Web masters

Spiders' silky skills hold the key to their evolutionary success.

Spider Webs and Silks: Tracing Evolution from Molecules to Genes to Phenotypes

by Catherine L. Craig

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Spiders are masters of the extended phenotype. The archetypal orb web spider, for example, manages to expand its effective body size by at least an order of magnitude. This remarkable extension is superbly matched to the local conditions, and total daily restoration is often thrown in for free. How does the spider perform this clever trick of morphological inflation? By building its trademark web; by matching and redesigning the structure to suit the changing circumstances of location, weather and prey; by rebuilding it daily; by recycling the silky hardware, so it can devote most of its resources to the software and the 'running costs' of building. Running, or rather walking, is the operative word here, as the web is a frozen record of the spider's path and its manual labour, written in silk.

Silk is the key to the spider's success, with behaviour playing merely a supporting role. Without their silk, spiders would be weaklings among their arthropod peers — if they had survived at all. They are soft-bodied and so are prone to physical damage; they breathe through lungs, and are in constant need of high humidity; and they are wingless, and their hydraulically driven legs buckle when overused. As a result, spiders would have been no match for the tough and virtually indestructible insects. But silk gives spiders a distinct edge, and has become the main weapon in an arms race with their insect relatives, which are both their main prey and major predators.

Mention silk to a polymer chemist and they will get dreamy eyes. It is a natural fibre to match the best man-made ones, but its production is as eco-friendly as it gets, occurring at ambient temperature and near-ambient pressure, with water as the solvent. How is it done? We don't know. Why is it so tough? We don't know. Actually, what is silk, exactly? We don't know. So there's lots of scope for research, then.

This is especially gratifying because state-of-the-art analytical techniques such as X-ray diffraction, Raman spectroscopy and mechanical testing have recently been refined to allow measurements on single silk filaments, which are often less than 2 µm in diameter. Today, single-filament analysis can be done online as the fibres are being spun by the animal; the speed at which the spider

Spinning a line? The silk produced by spiders, such as this golden orb spider, is stronger than that from silkworms.

reels the silk can be altered over five orders of magnitude by heating and cooling the spider.

Although we have no real answers to even general questions, we have come a long way in our understanding of silks, and Catherine L. Craig's *Spider Webs and Silks* is an extremely useful staging post. I don't agree with everything that Craig has written, but even so I can highly recommend the book as a comprehensive and up-to-date account of silk.

The four chapters on silk form the core of the book. The first outlines the history of silk evolution, and the second explores the genetic code behind the proteins that make up some silks. Next comes an investigation of how the mechanical properties of bulk silk depend on the protein skeleton of the filament. And it is all wrapped up by an explanation of the economics of silk synthesis and its effect on the evolution of the wide range of silk types that some spiders can produce.

There are also three intriguing chapters on spider webs and their role in feeding the beast, as well as in constraining the more social aspects of its evolution. These chapters are not so much a review as a personal voyage, relying heavily on the author's own work, which focuses on the interaction of insect vision and a web's architecture as well as the silk's structural properties. There is also a chapter on the absence of higher social development in spiders, which, in a twist, is linked to development and related silk-production costs. The brief final chapter summarizes the author's view on the forces that drive silk evolution.

The writing throughout is clear and well presented, and even though there is no glossary, an effort has been made to avoid jargon.

There is a good index and the references are, on the whole, comprehensive, although with some curious gaps and biases. Overall, the book provides excellent value for money on a number of levels.

Silk research has undergone something of a renaissance, with the focus of study shifting from the classic (and highly commercial) silkworm silk to the more esoteric spider silk. Silkworms spin through their mouth between their nippers, which means that they can cut the fibre at will. Most silkworm silk is collected from preformed cocoons that the worm has spun at its leisure, and it invariably contains numerous weak points resulting from the worm's typical spinning action. By contrast, spiders spin from their bottoms and cannot interfere with forced silking as long as their legs are kept clear, so spider silk is typically collected as it is spun under highly controlled conditions.

It may be that spinning conditions, rather than silk genes, are a major factor for fibre quality, as silkworm silk that is spun spider-fashion can be almost as tough as spider silk (Z. Shao & F. Vollrath *Nature* **418**, 741; 2002). Using spider silks produced under controlled conditions allows the construction and testing of hypothetical links between protein form and folding. In this way, spider silks provide a new way of studying fibrous proteins. For example, recent studies have shown that spider silk shares important protein-folding configurations with amyloids and prions (J. M. Kenney *et al. Eur. J. Biochem.* **269**, 4159–4163; 2002), which suggests that unravelling the spider's way of making a tough fibre might have surprising results.

Craig's book has the somewhat puzzling

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subtitle "Tracing evolution from molecules to genes to phenotypes". Most authors would have gone from genes to phenotypes without bothering with the molecular level. But not Craig, who states that one of her goals is "to illustrate the ease with which evolutionary studies of spiders and silk proteins can cross traditional molecular and organismal borders". Thus silk proteins are "the perfect system through which to study evolutionary conflicts among molecular genetic constraint, protein architectural constraint, protein diversity and selection". Indeed, silk has evolved to function as a dead material outside the animal's body. And silk is only one step (spinning) removed from the protein in its native form; the chain from gene to raw protein to dehydrated protein fibre is brief.

But more importantly, the fibre, once drawn — whether as a simple drag safety line or as a structural member in a web — is the phenotype that is selected more or less on its own, distinct from its creator. This is unusual for a protein and suggests that silk might allow for shortcuts in the study of protein evolution — yet another reason why studying silk might provide interesting insights into the more general aspects of protein folding.

Be that as it may, Craig's *Spider Webs and Silks* brings a fascinating and important subject to a potentially broad audience. And it might even turn some arachnophobes into arachnophiles. ■

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From genes to biochemistry

George Beadle, an Uncommon Farmer: The Emergence of Genetics in the 20th Century

by Paul Berg & Maxine Singer
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Genetics is a young science, having its roots just 100 or so years ago in the rediscovery of Gregor Mendel's work on inheritance in peas. These days, this history is left out of most textbooks and is rarely taught at university. Today's students learn only about what has happened in the past five years, not about the pioneering work that opened up their field — they know nothing of the giants on whose shoulders they stand. If you ask today's advanced genetics students about George Beadle (1903–1989), you would be met with a deafening silence. So it is fortunate that Paul Berg and Maxine Singer took the time to write a book about this great pioneer.

Field work: at Cornell, George Beadle (kneeling) studied maize genetics with Barbara McClintock (right).

They describe Beadle's family and his childhood and youth on a farm close to Wahoo, Nebraska. His father prevented his elder brother from going to agricultural college, but when this brother died after being kicked by a horse on the farm, George was allowed to go the agricultural college in Lincoln, where he developed an interest in maize genetics. His intelligence and hard work impressed his teachers, who sent him to Cornell University in Ithaca, New York, where he continued to work on maize genetics. There he met Barbara McClintock, who demonstrated that maize has ten chromosomes. But her supervisor was not amused when she published this under her own name without including him as a co-author.

Beadle's work on maize genetics earned him a PhD in 1929, after which he moved to the California Institute of Technology, which was an exciting place to be. Thomas Hunt Morgan had just moved there, and the authors describe his fly group in a separate chapter that is a must for students. I would have liked to hear more. For example, the authors mention that the undergraduate Alfred Sturtevant produced the first linear map of five genes of the fruitfly's X chromosome, and that Morgan allowed him to publish his results without demanding his own name on the paper. Berg and Singer don't comment on this, but how many professors would allow this today?

Beadle started collaborating with Boris Ephrussi, who was on sabbatical there, to try and understand what a gene produces. For Morgan and his group, the gene was abstract, but Beadle and Ephrussi wanted to come closer to biochemistry. They concentrated on *Drosophila* mutants with different eye colours, *vermillion* and *cinnabar*. After five years they concluded that tryptophan is converted by the *vermillion* gene into a substance of unknown structure. So it was a blow in 1940 when they read in the journal *Naturwissenschaften* that Adolf Butenandt had identified the compound as 3-hydroxykynurenine. Five years' work and then scooped!

Ephrussi then moved into a different field but Beadle stuck to the problem. During a lecture by his postdoc Edward Tatum, Beadle had the idea of treating micro-organisms with mutagens and isolating mutants that are unable to produce amino acids, hormones or other substances. These mutants will then show that one gene produces one enzyme. Tatum did the experiment using the fungus *Neurospora*. It worked like a charm, and hundreds of such mutants were isolated and analysed. What worked well with *Neurospora* worked even better with the bacterium *Escherichia coli*. One of Tatum's students, Joshua Leder-

berg, showed that such mutants could be isolated, and demonstrated genetic exchange between two mutants of *E. coli*. In 1958, Beadle, Lederberg and Tatum shared a Nobel prize for their work. As Ephrussi wrote to a friend: "I suddenly felt my life wasted."

But the story does not end here. When the experimental problem was solved and Beadle had convinced the sceptics, he moved into the field of administration at Caltech, first as chairman of the biological faculty and then as president. He excelled at hiring excellent faculty and defended Linus Pauling when he was attacked as a communist. Even after his retirement, Beadle returned to a familiar problem: was teosinte, a wild grass from Mexico, really the predecessor of maize?

The book tells us in detail about Beadle's two marriages, the salaries he earned (but not their equivalent values today), his journeys by ship and by train, and the fact that he succumbed to Alzheimer's disease. There is plenty here for everyone. Those interested in the history of genetics will want to read the whole book, but today's students would benefit from just a few chapters. ■

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A recipe for success?

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<http://www.interscience.wiley.com/db/os>
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John Mann

The total synthesis of complex natural products remains one of the most tangible and often elegant demonstrations of the chemist's craft. Some practitioners have turned these endeavours into something approaching an art form. It is also often