Preface

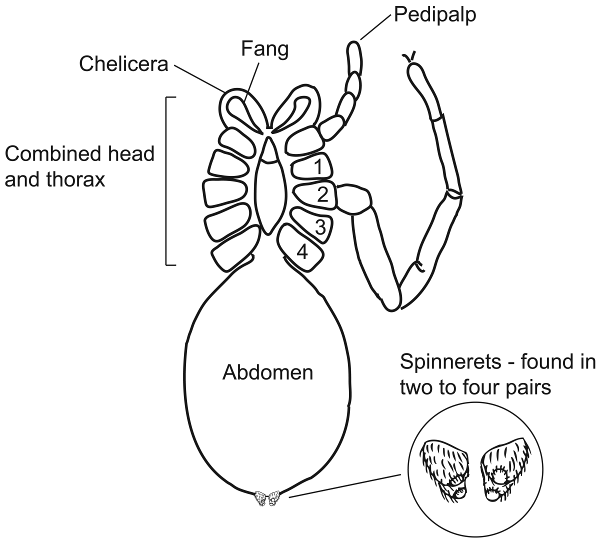
No matter where you are at this moment, you can probably spot some spider silk. Spiders are everywhere, and they often leave evidence of their presence in the form of a strand, web, or tangle of silk. More than forty thousand spider species have been identified, making them the third most abundant type of animal after the first-place insects and second-place ticks and mites. Biologists estimate that there may be forty to a hundred thousand more spider species yet to be discovered. And all spiders make silk. They paste and drape it in every place imaginable, from caves to tree-tops and even under water.

Spiders are best known for using silk to build orb webs, the wheel-shaped webs that look as if they were engineered. These webs, and the spider's ability to produce them using material generated in its own body, have fascinated humans for millennia. They have inspired weavers, civil engineers, and metaphor makers from poets to designers of computer networks. Geometrical, delicate to the point of transparency, yet super strong and super sticky, these webs can stop and hold insects hurtling with tremendous speed through the air. Spiders build orb webs by piecing together a minimum of four types of silk, each having a different form and function. One silk provides strength, another flexibility, and still another a scaffold to aid the spider during construction. Scientists and entrepreneurs have spent millions of dollars trying to copy what spiders accomplish on a budget of dead bugs.

How could anything as complex, functional, and beautiful as an orb web result from chance changes in genes rather than by design? All adaptations to an animal's environment, including spiderwebs, are the products of natural selection, which allows certain random changes in genes to be passed on to later generations. Natural selection is the major mechanism behind evolution, the process of change in a species over time. This change results from the accumulation of gene changes. The spiderweb has evolved gradually, over millions of years. Spiders, too, have evolved over time. Spiders and spider silks are thus like all animals and all adaptations.

But *unlike* most other animals and adaptations, spiders and their silks allow us to understand relatively easily how small changes in genes can lead to evolution at the species level. Nonbiologists may have trouble grasping how minute genetic changes can lead to anatomical, physiological, or behavioral alterations that help an animal survive. The evolution of spiders can help elucidate the workings of natural selection—and why Charles Darwin's phrase "descent with modification" so well describes evolution at both the genetic and the species level. The case of spiders can also help dispel some commonly held misconceptions about evolution, such as the notion that it always leads to a better organism or aims at a perfect adaptation to the environment. Indeed, the orb web is by no means a perfect adaptation, and some shockingly messy-looking spiderwebs evolved *after* the orb web.

Spiders are unusual because their survival hangs on their silk; in fact, without silk, a spider is not a spider. The scientific definition of a spider includes a precise list of physical characteristics ranging from the tips of the animal's legs to the hinge of its fangs. The spider's most salient features include a body divided into two main parts—a prosoma (com-



The Underside of a Spider
All spiders have all the features shown here, although the size, shape, and position of many features differ in different species. The numerals refer to the four pairs of legs. (Drawn by Peter Loftus)

bined head and thorax) and an abdomen—and four pairs of legs. At the front of its head is a pair of chelicerae (jaws), each tipped with a fang. Between the chelicerae and the legs is a pair of smaller limbs called pedipalps, which help with food-handling and object-moving chores. (Pedipalps also play a unique and bizarre role in the sex lives of spiders.) But an animal could possess all these features and still not qualify as a spider if it lacked abdominal silk spinnerets.

Spinnerets are the external parts of the spider's silk-making apparatus. Inside the abdomen, multiple silk glands feed silk dope to the spinnerets via ducts. Under a microscope spinnerets look like hairy, pointy teats. The "hairs" are actually spigots, tiny tubes through which silk extrudes. Different spider species have different numbers of spinnerets, and the spinnerets may jut out from the middle of the abdomen or from the hind end. Spiders are the only animals that have abdominal spinnerets.

Their silks, too, make spiders unique. Although many insects and other similar animals produce silk or silklike substances at some point in their lives, only spiders make silk throughout their lifetime, regardless of their sex. Silk is what has allowed spiders to remain so spiderlike even as they have diversified into tens of thousands of species.

Consider, in contrast, the insects. Comprising a million species, insects account for more than half of all known species of organisms now alive and are often lauded as the most evolutionarily successful animal. The forty thousand spider species may look unimpressive when stacked against the million insect species. But insects have undergone considerable contortions on the way to this evolutionary success. Some are carnivores, some herbivores, some scavengers, and some parasites, with mouthparts that vary accordingly. Flies and bees have wings; fleas and lice do not. Bristletails and silverfish stay the same shape all their lives; damselflies and dragonflies alter gradually as they mature; beetles and butterflies change form entirely. Because of their huge variety of body types and ways of life, insects can be found almost anywhere on the planet.

In the evolutionary context, then, spiders may seem boring compared to insects. All spiders are predators. Some spiders are bigger and huskier than others, but all spiders have a basically similar body plan. None has conspicuous additional features, like wings. And yet this is exactly what is so startling about spiders. Without undergoing major outward bodily change since they first evolved, spiders have nonetheless adapted to a vast array of conditions, from desert to rain forest, from valley bottom to mountaintop, from untouched wilderness to medicine cabinet.

Silk has made the spider's adaptation to these different environments possible. As spiders have evolved, they have developed many ways of using silk: to protect themselves and their eggs, to detect and catch prey, to travel to new habitats. They use some silks as glues, some as watertight packaging, some as rappelling rope, some as super-flexible impact-absorbing snare netting. When spiders use silk as trip lines or webs, they are able to extend their energy, their senses, and even their physical reach without changing the outlines of their anatomy. Modifications to the strength, flexibility, stickiness, and appearance of silk are the equivalents of the flea's jumping power, the stick insect's camouflage, the butterfly's wings, the wasp's venom.

Spiders also have the unique ability to make more than one kind of silk. "Living-fossil" spiders, which are almost identical to some of the oldest spider fossils yet found, make only a few different silks. Spiders that have evolved more recently, however, have six or more different silks at their disposal. Each is produced in a different type of gland and used for a different purpose. Each appearance of a major new type of silk correlates with explosive growth in the number of spider species. These new silks seem to have allowed spiders to forge trails into new ecological niches where they did not have to compete with ancestral spider species.

Silk is a protein, a substance made from highly complex molecules that are constructed from smaller molecules called amino acids. Different combinations of amino acids give rise to different proteins, each with specific properties. Spider silk proteins range from glue to adhesive but nongluey "wool" to fibers strong enough to bear the weight of the spider to bungee cord–like threads that combine enough strength, flexibility, and elasticity to absorb the impact of speeding insects. Some spider silk is as strong as steel and some is as tough as nylon.

Individual spider genes—certain segments of spiders' genome, or DNA—act as the "instruction manuals" for the production of individual spider proteins, including silk proteins. Research since the late 1990s has shown that most spider silk genes belong to the same gene family: although they vary, their variations indicate that existing silk genes have begotten new silk genes. This research allows us to see how a change in spider genes can enhance a spider's chances of surviving long enough to pass that change on to offspring. Spider genes therefore give us a glimpse into the operation of natural selection at the genetic level, where all biological innovation has its roots.

The opportunity to link gene changes in animals to an evident increased chance of survival is rare. Although the ability of scientists to identify gene changes is rapidly improving, singling out a particular gene change as mainly responsible for an easily observable beneficial adaptation is still difficult, because constructing a chain of gene-to-protein and then protein-to-survival links is often difficult. Most easily observable survival mechanisms—eyesight, flight, speed—involve a set of mechanisms so complex and interconnected that researchers often cannot identify all the genes involved, let alone tease apart the interactions among the genes' protein creations. We know that these adaptations *did* evolve —there is plenty of fossil and other evidence for that—but we do not have much idea *how*, genetically, they began, or how they continued, to evolve.

Spider silks thus offer us a rare chance to see how natural selection shapes evolution. In spiders a new gene evolves from an old one: for example, a new gene might dictate a silk protein that has more elasticity than the old silk proteins. As a result, fewer insects will break through a web, and the spider will nab more prey. This spider is therefore more likely to live long enough to reproduce and pass its genetic novelty on to subsequent generations. Given the right environmental circumstances, these descendants may establish a new species. A new gene arises and sometimes, eventually, a new species results. Evolution happens. Spiders can show us how if we follow their silk threads. Follow these threads and the natural selection trials that shaped them, and you may never again sweep away a cobweb without a twinge of remorse.

T • W • O

Living Fossils

In 1849 the Danish entomologist Jørgen Matthias Christian Schiødte examined a number of specimens he had received from a collector who captured animals on the island of Penang, off the Malay Peninsula, then under the control of the British East India Company. At that time interested colonists and professional collectors would take specimens out of the European colonies in Asia and Africa and bring or send them back to Europe, where they often made up the bulk of the "exotic" collections in Western natural history museums. Zoologists associated with these museums, like Schiødte, played an important role in describing and classifying these organisms, publishing their results in journals that were sent to libraries and private subscribers around the world. British, European, and American biologists knew Schiødte as a well-read and precise natural historian, and Charles Darwin later referred to his work on cave insects in *On the Origin of Species.*

One spider in particular caught Schiødte's attention. Like many such specimens, the spider was hardly in the condition it had been when it was captured. By the time Schiødte saw it, it was in "a dry state, having been opened along the middle line of the underside of the abdomen and, after extraction of the contents, stuffed with cotton; it was then placed in spirit of wine."[1] But Schiødte could immediately see that this spider was unlike any he had seen before. The abdomens of all the spiders he had ever examined were smooth. This spider's abdomen was segmented.

By 290 million years ago—nearly 100 million years after the death of the fossilized *Attercopus*—forests of tall trees covered much of the land. The evolution of tall plants led to a number of developments that would prove crucial to both insect and spider evolution. Probably most important was that the soil-covered land was no longer essentially two-dimensional but instead had become a three-dimensional space. Tall plants provided the potential for animals to live not just next to one another but also above and below one another. Each tall plant immensely increased the living area available to small arthropods.[2]

Taking advantage of this change in plant life, insects had diversified and multiplied. Once exclusively denizens of the ground, like spiders, millipedes, and centipedes, insects had started out as predators and eaters of predigested food, including animal waste and dead, rotten plant material that had been preprocessed by microorganisms. In eating the rotting plant material, the insects took the microorganisms into their guts, and a symbiotic relationship between the microorganisms and insects evolved, from which insects gained the ability to process low-protein, high-cellulose plant material into a more animal-friendly form. This in turn led to the ability to eat healthy, live plant parts. Once they had obtained the key to this gastronomic treasure trove, insects began to climb, jump, and fly. Beetles, crickets, cockroaches, and various flying insects began to proliferate. Meanwhile, four-legged amphibians, descended from fish, began to prowl farther and farther from the water's edge in search of food.[3]

While insects began to explore the world above the forest floor, spiders remained secure below it. We know this because 290 million years ago a member of the Mesothelae, the oldest surviving lineage of spiders, died on ground that is now part of France, and its remains eventually fossilized. Mesotheles give us the most complete view yet available of how the earliest spiders probably lived.[4]

The Malaysian spider that Schiødte described in 1849 and named *Liphistius desultor* was the first mesothele known to the Western scientific world, although arachnologists did not coin the word *mesothele* until decades later. Even though its segmented abdomen was unique, arachnologists first believed it to be a close relative of the tarantula. But in 1892, by which time a few more specimens had been catalogued, the eminent English arachnologist Reginald Innes Pocock wrote a paper giving "good reasons for assigning *Liphistius* a still greater classificatory value, and placing it in solitary grandeur over against all other known spiders." These "good reasons" referred to the strange anatomy of the spiders. Their front halves are similar to the front halves of other spiders, but their abdomens, topped by a series of plates called tergites, clearly connect them to more segmented arthropods in a way that is not obvious in other spiders (fig. 5). Based on their dissections of spiders and observations of internal segmentation, some arachnologists had hypothesized that the first spiders or their immediate ancestors had been outwardly segmented as well, and these *Liphistius* specimens provided physical evidence that this might be true. In addition, the spinnerets of all previously known spiders projected from the rear of their abdomens. Schiødte could not see any spinnerets on his pickled *Liphistius*. But the newer specimens showed that these spiders did indeed sport spinnerets—in fact, they often had a full complement of four pairs. (Apparently Schiødte's collector had destroyed them while slicing open and then stuffing the spider's abdomen.) Pocock proposed to place *Liphistius* in "solitary grandeur" under the title *Mesothelae* because its spinnerets, unlike those of any other known spider, projected from the middle (*meso-*) of the un-

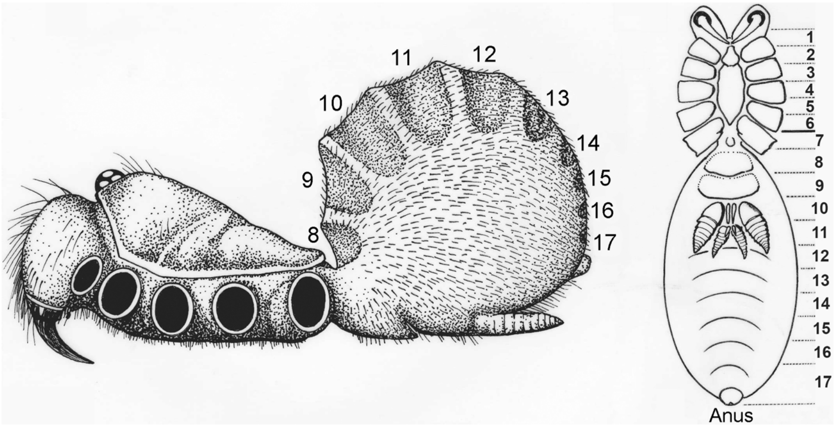


Fig. 5. Mesothele Anatomy
Note the tergites on the top of the abdomen and the position of the spinnerets in the middle of the abdomen. Each number indicates a body segment. (From Foelix, *Biology of Spiders,* p. 31, figs. 29a and 29b, after Millot, "Ordre des Aranéides." Reprinted by permission of Oxford University Press, Inc.)

derside of the abdomen. (*Thele* comes from the Greek for "teat," referring to the shape of spinnerets.)[5]

Taxonomists assign all spiders, living or extinct, to the order Araneae (from the Latin for "spider"). After years of analysis and controversy, arachnologists now generally believe that living spiders fall into two suborders, Mesothelae and Opisthothelae ("posterior teat"). Opisthothelae comprises two infraorders, Mygalomorphae (tarantulas and their closest relatives) and Araneomorphae, or "true spiders," the silk-spinning spiders that people are most familiar with. The Mesothelae and Opisthothelae suborders share a common ancestor. The Mygalomorphae and Araneomorphae infraorders share a more recent common ancestor.

Mesotheles are considered "living fossils" because many of them are almost identical to the 290-million-year-old fossil mesothele found in France. *Living fossil,* a term invented by Darwin, is one that many biologists do not like. To them it has the same ring as *primitive*—which they have also largely abandoned—for both terms conjure up images of an organism that has been left behind by evolution and is therefore a lesser organism than so-called advanced organisms. Other living fossils include the ginkgo tree, the platypus, and the coelacanth. All these organisms have characteristics that appeared early in their evolutionary history and have persisted virtually unchanged to the present. Not "lesser" at all, these organisms have been tested by great changes in their environments occurring over tens, and sometimes—as in the case of mesotheles—hundreds, of millions of years. And they have survived with their original characteristics mostly intact.

Because mesotheles have remained essentially unchanged, their behavior is probably similar to that of the first spiders and can give us insight into early life on land. They can also offer tremendous insights into early silk protein and gene evolution in all spiders. Yet few arachnologists study mesotheles because of the difficulties involved. Today, mesotheles live only in China, Vietnam, Japan, Malaysia, Sumatra, Thailand, and Myanmar, and they are often hard to find—males of some species have never been captured. In addition, there is no commercial interest in their silk proteins, so research funding is scarce. And they develop slowly, taking years to mature. Researchers who want to observe entire lifecycles need great patience to do so. Still, what little is known about mesotheles sheds light on some central questions about how silk enabled spiders to survive the perils of more than 300 million years of environmental change.

Mesotheles dig burrows into moist soil, preferring shaded banks and slopes. Shoveling out soil with its chelicerae and pedipalps, the mesothele tunnels into the ground, cramming its body against the burrow walls and ceiling, compacting the soil and reducing crumbling. Muscles spiraling throughout the spider's spinnerets from base to tip give them great agility; even though their position in the middle of the abdomen might seem awkward, the spinnerets are able to reach like tiny fingers to nimbly lay down a lining of gauzy silk around the burrow interior.

The spider then builds a trapdoor by dragging nearby soil and bits of debris to the burrow entrance. Coordinating its legs, chelicerae, pedipalps, and spinnerets, it uses silk protein to glue this material to the top of the burrow's doorframe. Continuing to glue soil and debris together, the spider works its way down the entrance opening until it has produced a swinging door (see plate 1). Because the spider attaches the second and each subsequent load of material to the leading edge of the previous load, rather than to the doorframe, the silk protein at the top of the doorframe becomes a hinge for the whole door. This process effectively camouflages the door and hides the burrow, for the door has been made from the debris and soil of its surroundings. By the time the spider is finished with the burrow, a thin sheet of silk protein coats the interior and the inside of the door. This silk-based trapdoor offers its maker a number of benefits. It hides the spider lurking behind it from both predators and prey and creates a membrane between the underground and aboveground air, moderating humidity within the burrow and even protecting the burrow from short-term flooding.

Silk also plays an important role in mesothele egg protection. The mother mesothele lays down a sheet of silk at the far end of her burrow on which she deposits her eggs (ranging in number from about thirty to more than three hundred depending on species) and then covers them with another silk sheet.

Mesotheles are almost entirely nocturnal, a habit that probably stems from the time when plants were too small to protect land arthropods from the sun. As night begins to fall, the mesothele waits for dinner, taken mainly in the form of small insects. Spurred by instinctive reactions to the waning light, the spider cracks open the trapdoor and sets its legs around the bottom rim of the doorframe. Now able to pinpoint nearby movements by gauging the ground vibrations it feels with its different legs, the mesothele is poised to pounce. Meanwhile, because the spider can pop the trapdoor closed and hold it firmly from inside the burrow, the door helps protect this hunter from competing predators who might enjoy seeing mesothele on the menu.

The spider senses movement just beyond the rim of the burrow . . . then lunges. Unlike spiders that evolved later, mesotheles lack silk fibers strong enough to tie up their prey and immobilize it, and they also lack venom glands with which to poison it. A steady grip and aggressive crunching with the pedipalps have to do the job.

Mesotheles so closely resemble one another that systematists—who classify organisms and study their evolution and evolutionary relationships—have assigned them to a single family, Liphistiidae. But mesotheles hunt in two different ways. Some mesothele species keep at least one foot in the door as they grab their prey. But other species use silk to extend their hunting ground beyond their immediate dooryard. They lay down six to eight trip lines that radiate a few centimeters from the doorframe. To the human eye, these trip lines look a bit like thick, rough sewing thread. Under a scanning electron microscope, however, they resemble irregular, loosely wound ropes held off the ground by less densely wound "stalks." Because they hang in the air, the trip lines transmit uninterrupted vibrations to the spider's legs at the doorframe. When passing prey hit a line, the spider knows exactly which way to charge. A rush over the top, out along the line, and the spider nabs its surprised victim. Reverse direction, retreat, flip open the trapdoor, barrel back inside, and the spider can dine in the security of its burrow.

To date arachnologists have identified about ninety mesothele species. The classification of a new species often rests on spiders' unique mating mechanism. As male spiders mature, they develop a palpal organ (basically, a modified foot) on each of their two pedipalps, the leglike appendages in front of the walking legs. They use this organ to insert sperm into a female's body. Masculine preliminaries take place under cover of darkness. To prepare for copulation, the male suspends a small ribbon of silk between two pebbles or other objects outside his burrow. He then limbos belly up under this “sperm web,” hobbling on his patellae (the spider equivalents of elbows and knees). As he passes underneath, he deposits sperm from his genitals onto the silk. He then rights himself and sucks the sperm up into the palpal organs. With his organs loaded, he creeps off in search of a female. The microscope reveals that parts of these palpal organs vary wildly in shape among species, from beaky prongs to angelfish tail horns to bulbish pods, and everything in between. More than any other external features, the males’ palpal organs and the females’ reciprocally fitted copulatory organs have become the spiders’ taxonomic identification cards. Arachnological systematists often seem genitally fixated, but this is not their fault. Spiders leave them few other options.

Other than these brief periods of excitement, a mesothele’s life is rather humdrum. Mesotheles are dine-at-homes and stay-at-homes. They hunker down in their burrows night and day, darting out only to hunt, to find a mate, or to scramble for cover if their burrow is attacked. For most of their lives, they sit perfectly still, using little energy and consuming little oxygen.[6]

Watching mesothele behavior, one might imagine that plants had never grown taller than they were when the early land arthropods lived 400 million years ago and that insect flight had never evolved. The world two meters away from mesotheles on the ground or a centimeter above them in the air holds no attraction. And yet their silk-lined burrows, evolved in the distant past, protect them from every new danger, such as flying and four-legged predators. They have not only survived virtually unchanged but also have thrived, diversifying into their ninety species.

Few creatures have managed to survive the traumas and changes that have taken place on earth over the past 290 million years. A common misperception about evolution is that as environments drastically change, organisms are forced to evolve equally drastically in order to survive. But according to the fossil record, mesotheles have evolved very little; they are constructed much as they were in the past, and their silk seems to have remained largely unchanged. The story of spider silk could have stopped with mesotheles, seemingly no closer to an orb web than it was at its beginning, but spiders and their silk systems evolved in many different directions. Why? And how?