minimalism is the 'web' of *Mastophora*, the Bolas spider, which consists of a single thread with a large ball of glue at the end. This spider emits a chemical which mimics the pheromones put out by female moths to attract a mate. When a male moth arrives, lured by the prospect of a mate, the spider swings the ball-and-thread round and round until it the moth gets stuck to the glue. Rather than the good time he was expecting, the moth becomes a juicy meal!

Other spiders, the cribellates, use a quite different method of producing sticky silk. These spiders have a comb of curved bristles, called a calamistrum, on the last pair of legs, with which they draw silk from the spigots across a plate bearing short spines (the cribellum) situated just in front of the spinnerets. This 'carding' process produces a woolly type of silk which insects' hairs will stick to readily, in just the same way as burrs stick to a woolly jumper Silk of the common house spider *Amaurobius* is cribellate, and has a typically bluish tinge. *Amaurobius* makes a silken tube in a wall or beneath bark, but some other cribellate spiders weave orb webs, *Uloborus* for example. Some *Uloborus* weave stabilimenta into their webs, and other cribellate orb-web weavers produce highly modified webs. *Hypiotes* makes a triangular web which is derived from one sector of an orb; it holds this taught between two twigs, letting it collapse around any insect which flies into it. Perhaps the most amazing cribellate orb web is that woven by *Deinopis*. This spider is large with long, twig-like legs. It has two enormous eyes directed forwards on the head, giving it the common name of Ogre-faced spider. *Deinopis* lives in tropical forests; at night it weaves a tiny but complete cribellate orb web between its four front legs. It stretches this out like a cat's cradle and holds it taut until an insect approaches, when it collapses the web over the insect rather like the Roman retiarius gladiator with his net.

So, just as in the araneid orb-web weavers, the cribellate forms have developed the orb web and then reduced it in various clever ways for specialized uses. The big question is: did the orb web evolve many times, in both cribellate and ecribellate spiders, or was there an ancestral cribellate orb-web weaver which gave rise to ecribellate orb-web and non-orb-web weavers? Current research based on living spiders suggests the latter, but palaeontology has some light to throw on these matters as well.

Fossil spiders are generally rather rare. They do not preserve well, and do so only under special circumstances. Perhaps the best known are those found in amber; for example that of Oligocene age from the Baltic region. Fossil spiders are also known from Tertiary rocks on the Isle of Wight, and in the Coal Measures. Few Mesozoic spiders were known until recently, when some were discovered in Cretaceous lithographic limestones in the Sierra de Montsec, a range in the foothills of the Pyrenees near Lleida, in north-east Spain. The fossil fauna found in limestones in old quarries in these hills was well known, and contained many beautifully preserved insects and plants. Excavations organized by Lleida Museum a few years ago enlisted the help of the Spanish army! During these digs, many exciting fossils were discovered, including fish, frogs, and even bird feathers and bones. Four spiders turned up as well, which were sent over to me for study, and they proved to be quite exciting.

On first examination, the spider fossils appeared simply as shapes in the rock, preserved as flakes of brown cuticle on, or just within, the slightly translucent fine limestone. A number of techniques were used to see them better Alcohol has many uses in palaeontology, and a drop on the specimen increases the contrast for light microscopy; but to see very fine details such as the pattern of hairs on the legs, or the spinnerets, a reflected light microscope, such as that used by ore mineralogists, was employed. In this microscope, light passes down the objective lens to be reflected back up the same lens. Thus, light could be brought to the specimens at very high magnification. Inspection of one of the spiders revealed it to be an adult male of an araneoid orb-web weaver. Evidence for this was found in the nature of the bristles and claws at the tip of each leg. Three claws (rather than two) suggests a web-weaver, and specialized curved, serrated bristles indicated an orb-web weaver Two more specimens could be identified as belonging to the modern family Tetragnathidae, also araneoid orb-web weavers. The fourth specimen was perhaps the most interesting of all. A curved calamistrum could clearly be seen on the fourth leg, together with a cribellum in front of the spinnerets. Additional evidence from the sensory hairs on the legs revealed this spider to belong to the superfamily Dinopoidea, and probably the family Uloboridae. These are orb-web weaving cribellates. Therefore, both cribellate and ecribellate orb-web weavers were present early in the Cretaceous (Montsec is dated at Berriasian–Valanginian, around 138 million years old). This does not solve the problem of which came first, the cribellum/ calamistrum or the

orb web, but it places their origins back into the Jurassic at least.

All but one species of British spider are araneomorphs, *Atypus affinis* is our only representative of the mygalomorph (or bird-eating, funnel-web, trapdoor, tarantula) spiders. These spiders differ from araneomorphs in that their cheliceral fangs strike down on prey rather than clasping it in a pincer-like sideways movement. Some (the so-called tarantulas) are large, but many are small and live in burrows; they are typical of tropical and southern hemisphere regions of the world. The Isle of Wight fossil spider is a mygalomorph, and a few have been described from Tertiary rocks. A couple of years ago some mygalomorphs were described from Cretaceous rocks in Siberia and Mongolia. Then, in 1990, I spent a few days in Strasbourg working with Professor Jean-Claude Gall, studying ten specimens of spiders from Triassic rocks there. Strasbourg is a pleasant city, with a fine cathedral built of Grès à Voltzia sandstone, an excellent freestone. This stone is quarried in the northern Vosges, and many of the quarries occasionally hit clay wayboards, rather like those which are responsible for the springs in the Triassic sandstone at Alderley Edge. The claystones represent shallow pools in a deltaic setting adjacent to the western margin of the Zechstein Sea. The Grès à Voltzia had long been known to produce exceptionally preserved fossils of plants, insects, vertebrates, and even jelly fish and gelatinous strings of eggs. The ten spiders turned out to belong to a single species of mygalomorph spider, which we called *Rosamygale* (Fig. 1). This is the oldest known fossil mygalomorph, and the find more than doubled the fossil record of the group. What was particularly interesting was that the family which it belongs to, the Hexathelidae, is mainly antipodean today It suggested that the family, and probably many other mygalomorphs, was widespread over the supercontinent Pangaea before its break-up later in the Mesozoic.

Going back in time, fossil spiders are known from Carboniferous Coal Measures in Europe and North America. All those I have seen have clearly segmented abdomens. This is a feature of the third main group of spiders alive today· the liphistiomorphs, represented by *Liphistius* in Malaysia. *Liphistius* lives in a silk-lined burrow with a trapdoor at the entrance and is considered to be the most primitive of all spiders alive today So, the fossil record appears to mirror our concept of spider evolution, with the Palaeozoic forms being the most primitive, mygalomorphs appearing first in the Mesozoic, and araneomorphs arriving later Are there any spiders older than this?

Carboniferous terrestrial faunas contain fossils not only of spiders but also of other arachnids in relative abundance (compared to the Mesozoic for example). Scorpions were at their most diverse then, and another group, the trigonotarbids, occur fairly frequently in some Coal Measure sequences. Trigonotarbids are extinct, but their fossil record goes back further than the Carboniferous. Our knowledge of the morphology of 'trigs' benefits greatly from their occurrence in the famed Rhynie Chert, a Lower Devonian hot-spring deposit in Aberdeenshire.

Animals and plants preserved in the translucent chert reveal their morphology in three dimensions, and serial sections can be useful as well. Study of Rhynie Chert 'trigs' showed that they are quite closely related to true spiders, and were important predators in these early terrestrial ecosystems.

Rhynie Chert arachnids had been known since 1923 but in the 1980s, trigs were discovered by palaeobotanists dissolving mudstone from the Upper Devonian of Gilboa, New York for well-preserved fossil plants. A number of trigonotarbids were described from Gilboa, but in 1989 a spider spinneret was recognized among the thousands of fragments of animal cuticle from this deposit. This was not only the earliest fossil spider but also the oldest evidence for silk production by any animal. That year I worked on the fauna with Professor Shear at Hampden-Sydney College, Virginia, and we described the fossil spider from many more fragments which had the same cuticle pattern as the spinneret. It turned out that a fragmentary animal we had described in an earlier paper as a probable trigonotarbid was actually the spider. What makes a spider differ from a 'trig' is the possession of spinnerets, but otherwise they are rather closely related.

The story of the fossil record of spiders does not quite end there. In 1990, Andrew Jeram, who was working here in Manchester on early land animals, discovered some interesting pieces of arthropod cuticle dissolved out of sediments just above the famous Ludlow Bone Bed at Ludlow, Shropshire. Fragments of fish teeth and spines have been chipped out of the Ludlow Bone Bed on the corner of Ludford Lane opposite the Youth Hostel in Ludlow by generations of fossil collectors. The danger of collapse of the overhanging rock at this corner prompted the Nature Conservancy Council to clean up the site and make it safe. Any rock removed was kept for study, and it was this material which produced the animals. One black speck turned out to be a trigonotarbid. The Ludlow Bone Bed lies on the boundary between the Ludlow and Prídoli stages of the Silurian period. This is dated at 414 million years old, and is 16 million years older than the previously known oldest terrestrial animals from the Rhynie Chert.

Trigonotarbids, spider relatives, are among the oldest known land animals, and we may yet find spiders in the Ludford Lane deposit as well. Man has been on this planet for about 2 million years, yet spiders have been weaving webs to catch insects for 400 million years. Surely, we should treat the spider with the respect she deserves!

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SEA DEFENCES ALONG THE NORTH WIRRAL COAST: RIVER MERSEY TO MEOLS

by HAZEL E. CLARK

Processes Common to all Beaches

A beach is an accumulation of unconsolidated material between the highest and lowest levels of spring tides. The size, sorting and quantity of material forming the beach are significant factors in determining its final form. The gradient, height in relation to the mean sea level and resistance to erosion affect the rate of coastline development.

Waves are the fundamental force operative on a beach. They are generated by the wind and their size is determined by the strength of the wind and the distance of water over which the wind can build the waves (the fetch).

On many coastlines the dominant wave direction is oblique to the shoreline and material is carried obliquely up the beach, but is then moved, under the influence of gravity, straight down the beach by the backwash. This process is called longshore drift and moves material sideways across the beach in a down drift direction. Tidal currents may also contribute positively or negatively to this process.

Left to itself, a beach will attain a profile that is in dynamic equilibrium with its environment, i.e. little change is taking place - for example the amount of material lost through erosion is equal to the amount gained from accretion. Wave action tends to build a profile which is in equilibrium.

GAINS		LOSSES
River Sediment Supply		
Coastal Erosion		Onshore Loss
Longshore Gain	BEACH	Longshore Loss
Organic Supply		Offshore Loss
Offshore Supply		

Human interference can have a marked effect on the beach. The building of structures such as groynes, sea walls and revetments, disturbs the natural movement of the beach material and may cause profound changes in their immediate vicinity Adjoining areas may be starved of sediment which can lead