THE SHAPE OF THE MAMMALIAN ERYTHROCYTE AND
ITS RESPIRATORY FUNCTION. II.*

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In a previous paper (1) it has been pointed out that a section through
the poles of a mammalian red cell of typical biconcave form approxi-
mates to one of the equipotential curves of Cayley, and that, although
such a curve does not fit the shape of the cell with any exactness, the
approach of the cell surface to an equipotential surface is interesting in
view of the respiratory function of the erythrocyte. The equipotential
surfaces considered were obtained by revolving equipotential curves
about their minor axis, a process which causes the two sinks associated
with the curves to form a ring; this ring was then regarded as a cir-
cular sink to which the rotated curves were equipotential surfaces.

Now this procedure is not quite accurate, and gives only an ap-
proximation to the true result. The rotated curve, strictly speaking,
does not form an equipotential surface to a ring, but a section through
the poles of that surface gives a curve equipotential to the two points
in which the ring is cut by the plane of section—a different thing,
although the difference may not be an obvious one. The difference
is not a great one, and in the paper referred to it was ignored, partly to
avoid such complexity as would have obscured the general principles
which were dealt with, and partly because the treatment was admit-
tedly more suggestive than complete. However, it has been since
suggested to us that, in view of the interest now attached to the ques-
tion of diffusion gradients in the erythrocyte, a more complete study
of these equipotential surfaces would be desirable; in this paper,
therefore, we shall treat the matter in a more rigid manner.

Suppose that we wish to find the equipotential surfaces to a circular

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source or sink of radius $a$. In Fig. 1, let $PB = r'$, the distance of a point $P$ on the required surface, from a point on the ring. Let the distance from the centre of the ring, $O$, to $P$ be $r$. Let the plane $OAP$ be perpendicular to the plane of the ring, and let $OA$ and $OB$ make an angle $\phi$, while $OA$ and $OP$ make an angle $\theta$.

![Diagram](image)

**Fig. 1.**

We first require $PB$ in terms of $\phi$ and $\theta$. By simple trigonometry we find that

$$PB = r^2 + a^2 - 2ar \cdot \cos \theta \cdot \cos \phi$$

The surface, to be equipotential to the ring, must have

$$P = m \int \frac{ds}{r}$$

or, since $ds = a \cdot d\phi$,

$$P = 2m \int \frac{a \cdot d\phi}{\sqrt{a^2 + r^2 - 2ar \cdot \cos \theta \cdot \cos \phi}}$$

Here $m$ is some constant, which we can ignore in the meantime. Continuing with the integral, and putting $\phi = 2\psi, \psi = \frac{\pi}{2} - \chi$.

$$\frac{P}{2} = \int \frac{2a \, dx}{\sqrt{a^2 + r^2 - 2ar \cdot \cos \theta \cdot (2 \cdot \sin^2 \chi - 1)}}$$

$$\frac{2a}{\sqrt{a^2 + r^2 + 2ar \cdot \cos \theta}} \int \frac{d\chi}{\sqrt{1 - k^2 \sin^2 \chi}}$$
where

$$k^3 = \frac{4ar \cdot \cos \theta}{a^2 + r^2 + 2ar \cdot \cos \theta}$$  (1)

This last integral is a well known form, being the first complete elliptic integral of the modulus $k$.

The necessary condition for the equipotential surface is, therefore, that

$$\frac{Kk}{\sqrt{a^2 + r^2 + 2ar \cdot \cos \theta}} = \text{a constant} = \psi$$  (2)

This is a very awkward expression to deal with, and admits of no further simplification. The best way to obtain the equipotential surfaces which it describes is to assign certain values to $r$ and $\theta$, and thus to arrive at the several surfaces in a semigraphical manner. We proceed as follows.

First we assign a convenient value to $a$, the diameter of the ring which is the circular source or sink—an easily worked value is 10 units. Next we proceed to introduce various values for $r$ and $\theta$ into (1) and (2), and to evaluate the constant, $\psi$, in each case. To facilitate labour, we first of all take cases where $\theta = 0^\circ$ and where $\theta = 90^\circ$, and obtain the following values for $\psi$.

<table>
<thead>
<tr>
<th>$r$</th>
<th>$\theta = 0^\circ$</th>
<th>$\theta = 90^\circ$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0</td>
<td>0.157</td>
<td>0.156</td>
</tr>
<tr>
<td>2.0</td>
<td>0.158</td>
<td>0.154</td>
</tr>
<tr>
<td>2.3</td>
<td>—</td>
<td>0.153</td>
</tr>
<tr>
<td>3.0</td>
<td>—</td>
<td>0.150</td>
</tr>
<tr>
<td>5.0</td>
<td>0.166</td>
<td>0.140</td>
</tr>
<tr>
<td>12.0</td>
<td>0.177</td>
<td>0.100</td>
</tr>
<tr>
<td>12.7</td>
<td>0.153</td>
<td>—</td>
</tr>
<tr>
<td>13.0</td>
<td>0.148</td>
<td>—</td>
</tr>
<tr>
<td>15.0</td>
<td>0.122</td>
<td>0.087</td>
</tr>
</tbody>
</table>

Now the value of $r$ when $\theta = 90^\circ$ gives us half the least thickness of the cell, and the value of $r$ when $\theta = 0^\circ$ gives the semidiameter. We know the ratio of these two measurements to be approximately 1:5.5, and we have, therefore, to select from the values of $\psi$ in the above table one which will give this ratio between $r$ when $\theta = 90^\circ$ and $r$ when
\( \theta = 0^\circ \). The value 0.153 is such a one, for it gives values for \( r \) of 2.3 and 12.7 respectively. The surface \( \psi = 0.153 \) is therefore one which will fit the red cell as regards its two axes, and is accordingly to be worked out in full. We obtain the following values:

\[
\begin{array}{ccccccc}
\theta & 0^\circ & 10^\circ & 20^\circ & 30^\circ & 45^\circ & 60^\circ & 90^\circ \\
 r & 12.7 & 12 & 10.6 & 8.0 & 4.5 & 3.0 & 2.3 \\
\end{array}
\]

The curve is shown in Fig. 2, in which the position of the ring, which is, of course, seen as two points in the section, is indicated by \( S \) in the quadrant shown. \( OS \), therefore, is equal to \( a \).

![Fig. 2.](image)

To this equipotential surface we may now apply the same tests as applied to the curves of Cayley, to see if it fits the form of the red cell. By construction, the ratio of the least thickness to the diameter is correct, being approximately 5.5. The ratio of the greatest thickness to the diameter is 3.1, and is rather large. The crucial test lies in the comparison of the volume enclosed by the surface with the volume of the cell, which is known with a fair degree of accuracy to be about 110 \( \mu^3 \). By the application of Pappus' theorem the volume enclosed by the equipotential surface works out as 144 \( \mu^3 \), if the major axis of the curve be reduced to a scale so that it equals 8.8, the mean diameter of the human erythrocyte. This volume is about 45 per cent too large. In the case of the curve of Cayley which provides the best fit for the cell (1), the volume was found to be 196 \( \mu^3 \); the equipotential surface here considered is therefore the better, but still does not fit the cell in more than an approximate way.
It will be observed that, since we have
\[
\frac{P}{2a \cdot \pi \cdot m} = \psi
\]
the effect of altering the value of \(a\), the diameter of the circular sink, will be to alter the numerical value of the equipotential surface, but not to alter its form.

Allied to the curves of Cayley and to the curves which we now describe is the family of curves known as the Cassinian ovals. Certain of these present an appearance suggestive of that of the erythrocyte. Although these curves are of no interest in connection with diffusion gradients in the cell, we have investigated them to see whether any of them might be taken as fitting the form of the cell; the result may be briefly stated by saying that the best of them encloses too great a volume, and that they may accordingly be dismissed from notice.

The summary of our previous paper thus remains unchanged. The surface of the red cell is not exactly an equipotential one to any simple source or sink, but it approximates to an equipotential surface, a fact which is of interest and importance in connection with its respiratory function.

BIBLIOGRAPHY.

1. Ponder, E., *J. Gen. Physiol.*, 1925-26, ix, 197