2. Structure of the Fibre

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Learning objectives

On completion of this topic you should have:

- the structure of wool as a complex tissue containing dead cells filled with proteins that provide it with the mechanical properties that make it a textile fibre.
- An overview of the properties of wool in relation to its structure

Key terms and concepts

- wool follicles develop from the interaction of epidermal and dermal cells
- the cell layers of a wool follicle are derived from streams of separate cell lineages that are determined by expression of controlling genes
- the population of follicles of fine wool sheep arises from an abundance of secondary derived follicles
- the fine wool fibre has two types of cell, cortical and cuticular that have different structures and physical properties and contain different proteins
- the fibre cortex contains keratin intermediate filaments separated by matrix proteins that are made up of several classes of proteins of different classes distinguished by amino acid composition and sequence
- the helical conformation of the proteins of the keratin intermediate filaments and interaction of the matrix proteins, determines the elastic behaviour of wool fibres
- the wool cuticle consists of overlapping cells that have a laminated internal structure of proteins and in addition there is a surface layer of fatty acids that cause the hydrophobicity of wool. The major component of the fatty acid layer is the unusual 18-methyleicosanoic acid (18-MEA) anchored to a surface protein that is not yet identified
- Wool proteins can be solubilized by vigorous chemical procedures such as reduction or oxidation in denaturing conditions
- The three main families of keratin proteins, low-sulphur (intermediate filament, IF) high-sulphur and high glycine/tyrosine proteins (matrix proteins) can be roughly fractionated by traditional solution methods involving salts (eg. zinc acetate) and pH
- The covalent bonds that hold wool proteins together are the disulphide bonds. Isopeptide bonds are also found in fibres but only when a medulla is present because this structure is constituted of a matrix-type protein called trichohyalin that is a major component of the inner root sheath of the follicle

- The location of disulphide bonds with and between amino acid sequences of IFs and matrix proteins in wool is mostly unknown; a factor in elastic behaviour of wool and a research task for the future.

Introduction to the topic

To understand the measurement (metrology) of the physical and chemical properties of wool fibres it is helpful to understand how fibres develop and the sources of variation of their shapes and composition. The skin of mammals is the largest of all the organs in the body and has many functions. Hair is found only in mammals. The skin acts as a barrier that protects the whole organism from the environment but it is also concerned with thermoregulation via sweat glands and hair. In sheep, the growth of the wool has been enormously influenced by selective breeding to increase the amount grown per animal and improving quality characters such as fineness and crimp.

The wool fibre is a cellular entity and a protein polymer and is complex at both of these levels. In recent years there has been a remarkable increase in our knowledge of the biological mechanisms operating during development of follicles and the maintenance of wool growth.

Wool is sheephair and belongs to the group of hard mammalian structures that include nails, claws and hooves. These structures are tissues and their cells are differentiated from epithelial cells and contain proteins that are called keratins. Mammalian keratins are different from keratins found in non-mammalian species such as the skin of reptiles, avian claw, beak and feather keratins. The evolutionary relationship of mammalian and non-mammalian keratins is as yet unclear.

2.1 The Structure of the Wool Fibre

General Features

The wool fibre is a dead tissue made up of two and sometimes three distinct types of cells. The core is the cortex consisting of spindle-shaped cells that are about 100um long and 5um at their widest width (Figure 2.2). The cortex is surrounded by a cuticle of overlapping flattened scale-like cells that form a protective layer - the appearance of the cuticle in a scanning electron microscope (SEM) is shown in Figure 2.1. The scale cells are rigid and protective as a result of their content of highly cross-linked proteins including the surface epicuticle. The overlapping of the scale cells allows the fibres to bend.

Wool fibres of fine wool sheep are about 20um in diameter but in coarse wool sheep the diameter of the fibres can be much greater and in such sheep the fibres can contain an inner core called the medulla as discussed later. The medulla can be continuous or discontinuous. In really coarse (kempy) fibres the medulla is continuous and its presence gives a white lustre to the fibre because of the light-reflecting effect of the air contained in the dead medulla cells.

An interesting feature that is still not completely understood is the bilateral structure of the cortex of fine wool that was discovered over 50 years ago by Horio and Kondo (1953). Basic dyes are preferentially taken up by the cells on one side of the cortex. called the orthocortex it follows the outermost aspect of the curvature of the fibre, as described above. The area that takes up the dyes less readily was termed the paracortex and is found on the innermost part of the curvature (Figure 2.4). In fine wool the orthocortex is larger in area than the paracortex (Figure 2.5). These basic features can be visualised in the light microscope but the higher resolution of the electron microscope (TEM) gives more detailed information as can be seen from Figures 2.4 and 2.5.
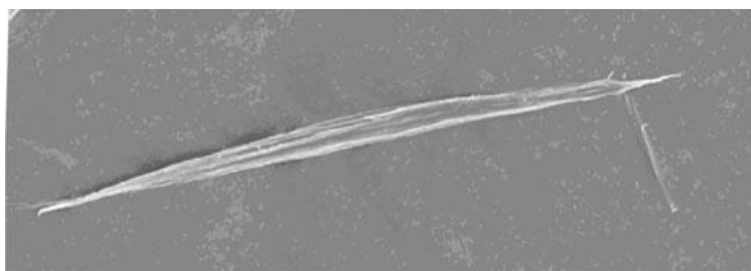
Figure 2.1 A cortical cell imaged by SEM. Note the fusiform shape. Cortical cells are about 100μm long and 5μm in their widest dimension. In the cortex of the fibre they are arranged axially but not in register. Source: Bryson, W. (2005, pers. comm.).
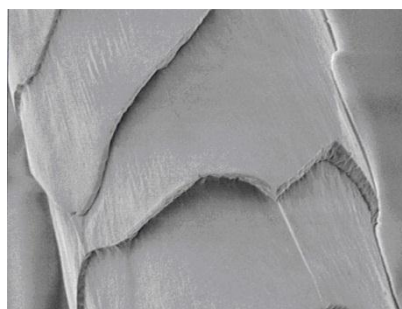

Figure 2.2   An SEM image of the surface of a wool fibre ~20μm diameter). The smooth surfaces of the overlapping scale cells have some striations and their edges are often raised from the juxtaposed surface. Chemical or physical damage to the surface of wool fibres can be readily detected by SEM.

Figure 2.3 The arrangement of the orthocortex (dark) and the paracortex around the three-dimensional curvature or curl of a wool fibre is shown. The bilateral structure can be revealed by the selective penetration of the orthocortex by dyes and examined by light microscopy. Adapted from: Mercer (1953).

2.2 The Wool Fibre at the Submicroscopic Level

The SEM can be used for examining the surface of wool fibres but for details of the inner structure of the cuticle and of the cortex, transmission electron microscopy (TEM) is necessary. In order to do this, wool fibres have to be sectioned in a special microtome, an ultramicrotome that can cut sections about 50nm thick ($1nm=10^{-9}m$). For sectioning, the fibres are pretreated to reduce some of the disulphide bonds and then the fibres are reacted with osmium tetroxide that is reduced to the heavy metal osmium within and between the keratin components. The fibres turn black and are dried and then embedded in an epoxy resin. The ultrathin sections are further stained with salts of

lead and uranium and then examined in the TEM. The heavy metal treatment is necessary in order to increase the contrast in the TEM between the different structures as seen in Figure 2.4. In particular orthocortical and paracortical cells, the two types of cortical cell, can be identified.
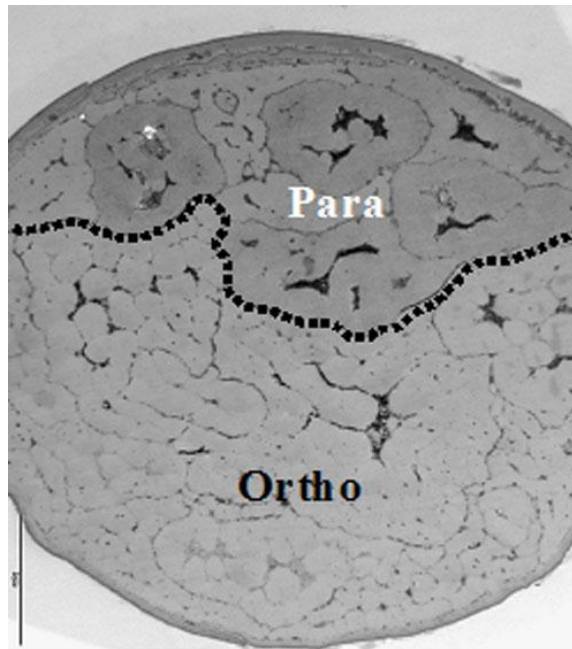

Figure 2.4 Low mag TEM of a 10 µm diameter wool fibre in cross-section. Above the dotted line individual paracortical cells can be distinguished and below the line are the cells of the orthocortex, the boundaries of which are less easily outlined. The paracortical cells appear denser because they have more cystine-rich proteins and take up more of the osmium stain.

The orthocortical cells are made up of macrofibrils; macrofibrils are aggregates of 8nm (1nm = 10^{-9} metre = 10 Angström units) diameter intermediate filaments (IF) visible at higher magnification (see Figure 2.6). The macrofibrils are delineated because there is dark-staining non-keratinous material between them and this explains the accessibility to dyes that diffuse more readily between the macrofibrils and reveal the bilateral asymmetry of the cortex. By comparison, macrofibrils in the paracortex are not so visible because they are fused together into a continuous mass of IFs and as a consequence the uptake of basic dye is not as rapid (Rogers 1959b). There is a clear difference in the organisation of the IFs in the cortex of fine wool (Figure 2.5). In the orthocortex the IFs are organised in a spiral fashion in the macrofibrils so that in cross-section the macrofibrils appear as "whorls" whereas in the paracortex the IFs are aligned parallel with the fibre axis and are closely–packed often in a hexagonal arrangement. In both the ortho- and the paracortex, the IFs are separated by a dense space that is called the matrix and the combination is often referred to as the "filament + matrix" complex.

The scale cells of the cuticle are laminated structures that can be clearly distinguished because of their relative electron densities in the TEM (Figure 2.6). The electron densities are correlated with the sulphur content of the layers. The outer layer is the exocuticle and a layer nearer to the surface is referred to as the "a" layer (Rogers 1959a). Beneath is the endocuticle that is thought to be cellular debris remaining after the proteins of the exocuticle have been synthesised.
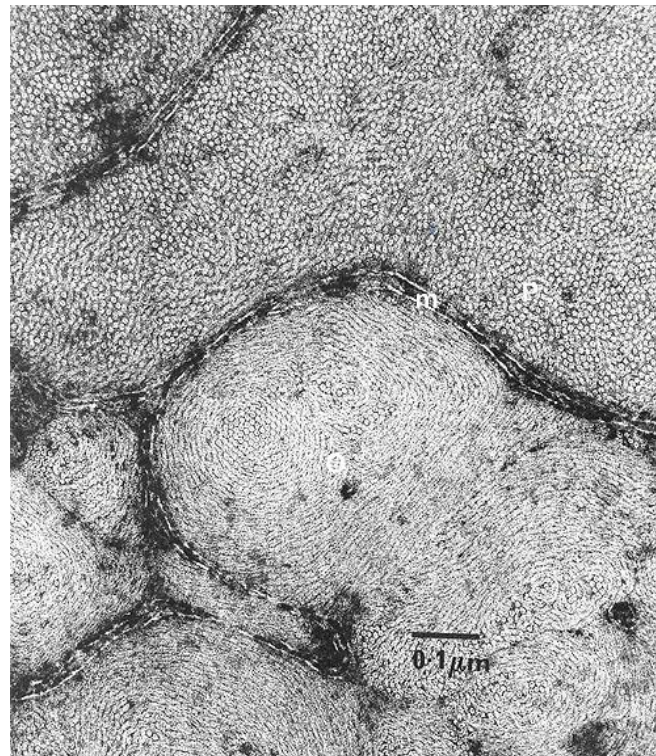
Figure 2.5   A TEM of a cross-section of a wool fibre at high magnification that reveals the 8nm diameter IFs packed in semi-crystalline arrays in the paracortex (P) and dark stained matrix between them that provides the contrast to see them. The IFs are also visible in the orthocortex (O) but there is less matrix and distance separating the IFs. Also the whorl pattern in the macrofibrils is clearly displayed. The structure 'm' is the cell membrane complex (CMC) that is between cortical cell s and cuticle cells. Osmium, lead and uranyl staining.
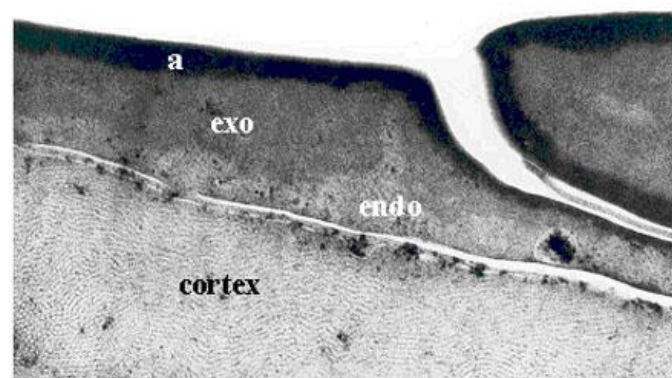

Figure 2.6 A TEM image of a cross-section through a scale cell of the wool fibre cuticle showing the three layers of the cuticle – 'a'-layer, exocuticle and endocuticle. The CMC separating the cortex from the cuticle can be seen.

The cell membrane complex or CMC is a dense layer about 15nm in wide (Figure 2.7) between cells of the cortex and cuticle. It is derived from the lipid bilayers of the original plasma membranes of the cells differentiating in the wool follicle. It plays an important role in the structural integrity of the wool fibre and hairs generally. When wool fibres are incubated with a proteolytic enzyme for long periods (days) the CMC is preferentially digested and cortical and scale cells are released. The process is called retting. A similar effect can be achieved if wool fibres are immersed in

swelling agents such as formic acid that preferentially swells the CMC. The cells of the fibres are released by sonication and cortical cells can be separated from scale cells by using fine sieves.

The medulla when it is present in wool it is a centrally placed core in the cortex and consists of a ladder of cells separated by gaps of air so that the medulla reflects lightand the fibres appear whiter than non-medullated fibres. The arrangement of the medulla cells can vary in sheep depending on the breed (Figure 2.8).
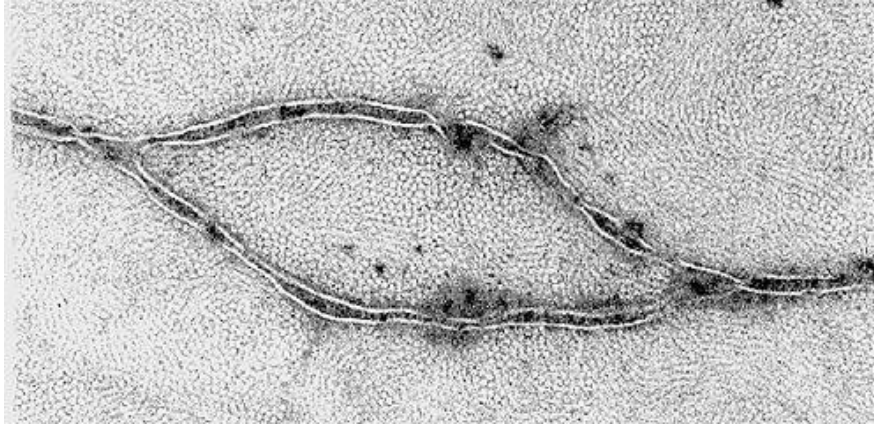

Figure 2.7 The modified cell membranes (cell membrane complex, CMC) separating several cortical cells.

The medulla is found in many other species and the type of packing of medullary cells can also vary within a species for example, the medulla in rabbit fur can vary along the length of a fibre because of cellular changes during growth and differentiation. The proteins within the medulla don't have a visible ultrastructure and are masses of amorphous protein material when examined in the TEM. The major protein is a specific protein called trichohyalin that has a matrix-type role in the inner root sheath cells of the follicle.
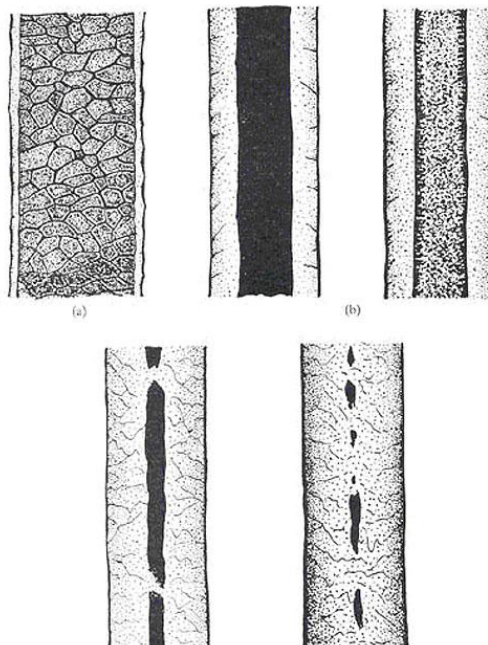

Figure 2.8 Diagrams illustrating the different types of medulla found in wool fibres. From left to right they are from kemp fibres, continuous, continuous with the air displaced by mounting medium (water can do this) and two types of discontinuous medullae. Source: Ryder and Stephenson (1968).

2.3 Proteins of the Wool Fibre Cortex

The proteins of wool and hairs are referred to as keratins or keratin proteins but more recently the term keratin has become restricted to that group of intermediate filaments (IFs), the keratin IFs, found primarily in the epidermis and hair. They are a family of proteins within a much larger IF superfamily of IFs. Other proteins in the cortex and the cuticle are called keratin-associated proteins and abbreviated to KAPs. They have a chemical structure that is markedly different from the IFs as will be explained. All of the proteins contain the amino acid cysteine (Figure 2.9) and hence disulphide (-SS-) bridges (Figure 2.10) are abundant and hold the proteins together.
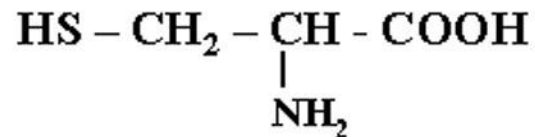
$$HS - CH_2 - CH - COOH$$
$$|$$
$$NH_2$$

Figure 2.9 Structural formula of the amino acid cysteine.
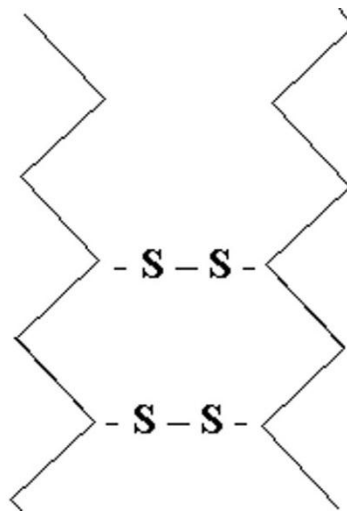

Figure 2.10 Diagram representing two polypeptide (protein) chains linked by two disulphide (SS) bonds formed from cysteine residues in each of the two chains.

Keratin proteins can be solubilized by breaking the disulphide bonds with a reducing reagent in the presence of a protein denaturing agent such as 8M urea and at alkaline pH (pH11). To prevent re-oxidation the dissolved proteins have to be blocked by reacting them with agents like iodoacetic acid ($I.CH_2.COOH$) that adds a carboxymethyl function (-$CH_2.COOH$) to them. When the extracted proteins are examined by electrophoresis on a gel (Figure 2.18) they are seen to separate into their major groups, the IF proteins, Type I and Type II and the KAPs, the cystine-rich KAP family and the glycine/tyrosine rich KAP family.
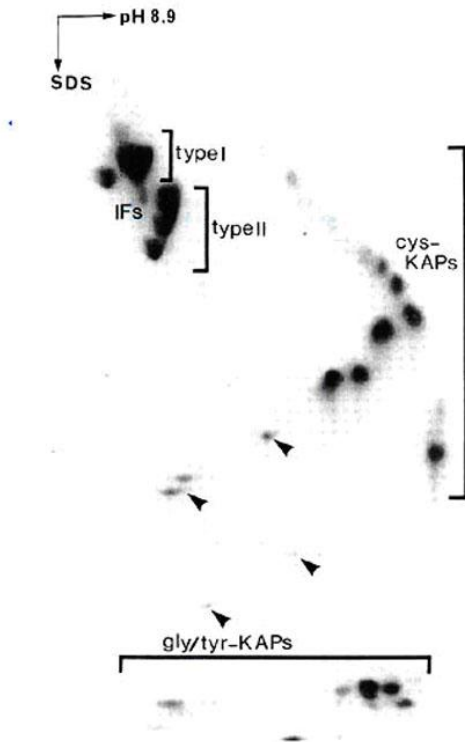
Figure 2.11 The two-dimensional gel pattern is actually an autoradiogram obtained from keratin proteins extracted from wool, carboxymethylated with ^{14}C- iodoacetic acid and run in an acrylamide gel at pH 8.9 in the presence of 8M urea in one direction followed by SDS in the other. The major classes of proteins can be distinguished – Type I and II IFs, the cysteine-rich KAPs and the glycine-tyrosine rich KAPs. Source: Powell and Rogers (1997).

There are two types of keratin IF proteins, Type I and Type II. They differ in their amino acid compositions although they are similar, as are their amino acid sequences. Moreover, the Type II IFs are slightly larger than the Type I's containing approximately 550 amino acid residues compared to 500 in the sequences, respectively. There is a further complexity in that each of the two groups of IFs are protein families. In the case of sheep the total is not known but three Type I and three Type II members respectively were identified (Bawden et al. 2001; Powell & Rogers 1997) but there should be many more because in the case of hair IFs there appears to be a total of 54 genes (Hesse et al. 2004).

The KAP proteins are of smaller molecular size than the IFs and vary from about 100-150 amino acids in length. There are two major KAP families that differ in amino acid composition. One group contains more cysteine residues (high-sulphur or cystine-rich KAPs) the other contains an abundance of glycine and tyrosine residues (high glycine/tyrosine KAPs) (Figure 2.12). The number of KAPs is not exactly known but is likely to be of the order of one hundred.

The interesting feature of all of the proteins is that each group, IFs and KAPs, is a large family of similar sequences. The reason why there are so many genes is not clear but may be related to the need for the rapid expression of the keratin genes to allow the rapid protein synthesis during fibre growth. There is now plentiful evidence to indicate that the KAPs constitute the matrix of the "filament + matrix" complex between the IFs.
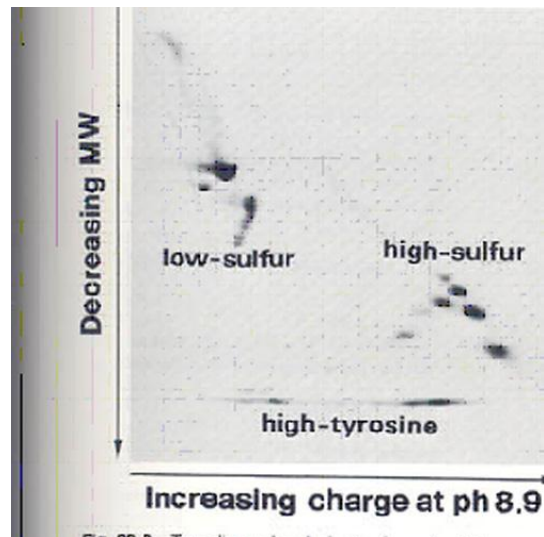
Figure 2.12 2D gel electrophoresis of wool keratin proteins labelled with C^{14} iodoacetic acid. Source: Gillespie (1991).

Table 2.1 Amino acid composition of the three classes of wool proteins*.

Source: Jones and Rogers (2006).

Amino acid	Low-sulphur SCMKA major fraction	High sulphur Total	High glycine tyrosine Total
Lysine	4.1	0.6	0.4
Histidine	0.6	0.8	1.1
Arginine	7.9	5.9	5.4
Cysteine (as SCMC*)	6.0	18.9	6.0
Aspartic acid	9.6	3.0	3.3
Threonine	4.8	10.3	3.3
Serine	8.1	12.7	11.9
Glutamic acid	16.9	8.4	0.6
Proline	3.3	12.5	5.3
Glycine	5.2	6.9	27.9
Alanine	7.7	2.9	1.5
Valine	6.4	5.6	2.1
Methionine	0.6	0.0	0.0
Isoleucine	3.8	3.6	0.2
Leucine	10.2	3.9	5.5
Tyrosine	2.7	2.1	15.1
Phenylalanine	2.0	1.9	10.4

* Adapted from Gillespie (1991). Expressed as moles per 100 moles

2.4 Mechanical Properties

Single wool fibres are not as strong as nylon or silk but stronger than cotton when compared in terms of the energy required to break them. The intrinsic strength is calculated as the force per unit area (Newtons/cm^2). However the common measure of wool strength is staple strength and for undamaged wool it is normally around 50 Newtons /kilotex. A kilotex is defined as 1g wool per metre and is a direct measure of staple cross-sectional area. Staple strength is not a biological property but a physical measurement of the strength of the wool material and is the result of all the growth processes involved in producing a wool staple.

The basis of wool's toughness is its extensibility. When wool (or hair) fibres are stretched with an applied force (stress) *in the presence of water* they first lengthen (strain) in a linear relationship up to about 2% and this is referred to as the Hookean region. The ratio, stress/strain, in this region is Young's modulus. Beyond the Hookean region the fibre lengthens with very little increase in stress, the yield region, until at about 30% extension it begins to stiffen again. This elastic behaviour of a wool fibre is graphically shown in Figure 2.13.

The stretching (Young's) modulus (stress/strain) depends on the relative humidity and water content. A dry fibre is about 2.5 times stiffer than a wet fibre (Figure 2.14). The mechanical properties of the fibre keratin when dry are isomorphic (physical properties the same both radially and longitudinally) and the fibre breaks with minimal extension.
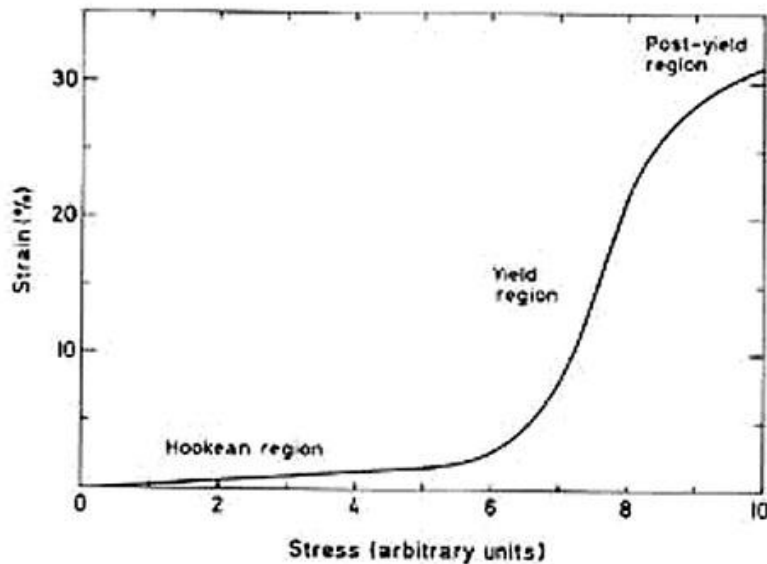
Figure 2.13 A typical stress strain curve of a wool fibre extended in water.
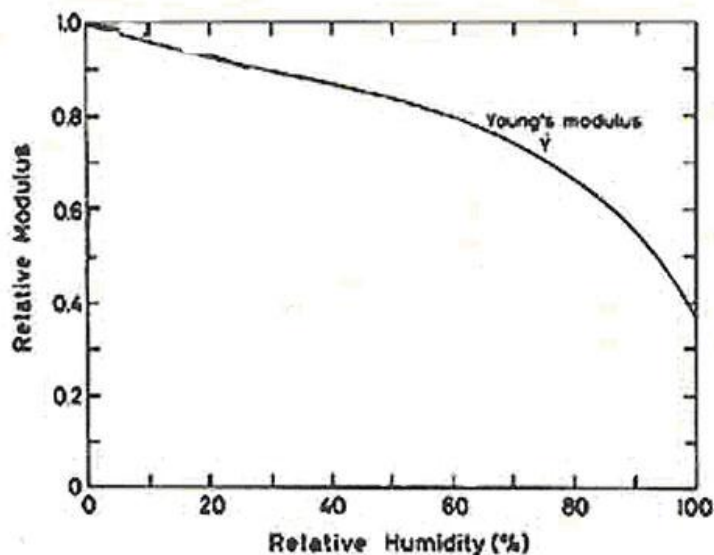
Source: Fraser, MacRae and Rogers (1972).

Figure 2.14 This graph demonstrates that as the available moisture to a hair fibre increases, Young's modulus decreases. The fibre is more elastic in the Hookean region. Source: Fraser, MacRae and Rogers (1972).

A wet fibre stretched to the end of the yield region will regain its original properties so that the load extension behaviour can be repeated. This is called hysteresis. If the extension proceeds into *the post-yield region* then the structural memory is lost and the fibre **will not** return to the initial state. The mechanical properties in the post-yield region are independent of water.

X-ray diffraction studies (high angle X-ray diffraction) show major shifts in the X-ray reflections when a fibre is extended and are indicative of major molecular structural changes. These occur in the yield region and were called the alpha - pattern to alpha-pattern transformation by W. T. Astbury in the 1940's. Water is essential for this behaviour. It is generally agreed that what occurs at the molecular level in the Hookean region is a stretching of the non-covalent bonds within the

2-12 _____ WOOL472/572 Wool Biology and Measurement

alpha-helices, mainly hydrogen bonds and between the alpha-helices including ionic bonds. However when extension reaches the yield region (Figure 2.13) hydrogen bonds are broken and the alpha-helical conformation of the IFs unwinds and the alpha -pattern detected by X-ray diffraction increases in proportion to the extension up to 30%. Then a restraint on the rate of extension in this post-yield region occurs because disulphide links between IFs or between the IFs and the matrix proteins come into play. The fibre finally breaks.

Wool is stable in water up to 100^0C but 30 degrees higher than that causes a contraction by about 25% and disruption of the helices of the IFs is observed by X-ray diffraction with the alpha - to alpha -pattern transformation. Another property of wool and (hair) fibres is supercontraction. If a fibre is elongated in steam and then released it will gradually contract to about 50% of its length. The molecular explanation of that phenomenon is that the alpha-helices stretch into a alpha -sheet conformation that collapse into folds. The supercontracted state is irreversible because the polypeptide chains are stabilised by the reformation of disulphide bonds.
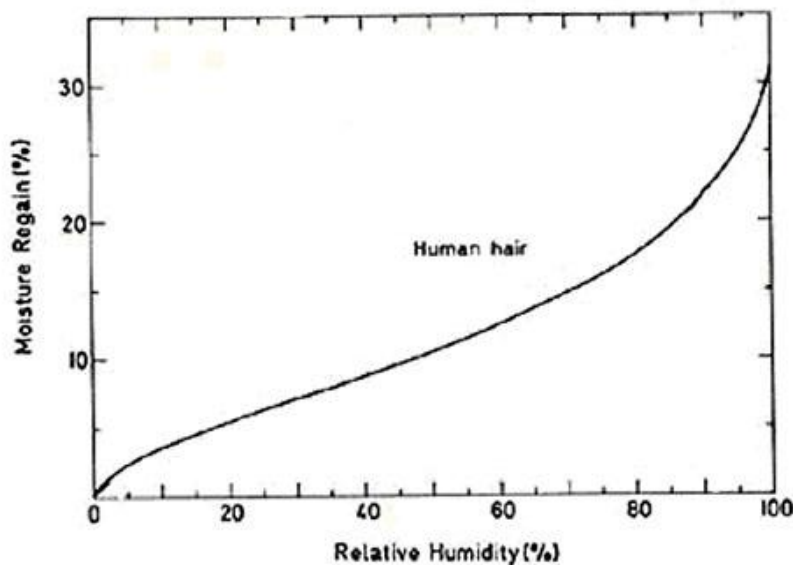

Figure 2.15 The graph shows the capacity of the wool fibre to take up water molecules as relative humidity increases. The water molecules penetrate the matrix proteins between the IFs and cause radial swelling of the fibre. Source: Fraser, MacRae and Rogers (1972).

When wool (or hair) is wet, constrained in a coiled fashion and dried, the wool remains in a curled state and the process is called "setting"or "cohesive set". It is one method of hair waving and is removed by high humidity or wetting. The molecular events are the breaking and remaking of hydrogen bonds in the IF structure. More permanent setting of fibres is achieved by breaking and reforming disulphide bonds while the fibres are in the deformed state. Such covalent changes can be introduced by raising the temperature of the water that brings about the formation of a small amount of sulphydryl groups by hydrolysis and then sulphydryl-disulphide bond exchange altering the location of disulphide bonds. Alternatively, reducing agents can be used to break the bonds and then re-oxidise them in a new configuration with the fibre in its curled state. The latter mechanism is the basis of permanent waving of human hair.

The elastic behaviour of wool fibres is not significantly influenced by the relatively inelastic cuticle. The inelastic cuticle is more likely to influence the force required to <u>bend</u> a fibre (the bending modulus) and this is especially so in human hair in which the cuticle is several scale cells thick compared to wool in which the cuticle is mainly one scale cell thick.

Water Sorption

Measuring of alterations in the separation between IFs in wool by low-angle X-ray diffraction has provided an insight into changes in wool structure in reponse to water sorption. The distance between adjacent IFs is of the order of 11nm and the space filled with the matrix proteins and separating the IFs is about 1.5nm, given that the IF diameter is 8nm. The separation distance of orthocortical IFs is somewhat less than that of the paracortex. It has been found that the IF separation increases by about 14% as the relative humidity (RH) increases to a maximum at 100% RH. The water content of wool in relation to relative humidity is referred to as the regain value (Figure 2.15) and at 65% RH it is about 14%. The swelling of a wool fibre in the presence of water vapour is anisotropic that is to say; the diameter of the fibre increases much more than the fibre length and is the result of penetration of water molecules between matrix protein molecules. The IFs extend no more than 1% when water penetrates.

The behaviour of wool in the presence of water has important practical consequences. Wool textiles are exothermic when water vapour penetrates and this is one of the reasons why wool is protective in cold and wet weather through the penetration of water vapour. On the other hand the surfaces of wool fibres are hydrophobic and this delays the wetting of wool textiles by liquid water.

Relevance of the Basic Knowledge to Wool Processing

The felting of wool fibres and the shrinkage of woollen garments are unique properties of wool. The friction of a fibre is greater when rubbed in the tip to root direction than the reverse because of the scale cell protrusions; this is known as the differential friction effect (DFE). Wool felts when fibres are rubbed together especially when wet. There are several theories of felting and factors that increase the rate of felting includes the fineness of the fibres, their elastic properties and the sinusoidal type of crimp.

The felting property is used for producing felted products but in the form of woollen garments felting causes shrinkage. Methods for reducing shrinkage necessarily involve modifying the surface to reduce the DFE. The initial process of shrinkproofing of wool tops by using chlorine was discovered empirically and is effective but the wool is harsh to handle. Shrinkproofing has been refined through research; the modern process is the Hercosett process and includes the deposition of a surface polymer after chlorination to give a better product that is softer. An interesting aspect of this problem is the finding by Tony Schlink that sheep can be selected for wool that has low shrinkage properties (see useful weblinks) so there is a potential for a biological approach. However it would be important that other characters are not compromised such as fibre diameter, crimp and staple strength.

Similarly, the setting of fibres when in fabric form by steam was discovered but improved through basic knowledge of the disulphide bond. Partial cleavage of the bonds has led to a commercial method of permanent creasing. It is to be expected that new processes will be introduced through continued research. The CSIRO's OPTIMA process for example, is based on fundamental knowledge and produces wool that is softer. In this process wool tops are lightly treated to reduce some of the disulphide bonds, stretched in steam and then set. The fibre diameter is decreased by 2-3μm.

A major problem with woollen garments is that they slowly yellow in sunlight if white or change colour if dyed. Overcoming this problem is a major challenge and a practical solution to it will come from the increasing knowledge of wool structure and chemical properties of the proteins, especially those in the cuticle where the yellowing process is greatest.

There is another aspect that can be considered here and that is what might be done with wool waste; wool that cannot be converted to yarn. One practicable solution would seem to be to dissolve the wool by known methods and to spin fine fibres from the dissolved proteins through a chemical stabilising bath. So far the fibres that have been produced were relatively weak and the process is expensive because of the cost of chemicals and energy requirements.

Readings

The following readings are available on web learning management systems

1. Fraser, R.D.B., MacRae, T.P. and Rogers, G.E. 1972, *Keratins: Their Composition, Structure and Biosynthesis*, Charles C. Thomas, Springfield, Illinois.

2. Hardy, M. H. 1992, 'The secret life of the hair follicle,' *Review,* vol. 8(2).

3. Hearle, J.W.S. 1997, 'Can genetic engineering enhance the miracle of wool? Part 3: Why worry about fibre strength?,' *Proc. of Textile Horizons,* Aug/Sept 1997.

4. Rogers, G.E. 2004, 'Hair follicle differentiation and regulation,' *International Journal of Developmental Biology,* vol 48, pp. 163.

References

Bates, E.J., Hynd, P.I., Penno, N.M. and Nancarrow, M.J. 1997, 'Serum-free culture of wool follicles: effects of nutrients, growth factors and hormones,' British Journal of Dermatology, vol. 137, pp. 498.

Bawden, C.S., McLaughlan, C., Nesci, A. and Rogers, G. 2001, 'A unique type I keratin intermediate filament gene family is abundantly expressed in the inner root sheaths of sheep and human hair follicles,' J. Invest. Dermatol., vol. 116, pp. 157.

Bond, J.J., Wynn, P.E. Brown, B.N. and Moore, G.P.M. 1994, 'Growth of wool follicles in culture,' Vitro Cell Development and Biology, vol. 30(A), pp.90.

Chase, H.B. 1965, Cycles and waves of hair growth, in: Biology of the Skin and Hair Growth, A.G. Lyne and B.F. Short (eds.), publ. Angus and Robertson, Sydney, pp. 462

Cotsarelis, G., Sun, T.-T. and Lavker, R.M. 1990, 'Label-retaining cells reside in the bulge area of the sebaceous unit: implications for follicular stem cellls, hair cycle and skin carcinogenesis,' Cell, vol. 61, pp.1329.

Ferguson, K. 1995. 'The evidence for selecting sheep the Watts way,' Australian Farm Journal, November, pp. 28.

Fraser, I.E.B. 1964, 'Studies on the follicle bulb of fibres. I. Mitotic and cellular segmentation in the wool follicle with reference to ortho- and parasegmentation,' Australian Journal of Biological Science, vol. 17, pp. 521.

Fraser, R.D.B., MacRae, T.P. and Rogers, G.E. 1972, Keratins: Their Composition, Structure and Biosynthesis. Charles C. Thomas (ed.) , Springfield, Illinois.

Fraser, R.D.B. and Rogers G.E. 1954, 'The origin of segmentation in wool cortex,' Biochemical and Biophysical Research Communications, vol. 13, pp. 297.

Gillespie, J.M. 1991. The structural proteins of hair: isolation, characterization and regulation of biosynthesis. *In* Physiology, Biochemistry and Molecular Biology of the Skin. Vol. I. L.A. Goldsmith, editor. Oxford University Press, Oxford. 625-659.

Hardy, M.H. 1969, The differentiation of hair follicles and hairs in organ culture, in: Advances in Biology of Skin, vol. 9. W. Montagna and R.L. Dobson, (eds.) Pergamon Press, Oxford, pp. 35.

Hardy, M.H. 1992, 'The secret life of the hair follicle,' Trends in Genetics, vol. 8, pp. 55.

Hardy, M.H., and Lyne, A.G. 1956, 'The pre-natal development of wool follicles in merino sheep,' Australian Journal of Biological Science, vol. 6, pp. 423.

Horio, M. and Kondo, T. 1953, 'Crimping of wool fibres,' Text. Res. J., vol. 23, pp. 373.

Jones, L.N. and Rivett, D.E. 1997, 'The role of 18-methyleicosanoic acid in the structure and formation of mammalian hair fibres,' Micron, vol. 28, pp. 469.

Moore, G.P., Jackson, N. Isaacs, K. and Brown, G. 1998, 'Pattern and morphogenesis in skin,' J. theoret.Biol., vol. 191, pp. 87.

Nagorcka, B.N. and Mooney, J.R. 1989, The reaction-diffusion system as a spatial organizer during initiation and development of hair follicles and formation of the fibre, in: The Biology of Wool and Hair, G.E. Rogers, P.J. Reis, K.A. Ward, and R.C. Marshall, (eds.), publ. Chapman and Hall, London, New York, pp. 365.

Parry, D.A.D. and Steinert, P.M. 1995, Intermediate filament structure, Springer-Verlag, Heidelberg.

Philpott, M.P., Green, M.R. and Kealey, T. 1990, 'Human hair growth, in vitro,' Journal of Cell Science, vol. 97,pp. 463.

Powell, B.C. and Rogers, G.E. 1997, The role of keratin proteins and their genes in the growth, structure and properties of hair, in: Formation and structure of hair, P. Jolles, H. Zahn, and H. Hocker, (eds.) Birkhauser Verlag, Basel. pp. 59.

Reynolds, A.J. and Jahoda, C.A. 2004, 'Cultured human and rat tooth papilla cells induce hair follicle regeneration and fiber growth,' Differentiation, vol. 72, pp. 566.

Rogers, G.E. 1959a, 'Electron microscope studies of hair and wool,' Ann. N.Y. Acad. Sci. vol. 83, pp. 378.

Rogers, G.E. 1959b, 'Electron microscopy of wool,' Journal of Ultrastructure Research, vol. 2, pp. 309.

Rogers, G.E. 1999, Cells and molecules in the properties of hair and wool, in: Supramolecular and Colloidal Structures in Biomaterials and Biosubstrates, Lal, M. (ed.).

Rogers, G.E. 2004. 'Hair follicle differentiation and regulation,' Int J Dev Biol., vol. 48, pp. 163.

Ryder, M.L. and Stephenson, S.K. 1968, Wool Growth. Academic Press, London, New York.

Stryer, L. 2002. Biochemistry. W. H. Freeman (ed.), New York.

Glossary of terms

Cell lineage	The specific pathway of differentiation that a group of cells follows
Dermal cell	Fibroblast cells that synthesise collagen, the fibrous protein that composes the deep layer beneath the epidermis and that surrounds hair follicles

Dermal sheath	The layer consisting of a type of fibroblast, adjacent to the outer root sheath of the follicle, continuous with the dermal papilla and makes collagen Type IV and mucopolysaccharides
Epithelium	The layer of cells of ectodermal origin that makes up a tissue surface
Hair cycle	The different stages of follicle activity of hair production (anagen), partial regression of the follicle (catagen) and a dormant stage (telogen). The stages vary greatly between different species. In sheep, anagen can last for 2 years whereas in mice it is a few weeks
Involucrin	A protein found in cell envelopes that modifies the plasma membrane of keratinocytes to become a physically tough membrane
Isopeptide bond	Found as a cross-link in some proteins and connects the epsilon amino group of a lysine side chain with the gamma carboxyl group of a glutamic acid side chain. The normal peptide bond of proteins connects amino acids via the alpha carboxyl group of any amino acid to the alpha amino group of another
Keratinocyte	The differentiated cells of skin and related tissues that A protein found in cell envelopes that modifies the plasma membrane of keratinocytes to become a physically tough membrane produce keratin intermediate filaments and keratin associated proteins as their major cytoskeleton products
Loricrin	A cystine-rich protein found in cell envelopes with involucrin that modifies the plasma membrane of keratinocytes to become a physically tough membrane
Matrix cells	The dividing cells in the bulb of hair follicles. The term matrix is also used to describe the proteins that occur between the intermediate filaments of hair and epidermis
18-methyleicosanoic acid	An unusual 21-carbon fatty acid with a methyl group branched from carbon-18
SEM	Scanning electron microscope/microscopy
Sulphydryl-disulphide exchange	A process involving the switching of a disulphide bond through interaction with a free sulphydryl group between two protein chains
TEM	Transmission electron microscope/microscopy