

Fig. 4. Example of lee waves over Colorado, observed in the water-vapor channel of the MODIS instrument on October 3, 2005, 1945 UTC. (Courtesy Kris Bedka, CIMSS, University of Wisconsin-Madison)

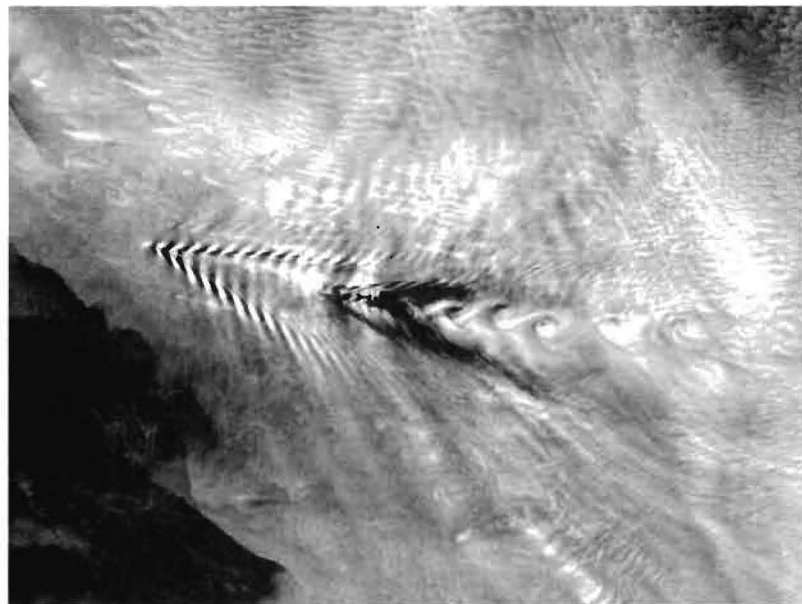


Fig. 5. Atmospheric ship-wave pattern and wake vortices behind two islands in the Crozet Island Archipelago in the southern Indian Ocean, as observed in MODIS visible satellite imagery on November 4, 2004. (NASA, <http://visibleearth.nasa.gov>)

4). In regions of constructive interference, wave amplitudes may become large enough to initiate wave breaking and turbulence.

The ship-wave pattern is generally possible in any system in which the wave propagation is dispersive (that is, the wave speed depends on the wavelength) and there is a point-source disturbance. As discussed above, this is the case for free-surface water ship waves and atmospheric gravity waves forced by flow over isolated obstacles (such as an island or an overshooting convective tower atop a thunderstorm) in the atmosphere and oceans, and for inertio-gravity waves (where rotational effects are significant). It is also the case for lightning-generated "whistlers" (audio-frequency electromagnetic waves that propagate along the Earth's magnetic field lines).

For background information see ATMOSPHERE; FROUDE NUMBER; KÁRMÁN VORTEX STREET; VORTEX; WAKE FLOW in the McGraw-Hill Encyclopedia of Science & Technology.

Robert Sharman

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## Silk and the earliest spiders

Spiders are familiar animals whose intricate webs have been marveled at by humans for thousands of years. Silk production is not unique to spiders; indeed, silk is made by arthropods as diverse as silkworms, the spectacular glowworms of New Zealand, and other arachnids including pseudoscorpions. All spiders produce silk, and the possession of silk glands in the abdomen (opisthosoma) is a characteristic feature of the arachnid order Araneae. Other characters of spiders include venom glands in the forepart of the body (prosoma), which emerge from a pore in the cheliceral fang, and the presence of hairless fangs separates spiders from closely related arachnids such as Amblypygi (tailless whip scorpions). During spider evolution, not all of these characters appeared at the same time. For example, the most primitive living spiders, members of the suborder Mesothelae, lack venom glands and hence have no pore in the fang. All other spiders (the suborder Opisthothelae) possess venom glands, except rarely when they have been secondarily lost. New evidence from 380-million-year-old fossil spiderlike animals shows that they lacked venom glands. However, like true spiders, they had silk glands and spigots. The weaving apparatus was different, though, and thus we can speculate on how the silk was used. Arachnologists can now see more clearly the evolutionary pathway of silk production and silk use in early arachnids.

**Silk.** Spider silk consists of proteins together with many different organic and inorganic components, including neurotransmitter peptides, glycoproteins, lipids, sugars, phosphates, calcium, potassium, and sulfur. There are many different kinds of spider silks, each with its own mode of formation and function, even within a single species. Simple dragline silk is composed of a liquid-crystal protein complex and is remarkable for its strength and elasticity; it is produced constantly by running and jumping spiders, and is the main structural silk in webs. Cribellate silk (produced from the cribellum, which is a specialized, flattened spinning organ) has an outer layer of extremely fine strands that can entrap insect legs and hairs like burrs on sheep's wool. The capture spiral of araneoid orb webs (such as those of garden spiders) is covered with glue droplets to which insects adhere. Other silks are modified for use in lining burrows, entrance doors, trip lines, egg sacs, sleeping bags, sperm webs, parachuting or ballooning,

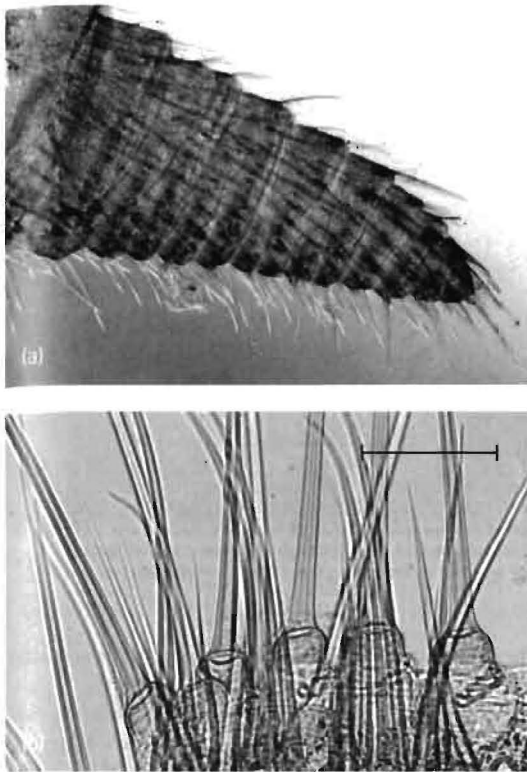


Fig. 1. Spinnerets and spigots of extant mesothel spiders. (a) Anterior lateral spinneret of *Liphistius* showing spigots. (b) Spigots of *Heptathela*. Scale bar = 50  $\mu\text{m}$ .

wrapping prey, hibernating and molting chambers, retreats, and nursery webs for spiderlings.

Different types of glands produce different types of silk; for example, in araneoid orb weavers, one type of gland produces dragline silk, another provides the core of the threads of the capture spiral, and the glue coating is supplied by a third gland type. Spider silk glands consist of a chamber that leads to a duct that emerges to the outside through a spigot. Spigots are hollow hairs (setae), often modified in some way. Simple spigots (Fig. 1) appear different from normal setae by their bell-shaped bases. In modern spiders, the spigots are found on spinnerets, which are modified opisthosomal appendages. One exception to this is the row of spigots (called fustules) along the anterior edge of the epigastric furrow (the posterior edge of opisthosomal segment 2) in adult male spiders. This silk, from the epigastric glands, is used to make a tiny web on which the male spider deposits his sperm before charging his palps with it to inseminate the female.

The spinnerets of spiders are unusual in being opisthosomal appendages, which all other arachnids have lost. The spinnerets can be shown embryologically to represent homologs of biramous appendages (that is, appendages having two branches) of opisthosomal segments 4 and 5. The primitive cheilicerate *Limulus* shows biramous appendages in this position in the form of a segmented median branch and a lateral branch with a plate covering lamellate gills. The most primitive spiders, the mesotheles, have a maximum of eight spinnerets, with two pairs

on opisthosomal segments 4 and 5, called anterior and posterior medians and laterals; even in living mesotheles, though, the anterior medians are non-functional. The anterior medians, at least, are missing in mygalomorph opisthotheles (tarantulas, and funnel-web and bird-eating spiders), and they are either modified to a cribellum or absent in araneomorph opisthotheles.

**Webs.** Most people tend to think of spiders as using silk to make webs for prey capture, but the more primitive kinds of spiders, in the suborder Mesothelae, live in burrows. They use silk for wrapping eggs, lining the burrow entrance, weaving the entrance door, and making radiating trip wires that the spider uses to detect passing prey. Mesotheles are known as fossils from as old as the Pennsylvanian period [ca. 300 million years ago (mya)], by which time insects had already taken flight, and the aerial prey-capture web is thought to have developed to follow the insects into the air to harvest this vast food resource. There are many different kinds of prey-capture webs. For example, a sheet web, as used by the Agelenidae (funnel-web spiders), consists of a dense meshwork of fine strands stretched out from a retreat inside a bush. This kind of web captures grasshoppers and other jumping insects most effectively. When the prey struggles, the vibrations are transmitted to the spider, which runs out and immobilizes the insect. Orb webs are constructed in gaps in vegetation through which insects might fly. Orb webs can use cribellate silk or silk with glue (ecribellate). Uloboridae (the hackled-band orb weavers) make cribellate orb webs and araneoids make the ecribellate type, but both catch prey in the same way. An insect flying through what appears to be an empty space hits the web and sticks to it, and its flight velocity is quickly dampened by the nature of the structural silk. The spider senses the struggling insect, emerges from its retreat, and immobilizes the prey by injecting venom and/or wrapping it in silk. One of the problems with a static prey-capture web is that predators, such as small birds or spider-hunting wasps, develop a search image for a web and its associated occupant, regardless of how the spider attempts to conceal itself. Consequently, many spider families have abandoned the prey-capture web and stalk their prey by sight or other senses. This is especially noticeable in the most diverse of all spider families today, the Salticidae (jumping spiders), whose greatly enlarged anterior median eyes enable them to pinpoint prey and jump on it with great accuracy.

**Origin and evolution of silk.** Although it is clear that silk has been employed by spiders for many diverse uses, several theories have been put forward regarding its origin and early evolution. One idea is that it was used first for lining burrows to prevent their collapse, as is done by modern mesotheles. Similarly, a mesothel dashes out of its burrow to capture prey and then needs to be able to find its way back, so a silken trail would be useful for homing, which could later evolve into a trip wire. Silk is used in many ways during reproduction, for example, in sperm webs

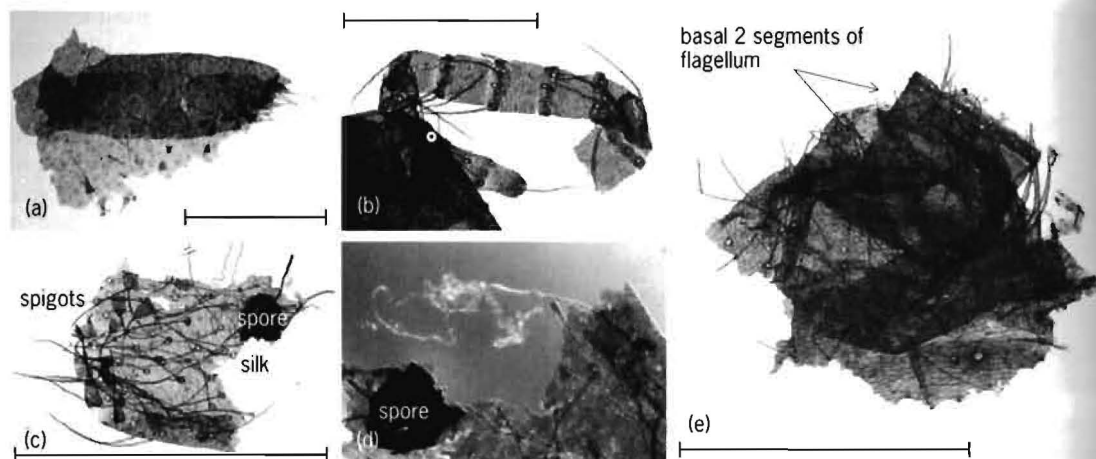


Fig. 2. *Attercopus fimbriunguis*, Devonian of New York. (a) First-described "spinneret"; the darkness of the cuticle reflects the number of layers, so the fragment is folded over twice. (b) Flagellar structure with 12 segments (including the possible distalmost one) from the original Gilboa locality; segments show distal collars and setae. (c) Piece of cuticle from a corner of the opisthosomal ventral plate showing setae, spigots, and a possible silk strand. (d) Close-up of panel c showing the possible silk strand emerging from the spigot shaft. (e) Two flagellar segments emerging from the posterior part of the opisthosoma. Scale bars = 0.5 mm.

and egg sacs, which has led to suggestions that this was its primary function.

Of course, it is unlikely that the silk glands, spigots, and spinnerets appeared together during evolution, so which came first? It is apparent from the discovery of fossils showing spigots arranged along the posterior edge of an opisthosomal plate (Fig. 2c) that the silk glands and spigots developed before the spinnerets appeared. Therefore, it seems likely that the genetic mechanism for the production of a biramous appendage, which had been suppressed in the ancestors of Araneae, was switched back on when the advantage of having spigots on appendages—the maneuverability for weaving webs—became selected for. A strand of material apparently issuing from a spigot (Fig. 2d) may be the oldest fossil occurrence of silk, although it would be difficult to analyze chemically. Silken strands occur alongside the earliest spiders in amber of Cretaceous age (ca. 140 mya).

**Early fossil arachnids.** In the 1980s, paleobotanists macerating Devonian (ca. 380 mya) shales from Gilboa, New York, for fossil plant cuticles found tiny fragments of animals: the oldest land animals from North America. One specimen appeared to be a nearly complete spider spinneret bearing about 20 spigots (Fig. 2a). On the basis of the simple spigot type and the lack of tartipores (vestigial spigots from earlier molts), the fossil spinneret was compared most closely with posterior median spinnerets of mesotheles. The distinctiveness of the cuticle enabled association of the spinneret with remains previously referred tentatively to another kind of arachnid: a trigonotarbid. Detailed study of this material resulted in a fuller description of the animal, *Attercopus fimbriunguis*, which was at that time thought to be the oldest known spider. The appendicular morphology of *Attercopus*, but little of the body, is now known in great detail. A number of other arachnids, including other trigonotarbids, were described alongside *Attercopus* from Gilboa,

including some enigmatic fragments that resembled multisegmented flagella (Fig. 2b).

Later collections made in the 1990s at South Mountain, New York, yielded more *Attercopus* material, including some specimens with spigots. With more specimens available for study, it became clear that the original spinneret was actually a rolled-up piece of cuticle and that the spigots were arranged in two rows along the edge of plates. These are ventral opisthosomal plates, features that occur in relatives of Araneae, such as trigonotarbids and Amblypygi, but which have been lost in true spiders.

The fossil record of spiders is sparse. For example, they were unknown from strata of the Permian period (ca. 300–250 mya) until 2005. Then, *Permarachne*, from the Urals of Russia, was described as an unusual mesothele because it appeared to have a long structure emerging from the posterior of its opisthosoma: an anal flagellum (Fig. 3). Moreover, while the main part of the fossil showed the ventral side, there were plates on the opisthosoma. Because nothing like it was known from mesothele spiders, the flagellum was interpreted as a long spinneret (the other spinnerets were presumed to be absent in the fossil) and the opisthosomal plates were presumed to be dorsal.

Finally, comparing *Permarachne* with the new interpretation of *Attercopus*, it became clear that forcing these animals into a modern definition of spiders did not work. One specimen proved that the structures found with *Attercopus* are really anal flagella, as is the supposed spinneret of *Permarachne*, and the plates on *Permarachne* are ventral, not dorsal (Fig. 2e). Thus, these animals form the basis of the new arachnid order Uraraneida ("tailed spiders"). The spigot location in *Attercopus* suggests that the original use of silk in these protospiders was to produce sheets, perhaps used as burrow linings, as homing trails, or to cover egg masses. The evolution of spinnerets, which would allow more precise weaving of webs, by some mutation that switched back on

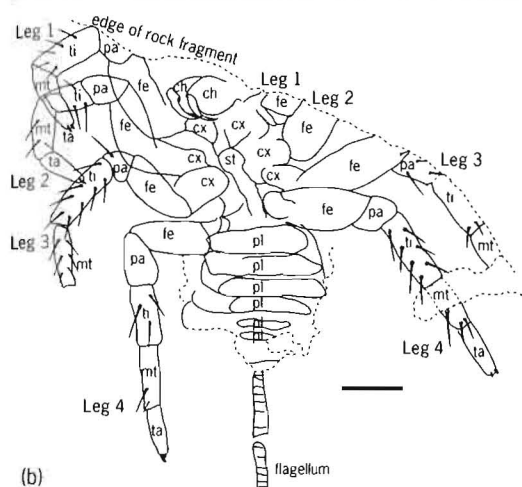
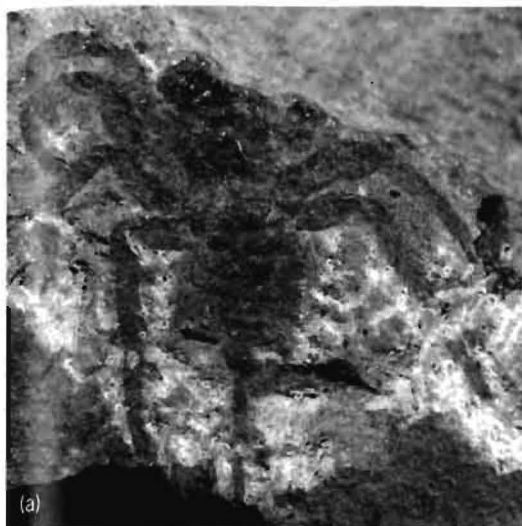


Fig. 3. *Permarachne*, Permian of Russia. (a) *Permarachne* in rock matrix. (b) Explanatory drawing of panel a. Abbreviations: ch, chelicera; cx, coxa; fe, femur; mt, metatarsus; pa, patella; pl, ventral plate; st, sternum; ta, tarsus; ti, tibia. Scale bar = 1 mm.

the genes for opisthosomal appendages, occurred in their relatives, that is, the true spiders.

For background information see ARACHNIDA; ARANEAE; ARTHROPODA; FOSSIL; INSECTA; NATURAL FIBER; ORGANIC EVOLUTION; PREDATOR-PREY INTERACTIONS; SILK; SPIDER SILK in the McGraw-Hill Encyclopedia of Science & Technology. Paul A. Selden

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## Sirtuins

Aging is influenced by complex interactions between genetic and environmental parameters. Sirtuins are a family of nicotinamide adenine dinucleotide (NAD)-dependent protein deacetylases (which remove acetyl groups from protein molecules) and adenosine diphosphate (ADP)-ribosyltransferases (which catalyze the transfer of the ADP-ribose moiety from NAD<sup>+</sup> onto specific substrates) that are thought to play an important role in modulating these interactions. Mammalian sirtuins have been recently implicated in a variety of aging-related processes, and it has been suggested that these enzymes may prove to be effective therapeutic targets for treating age-associated diseases in humans.

**Function.** Sirtuins are named for the founding member of the family, that is, the budding yeast Silent Information Regulator 2, Sir2. Sir2 is a histone deacetylase that promotes the formation of silenced chromatin at three cellular loci in yeast: the telomeres (the ends of chromosomes), the silent mating loci, and the ribosomal DNA (rDNA). [Note that chromatin is the deoxyribonucleoprotein complex forming the major portion of the nuclear material and of chromosomes; histones are a group of positively charged proteins that aid in compaction of the chromatin.] Modulation of the histone acetylation state is an important mechanism for regulating gene expression. Chromatin with highly acetylated histones tends to be permissive for messenger ribonucleic acid (mRNA) transcription, whereas removal of histone acetyl groups reduces transcription by creating a more compact chromatin structure. Yeast cells that lack Sir2 have defects associated with loss of transcriptional silencing at these loci, including sterility, reduced telomere length, genomic instability at the ribosomal DNA, and shortened life span.

The enzymatic activity of Sir2 differs from non-sirtuin deacetylases in that the reaction uses NAD<sup>+</sup> as a substrate and produces 2'-O-acetyl-ADP-ribose and nicotinamide as products (see **illustration**). Nicotinamide and NADH (the reduced or hydrogenated form of NAD) are both inhibitors of sirtuin activity and are believed to be biologically relevant regulators in vivo. Based on this unique catalytic mechanism, Sir2 is defined as a class III histone deacetylase. Sir2 also has ADP-ribosyltransferase activity, in which the ADP-ribose moiety of NAD<sup>+</sup> is covalently joined to the substrate protein, but this activity is believed to be relatively low in vivo. Most sirtuins studied thus far appear to have the capacity to catalyze both reactions under appropriate conditions in vitro.

The sirtuin family is highly conserved from yeast to mammals. Sirtuins have been classified into homology groups (I, II, III, and IV) based on their protein sequence similarity and presumed evolutionary divergence (see **table**). Yeast have five sirtuin proteins, that is, Sir2 and four homologs of Sir2, Hst1–4, all of which are group I sirtuins. The nematode *Caenorhabditis elegans* has four sirtuins, the fruit fly *Drosophila melanogaster* has five sirtuins, and both mice and humans have seven sirtuins