ELASTIC DOUBLE SYSTEM AND SELECTIVE PERMEABILITY TO CATIONS IN THE STROMA OF THE RABBIT CORNEA

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In the previous work (1), the submicroscopic structure of the rabbit cornea was studied from the viewpoints of polarization optics and thermoelasticity. It was shown that the cornea is composed of many layers of two-dimensional networks of long chain molecules.

The purpose of the present work is to evaluate the importance of the negatively charged ionized groups fixed on the long chain molecules in the mechanical behavior and the ion permeation.

The thermoelastic studies showed that the entropic tension is balanced by an outwardly directed energetic tension which arises from the energy of electrostatic repulsion between ionized groups of like sign.

The presence of these ionized groups was confirmed by the studies on the selective permeability to ions.

I. ELASTIC DOUBLE SYSTEM

Theoretical treatment

In a deformed crystal or glass, atoms are lifted from their potential wells by the deformation, and interatomic attraction tends to restore the previous state; the elastic mechanism is energetic. In rubber-like substances only the arrangement of the atoms is changed on stretching, becoming more regular and less probable: the twisted long chain molecules are straightened on stretching. Thermal motion causes the chains to return to any statistically more probable (twisted) form, as soon as the deforming force is removed; the elastic mechanism is entropic.

In stretching a fiber, free energy is stored in the form of an altered internal energy (potential energy of a distorted valence skeleton, electrostatic energy of a configuration of ionized groups), or of a reduced configurational entropy.

This is the assumption in the usual Wiegand Snyder equation

\[
K = (\partial E/\partial l)_{T} - T(\partial S/\partial l)_{T}
\]

\[
= (\partial E/\partial l)_{T} + T(\partial S/\partial T)_{l}
\]

where \(K\) is the elastic force, \(E\) and \(S\) are, respectively, the internal energy and the entropy of the system, \(l\) is the length, and \(T\) is absolute temperature.

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Much interest attaches not only to the absolute value of the “entropic tension”, \(-T(\partial S/\partial l)_T\), but also to its importance relative to the “energetic tension”, \((\partial E/\partial l)_T\). For many fibers, \((\partial E/\partial l)_T\) is small relative to \(K\), up to moderate stretching, and, in accordance with statistical-mechanical theory, it is concluded that the elastic mechanism of such a system is largely entropic; in great stretching, however, \((\partial E/\partial l)_T\) becomes large relative to \(K\), and the entropic mechanism becomes correspondingly less important.

A positive entropic tension (a negative value of \((\partial S/\partial l)_T\)) is attributed to the decrease of configurational entropy resulting from straightening of long chain molecules by the stretch. On the other hand, a positive energetic tension is usually attributed to the elastic deformation of valence bond distance or angle as a result of the stretch (2), (3).

Especially in the case of protein fibers immersed in water, e.g., actomyosin threads (4), electrostatic interactions between charges fixed on the chain molecules (e.g., charges arising from ionization) can contribute to \(E\), and, insofar as these interactions depend on macroscopic length, also to \((\partial E/\partial l)_T\).

In the stroma of cornea, the collagen molecules lie enmeshed in the mucoid; in this system, water content is about 80% of the total weight (5). The condition is in favour of ionization. It is therefore reasonable to consider that the collagen chains bear fixed ions which are counter-balanced by mobile ions of the opposite sign. Accordingly an energetic tension either positive or negative can, in the case of cornea, be attributed to an electrostatic contribution of the type just mentioned.

**Method**

To determine the tension-temperature relations of the cornea, the same procedure as in the previous work (1) was followed. A strip of cornea of 4 mm. width was mounted to the apparatus of Polanyi (6), then a change in elastic force with increasing or decreasing temperature was measured, under practically isometric conditions, by the aid of a system of optical levers with an accuracy of \(\pm 0.01\) g.

**Calculation**

The entropic and energetic tensions were calculated from the tension-temperature relations obtained. A few example of the tension-temperature relations at slight and intermediate elongations are shown in fig. 1. Over a small range of temperature, \(K\) may be treated as a linear function of \(T\). The equation of this straight line is

\[
K = a + bT,
\]

where \(a = (\partial E/\partial l)_T\) and \(b = (\partial K/\partial T)_T = -(\partial S/\partial l)_T\). The experimental value for \((\partial K/\partial T)_T\) was taken from the tangent drawn graphically to the curve (fig. 1).

Since \(K\) can be measured independently of \((\partial K/\partial T)_T\), the energetic contribution was obtained by simple transposition of equation (1). The resolution of the net tension into entropic and energetic fractions was done by dividing equation (1) by \(K\).
Results

The experimental results are given in tables 1 and 2, in which the net tension was resolved into entropic and energetic contributions.

The entropic and energetic fractions are plotted against elongation in fig. 2.

Over the range of moderate extensions it was found that:

1. positive tension is due entirely to the entropic contribution,
2. the internal energy makes a negative contribution to the tension.

These results can be taken to mean that the tension of the cornea is, at least in part, due to the thermal motion of segments of long chain molecules straightened by the stretch; some length-dependent process other than straightening must also be contributing to the entropy, otherwise $-T(\partial S/\partial l)_T$ should increase with the length (fig. 2).

Further, these results suggest that the negative energetic contribution arises from the energy of electrostatic repulsion between charged groups of like sign fixed along the molecular

![Diagram](image)

**Fig. 1.** Curves showing the elastic force, $K (g)$, exerted by different strips at slight and intermediate elongations, plotted as a function of the absolute temperature, $T$. The tangents are drawn to the upper portions of the ascending limbs. $OA$: net tension, $AB$: entropic tension, $OB$: energetic tension. Arrow indicates the ascending limb.

**Table 1.** Tension-temperature Data for Corneas Stretched in the Fiber (Radially Arranged Fiber) Direction

<table>
<thead>
<tr>
<th>Per cent extension (%)</th>
<th>Net tension $K$ g. for sectional area* at 30°C.</th>
<th>Entropic tension $T(\partial K/\partial T)_T$</th>
<th>Energetic tension $1/(\partial E/\partial l)_T$</th>
<th>Entropic fraction $T(\partial K/\partial T)_T$</th>
<th>Energetic fraction $1/(\partial E/\partial l)_T$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.33</td>
<td>4.00</td>
<td>-3.67</td>
<td>12.1</td>
<td>-11.1</td>
</tr>
<tr>
<td>0</td>
<td>0.31</td>
<td>2.89</td>
<td>-2.58</td>
<td>9.32</td>
<td>-8.32</td>
</tr>
<tr>
<td>0</td>
<td>0.28</td>
<td>2.78</td>
<td>-2.50</td>
<td>9.93</td>
<td>-8.93</td>
</tr>
<tr>
<td>3</td>
<td>0.95</td>
<td>4.52</td>
<td>-3.57</td>
<td>4.76</td>
<td>-3.76</td>
</tr>
<tr>
<td>5</td>
<td>0.78</td>
<td>2.24</td>
<td>-1.46</td>
<td>2.87</td>
<td>-1.87</td>
</tr>
<tr>
<td>6</td>
<td>1.10</td>
<td>3.16</td>
<td>-2.06</td>
<td>2.87</td>
<td>-1.87</td>
</tr>
<tr>
<td>8</td>
<td>0.82</td>
<td>1.60</td>
<td>-0.78</td>
<td>1.95</td>
<td>-0.95</td>
</tr>
<tr>
<td>9</td>
<td>0.90</td>
<td>1.67</td>
<td>-0.77</td>
<td>1.86</td>
<td>-0.86</td>
</tr>
</tbody>
</table>

* The elastic force is given for the sectional area of a strip of 4 mm. width.
TABLE 2. Tension-Temperature Data for Corneas Stretched at Right Angles to the Fiber (Radially Arranged Fiber) Direction

<table>
<thead>
<tr>
<th>Per cent extension (%)</th>
<th>Net tension K g. for sectional area at 30°C.</th>
<th>&quot;Entropic tension&quot; $\frac{\partial K}{\partial T}$</th>
<th>&quot;Energetic tension&quot; $\frac{\partial E}{\partial l}$</th>
<th>&quot;Entropic fraction&quot; $\frac{K}{K(T)}$</th>
<th>&quot;Energetic fraction&quot; $\frac{1}{K} \left(\frac{\partial E}{\partial l}\right)_T$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.45</td>
<td>10.52</td>
<td>-10.07</td>
<td>23.4</td>
<td>-22.4</td>
</tr>
<tr>
<td>3</td>
<td>0.67</td>
<td>5.57</td>
<td>-4.90</td>
<td>8.31</td>
<td>-7.31</td>
</tr>
<tr>
<td>6</td>
<td>0.98</td>
<td>5.06</td>
<td>-4.08</td>
<td>5.16</td>
<td>-4.16</td>
</tr>
</tbody>
</table>

* The elastic force is given for the sectional area of a strip of 4 mm. width.

chain; this notion is in keeping with the fact that $(\partial E/\partial l)_T$ becomes less negative with stretch.

Summarizing these considerations, it may be stated that the entropic tension is balanced by an outwardly directed energetic tension which arises from the energy of electrostatic repulsion between charged groups of like sign. *i.e.* the cornea contains two elastic systems which oppose each other. Thus the chain molecules bearing charged groups of like sign can be envisaged as a sort of "elastic double system" (*4*, *7*); the repulsion of the charged groups tends to stretch the chains, whereas the thermal motion of the segments tends to compress them (fig. 3).

**Crystallization**

The internal energy $E$ diminishes during isothermal stretching of the cornea (1). Since $dE = dA + TdS$, it follows that the decrease of $TS$ must be greater than the increase of the free energy $A$. As the heat given off equals $TdS$, this heat is greater than $dA$, the work absorbed.

This is consistent with, but does not prove, the hypothesis that

![Fig. 2. Fractions of tension of entropic and energetic contributions. Heavy line represents the cases which were stretched in the direction parallel to the radial fibers, light line those stretched at right angles to the radial fibers.](image)

![Fig. 3. Diagrammatic representation of chain molecules stretched by ionized groups of equal charges.](image)
crystallization is increased by stretching, i.e. the increase in orientation proceeds with evolution of latent heat during an isothermal stretch; other reversible exothermic processes might be coupled with mechanical extension.

The tension of the cornea is due to the thermal motion of segments of long chain molecules straightened by the stretch, however, the present investigation has suggested that some length-dependent process other than straightening must also be contributing to the entropy, otherwise the entropic tension $-T(\partial S/\partial l)_T$ should increase with the length.

It is generally believed that birefringence is exhibited by the oriented region, on the other hand, long-range extensibility and elasticity are confined to the amorphous region, and disappear if crystallization is complete. The entropic tension will decrease, if the amorphous region is reduced by crystallization on stretching; such is the case in the stroma of the cornea.

Thus the fact that the entropic tension decreases with increasing length is reasonably accounted for by the assumption of crystallization occurring in the protein constituents of the stroma.

II. SELECTIVE PERMEABILITY TO IONS

To get further experimental evidence for the presence of the charged groups of like sign fixed on the protein network, the behavior of the stroma of the cornea towards ion permeation was investigated.

*Theoretical treatment*

If a membrane, permeable or semipermeable, is put between two solutions of one electrolyte in different concentrations, a potential difference arises, which may be considered simply as a diffusion potential. Its magnitude can be calculated by application of Nernst's formula for the diffusion potential

$$E = \frac{RT}{nF} \ln \frac{C_1}{C_2}$$  \hspace{1cm} (2)

where $u$ and $v$ are, respectively, the mobilities of the cations and anions within the membrane, $C_1$ and $C_2$ the activities of the electrolyte on the two sides of the membrane, $n$ is valency, $R$ is gas constant, $T$ is absolute temperature and $F$ is Faraday constant (8).

Substituting the values of the constants:

$$E = 0.059 \frac{u - v}{u + v} \log \frac{C_1}{C_2} \text{ volts at 22}^\circ \text{C. to 26}^\circ \text{C.},$$

$$E = 0.060 \frac{u - v}{u + v} \log \frac{C_1}{C_2} \text{ volts at 27}^\circ \text{C. to 31}^\circ \text{C.}$$  \hspace{1cm} (3)

where $n$ was taken as 1.

In case the membrane is semipermeable to the electrolyte used, the P.D. can be calculated by taking the mobility of either ion as zero; the value $\frac{u - v}{u + v}$ then equals 1 or −1 and the concentration potential reaches its thermodynamic maximum.
It is possible to calculate the mobilities of the ions within the membrane, at least relatively, from the values of the P.D.'s. From (3) it follows,

\[
\frac{v}{u} = \frac{0.059(0.060) \log \frac{C_1}{C_2} - E}{0.059(0.060) \log \frac{C_1}{C_2} + E}
\]

(4)

In the case of CaCl₂, the formula (2) becomes:

\[
E = \frac{0.059(0.060)}{2} \cdot \frac{u - v}{u + v} \log \frac{C_1}{C_2} \text{ volts}
\]

where \( n \) was taken as 2.

Then let \( v = 0 \), the equation will be:

\[
E = \frac{0.059(0.060)}{2} \log \frac{C_1}{C_2} \text{ volts}
\]

(5)

This is the thermodynamically possible maximum value for the case of CaCl₂, and does not exceed 30 mV, if \( C_1 : C_2 = 10 : 1 \).

**Method**

An excised cornea, of which the epithelial and endothelial layers had previously been completely rubbed off with absorbent cotton, was mounted, directing the anterior surface downward, between two vertical glass tubes filled with the two solutions of one electrolyte of the concentration ratio 10:1, thus a concentration chain was established. The electrodes (Ag-AgCl type) having been installed in the tubes, the P.D. of the chain was measured by means of a potentiometer (fig. 4).

The experiments were carried out with the chlorides of Na, K and Ca. The concentrations of the two solutions were always in the proportion of 10:1, but their ranges were varied. Four sets of experiments were made for each electrolyte (table 3).

After the measurements, the degree of removal of the cell layers was checked microscopically by the aid of the staining with Haematoxylin and Eosin.

**Results**

Fig. 5 shows the time course of the P.D.'s with the chlorides of Na, K and Ca. In all cases the concentration potentials were positive on the side of the more dilute solution in the external circuit.
TABLE 3. Concentration Chains

<table>
<thead>
<tr>
<th>Solution</th>
<th>Experiment</th>
<th>Upper tube</th>
<th>Lower tube</th>
<th>Mean value of the P.D.</th>
<th>$v/u$</th>
</tr>
</thead>
<tbody>
<tr>
<td>NaCl</td>
<td>A</td>
<td>0.165 M</td>
<td>0.0165 M</td>
<td>41.38 mV at 22° to 26°C.</td>
<td>Cl : Na = 1 : 7</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>0.0165</td>
<td>0.165</td>
<td>42.98 &quot; &quot;</td>
<td>&quot; &quot; 1 : 8</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>1.65</td>
<td>0.165</td>
<td>40.68 &quot; &quot;</td>
<td>&quot; &quot; 1 : 6</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>0.165</td>
<td>1.65</td>
<td>44.45 &quot; &quot;</td>
<td>&quot; &quot; 1 : 9</td>
</tr>
<tr>
<td>KCl</td>
<td>A</td>
<td>0.165 M</td>
<td>0.0165 M</td>
<td>52.08 mV at 22° to 26°C.</td>
<td>Cl : K = 1 : 50</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>0.0165</td>
<td>0.165</td>
<td>53.45 &quot; &quot;</td>
<td>&quot; &quot; 1 : 150</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>1.65</td>
<td>0.165</td>
<td>48.54 &quot; &quot;</td>
<td>&quot; &quot; 1 : 19</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>0.165</td>
<td>1.65</td>
<td>49.66 &quot; &quot;</td>
<td>&quot; &quot; 1 : 25</td>
</tr>
<tr>
<td>CaCl₂</td>
<td>A</td>
<td>0.11 M</td>
<td>0.011 M</td>
<td>32.82 mV at 27° to 30°C.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>0.011</td>
<td>0.11</td>
<td>37.23 &quot; &quot;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>1.1</td>
<td>0.11</td>
<td>31.05 &quot; &quot;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>0.11</td>
<td>1.1</td>
<td>33.75 &quot; &quot;</td>
<td></td>
</tr>
</tbody>
</table>

0.165 M being taken as isotonic for the cornea. NaCl solutions are buffered with NaHCO₃, pH 7.2. KCl solutions are buffered with KHCO₃, pH 7.4. CaCl₂ solutions, pH 6.8.

For convenience, the P.D. values at 10 minutes after making the circuit were averaged separately for each chain to represent the P.D.'s of the chains (shown in table 3).

From these figures the mobility ratios of the cations and anions within the stroma were calculated after the formula (4), in which either 0.059 or 0.060 was employed according to the temperature of the experiments; in the calculation of $C_1/C_2$, the activities of the ions were used, i.e. the molal concentration was multiplied by an activity coefficient (9) (table 4).

TABLE 4. Activity Coefficient

<table>
<thead>
<tr>
<th>Concentration of NaCl</th>
<th>Activity coefficient at 25°C.</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0165 M</td>
<td>0.884</td>
</tr>
<tr>
<td>0.165</td>
<td>0.754</td>
</tr>
<tr>
<td>1.65</td>
<td>0.659</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Concentration of KCl</th>
<th>Activity coefficient at 25°C.</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0165 M</td>
<td>0.875</td>
</tr>
<tr>
<td>0.165</td>
<td>0.726</td>
</tr>
<tr>
<td>1.65</td>
<td>0.572</td>
</tr>
</tbody>
</table>

FIG. 5. Time course of the P.D.'s of the concentration chains with the chlorides of Na, K and Ca.

Solid line: experiment B, broken line: experiment A. The experiments C and D are not shown for simplicity, but the curves agreed closely with those of A and B.
The results are shown in the last column of the table 3.
The ratio of the mobilities of the cations and anions depends both on the range of the concentration and on the direction of the concentration gradient. For instance, in the case in which the concentration falls from 0.165 M to 0.0165 M from the anterior to the posterior surface of the stroma (exp. B), the mobility of Na is about 8 times as great as that of Cl, and that of K is about 150 times as great as that of Cl; K is more effective than Na. In the case in which the concentration falls from 1.65 M to 0.165 M from the posterior to the anterior surface of the stroma (exp. C), the mobility of Na is about 6 times as great as that of Cl, and that of K is about 19 times as great as that of Cl; K is more effective than Na.

In all cases, it is evident that the mobilities of Na and K are considerably greater than that of Cl.

In the case of CaCl₂, the P.D.'s of the chains (table 3) obviously surpass the thermodynamical maximum value (30 mV), therefore, they can not be regarded as simple diffusion potential. Accordingly, it is impossible to calculate \( \frac{v}{u} \) in such a manner as practiced for NaCl and KCl. The extraordinarily great P.D.'s must be due to the specific properties of Ca ions.

In brief, the anions suffer a relative loss of mobility in the stroma as compared with the cations. The retardation of the anion mobility could easily be anticipated by the negative charges fixed on the protein molecules (10). In the case of the stroma, the cations would be able to enter into the meshes of the protein networks with negatively charged ionized groups, while the anions must be repelled electrostatically, i.e. the stroma is selectively permeable for cations.

It is of importance to include the information on the negatively charged ionized groups to the submicroscopic structural diagram of the cornea. Besides, since the previous work (1) has dealt exclusively with the radial fibers, it becomes desirable to supplement this point.

### III. ARRANGEMENT OF THE FIBERS

**Method**

The excised cornea under freezing were sectioned tangentially or vertically to the surface into convenient thickness (100-120 \( \mu \)) for birefringence study. These sections were moderately dried at a room temperature, and mounted in Canada balsam to be observed under a polarizing microscope with crossed polars.

**Results**

It was found by preliminary experiments that the presence of epithelial and endothelial layers hardly interferes with the birefringence of the stroma.

The fibrous structure of the cornea which is revealed by the present investigation is the following.

**Peripheral region**

In the posterior two-thirds of the cornea, the majority of the fibers are arranged in a radial manner, with a small number of intersecting fibers (fig. 6).
On the other hand, in the anterior one-third, the radial fibers are intersected closely with the other fibers, forming an appearance of meshwork (fig. 7).

![Fig. 6. Radially arranged fibers (Tangential section, peripheral region).](image1)

![Fig. 7. An appearance of meshwork. The radial fibers are intersected closely with the other fibers (Tangential section, peripheral region).](image2)

**Central region**

In all layers, the fibers intersect each other, resulting in an appearance of meshwork (fig. 8).

Fig. 9 shows the modes of vertical section. In figs. 10 and 11, actual manner of fiber arrangement are shown. When stretch, it was found that the radial or circular fibers as the case may be, fibers which happened to lie parallel to the stretch was selectively brought up in view (figs. 12, 13 and 14).

The average thickness of these fibers was found to be about 6 μ by the use of an ocular micrometer. In Schwarz's electron microscopic studies of the human sclera and cornea (11), it was shown that the corneal fibrils are arranged in bundles 2.5 to 8 μ in thickness with a masking of cement.

![Fig. 8. An appearance of meshwork (Tangential section, central region).](image3)
FIG. 9. Two modes of vertical section. The vertical sections were made both parallel and crosswise to the radial fibers.

FIG. 10. A side view of the radially arranged fibers (Peripheral region, vertical section).

FIG. 11. A cross section of the radially arranged fibers (Peripheral region, vertical section).
substance. The order of magnitude of the thickness of the bundle is consistent with that of the fiber. It is then permissible to suppose that the corneal fiber is identical with the bundle of submicroscopic fibrils, though the species of the animals examined by Schwarz and the present author are different.

Jakus (12) studied with an electron microscope the appearance, dimensions, and orientation of the collagen fibrils in the stroma of the rat cornea. Descemet’s membrane, even at high degree of resolution, seemed to be structureless.

Bowman’s membrane is generally believed not to exist in rabbits.

Nevertheless, no other structure was recognized with a polarizing microscope beside the fibrous structure in the stroma.

![FIG. 12. Effect of the stretch.](image)
When stretched at right angles to the radial fibers, the circular fibers become evident selectively. When stretched in the direction parallel to the radial fibers, the radial fibers alone are seen. Arrow indicates the direction of the force.

![FIG. 13. Circular fibers. Arrow indicates the direction of the force.](image)

![FIG. 14. Radial fibers. Arrow indicates the direction of the force.](image)
In the central region, the fibers intersect each other, i.e. the fibers run equally in all directions. Therefore although constituent micelles of the fiber assume an orderly arrangement, over-all distribution of them becomes random and the birefringence of the micelles cancels each other. In the peripheral region, on the other hand, majority of the fibers are arranged in the radial direction with less number of the circular one. Consequently the radial fibers predominate and govern the optic condition of this region. Fig. 15 represents the notion the author has arrived at concerning the submicroscopic structure of the radial fibers. This schema covers a wide scope of information extending over the polarization optic and thermoelastic properties, as well as the selective permeability to ions.

**SUMMARY**

The attempt was made to cover the thermoelastic behavior and the selective permeability to ions of the cornea by taking into account the presence of negatively charged ionized groups fixed on the protein chains.

The tension-temperature relations of the cornea were determined, and the entropic and energetic contributions to the net tension were calculated on the basis of the thermodynamic considerations.

Over the range of moderate extensions,

1. positive tension is due entirely to the entropic contribution,
2. the internal energy makes a negative contribution to the tension.

These results can best be explained by the superposition of two systems which oppose each other, *i.e.* an entropic system and the other in which electro-
static repulsion between charged groups of like sign causes the tension.

The long chain molecules bearing ionized groups of like sign can thus be envisaged as a sort of “elastic double system”; the repulsion of these groups tends to stretch the chains, whereas the thermal motion of the segments tends to compress them.

Further evidence for the presence of ionized groups on the protein chains was provided by the experiments on the permeability to ions. The concentration chains with the chlorides of Na, K and Ca were measured; from the values of the P.D.'s the mobility ratios of the cations and anions within the stroma were calculated.

The anion mobility is relatively more suppressed within the stroma as compared with the cation, i.e. the stroma is permeable selectively for cations. This could satisfactorily be explained by the negatively charged ionized groups of the protein molecules.

Further, the fiber arrangement was studied in detail, and the radial fibers are, in the polarization optic sense, considered as dominant.

The diagram is given showing a possible submicroscopic structure which can cover the known mechanical and optical characteristics and also the selective permeability to ions.

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REFERENCES