AN ULTRASTRUCTURAL STUDY OF THE MEMBRANES OF KERATINIZING WOOL FOLLICLE CELLS

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SUMMARY

Measurements of the widths of apposed plasma membranes and of the spaces between them were made at different stages of differentiation of keratinizing and hardening cells of the wool follicle. In contrast to findings in the hair follicle, no changes were detected for apposed cortex, cortex/fibre cuticle and fibre cuticle/fibre cuticle cells until keratinization had taken place. The trilaminar appearance of the plasma membranes was then lost and the intercellular material decreased in width.

However, the inner root sheath cells developed a 'membrane complex' in enlarged intercellular spaces prior to hardening. Desmosomes are apparently retained in the hardened 'membrane complexes'. A band of cytoplasmic material was also formed adjacent to the inner lamellae of the plasma membranes immediately before hardening of the cells.

The presence of gap and tight junctions in differentiating cell lines of the wool follicle was noted.

INTRODUCTION

Changes occurring in the plasma membranes and in the spaces between them have been described in keratinizing and hardening cell lines of the hair follicle by Birbeck & Mercer (1957a–c) and Parakkal (1967). The distance between apposed cell plasma membranes of cortex and fibre cuticle cells was found to increase from 12–15 to 20–30 nm in the lower regions of the keratogenous zone (Birbeck & Mercer, 1957a, b; Rogers, 1964; Parakkal, 1967) and the plasma membranes themselves increased in width (Parakkal, 1967). The intercellular material formed a central dense component (8) after keratinization (Rogers, 1959).

In the human hair follicle, the distance between the plasma membranes of inner root sheath (IRS) cells showed an increase from 12–15 nm to as much as 30–40 nm, commencing at the fibrous transformation of trichohyalin and being complete just before the hardening of the cells (Birbeck & Mercer, 1957c). In addition, the formation of dense material on the cytoplasmic surface of the plasma membranes and the formation of a 'complex' in the space between apposed plasma membranes was described by these authors. The complex was pentalaminar in appearance and was composed of the 2 plasma membranes, intercellular material of low electron density, and a denser central band. In the mouse hair follicle, the plasma membranes were reported as widening to about 15 nm late in differentiation, the widened intercellular spaces becoming filled with an amorphous material (Parakkal, 1967).
The cell lines which keratinize (harden) in the wool follicle have been studied to
determine whether similar changes occur in the plasma membranes and the distances
between them.

 MATERIALS AND METHODS

Electron microscopy

Follicles from 4 Romney wethers were fixed at 4 °C for 4 h in Karnovsky's glutaraldehyde-
formaldehyde fixative in 0.1 M cacodylate buffer, pH 7.4. After 3 washes at 4 °C in 0.1 M
cacodylate buffer containing 7.5 % sucrose, pH 7.4, the follicles were fixed for 2 h in 1 %
OsO₄ in 0.1 M cacodylate buffer, pH 7.4, washed once in 0.1 M acetate buffer, and stained in
2 % uranyl acetate in the same buffer. The follicles were dehydrated in a graded series of ethanols
before being embedded in Epon. Grey-to-silver sections were stained with uranyl acetate and
lead citrate for examination in a Philips EM 300 electron microscope operating at 60 kV. A
thin foil (30 µm) objective aperture was used.

Photography

Photographs were taken of apposed cell plasma membranes of the following cell lines: cortex;
cortex/fibre cuticle; fibre cuticle/fibre cuticle; inner root sheath cuticle (IRSC); and Henle’s.
The film magnification for the photographs was ×9000, 12 000 or 15000. Kodak fine grain
release positive 35-mm film was used and was processed under standard conditions. The
negatives were printed at final magnifications of ×100 000, 166 000 or 204 000 on Ilfoprint paper,
grade 4, which has a dimensional stability of 0.1 %. In most cases, all the negatives of each cell
line to be measured were printed at the one printing session. Prints judged to be out of focus
were discarded.

Measurements

Five to 20 measurements of the various membrane components were made on each print,
using an ocular micrometer (×7) with a millimetre scale graduated to 0.1 mm. At the print
magnifications used, 0.1 mm represented 0.99 nm at ×100 000, 0.602 nm at ×166 000, and
0.489 nm at ×204 000. Measurements were made only where the plasma membranes had com-
paratively sharp edges, in an effort to avoid those which had been sectioned slightly obliquely
and to reduce the errors resulting from the difficulty of defining the exact limits of the diffuse
image produced by the membrane edges at these magnifications (Yamamoto, 1963).

The various components of apposed cell plasma membranes that were measured are shown
in Fig. 1. Two observers worked independently and their measurements were pooled.

Only 2 cell lines of the IRS were examined. Apposed inner root sheath cuticle (IRSC)
plasma membranes were chosen as representative of IRS cells which form a membrane complex
during hardening. Apposed Henle’s cells are an example of IRS cells between which desmo-

somes are common and are included in the hardened cell surfaces. Membrane differentiations
other than desmosomes in hardened Henle’s cells were not measured.

Because of the differing lengths of wool follicles and the difficulty of precisely relating ultra-
structural features to the features commonly used to identify regions in the light microscope,
a system of morphological markers was used to identify the same region in different follicles
(Fig. 2). The regions used and the markers delineating them are as follows:

Zone A: from the bottom of the follicle to level with the top of the dermal papilla. This
includes the mitotic zone.

Zone B: from zone A to the level where Henle’s cells harden. This includes the pre-elongation
and elongation zones.

Zone C: from zone B to the level where the plasma cell membrane of fibre cuticle cells opposed
to IRSC cells has a continuous layer of fibre cuticle keratin associated with it. This zone
includes approximately one third of the keratogenous zone.
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Fig. 1. Diagrammatic representation of apposed cell plasma membranes at different stages of differentiation to show the features measured.

A, differentiating cortex, fibre cuticle or inner root sheath (before complex formation) apposed membranes. Total width \( (tw) \) is the distance between cytoplasmic edges of the inner lamellae \((il)\). The intercellular gap \((ig)\) is the distance between the outer lamellae \((ol)\). The width of a single plasma membrane \((pm)\) includes the outer and inner lamellae.

B, keratinized cortex or fibre cuticle apposed membranes. Total width \( (tw) \) is the distance between the edges of the cytoplasmic material \((cy)\). The intercellular gap \((ig)\) is the distance between the edges of the dark central band.

C, apposed plasma membranes of hardened inner root sheath cuticle cells. The membrane complex \((c)\) lies between the exterior edges of the cytoplasmic bands \((cb)\). The intercellular gap \((ig)\) is the distance between the outer lamellae \((ol)\).

D, desmosome. Hardened Henle’s cells. Total width \( (tw) \) is the distance between the exterior edges of the cytoplasmic bands \((cb)\).

Zone D: from zone C to the level where the remaining IRS cell layers harden. This includes the remainder of the keratogenous zone.

Zone E: above zone D. This includes fully keratinized and hardened cells of all cell layers except the outer root sheath and companion cells (Orwin, 1971).

Measurement errors

The errors in measuring membranes have been assessed by Yamamoto (1963) and Lillibridge (1968). The latter has determined that the maximum errors resulting from drift in the electron microscope, out-of-focus negatives, peripheral distortion of micrographs, lens hysteresis and
Fig. 2. Diagrammatic representation of the lower wool follicle. The letters refer to the approximate limits of the zones used in this study (see Materials and Methods).

improper compensation for astigmatism amount to ± 0.75 nm. Calibration of our electron microscope with a carbon diffraction grating with 2160 lines/mm (Ernest Fullam and Co.) at different times during the study showed a maximum error of 6.5% for the lowest magnification and less at the higher magnifications. In view of the fact that the increase in membrane widths and in the spaces between the membranes is reported as 6-20 nm, it is unlikely that such differences will be obscured by these errors. The maximum error due to measuring the same negative at different magnifications was ± 6.9%. This would, of course, tend to zero over a number of negatives and again it should not obscure the large differences reported.
RESULTS

The membrane changes that were found are detailed below. In addition, 2 types of membrane junction not previously reported for wool follicle cells were observed, though not included in the measurements. These had the typical appearances of gap and tight junctions (Fig. 3). In both cases the plasma membranes were more closely apposed than normal but, in gap junctions, a narrow gap remained between the outer lamellae of the membranes. Tight junctions did not show this gap and they were sometimes found between typically apposed membranes and gap junctions (Fig. 3). Gap junctions were found in all cell lines of the follicles.

Membrane changes during keratinization

General. In the mitotic zone (A) the mean total width of apposed plasma membranes was found to be 33.8 ± 1.4 nm. Many regions appeared not to have attained their final degree of apposition (Fig. 4). In contrast, the mean total width of apposed plasma membranes in zone B was 26.3 nm, this being composed of 2 plasma membranes of 7.3 ± 0.3 nm each, separated by a gap of 11.7 ± 1.1 nm (Table 1; Fig. 1a). These measurements are regarded as characteristic of fully apposed plasma membranes of cells in the early stages of differentiation. Changes in the various apposed plasma membranes as differentiation proceeds in different cell lines are shown in Table 1.

Cortex and fibre cuticle. The mean total width of apposed plasma membranes of these cell lines showed very little difference in zones B, C or D. In zone E, however, a marked decrease in mean total width was found, i.e. after keratinization. Two contributory factors were involved. First, a false decrease in total width was caused by the exclusion from the measurements of the inner lamellae which were indistinguishable from the keratin lying next to them. Secondly, a real decrease in total width resulted from the reduction of the intercellular gap width from 11.7 ± 1.1 nm to 6.6 ± 2.1 nm. In addition, the outer lamellae could not be distinguished from the intercellular material and presumably they were measured as part of the intercellular gap. This would result in the actual width of the intercellular gap being even narrower than indicated.

Typical appearances of apposed plasma membranes in various zones are shown for cortex cells in Figs. 5, 6; cortex/fibre cuticle cells in Figs. 7, 8; and fibre cuticle/fibre cuticle cells in Figs. 9, 10. It is noteworthy that the intercellular gap of cortex cells in zone E shows greater variability in width than in the other cell lines portrayed. Also, the intercellular gap shows greater electron density in zone E than in zones B, C or D, except in the case of apposed fibre cuticle cells (Fig. 9). Here, the increased electron density of the intercellular material can be observed as early as zone C (Fig. 11). Structures which could be interpreted as desmosomes were not seen in zones D and E between apposed cortex or fibre cuticle cells.

Although not included in the measurements, the apposed plasma membranes of fibre cuticle and IRSC cells are of interest as they separate to set the fibre (cortex and fibre cuticle) free in the follicle. The apposed plasma membranes have the usual appearance in zones B and C, but in upper zone D separation may occur. Although it is difficult to define the exact point at which this occurs and to determine the effect
Table 1. Width measurements of apposed plasma membranes of keratinizing and hardening cell lines of the wool follicle

<table>
<thead>
<tr>
<th>Keratinizing and hardening cell lines</th>
<th>Zone</th>
<th>Width measured</th>
<th>nm ± S.D.</th>
<th>No. of readings</th>
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<tbody>
<tr>
<td>Cortex/cortex</td>
<td>A</td>
<td>Total*</td>
<td>33.8 ± 1.4</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>upper B</td>
<td>Total</td>
<td>26.3 ± 1.2</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>Total</td>
<td>26.5 ± 1.0</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>Total</td>
<td>26.9 ± 4.7</td>
<td>130</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>Total†</td>
<td>13.9 ± 2.8</td>
<td>250</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>Intercellular gap</td>
<td>6.6 ± 2.1</td>
<td>250</td>
</tr>
<tr>
<td>Cortex/fibre cuticle</td>
<td>B</td>
<td>Total</td>
<td>27.0 ± 2.5</td>
<td>110</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>Total</td>
<td>27.0 ± 2.1</td>
<td>230</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>Total</td>
<td>24.7 ± 2.5</td>
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<tr>
<td></td>
<td>E</td>
<td>Total†</td>
<td>14.4 ± 4.0</td>
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<tr>
<td>Fibre cuticle/fibre cuticle</td>
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<td>Total</td>
<td>25.8 ± 1.8</td>
<td>120</td>
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<tr>
<td></td>
<td>C</td>
<td>Total</td>
<td>26.0 ± 2.3</td>
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<tr>
<td></td>
<td>D</td>
<td>Total</td>
<td>25.9 ± 2.3</td>
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<td>E</td>
<td>Total†</td>
<td>14.4 ± 4.0</td>
<td>80</td>
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<tr>
<td>IRS cuticle/IRS cuticle</td>
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<td>Total</td>
<td>25.7 ± 2.6</td>
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<tr>
<td></td>
<td>B-C</td>
<td>Intercellular gap</td>
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<td></td>
<td>D†</td>
<td>Total</td>
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</tr>
<tr>
<td></td>
<td>D†</td>
<td>Intercellular gap</td>
<td>16.8 ± 1.9</td>
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<td>E</td>
<td>Intercellular gap</td>
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<td></td>
<td>E</td>
<td>Cytoplasmic band</td>
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<tr>
<td>Henle'sHenle's</td>
<td>E</td>
<td>Desmosome</td>
<td>39.4 ± 4.1</td>
<td>130</td>
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</table>

* Two membranes and the intervening gap.
† See text.
‡ Complex formed.

of mechanical stresses during sectioning, separation appears to occur in the region involving the intercellular material and membrane of the fibre cuticle (Fig. 12).

Inner root sheath cuticle. The appearance and total width of the plasma membranes in zones B and C corresponded closely with those of plasma membranes of the other cell lines measured in these zones. In upper zone D, however, a complex is often found in the intercellular gap between cells undergoing the terminal stages of differentiation before hardening. At this level, the total width of the apposed plasma membranes still includes the inner lamellae of the membranes in contrast with the membranes in hardened cells where the inner lamellae are no longer distinguishable. Measurements showed that there was an increase in total width to 30.2 ± 2.5 nm in zone D, which resulted from an increase in the intercellular gap to 16.8 ± 2.9 nm.

The plasma membranes of IRSC cells in zone E showed further changes on hardening. The mean total width of the 'membrane complex' which, as mentioned previously, does not include the inner lamellae of the plasma membranes (see Fig. 1c) increased to
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33.9 ± 2.3 nm. An increase in the mean distance between membranes to 23.0 ± 2.3 nm was also noted.

Another change was the appearance of a band of material adjacent to the cytoplasmic side of the inner lamellae of the membranes. This band was laid down 1 cell before hardening occurred and was of similar electron density to the inner lamellae of the membrane, thus making it indistinguishable in most areas. The mean width of this band was about 12.4 ± 0.4 nm and it was found in all hardened IRS cells.

Fig. 13 shows the appearance of apposed cell membranes in zone D. The complex in the intercellular gap with its darker central band is visible but no cytoplasmic band has been laid down next to the inner lamella. In Fig. 14, a cytoplasmic band has been laid down against the inner lamella of the IRSC cell on the point of hardening but not against that of the less-differentiated IRSC cell next to it. The appearance of the apposed cell surfaces of hardened IRSC cells is shown in Fig. 15. The 'membrane complex' and cytoplasmic bands of both cells are readily apparent.

Henle’s layer cells. The membrane complex between the apposed plasma membranes of hardened Henle’s cells was more poorly defined and some regions still retained the convoluted form of the ‘unhardened’ membranes. However, many regions occurred in which short lengths of well defined membrane complex could be discerned. These regions were interpreted as being derived from the desmosomes common between these cells prior to hardening (Figs. 16, 17). Fig. 18 shows apposed Henle’s plasma membranes after hardening. The ‘desmosomes’ were found to have a mean ‘width’ (see Fig. 1D) of 39.4 ± 4.1 nm.

DISCUSSION

Measurements of various plasma membranes in the wool follicle showed marked differences from those reported for the hair follicle. The 7.3-nm width of plasma membranes of differentiating cells reported here is lower than the 8-9 nm reported by Parakkal (1967) for mouse hair follicle cells and is more in line with the 7.7 nm reported for human oral epithelium (Frithiof, 1970) and 7-8 nm for amphibian epidermis (Farquhar & Palade, 1965). There seems to be only approximate agreement on the width of the space separating the plasma membranes, with 11.7 nm measured in the wool follicle, about 10 nm in the cortex of the mouse hair (Parakkal, 1967) and 12-15 nm in human hair (Birbeck & Mercer, 1957a). The extent to which these and other differences reported here are due to species differences or to the techniques used has yet to be resolved.

In the wool follicle, the greater total width (33.8 nm) of the membranes in zone A compared with zone B appears to be an anomaly. This may result from the finding that surface contact between loosely attached cells leaving the mitotic zone increases (Birbeck & Mercer, 1957a). The measurements reported here probably included data from regions where the final state of cell-to-cell contact had not been reached so that greater total widths were measured for the loosely attached cells in zone A.

Both Birbeck & Mercer (1957a) and Parakkal (1967) reported an increase of about 10 nm in the width of the intercellular gap in the keratogenous zone of the cortex.
The results for the wool follicle show clearly that there is no increase in total width of the apposed membranes prior to keratinization, indicating that there has been no change in the width of individual components. That a decrease in individual membrane widths has not occurred to compensate for an enlarged intercellular gap, as reported in the hair follicle, is indicated by the following. An increase of 10 nm in the intercellular gap of wool cortex cells would result in a reduction of membrane widths to about 2 nm each. Both visual observation and the low standard deviation (7.3 ± 0.3 nm) of measurements of individual plasma membrane widths from all zones studied, including those in question, indicate that this is not the case.

Parakkal (1967) also reported an increase in plasma membrane widths of fully keratinized cells of the cortex and fibre cuticle. This observation could not be confirmed for the wool follicle because, as described previously, the inner and outer lamellae of the plasma membrane could not be distinguished, making measurements of the total width of the membrane impossible. The appearance of the cell membrane complex is similar to that described by Rogers (1959) in hair and wool fibres. In contrast to Rogers's findings, marked variation in the width of this complex was found in this study and this may account for the different mean width reported here.

The membranes of the wool follicle fibre cuticle/fibre cuticle cells also do not differentiate in the way reported for the human hair follicle (Birbeck & Mercer, 1957b) and anagen mouse hair follicle (Parakkal, 1967). The results presented here give no indication of an increase in the gap between the plasma membranes occurring during differentiation found in hair follicle fibre cuticle cells, nor was the intercellular material arranged in layers as described by Birbeck & Mercer (1957b). As in the cortex, a decrease in membrane widths to compensate for an enlarged intercellular gap was discounted for previously outlined reasons.

In the wool follicle the intercellular material of differentiating zone D fibre cuticle cells was more electron-dense than that between cortex cells. This may be an indication that the intercellular material between apposed fibre cuticle cells has a composition different from that between apposed cortex cells. Similarly, the loss of the trilaminar appearance of the plasma membrane of keratinized cortex and fibre cuticle cells possibly reflects a biochemical change in their structure.

The same sort of membrane complex as described by Birbeck & Mercer (1957c) for the human hair follicle developed in the space between the plasma membranes of IRS cell lines in the wool follicle. The complex could first be detected about 10 cells before hardening and it involved an increase in the distance between apposed plasma membranes. This development was in marked contrast to the decrease in width of the intercellular gaps found for apposed cortex and fibre cuticle cell lines after keratinization. This further indicates that the intercellular material of different cell lines may have different biochemical compositions. However, the extent to which other factors, e.g. dehydration, occurring during hardening and keratinization can modify the intercellular material to produce the structures seen in this study has not yet been determined.

The laying down of a band of material against the cytoplasmic side of the inner lamellae of IRS membranes 1 cell before hardening meant that plasma membrane
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widths could not be measured. Therefore, it was not possible to confirm for the wool follicle the increase in width of the plasma membranes recorded by Parakkal (1967). This cytoplasmic band of material does result in the membrane complex having a similar appearance to desmosomes in undifferentiated tissue and may indicate basic structural similarities.

In contrast to the findings of Birbeck & Mercer (1957c), the formation of the membrane complex in the space between apposed Henle cell plasma membranes was more poorly defined and the major regions of attachment seemed to be hardened desmosomes. These desmosomes had widths comparable with the largest measurements reported by Birbeck & Mercer (1957c) for membrane complexes. The more poorly defined nature of apposed hardened Henle's cells may allow transport of metabolites across this cell layer, while Huxley's and IRSC cell layers are still differentiating. It is more likely, however, that gap junctions are specialized sites for intercellular transport within the differentiating regions of the wool follicle as has been found in other tissues (Payton, Bennett & Pappas, 1969).

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REFERENCES


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Fig. 3. Zone A. Gap junction. Upper arrow points to the narrow gap between the outer lamellae. A tight junction (tj) occurs between the gap junction and normally apposed plasma membranes. × 166,000.

Fig. 4. Zone A. Apposed plasma membranes showing regions of markedly different widths (arrows). × 166,000.

Fig. 5. Zone C. Apposed cortex cell plasma membranes. The intercellular gap is relatively uniform. mf, macrofibril. × 166,000.

Fig. 6. Zone E. Apposed keratinized cortex cell surfaces. The trilaminar appearance of the membranes is not distinguishable. The intercellular gap is not as wide as in Fig. 5 and shows marked variations in width. × 166,000.

Fig. 7. Zone C. Apposed cortex (co)/fibre cuticle (cu) cell plasma membranes. The trilaminar appearance of the membranes is readily apparent. mf, macrofibril. × 166,000.

Fig. 8. Zone E. Apposed keratinized cortex (co) and fibre cuticle (cu) cell surfaces. The trilaminar appearance of the membranes has been lost. × 166,000.
Fig. 9. Zone C. Apposed fibre cuticle (cu) cell plasma membranes (pm). The material in the intercellular gap (ig) between the trilaminar-appearing membranes is more electron-dense than that shown in Figs. 5 and 7. \( \times 166000 \)

Fig. 10. Zone E. Apposed keratinized fibre cuticle (cu) cell surfaces. The trilaminar membranes are not distinguishable. im, intercellular material. \( \times 166000 \).

Fig. 11. Zone B. Apposed fibre cuticle (cu) cell plasma membranes. The increase in electron density of the intercellular material has occurred in one region (lower arrow) but not yet in another (upper arrow). \( \times 100000 \).

Fig. 12. Zone D. Apposed membranes of fibre cuticle (cu) and inner root sheath cuticle (irc) cells. The separation of these 2 cell types appears to involve the intercellular material and the membrane of the fibre cuticle cell (arrow). im, intercellular material; pm, plasma membrane. \( \times 166000 \).

Fig. 13. Zone D. Apposed inner root sheath cuticle (irc) cells. The pentalaminar nature of the complex (i.e. membrane (pm) - intercellular material of lower electron density - central more electron-dense material (c) - intercellular material of lower electron density - membrane) is apparent. d, desmosome. \( \times 166000 \).

Fig. 14. Zone D. Apposed inner root sheath cuticle (irc) cells just prior to hardening. A cytoplasmic band (cb) has formed against the inner lamella of the membrane of the last cell before hardening occurs but not against the inner lamellae of the apposing less-differentiated cell. The membrane complex (c) is well defined. \( \times 166000 \).
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Fig. 15. Zone E. Fully hardened inner root sheath cuticle (irc) cell surfaces. The cytoplasmic band (cb) is present against both inner lamellae of the membranes making them difficult to resolve. The membrane complex (c) remains unchanged in appearance. × 166,000.

Fig. 16. Zone B. Apposed Henle's (he) cell plasma membranes. A large number of desmosomes occur at these surfaces; 4 are indicated by arrows. × 22,000.

Fig. 17. Zone B. A desmosome (d) at higher magnification, showing similarities to desmosomes in hardened Henle's cells (compare Fig. 18). × 166,000.

Fig. 18. Zone C. Apposed surfaces of hardened Henle's (he) cells. The increase in width of the intercellular gap (ig) at the desmosome (d) is apparent. The membrane complex (c) is not well defined, although it is similar in appearance to the desmosome. × 166,000.
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