Physical properties of honeybee silk: a review

H. Randall Hepburn[1], Orawan Duangphakdee[2], Christian W. W. Pirk[3]

[1]Department of Zoology and Entomology, Rhodes University, Grahamstown, South Africa
[2]Ratchaburi Campus, King Mongkut's University of Technology, Thonburi, Bangkok, Thailand
[3]Social Insect Research Group, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

Abstract – Honeybee silk is released from secretory cells and polymerises as birefringent tactoids in the lumen while silk is spun by a spinneret at the tip of the labium–hypopharynx and contains ά-helical proteins arranged in a four-strand coiled-coil structure. Wet fibres are only half as stiff as dried ones, but are equal in strength. The fibroin is hygroscopic and lithium thiocyanate and urea eliminate the yield point tested on both dry and wet fibres. The slopes of the solvent-related curves are reduced compared to those tested in water. Silk sheets are independent of temperature when deformed in tension. This fibre is rather crystalline and its hydration sensitivity, expressed as the ratio of the elastic modulus of wet to that of dry fibre, is 0.53. The ά-helical fibroins are predicted to have an antiparallel tetrameric configuration that is shown as a possible structural model. The molecular structure of ά-helical proteins maximizes their robustness with minimal use of building materials. In conclusion, it appears that the composition, molecular topology and amino acid content and sequence are a highly conserved feature in the evolution of silk in *Apis* species.

honeybee / silk / ά-helix / fibroin

1. INTRODUCTION

The honeybee nest contains areas for the storage of nectar and pollen and for the rearing of brood. While wax, in its hexagonal structure (Pirk et al. 2004), is the basic building material for the nest, with continued use the combs become modified by the additions of silk and propolis (Hepburn and Kurstjens 1988). Thus, much of the honeybee nest gradually changes from a single phase (wax) to a composite (wax/silk) material. Some of the material properties of the individual phases of the honeybee nest have previously been characterized (Hepburn 1986; Hepburn et al. 1979; Hepburn and Kurstjens 1988; Kurstjens et al. 1985, 1990), but particularly important recent studies on the molecular structure of honeybee silk (Sutherland et al. 2006 et seq.) necessitate a review on the composition and properties of honeybee ά-helical silk (Figure 1), the elastic element in combs of all honeybee species.

"Silk" is a functional term used to describe protein fibres spun by honeybees, many different kinds of insects and other invertebrate animals (Figure 1) The spinning of silk by honeybees does not involve either rotating or twisting fibres as is done in commercial fibre production, but refers to the process of making an insoluble filament from an aqueous protein solution (Sutherland et al. 2010a). In the case of honeybees, just before pupation, the larvae cover the waxen walls of their cells with silk (Huber 1814; Arnhart 1906), paying out the fibres randomly so that, by the end of the spinning, the walls are covered by thin sheets of

Corresponding author: C.W.W. Pirk,
cwwpirk@zoology.up.ac.za

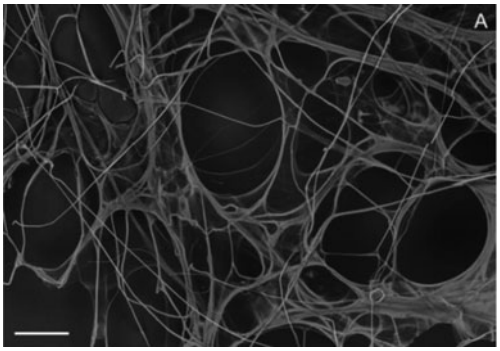

Figure 1. Scanning electron photomicrograph of ά-helical silk fibres produced by larvae of *A. mellifera*. *Scale bar* is 100 μm. Late final instar honeybee larvae were induced to spin silk within plastic tubes and the clean silk removed before the larvae added any further material (with kind permission of the publishers from Sutherland et al. 2011b).

silk in which the individual fibrils are readily discernible (Jay 1964; Zhang et al. 2010a).

Jay (1964) observed that fibres were formed when the honeybee spinneret was drawn away from the cell wall. In contrast, films were formed when the spinneret was dragged over the cell wall, presumably because the substrate stabilized the thin film. Jay (1964) reported that silk is generated from the labial gland as the larvae perform random head movements in all directions whilst moving in slow somersaults within the cell. Inasmuch as this behaviour may last up to 48 h, it ensures that the final product (the cocoon) will be a randomised and mechanically, planar isotropic structure. The colourless silk of about 3 μm diameter (Zhang et al. 2010a) is produced through a slit-like spinneret located at the tip of the combined labium–hypopharynx.

The inference that silk proteins are highly organized in the gland lumen before the larvae actually begin spinning (Flower and Kenchington 1967) was recently confirmed by Silva-Zacarin et al. (2003), who showed that silk formation starts during the middle of the fifth instar and finishes at the end of the same instar. This process begins in the distal secretory portion of the gland, going towards the proximal secretory portion and from the periphery to the centre of the gland lumen. The silk proteins are released from the secretory cells as a homogeneous substance that polymerizes in the lumen to form compact birefringent tactoids. Secondly, the water absorption from the lumen secretion, carried out by secretory and duct cells, promotes aggregation of the tactoids that form a spiral-shape filament with a zigzag pattern. This pattern is also the result of the silk compression in the gland lumen and represents a high concentration of macromolecularly well-oriented silk proteins.

After spinning the larvae smear, a small amount of material from the Malpighian tubules onto the hardened silk layers and faeces are also excreted between silk layers (Jay 1964). Subsequently the larvae produce a colourless pollen-free substance and then a yellow pollen-bearing one (from the anus), both of which are applied in turn to the silk base (Verlich 1930; Jay 1964). Nothing further is known of these four substances, but they invite the analogy of a sizing in paper manufacture, which is the incorporation of other material, in particular papers to act as a protecting glaze by changing the physical characteristic of the material (paper/wax).

Successive generations of brood apply more silk to the walls, the cells become smaller and the mass ratio of silk to wax greater (Chauvin 1962). Thus, old brood combs are heavily impregnated with silk (Figure 2) which is inseparable from the wax except by chemical and/or heat treatments. The development and maturation of brood comb proceeds from a single-phase material, pure white wax, to a coloured fibre-reinforced two-phase

Figure 2. Longitudinal section of an old comb from *A. mellifera capensis*, indicating layers of silk inside the base and walls of cells (from Hepburn et al. 2007).

composite (Hepburn and Kurstjens 1988; Z h a n g et al. 2010a). The physical significance of these observations can be illustrated by comparing the properties of the native fibroin, wax-free sheets of silk, silk-free wax, propolis and the final wax–silk composite (Kurstjens et al. 1985).

2. HONEYBEE SILK: AN α-HELICAL PROTEIN

Fifty years ago, the crystallographer, K.M. Rudall (1962, 1965), demonstrated in his X-ray fibre diffraction data that silk threads drawn from honeybee silk glands contained ά-helical proteins assembled into ordered coiled-coil structures and that their meridional reflections suggested an axial periodicity of about 28 nm. The patterns from honeybee silk fibres were considered most consistent with a four-strand coiled-coil structure with a tighter than expected super-helix radius of about 0.52 nm (Atkins 1967). In contrast, the dominant molecular structure in silk of other hymenopteran species is extended β-sheets (Warwicker 1960; Sutherland et al. 2007)

So, honeybee silk is an ά-helical fibroin (Rudall 1962), the micelles or crystallites of which form a four-stranded array of coiled-coils parallel to the fibre axis (Atkins 1967). Honeybee fibroin is crystalline relative to other insect silks (Lucas and Rudall 1968) while the hydrated fibre is only half as stiff as dry ones although they are equal in strength (Hepburn et al. 1979). The fibroin is hygroscopic and when solvated is highly distensible, largely owing to its conformation (Lucas and Rudall 1968). These properties of the fibroin are largely suppressed by the cocoon-spinning larvae because the silk is pressed into the wax of the cell wall, possibly aided by the anal secretions, and this immediately water-proofs and checks the susceptibility of the silk fibroin to solvation. Thus, it is also likely that inter-micellar friction is enhanced (Warwicker 1960) and the possibility of conformational change restricted (Rudall 1962), effects consistent with a good stiffness and reduced distensibility (Hepburn et al. 1979). That the silk fibres are spun and randomly arranged in the cell wall overcomes the basic anisotropy of the material; dewaxed sheets of cocoon silk are planar isotropic on tensile deformation. Alternatively, a hygroscopic silk could serve as a respiratory water sink.

3. BEHAVIOUR OF SILK AT DIFFERENT TEMPERATURES

Natural variations in the temperature of honeybee nests invite a consideration of silk behaviour in a variable thermal regime. The independence of the mechanical properties of *Apis mellifera scutellata* silk sheets when deformed in tension at a fixed rate to different temperatures is given in Table I.

Sheets of silk maintain the same relative strength and distensibility between 25 and 45 °C and staunch the plastic flow and ultimate collapse of wax at the higher temperatures. Consequently, changes in stiffness or the energy to fracture the sheet, an index of its relative workability, were not observed. The tensile properties of silk sheets over this range of temperatures are in sharp contrast to those of pure wax (Hepburn et al. 1983), propolis (Hepburn and Kurstjens 1984), and the wax–silk composite of brood combs.

In addition to crystal structure, white comb wax is also affected by the presence of a protein fraction (Kurstjens et al. 1985, 1990). This material is present, quite apart from silk, in both wax scales and in newly constructed combs. In both cases, this partially characterised protein (Kurstjens et al. 1990) is positively associated with enhanced stiffness in both scales and comb. Nothing is known of the molecular behaviour of this protein or how it might contribute to the stiffness of wax.

4. RELATIVE CRYSTALLINITY

Lucas et al. (1960) estimated the relative crystallinity of moth fibroins by calculating short-side-chain–long-side-chain ratios. When Hepburn et al. (1979) did the same for honeybee silk, the result suggested that this silk was anomalous because crystalline fibroins generally have a high glycine content but honeybee silk

Table I. Tensile mechanical properties of dewaxed, worker honeybee, *A. mellifera scutellata*, cocoon silk (Hepburn and Kurstjens 1988).

Temperature (°C)	Relative tensile strength (N mm^{-1})	Breaking strain (%)	Relative stiffness (N mm^{-1})	Work (MJ m^{-3})
25	32±16	98	33±14	29±20
30	32±18	81	40±13	28±23
35	26±10	85	31±8	22±14
40	39±17	105	37±14	38±22
45	43±20	106	41±14	48±30

Mean and standard deviation are shown. For each value, $n=10$

has a very low glycine content but, nevertheless, is relatively crystalline (Atkins 1967; Lucas and Rudall 1968). These authors subsequently turned to cellulose because one feature of cellulose is that the degree of crystallinity is reflected in the sensitivity of its fibres to solution effects. Water can penetrate amorphous regions in a capillary manner thus diminishing the interactions between crystallites or, alternatively, compete for potential hydrogen-bonding sites within the fibre (Wainwright et al. 1976).

In the work on cellulose, it was assumed that hydration loosened the interaction between neighbouring crystalline regions thereby reducing stiffness. It was further assumed that the elastic modulus of the dry cellulose approached that of crystalline cellulose. From that, the ratio of modulus wet to modulus dry provided an approximate index of the degree of crystallinity, a ratio of 1 indicating complete and lesser values of progressively less crystallinity. When honeybee silk was examined for hydration sensitivity expressed as the ratio of the elastic modulus of wet to that of dry fibre, a value of 0.53 showed that this fibre is rather crystalline, a result consistent with other forms of measurement (Lucas and Rudall 1968).

Tensile stress–strain curves for wet and dry ά-helical honeybee, *A. mellifera scutellata*, silk are shown in Figure 3. Honeybee silk, either wet or dry, are characterised initially by linear regions which terminate in marked yield points at about 0.1 and 0.3 strain, respectively, for wet and dry silk. A yield point is defined as a marked decrease in the slope of the stress–strain curve which occurs over a very small region of strain and, for an ά-helical structure, most likely associated with the onset of a transconformational change from the ά to the //β state (Rudall 1962, 1965).

More recently, Zhang et al. (2010b) reported on the microstructures and mechanical properties of honeybee, *A. mellifera ligustica*, and silkworm silks that they examined by environment scanning electron microscopy, scanning probe microscopy, tensile tests, and nano-indentation. They concluded that honeybee silk, unlike silkworm silk, is a single fibre with a circular cross section and has a much finer and smoother texture than the silkworm silk. The honeybee silk exhibits a distinct linear and brittle elastic mechanical behaviour. Moreover, their nano-indentation measurements showed that the honeybee silk is much less anisotropic than the silkworm silk. The ratio of the longitudinal modulus to the transverse modulus of the honeybee silk is 2.0, whereas that of the silkworm silk is 18.9. Added to this, it is probable that the different structural and mechanical properties of honeybee and silkworm silks are likely the result of their specific biological functions (Zhang et al. 2010b).

5. SOLVENT EFFECTS ON SILK

A large amount of empirical information on the effects of solvents has accumulated over the past 100 years from the wool, leather and silk industries. A few of these solvents have been studied in considerable detail and their effects well documented in the general chemical liter-

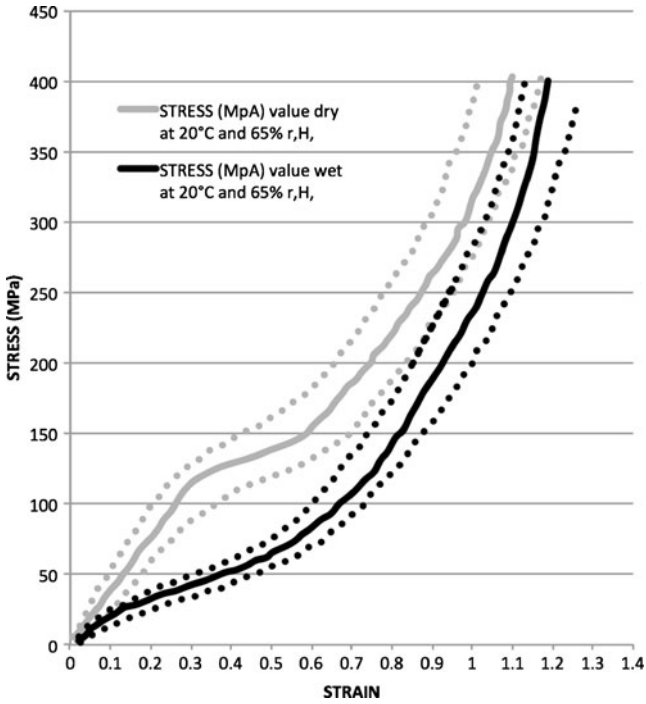

Figure 3. Generalised tensile stress–strain curve for ά-helical silk of the honeybee, *A. mellifera scutellata*, tested dry (**a**) and then wet (**b**) (from Hepburn et al. 1979). *Dotted lines* indicate upper and lower limits.

ature. Of these solvents, Hepburn et al. (1979) selected lithium thiocyanate, urea and formamide as high affinity hydrogen bond competitors and specimens of honeybee silk were tested in these solutions to assess the possible role of distilled water having more than capillary sorptive effects on the general tensile behaviour of the fibres.

In the case of honeybee silk, lithium thiocyanate and urea virtually eliminated the marked yield point characteristic of honey bee silk tested both dry and in distilled water. Secondly, the entire slope of the solvent-related curves is markedly reduced, as are the associated values of stress, point for point, along the curves (cf. Figures 4 and 5).

These differences can be explained in the following way. An aqueous environment facilitates microfibrillar lubrication as evidenced by decreasing values of the elastic modulus and in increasing total extensibility in honeybee silk. On the other hand, organic solvents drastically reduced modulus and stress in honeybee silk and virtually eliminated the transition from linearity to non-linearity in these curves. We suggest that, in these cases, the solvents are in fact directly acting on hydrogen bonds so that during tensile deformation the silks essentially behave as loose collections of unconnected bends (like a bowl of cooked spaghetti) requiring very small loads to unfold them.

Loose fibres of honeybee silk placed in a 7-M solution of formamide or urea and in a 4-M solution of lithium thiocyanate showed no change in length but were remarkably rubbery to the touch and very easily distended. This distensibility was reversible over the ranges examined, 100–200 % (ε_1=0.69–1.1), and the silk was rubbery in nature and highly reminiscent of solvated resilin (Andersen and Weis-Fogh 1964) and other rubber networks with moderate cross-linking.

However, there are basic differences between solvated fibroins and rubber networks; the integrity of the former lies in the secondary hydrogen bonding topology of the structure while in the latter bonding is usually of the sulphydryl covalent type. Thus, we conclude that solvation of honeybee silk in lithium thiocyanate, urea and formamide and even

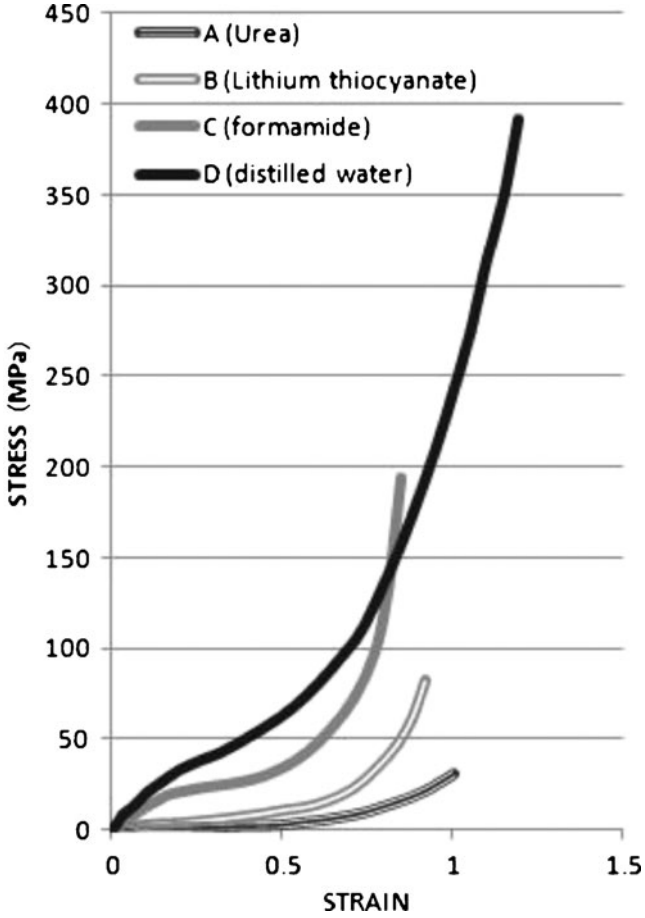

Figure 4. Stress–strain curves (to failure) of honeybee (*A. mellifera scutellata*) silk at 20 ° C in various hydrogen bond-disruptive solutions: *A*=7 M urea, *B*=4 M lithium thiocyanate, *C*=7 M formamide, *D*=distilled water (Hepburn et al. 1979).

distilled water disrupt the crystalline organisation of the fibroin by directly reducing hydrogen bonds in the structure. Properties of the proteins of the ά-helical honeybee silk are shown in Table II.

6. HONEYBEE SILK: AN α-HELICAL SILK AND A COILED-COIL PROTEIN

It appears to be a general property of natural silks that the components, hierarchical structure and the conditions of their production all affect their mechanical properties (Vollrath and Knight 2001; Shao and Vollrath 2002). So, it is not surprising that the discovery of the amino acid sequence in honeybee silk protein provided an explanation of why the coiled-coil packing was atypically tight: While the core of coiled-coils usually contains large hydrophobic residues such as leucine and isoleucine, in coiled-coil silk the most abundant core residue is the small amino acid alanine (Sutherland et al. 2007).

Lucas and Rudall (1968) suggested that the pattern of coiled-coil proteins occurring in the silk gland could be to prevent agglutination of the proteins within the silk gland. Another, not incompatible, reason put forward by Sutherland

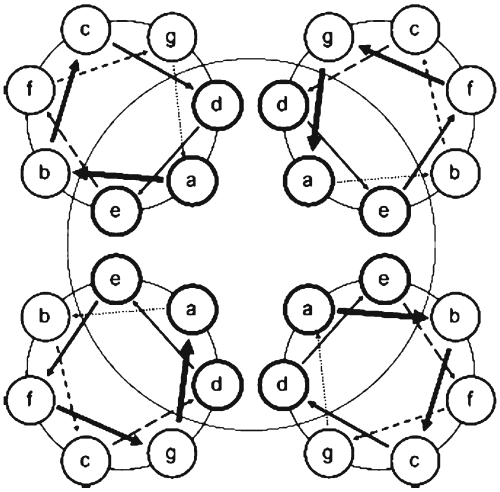

Figure 5. A structural model for a coiled-coil silk as produced by honeybees. The ά-helical strands corresponding to each of the fibroins are arranged in an antiparallel tetrameric configuration (direction indicated by *arrows*). Three residues (*a*, *d*, *e*) from each heptad repeat are buried in the core (with kind permission from Sutherland et al. 2007).

et al. (2007) is that it could provide a mechanism to reduce the flow viscosity of the protein solution in order to allow the concentrated silk rope to pass through the spinneret. Obviously, the behaviour of silk must be based on its chemical composition. Sutherland et al. (2006) were able to identify the coiled-coil silk sequences from silk gland cDNA libraries from European *A. mellifera* and determined the amino acid sequence of the coiled-coils.

Sutherland et al. (2007) confirmed that honeybee silk is formed from four coiled-coil proteins (fibroins), as originally suggested by Rudall (1962, 1965) on the basis of his X-ray diffraction data. The fibroin proteins contained extensive coiled-coil regions of conserved length flanked by largely unstructured termini. Sutherland et al. (2007) proposed a structural model for coiled-coil silks (Figure 5), whereby the ά-helical strands corresponding to each of the fibroins are arranged in an antiparallel tetrameric configuration (direction indicated by arrows).

Each fibroin contains a continuous predicted coiled-coil region of around 210 residues, flanked by 23–160 residue length N- and C-termini. The cores of the coiled-coils were unusually rich in alanine, a hydrophobic amino acid, in the a and d core positions (Figure 5).

Sutherland et al. (2011a) further provided a schematic top-down view of one strand of a coiled-coil generated from coiled-coil silk proteins such as those that occur in honeybees (Figure 6). Three residues (a, d, e) from each heptad repeat are buried in the core. Most known coiled-coils contain predominantly large hydrophobic residues at these positions to maximise the hydrophobic forces stabilising the core (Woolfson 2005). Sutherland et al. (2007) ascribed the atypical composition of the coiled-coils in bee silks possibly to the metabolic constraints of having to produce a continuous and copious secretion of silk during the many hours of larval spinning.

Amino acid sequence comparisons indicate that different regions of silk proteins have different levels of sequence constraint. A pairwise alignment of the closely related silk proteins from European *A. mellifera* (Sutherland et al. 2007) and *Apis cerana* (Shi et al. 2008) shows, on average, 3 % amino acid changes in predicted coiled-coil core positions, 8 % amino acid changes in predicted coiled-coil noncore positions and 14 %amino acid changes in the N- and C-termini regions (Sutherland et al. 2011a). Thus, composi-tion, molecular topology and amino acid content and sequence appear to be a highly conserved feature in the evolution of silk in *Apis* species.

7. MOLECULAR DYNAMICS OF α-HELICAL PROTEINS

Over the past few years, the molecular dynamics of ά-helical protein behaviour has gained enormous momentum, particularly in the works of Ackbarow et al. (2007) who have published a highly significant work on how hierarchies, multiple energy barriers and robustness govern the fracture mechanics of ά-helical and β-sheet protein domains. The authors point out that the fundamental fracture mechanisms of protein materials remain largely unknown, in part, because of a lack of understanding of how

Table II. Properties of the proteins of the ά-helical honeybee silk of *A. mellifera* compared with other insects silks (with kind permission from the publishers from Sutherland et al. 2007).

Species	Protein name	Number of amino acids	Percent of cDNA library clones[a]	Normalized expression levels[b]	LC/MS identification score[c]
Fibrous proteins					
Bumblebee	BBF1	327	4	1.0±0.16	180
	BBF2	313	14	1.1±0.22	100
	BBF3	332	20	1.3±0.19	218
	BBF4	357	32	1.0±0.15	137
Bulldog ant	BAF1	422	16	1.0±0.09	99
	BAF2	411	30	2.3±0.41	90
	BAF3	394	26	1.6±0.26	88
	BAF4	441	24	1.7±0.24	116
Weaver ant	WAF1	391	35	2.4±0.18	228
	WAF2	400	22	1.7±0.11	191
	WAF3	395	13	1.9±0.2	156
	WAF4	443	17	1.0±0.07	148
Honeybee	AmelF1	333	6d	1.0±0.05	52[d]
	AmelF2	309	7d	1.3±0.06	51[d]
	AmelF3	335	11d	1.2±0.07	107[d]
	AmelF4	342	7d	1.5±0.14	88[d]
Glue-like proteins					
Bumblebee	BBSA1	>501	3	Not done	138
Honeybee	AmelSA1	578	13d	Not done	40[d]

[a] Total number of cDNA sequenced: honeybee 82, bumblebee 117, bulldog ant 131, weaver ant 23

[b] Normalized ratio of expression levels determined by quantitative RT-PCR as described in the "Materials and methods in Sutherland et al. 2007"

[c] The default score in Spectrum Mill software required for confident identification of a protein greater than 20

[d] Data from Sutherland et al. (2006)

individual protein building blocks respond to mechanical loads. As an example, they report that there is uncertainty as to whether the unfolding behaviour of ά-helical proteins consists of multiple transition state changes continuously with the pulling velocity. Ackbarow et al. (2007) reported on a direct atomistic simulation over four orders of magnitude in time scales of the unfolding behaviour of ά-helical protein in which they found that two discrete transition states corresponded to two fracture mechanisms.

Whereas the unfolding mechanism at fast fibre extensions involves the sequential rupture of individual hydrogen bonds, unfolding at slower rates involves the simultaneous rupture of several hydrogen bonds. Ackbarow et al. (2007) derived a theory that explicitly considers the hierarchical architecture of proteins, providing a rigorous structure–property relationship. Their results provide evidence that the molecular structure of ά-helical proteins maximises their robustness with minimal use of building materials (Ackbarow et al. 2007; Buehler and Ackbarow 2007).

Although not directly pertinent to the present discussion, it is of considerable interest to learn of the existence of both reconstituted honeybee silks and others produced by recombinant techniques. The coiled-coil silk proteins of honeybees are small compared with the fibrous silk proteins of spiders and silkworms and therefore can be

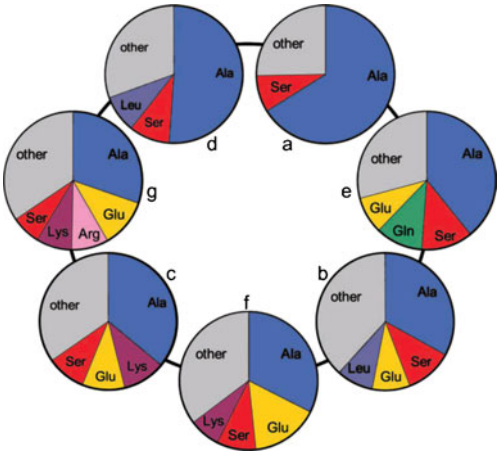

Figure 6. Schematic top-down view of one strand of a coiled-coil generated from coiled-coil silk proteins. Formation of coiled-coils occurs when two strands of protein containing repeats of amino acids in the pattern HPPHPPP (where H are generally hydrophobic residues and P are generally polar residues) come together to shield the hydrophobic residues from the solvent. The heptad repeat is commonly denoted as *a*–*g* with the *a* and *d* positions corresponding to the core residues. The relative abundance of different amino acids in each position, averaged over all silk proteins for seven species, is shown in pie chart form (with kind permission of the publishers from Sutherland et al. 2011b).

produced as full-length proteins by fermentation in the bacterium *Escherichia coli*. The native coiled-coil silk self-assembles within the silk gland before spinning (Flower and Kenchington 1967), and key elements of this self-assembly are replicated in reconstituted or recombinant silk, potentially allowing straightforward capture of native silk functionality in a biomaterial (Sutherland et al. 2007, 2011a, 2012). Moreover, in future, this work will very likely come within the gambit and purview of patent offices around the world (Sutherland et al. 2010b).

8. GENETIC BASIS OF HONEYBEE α-HELICAL FIBROIN

Sutherland et al. (2006) published the results of some pioneering work that described a highly divergent gene cluster in honeybees that actually encodes a novel silk family. Using the combination of genomic and proteomic techniques, they identified four honeybee fibre genes (*AmelFibroin*1–4) and two silk-associated genes (*AmelSA*1 and 2). The four fibre genes are small, each consisting of a single exon, and are clustered on a short genomic region where the open reading frames are GC-rich amid low GC intergenic regions. The genes encode similar proteins that are highly helical and predicted to form unusually tight-coiled coils. Despite the similarity in size, structure and composition of the encoded proteins, the genes have low primary sequence identity. Sutherland et al. (2007) proposed that the four fibre genes have arisen from gene duplication events but have subsequently diverged significantly. The silk-associated genes encode proteins likely to act as glue (*AmelSA*1) and are involved in silk processing (*AmelSA*2). Although the silks of honeybees and silkmoths both originate in larval labial glands, the silk proteins are completely different in their primary, secondary and tertiary structures as well as the genomic arrangement of the genes encoding them.

This implies independent evolutionary origins for these functionally related proteins. Six honey bee silk genes have been identified by a combination of genomic and proteomic techniques (Sutherland et al. 2006). Five of these genes, encoding the four AmelFibroin proteins and the AmelSA1 glue protein, are completely novel and show no sequence similarity found in any known gene. The four *AmelFibroin* genes are physically clustered in the genome, and although they encode proteins with similar amino acid composition, helical conformation and heptad substructure, AmelFibrion 1 identity with AmelFibrion 2, 3 and 4 is only between 25.1 and 30.6 % and even lower among the other three (cf. Table II in Sutherland et al. 2006). In coiled-coil formation, these four related but diverged genes may have different roles, and all of them might be required at specific ratios for proper silk formation. Alternatively and not mutually exclusive, the variation in the expression of the different genes might allow honeybee silk to adapt rapidly to environmental changes or they are simply serve as functionally equivalent with gene duplication required to support the very high

level of expression (Sutherland et al. 2006).

The important and burgeoning field of genomics is concerned with the study of genes and their effects on macroscopic functions and has led to considerable advances. However, as Ackbarow et al. (2009) have noted, genomics does not illuminate material properties, nor the mechanistic relation of hierarchical multi-scale structures and their resulting properties. Elucidating the relation between structure and material properties and multi-scale behaviour of protein assemblies such as the honeybee ά-helical silk represents a grand challenge at the interface of materials science and biology (Ackbarow et al. 2009). This gap in understanding can be closed by systematically studying the material properties of hierarchical protein struc-tures and their effect on the macroscopic proper-ties, an approach part of a larger effort to study the role of materials in biology, referred to by Buehler and Keten (2008) as materiomics.

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Propriétés physiques de la soie produite par les abeilles: synthèse des connaissances

Abeille / Apidae / soie / fibroïne / hélice alpha

Physikalische Eigenschaften der Seide von Honigbienen: Ein Review.

***Apis* / Honigbiene / alpha-Helix / Fibroin**

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