THE ELECTRON MICROSCOPY OF THE HUMAN HAIR FOLLICLE*

PART 1. INTRODUCTION AND THE HAIR CORTEX

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PLATES 50 TO 53

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INTRODUCTION

This series of papers will describe the fine structure of the hair follicle as revealed by electron microscopy of thin sections. Particular attention has been given in the study to the differentiation of the various cell layers and to the synthesis of the intracellular products.

There are many descriptions of the hair follicle in the literature, and the most useful have been found to be those by Hoepke (17), Maximow and Bloom (21), and Sharpey-Schafer (30) on human hair and Auber (6) on wool. The recent book by Montagna (24) contains a valuable review of the histochemistry.

From the matrix of the follicle (Text-fig. 1.1) six distinct cell streams may arise, as a consequence of continuous cell division, to form the hair and the inner root sheath. Together these structures comprise: (1) the medulla, (2) the hair cortex, (3) the hair cuticle, (4) the cuticle of the inner root sheath, (5) the Huxley layer, and (6) the Henle layer. Layers 1, 2, and 3 comprise the emergent hair, layers 4, 5, and 6 the inner root sheath. The earlier work by light microscopy has shown that the differentiation and development in each of these cells are distinct from those in adjacent streams.

The hair follicle is an attractive object for a study of morphogenesis and differentiation for several reasons. First the hair is a small organ, not too large for surveying at high magnifications with the electron microscope; second there are available extensive chemical and histochemical data to be correlated with fine structure; finally the organ, since it is on the external surface of the

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body, is readily accessible. It is clear that an understanding of morphogenesis in any particular instance will be greatly advanced when, by means of microscopy, the fine structures of the cells involved and the structural aspects of their interactions are minutely visualised. Accordingly the object in this work has been to determine, in as much detail as is possible, the life history of the individual cells in the several differentiating cell streams.

An account of some of this work (9-11), particularly where it relates to pigment formation, has already appeared. The present account will be divided for convenience into three Parts. Part 1 will deal with the formation of the cortex and the structure of keratin, Part 2 with the cuticle, and Part 3 with the inner root sheath. The section describing materials and methods included here applies to all three parts. A description of the outer root sheath, and the associated dermal structures of the hair, including the papilla, will be given in subsequent papers.

Materials and Methods

Follicles from man, rat, mouse, and sheep have been studied, but this report will be confined to the human follicle on which most of the work has been done. In some animals portions of skin may be excised, fixed, and embedded. This procedure was not often practicable in the human case; but the simple operation of plucking was found to provide satisfactory material. The parts of the follicle which are removed by plucking vary from one individual to another and also with the particular phase of the hair growth cycle. For the limited purpose of studying the growth of the hair in the steady state, follicles with a well developed bulb attached were chosen. In most cases the plucked follicles were without papilla and germinal layers, but occasionally the complete papilla and its enclosed structures were obtained. Immediately after it had been plucked, the root was immersed in the standard buffered osmium tetroxide fixative (25) (1 per cent OsO₄ and veronal-acetate buffer at pH 7.3, cooled to about 5°C.). The follicles were fixed usually for 2 hours, after which they were washed, dehydrated, and embedded in the usual way. Mixtures of one part methyl and five parts butyl methacrylate were used for embedding. Some preparations were embedded in an epoxide resin. A few special preparations of hair or chemically treated hair and wool will be described in the text.

The sections were cut with a modified Cambridge rocker microtome and examined with either a Siemens Elmiskop 1 or a Philips E.M.100 electron microscope.

Location of Micrographs

Longitudinal and cross-sections of the lower quarter of the follicle, which includes the whole of the region in which cell growth and differentiation take place, were obtained in the course of this study.

The location of the regions shown in the figures will be facilitated by reference to Text-fig. 1.1, which shows a longitudinal section of the lower part of a follicle. The follicle is shown divided into two symmetrical halves by a vertical line. On the left of this line are shown the several zones into which, for convenience in the subsequent discussion, the base of the follicle may be divided;

the limits of these zones are only approximate. On the right of the line the locations of the various electron micrographs are indicated. The numbers in the squares are the numbers of the particular micrographs; e.g., 1.3 is Fig. 3 of Part 1. In most cases these locations were determined both by light microscopy of thick sections, cut adjacent to those examined in the electron microscope and also by low power electron micrographs. The time scale on the right hand side has been added to show the rate of movement of the cell stream and the duration of the various changes. It has been computed by assuming an average value of 0.3 mm./24 hours for the rate of growth of hair (29). Since no measurements were possible of the growth rate of the actual hairs used, the scale can only be approximate.

The Formation of the Cortex and the Structure of Keratin

OBSERVATIONS

The Undifferentiated Matrix.—All the cells forming the hair and the inner root sheath derive from the undifferentiated matrix (U in Text-fig. 1.1). Below this zone is the germinal layer R in which the cells have a columnar form and are attached at one end to the basement membrane of the papilla. A fuller account of the germinal layer will be given in a subsequent paper describing the papilla. The presumptive cortical cells are derived from the inner part of the undifferentiated region U (Text-fig. 1.1); they form the solid cylinder of cells, which in non-medullated hairs, occupies the central part of the follicle.

The nuclei of the cells of the matrix are roughly spherical, sometimes with a single indentation; they are extremely granular particularly those regions adjacent to the nuclear membrane. The nuclear/cytoplasmic ratio is large (Fig. 1.1). Nucleoli are conspicuous and granular. In the zone D typical division figures were occasionally noted. The mitochondria (M) are long and thin, but otherwise appear normal. There are regions containing clusters of empty agranular vesicles, which are similar to the Golgi regions described in other cells. The most characteristic feature of the cytoplasm is the numerous clusters of small dense particles (150 to 200 A diameter) (Fig. 1.1 P). The cell cytoplasm is relatively empty at this level and no accumulation of amorphous material, which might be a precursor of the fibrous keratin, has been observed.

The cells are rounded, but their surfaces are thrown into numerous corrugations and finger-like projections or pseudopods. Contact between the cells is limited to small local areas, which are made conspicuous both by the increased density of the membranes and also by the material which occupies the space between them (120 to 150 A). Contacts of a similar, but more elaborate kind, are very conspicuous in the outer root sheath and in the epidermis (28, 33). In the presumptive cells of the cuticle and sheaths these contacts spread and the surface irregularities are smoothed out. The morphogenetic importance of
these contacts will be discussed in Parts 2 and 3. In contrast to their behaviour in the cuticle and sheath, the contacts in the presumptive cortical cells remain localised and intercellular gaps (up to 2 to 3 μ) are common. These gaps persist as the cells flow past the melanocyte rest (M) and leave the bulb. At this level (region F, Text-fig. 1.1) they rapidly elongate and the intracellular inclusions, nuclei, and mitochondria become oriented parallel to the axis of the follicle (Fig. 1.2).

**Text-Fig. 1.1.** Key to location of electron micrographs. The drawing shows a longitudinal section of the bulb region of a human hair follicle (shown in full in the inset). P is the papilla, R the germinal layer, D division region, U the undifferentiated matrix, M the zone of melanocytes. The regions of the hair and sheaths, indicated by the small numbers 1 to 6, are the cortex, hair cuticle, sheath cuticle, Huxley's layer, Henle's layer, and the outer root sheath respectively. The numbers enclosed in squares are those of the micrographs illustrating the text. The first number refers to the part and the second to the number of the figure; e.g., 3.1 refers to Fig. 1 of Part 3. The position of the square indicates the region covered by the section. Certain figures, whose location is above the area shown on the diagram, are not indicated. F is the region in which fibrous keratin is formed and K is the beginning of the keratinisation zone.
In the mid- and upper part of the bulb (region F, Text-fig. 1.1) the gaps between the cortical cells are occupied by the long processes of the melanocytes. Pseudopods still project from the cortical cells at this level and seem active in the neighbourhood of the pigment-bearing ends of the processes. Occasional bundles of pigment granules, surrounded by two membranes, have been found within the cortical cells.

The Formation of Keratin.—Fibrous keratin first appears as wispy clumps of fine filaments in the cells of the mid- and upper bulb (F in Text-fig. 1.1). These filaments, less than 100 A in width, which seem to be definite structural units, are oriented parallel to the elongated nuclei, mitochondria, and the long axis of the cell. There is no obvious connection between the filaments and the clusters of dense particles. The particles seem to reside in patches of amorphous ground substance (Fig. 1.3).

As the cells move towards the neck of the bulb, the bundles of filaments rapidly increase in length and width by the accretion of further filaments, until they reach a size visible in the light microscope. Histologists have previously referred to these fibrous structures as fibrils, therefore this term will be used here for such aggregates of filaments, but without restriction as to size. Many fibrils lie close to and parallel to the nuclear and cell membranes and some are twisted slightly around their long axis. The pigment granules lie in rows between the growing fibrils.

Keratinisation.—Above the constriction of the follicle is the region (K) (Text-fig. 1.1) referred to as the zone of keratinisation (6, 14). Here both the large fibrils and their component fine filaments become more clearly defined (Fig. 1.4). This is partly due to an increased regularity in the packing of the fine filaments, which over considerable areas approximates to hexagonal close packing, and partly to an increased contrast resulting from the appearance of a denser material between the filaments. The filaments within the fibrils now appear light on a darker ground (Fig. 1.6). Cells in which this change had occurred were found contiguous to others yet unchanged (Fig. 1.4). In addition to the hexagonal arrangement of the fine filaments, other patterns resembling those of finger prints are common. These patterns will be referred to as "whorls" (Fig. 1.7).

The large intercellular gaps, common at a lower level, disappear in the neighbourhood of the neck of the follicle. However, higher in the keratinisation zone, a uniform dilation of the membranes occurs, which results in a final spacing of about 200 to 250 A. A similar separation of cell membranes occurs in the cuticle and sheaths and will be described in Parts 2 and 3.

In the keratinisation zone more filaments together with interfilamentous material are added to the existing bundles of filaments, which become rather more uniform in diameter. Finally many fibrils fuse laterally to form large masses in the interstices of which the nuclear and cytoplasmic remnants are trapped (Fig. 1.5).
Although sections of the fully hardened hair can be cut only with difficulty, the results have shown (Fig. 1.8) that the keratin has a rather uniform appearance in cross-section and the fibrillar structure is rarely visible. In unstained and unfixed material the cell membranes, nuclei, and other condensed inclusions, appear more dense than the keratin. When the keratin is removed, by first oxidising the cystine with peracetic acid and then extracting the oxidised protein with dilute alkali (1), these non-keratinous constituents are readily demonstrated (Fig. 1.9). The fibrillar structure in hair becomes more apparent after prolonged treatment of the hair in the osmium fixative, or after a preliminary reduction combined with heavy metal staining.

**DISCUSSION**

_Differentiation in the Bulb._—A discussion of differentiation will be found in Parts 2 and 3 of this series following the description of the cuticle and inner root sheath. However, one aspect of the cell membranes may be conveniently discussed here. In the matrix (M, Text-fig. 1.1) the outlines of the cells are very irregular and intercellular gaps are common. These features may be interpreted as evidence of flexibility and lack of adhesiveness of the plasma membranes. In the presumptive cortex, in contradistinction to the cuticle and inner root sheath, this condition persists until the level of the neck of the follicle. The long melanocyte processes seem able to take advantage of the gaps to penetrate between the cells (10). Their tips, packed with pigment granules, have been found sometimes completely within cortical cells and sometimes partly enveloped by the cell membranes. It is possible that an active phagocytosis by the cortical cells is the mechanism by which the pigment enters the cells.

_Protein Synthesis._—All the cells of the matrix have similar cytoplasmic constituents, although they subsequently make very different products. There are many mitochondria, a few agranular vesicles (Golgi vesicles ?), and many small dense particles 150 to 200 A, that may be identified with Palade’s “small particulate component” (26). The cells are rich in ribonucleic acid (16, 24). There is no organised endoplasmic reticulum (27), but the particles associate in small clusters, which later become centres of a denser ground substance. A similar situation is found in skin (28, 32), and may be common to all epidermal cells. In the cortex, when keratin filaments appear, they bear no obvious spatial relation to the particles, suggesting that any precursor formed on the particles passes to the filaments in a form, which is either not preserved, or too small to see. These epidermal cells function for a short time only (48 hours) and accumulate their products without secreting them externally. This is quite a different situation to that found in secretory cells which continuously synthesise and secrete protein; these cells develop an elaborate reticulum.
Keratin Formation.—The formation of the fibrous keratin itself can be divided into two stages, first the formation of fine filaments and second the condensation of these into larger fibrils.

The filaments begin to appear in quantity in the upper bulb, where it has previously been shown (31) that the birefringence rises rapidly. An oriented α-type x-ray diffraction pattern can also be obtained from the follicle immediately above the constriction (22). There is little doubt therefore in identifying the filaments as the crystalline fibrous component of keratin. Porter (28) and Selby (32) have described the appearance of similar bundles of fine filaments in epidermal cells. They will be referred to as α-filaments, and it is considered that their internal structure is essentially unchanged in the final hair. Their diameter cannot be measured very accurately at this level, but it is substantially less than 100 A. At a higher level, where it is possible to make more accurate measurements, the diameter lies between 60 and 80 A. In longitudinal sections the filaments reveal a granular appearance, which may be due to a poorly resolved fine structure.

The filaments, when first formed, cluster in loosely knit bundles which may be tactoids. They are oriented parallel to the fibre axis as soon as they appear. This orientation, which is common to all components of the cortex, may be due to the narrowing of the follicle above the papilla tip, which constrains the cells to adopt a long spindle shape. The nuclei suffer the same deformation and the elongated mitochondria are also oriented.

The subsequent condensation of the filaments into more coherent large fibrils seems a different type of association which can develop suddenly cell by cell (Fig. 1.4). The most remarkable feature is that the filaments are now seen to be separated by a new substance which is denser than the filaments themselves. Because it improves the compactness of the bundles of filaments, it may be inferred that it functions as an adhesive cement. The appearance of this interfilamentous cement coincides with the rapid increase in the thiol (SH) content of the cortex (13, 16, 24). Bahr (7) has emphasised that there is a strong reaction between osmium tetroxide and cysteine or cystine. Further the length of the follicle which is stained a very dark brown by the fixative coincides with the keratinisation zone. Therefore as the osmium functions as a visible stain for thiol groups in this region, it may also function as an electron stain. Assuming that the high apparent density of the interfilamentous substance is due to its osmium content, it may be inferred that this substance has a higher cysteine content than the filaments.

The "whorl" structure shown in Fig. 1.7 and Text-fig. 2 (b) (10) becomes conspicuous as keratinisation increases, although areas of hexagonal packing persist in the centre of the fibrils. The interpretation of the whorls cannot be definitely established from our present data. However they may indicate a small twist in the bundle of filaments developing in the later stages of growth.
Keratin, using this name for the hardened fibrils which ultimately fill the cells of the cortex, would thus not be of uniform composition at the electron microscope level. In a sense it may be said to consist of two proteins in close association, one of which is fibrous and the other amorphous (Text-fig. 1.2). It is desirable in view of the importance of this concept to point to chemical evidence in its favour. Goddard and Michaelis (15) dissolved wool in alkaline thioglycolate solution and fractionated it into two proteins. Similarly Alexander and Earland (1) oxidised wool with peracetic acid to destroy the cystine cross-linkages and extracted the keratin with dilute ammonia. The residue (Fig. 1.8) consists of cell membranes, nuclei, and other cytoplasmic constituents (23).

Text-Fig. 1.2. (a) Proposed structure of the keratin fibrils showing the α-filaments embedded in a continuous, amorphous, interfilamentous cement (γ). The α-filaments are about 60 Å in diameter and are considered to be responsible for the α-type x-ray pattern. Ideally the arrangement of the filaments is hexagonal, but more frequently the whorl structures (b) and (c) appear.

(b) and (c) Arrangements of filaments within the keratin fibrils giving the appearance of whorls or finger prints which are shown in Fig. 1.7. The association of the filaments may be stronger in one direction than in the other. The spirals, which may be single (b) or multiple (as in c), develop around areas of quasihexagonal packing, perhaps as a result of a dislocation. The geometrical similarity to surface structures formed during crystal growth may be noted.

The extract may be fractionated into two main constituents, one a fibrous protein (α-keratose) which gives the same oriented x-ray pattern as hair, and the other a lower molecular weight, higher sulfur content protein (γ-keratose) incapable of being drawn into fibres. It seems likely that α-keratose is derived from the α-filaments and γ-keratose from the interfilamentous cement. Accordingly the designations α- and γ-keratin will be used to label the two constituents of the keratin complex (Text-fig. 1.2). Alexander and Hudson (1) report that the γ-keratose amounts to 30 to 40 per cent of the extractable keratin of wool. The approximate figure, derived from the areas of the two constituents in the cross-section of fibrils in hair, is nearer to 50 per cent. This may be regarded as good agreement, since the amount of γ-keratin to be expected from the hair (5 per cent sulfur) is greater than in wool (3.5 per cent sulfur).
Relation to X-Ray Diffraction Data.—The wide-angle, fibre-type x-ray diffraction pattern (α-pattern) common to all mammalian keratins (2, 8, 20) must arise from the oriented α-filaments. The slight twist of the bundles of filaments, which is inferred from the existence of the whorl structure may contribute to the arcing of the diffraction spots. The γ-keratin presumably contributes only to the diffuse haloes, which are found in all the x-ray photographs (4, 5). That the sulfur is largely in the amorphous fraction is corroborated by the fact that reduction of cystine followed by substitution of the H of the thiol group by alkyl radicals, makes little change in the fibre-type pattern. Any attempt to relate the chemical composition to the crystalline structure of the α-filaments is difficult, as Astbury has pointed out (3), in the absence of determinations of the amino acid composition of the two separate fractions, α- and γ-keratin.

The small-angle x-ray diffraction pattern given by many keratins contains both lateral and longitudinal spacings (8, 20), indicating structures within the range of electron microscopy. The lateral spacings of the order of 70 to 80 Å may well arise from scattering by the complex, “filaments plus cement.” This complex consists of a system of rodlets (diameter ca. 60 Å), in approximate hexagonal array with centres spaced 70 to 80 Å apart, embedded in cement of different scattering properties. The longitudinal long spacings cannot be accounted for so readily. The filaments appear granular in longitudinal sections, which suggests a poorly resolved fine structure, but no regular spacing of the order expected (100 to 200 Å) has been observed.

Comparison with Electron Microscopy of Fragments of Fibres.—The present conclusions concerning the structure of keratin are in good agreement with those drawn from an examination of fragments of fibres which have been disintegrated by chemical procedures designed to reverse the process of keratinisation (19). Farrant, Rees, and Mercer (12) reduced, ethylated, and digested wool with pepsin to free the fibrils and obtained suspensions of fine filaments about 100 Å in diameter; these are probably the same structures as those now found in sections. Similar preparations have been obtained by Jeffrey, Sikorski, and Woods (18), who, however, report that their filaments are associated in sheets. There is, in many sections (Fig. 1.7) of the whorls, a suggestion that the filaments are attached to the adjacent unit more strongly in the tangential direction than in the radial one; certain forms of disintegration might separate these into sheets.

SUMMARY

1. The presumptive cortical cells of hair in the undifferentiated matrix of the bulb contain mitochondria, agranular vesicles, and many small dense R.N.P. particles, but no keratin, pigment granules, or endoplasmic reticulum.
2. In the mid-bulb region intercellular adhesion is limited to small localised
areas. Intercellular gaps are common and the cell surfaces are irregularly convoluted. The melanocyte processes penetrate the cell gaps. The relation between their pigment-bearing tips and the involutions of the cell membranes suggests an active phagocytosis of the tips.

3. Fibrous keratin first appears in loose parallel strands of fine filaments (ca. 60 A diameter) in the mid-bulb. The filaments, the long mitochondria, and elongated nucleus are all parallel to the long axis of the cell and the axis of the follicle.

4. At the level of the constriction of the bulb and above, a dense amorphous substance appears between the fine filaments and apparently acts as adhesive cement. The bundles of filaments now form well defined fibrils. The packing of the filaments within the fibrils is in places hexagonal and elsewhere in the form of "whorls."

5. At higher levels further filaments and interfilamentous cement are added together and the whole cytoplasmic space becomes packed with fibrils which finally condense to massive blocks of keratin. The residual cellular material occupies the interstices.

6. The addition of the interfilamentous substance is regarded as an essential factor in keratinisation. Keratin is considered to be a complex made of fine filaments (α-filaments) embedded in an amorphous substance (γ-keratin) which has the higher cystine content.

7. The wide-angle fibre-type x-ray pattern is thought to be due to scattering by the fine α-filaments and some low angle lateral spacings to the filament-plus-cement structure.

REFERENCES

EXPLANATION OF PLATES

PLATE 50

The magnifications of the electron micrographs are indicated by a line with the length shown.

Many of the micrographs contain dense spherical particles, often aggregated, about 200 Å diameter. These are particles of colloidal gold, which are added to facilitate focusing.

Fig. 1.1. An electron micrograph of cells of the undifferentiated matrix of the hair bulb (region U, Text-fig. 1). These cells have a high nuclear/cytoplasmic ratio. The nuclei (N) and nucleoli (n) are conspicuous. The cytoplasm contains mitochondria (M), Golgi elements (G), and numerous dense particles (P). The wide intercellular gaps (possibly here enhanced by fixation), suggest that the cellular adhesion is poor. The surfaces have numerous finger-like pseudopods (S). × 16,000.

Fig. 1.2. A longitudinal section of the cortical cells in the mid-bulb region where keratin filaments are rapidly accumulating. The cells are greatly elongated in the direction of the axis of the growing hair. Intercellular gaps appear at G and cell contacts at C. The mitochondria (M) are elongated and oriented. Clusters of dense particles (P) fill the cytoplasm. Fibrils of keratin (F) are seen running parallel to the long axis of the cells. × 24,000.

Inset.—Micrograph at higher magnification of a fibril (F), which consists of a loose association of filaments (f). × 80,000.
FIG. 1.3. Cross-section of two cortical cells in the upper bulb region (about the same level as Fig. 1.2) showing cross-sections of fibrils at F. Cell membranes (B) showing gaps (G) cross the field. An elongated mitochondrion is cross-sectioned at M. The fibrils are loose and poorly consolidated in comparison with later forms (cf. Figs. 1.5 and 1.8). × 120,000.

FIG. 1.4. Cross-section of portions of two cortical cells immediately above the constriction of the bulb. Two adjacent cell membranes cross the field in a sinuous curve separating the two cells. These two cells show different degrees of keratinisation; the lower cell is at an earlier stage than the upper. The bundles of keratin filaments in the lower cell are less densely stained and relatively poorly organised. In the upper cell the bundles are more deeply stained (higher cysteine content) and a regular internal structure is developing, (quasi-hexagonal at H and in whorls at W). The bundles are more discrete and coherent and now may be recognised as fibrils. × 120,000.
(Birbeck and Mercer: Human hair follicle. Part 1)
Fig. 1.5. Cross-section of cortical cells in the upper keratinous zone showing an advanced stage of fibril formation. Nuclei (N) are granular and condensed but their membranes can still be seen. Cell membranes appear at B. The large keratin fibrils are shown in cross-section and almost fill the cytoplasm. Their diameter varies and some are fusing into massive formations which run parallel to nuclear and cell membranes, but from which they are separated by a distinct gap. Other cytoplasmic components (particles P and mitochondria M) are crowded within the interfibrillar space. Sections of pigment granules are shown at G. × 24,000.

Fig. 1.6. Micrograph at higher magnification of a cross-section of a cortical cell in the upper keratinous zone (same as Fig. 1.5) showing cross-sections of several massive keratin fibrils. The fine filaments (α-keratin) appear light on the darker ground (γ-keratin). It is probable that the interfibrillar material is strongly stained by reaction with the osmium fixative, presumably due to its high cysteine(cystine) content. (See Text-fig. 2.)

The filaments within the fibrils are in some areas packed in a quasihexagonal array; in other areas the whorl formation may be seen (see also Fig. 1.7). Fusion of the fibrils into a larger continuous structure of rather uniform texture may also be seen. The ill formed material between the fibrils is the cytoplasmic residue. × 120,000.

Inset shows a reversal of a portion of the section. Here the filaments appear as dark dots on a light ground. × 120,000.
(Birbeck and Mercer: Human hair follicle. Part 1)
PLATE 53

Fig. 1.7. Cross-section of a part of a cortical cell in the upper keratinous zone with keratin fibrils showing whorl formations. These formations become more obvious as keratinisation proceeds, and may be due to the packing of the fine filaments which is a result of the cementing action of the dense interfilamentous cement (γ-keratin in Text-fig. 1.2). In some limited areas particularly in the centre of the fibrils the packing is hexagonal; peripherally the structure usually develops a whorl, characterised by the sections of the filaments (light areas) forming parallel lines separated by darker layers of cement. × 80,000.

Fig. 1.8. Cross-section of the cortex of a fully hardened hair showing the homogeneity of the condensed keratin (K). Pigment granules (P), the interlocking cell membranes (B), which are denser than the keratin, and various dense cytoplasmic inclusions (D), may be seen. × 12,000.

Fig. 1.9. Cross-section of the cortex at the same level as Fig. 1.8 after the extraction of the keratin (for method see text). The cell membranes remain as dense structures (B), nuclear and other remnants appear at N. The membranes appear as double lines at arrow and an intermembranal deposit is still present. × 25,000.
(Birbeck and Mercer: Human hair follicle. Part 1)