

When he began this work, three years ago, little was known of the connection between the physiology of the muscle and that of human muscular exercise. Three years of continual labour—years, perhaps, the happiest of his life, for he was never so happy as when “going all out”—have discovered and explored a new subject, that of the recovery process after muscular effort in man. We are glad to believe that, to the scientific world, the subject of these papers will remain associated with his name: to us it will always recall the unceasing devotion and the simple goodness of our friend.

A. V. H. C. N. H. L.

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*On the Balloon-like Structure of the Mammalian Erythrocyte.*

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It is well known that for many years there have been two principal views regarding the structure of the red cell of mammals. According to the first view, advocated by Rollett, the erythrocyte is made up of a more or less dense stroma, in the meshes of which the hæmoglobin is held contained. According to the second view, originally held by Schwann and by Schafer, as well as by many other physiologists, the red cell is composed of a membrane, containing a fluid or semi-fluid content.

In this paper it is not proposed to review or to discuss the evidence already brought forward, but to treat the problem in a direct way. It will be shown that (i) a body possessing a stroma such as Rollett's view of the red-cell structure postulates, will behave in a certain manner when its volume is increased, undergoing definite changes of form. Thereafter, (ii) the alterations in form which will occur in a balloon-like body, such as Schwann supposed the erythrocyte of the mammal to be, when the volume of such a body is increased, will be considered, and shown to be quite different from the changes which occur in (i). Finally, (iii) the changes in form of the mammalian red-cell when its volume increases by the passage of fluid into it will be dealt with, and it will be shown that these changes cannot be explained on Rollett's hypothesis, but

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that they are, in fact, the very changes which occur in a balloon-like body when distended.

(i) Consider the change in form of a spheroidal body composed of some dense material in a network form—a body like a sponge—when its volume is increased by the passage of fluid into it from without. Without going into unnecessary detail, we may say that the change of form accompanying an increase of volume will be an increase in the lengths of the polar and of the equatorial axes of the body, this lengthening being some function of the volume in the case of each axis. This is, of course, obvious, and more detailed consideration is unnecessary for our purpose. The point to be emphasised is that, under no circumstances, will the equatorial axis decrease in length with increase of volume of the body—unless some very complicated and improbable arrangement of the sponge-work be postulated.

(ii) We may now consider the changes which occur in a spheroidal body like a balloon, possessing an elastic membrane, when it is distended. This problem is rather complicated, and may be approached in the following way:—

Let us calculate the energy in stretching a small rectangle of membrane. In the deformation which results two perpendicular lines will remain perpendicular, and no others. Take these lines for axes. Then the number  $\frac{(\text{extended length} - \text{old length})}{\text{old length}}$  is called the extension ratio. Call the two

lengths  $s_1, s_2$ . The energy of stretching will be

$$W = \frac{1}{2} \lambda (s_1^2 + s_2^2) - \mu s_1 \cdot s_2$$

per unit area, where  $\lambda$  and  $\mu$  are elastic constants. To give them a meaning, let us take a square centimetre of membrane and stretch it without supporting the sides. The tension is

$$T = \frac{\delta W}{\delta s} = \lambda s_1 - \mu s_2,$$

and, assuming that there is no cross force,  $\lambda s_2 - \mu s_1 = 0$ . Therefore,

$T = \frac{\lambda^2 - \mu^2}{\lambda} s_1$ , and  $\frac{\lambda^2 - \mu^2}{\lambda}$  is the elastic modulus, as in Hooke's law.

Further  $\frac{s_2}{s_1} = \frac{\mu}{\lambda}$  is the ratio of lateral contraction to elongation, or Poisson's ratio.

In the case of the balloon the principal areas of strain will be the meridian and the circumference of latitude by symmetry. Let us describe a point by  $s$  the length of arc from the origin 0. Then, when the membrane is undistended



we have any point of it as  $x, y$ , functions of  $s$ . On distension, let these go to  $x + \xi, y + \eta$ , where  $\xi$  and  $\eta$  also depend on  $s$ . Then  $x + x'ds, y + y'ds$  goes to  $x + \xi + (x' + \xi') ds, y + \eta + (y' + \eta') ds$ , writing  $x' = \frac{dx}{ds}$ , and  $y' = \frac{dy}{ds}$ .

The extended length along the meridian will be

$$ds\sqrt{(x' + \xi')^2 + (y' + \eta')^2} = ds(1 + x'\xi' + y'\eta')$$

approximately: therefore the extension ratio is  $(x'\xi' + y'\eta')$ .

In the circle perpendicular to this the radius increases from  $y$  to  $(y + \eta)$ , and so the extension ratio is  $\eta/y$ .

The ring corresponding to this length has unextended area  $2\pi y ds$ . The whole potential energy of stretching is therefore,

$$W_s = \frac{1}{2}2\pi y ds \left\{ \lambda \left[ (x'\xi' + y'\eta')^2 + \frac{\eta^2}{y^2} \right] - 2\mu (x'\xi' + y'\eta') \frac{\eta}{y} \right\}.$$

The work done in distending the balloon must be subtracted, as in expanding the pressure,  $p$ , does work instead of receiving it. The volume is

$$\begin{aligned} \int \pi (y + \eta)^2 \cdot d(x + \xi) &= \pi \int (y^2 + 2\eta y + \dots) (x' + \xi') ds \\ &= V_0 - \pi \int (2\eta y x' + y^2 \xi') ds. \end{aligned}$$

As  $\eta$  is small only the terms of the first order of magnitude are considered. We now require the minimum of

$$\begin{aligned} W/\pi &= \int ds \left\{ \lambda \left[ y (x'\xi' + y'\eta')^2 + \frac{\eta^2}{y^2} \right] \right. \\ &\quad \left. - 2\mu (x'\xi' + y'\eta') \eta - p (y^2 \xi' + 2x' y \eta) \right\}. \end{aligned}$$

We can regard  $x$  and  $y$  as known functions of  $s$ , and adjust  $\xi$  and  $\eta$  so as to make  $W$  a minimum for the form. To do so, vary  $W$ . We can put for short,

$$W/\pi = \int F(\xi', \eta', \eta) ds.$$

$$\begin{aligned} \delta W/\pi &= \int \frac{\partial F}{\partial \xi'} \delta \xi' + \frac{\partial F}{\partial \eta'} \delta \eta' + \frac{\partial F}{\partial \eta} \delta \eta \cdot ds, \\ &= \frac{\partial F}{\partial \xi'} \cdot \delta \xi + \frac{\partial F}{\partial \eta'} \cdot \delta \eta - \int \delta \xi \cdot \frac{d}{ds} \cdot \frac{\partial F}{\partial \xi'} + \delta \eta \left[ \frac{d}{ds} \cdot \frac{\partial F}{\partial \eta'} - \frac{\partial F}{\partial \eta} \right] \cdot ds = 0. \end{aligned}$$

The lower limit has  $\xi, \eta = 0$ . The upper limit has  $\eta = 0$ , but, as lengthen-

ing may take place,  $\delta\xi$  is not necessarily zero. We require  $\partial F/\partial\xi'$  to be zero at this end, and also at all points along

$$\frac{d}{ds} \frac{\partial F}{\partial \xi'} = 0, \quad \frac{d}{ds} \cdot \left( \frac{\partial F}{\partial \eta'} \right) - \frac{\partial F}{\partial \eta} = 0,$$

and  $\frac{\partial F}{\partial \xi'} = 0$ , everywhere. Then,

$$2\lambda y (x'\xi' + y'\eta') x' - 2\mu\eta x' - py^2 = 0,$$

$$\frac{d}{ds} [2\lambda y (x'\xi' + y'\eta') y' - 2\mu\eta y'] = \frac{2\lambda\eta}{y} - 2\mu (x'\xi' + y'\eta') - 2px'y.$$

Substituting for  $x'\xi' + y'\eta'$  out of the first equation,

$$\frac{d}{ds} \cdot \left( py^2 \cdot \frac{y'}{x'} \right) = \frac{2\lambda\eta}{y} - 2\mu \frac{py^2 + 2\mu\eta x'}{2\lambda y x'} - 2px'y.$$

Therefore

$$\eta \left[ \frac{2\lambda}{y} - \frac{2\mu^2}{\lambda y} \right] = 2px'y + \frac{\mu}{\lambda} \cdot p \cdot \frac{y}{x'} + \frac{d}{ds} \cdot \left( py^2 \cdot \frac{y'}{x'} \right).$$

From which

$$\eta = \frac{\frac{1}{2}\lambda p}{\lambda^2 - \mu^2} \cdot y \left[ 2x'y + \frac{\mu}{\lambda} \cdot \frac{y}{x'} + \frac{d}{ds} \cdot \frac{y^2 y'}{x'} \right].$$

Whether there is contraction or expansion of the membrane at this point depends on the sign of the bracket in the equation derived from this by simplification,

$$\eta = \frac{1}{2} \frac{p}{\lambda^2 - \mu^2} \cdot y \left[ \lambda \left( 2x'y + \frac{d}{ds} \cdot \frac{y^2 y'}{x'} \right) + \frac{\mu y}{x'} \right].$$

An expression could also be found for  $\xi$ , but it will not integrate, and is not simple. The expression for  $\eta$  verifies completely for a sphere. Continuing with the expression for  $\eta$ ,

$$\eta = \frac{1}{2} \frac{p}{\lambda^2 - \mu^2} \cdot y \left[ \lambda \left( 2x'y + 2y \cdot \frac{y'^2}{x'} + y^2 \cdot \frac{d}{ds} \cdot \frac{y'}{x'} \right) + \frac{\mu y}{x'} \right],$$

and changing to  $x$  as independent variable,

$$= \frac{1}{2} \frac{p}{\lambda^2 - \mu^2} \cdot y^2 \left[ \frac{2\lambda + \mu}{x'} + \lambda y \cdot \frac{d}{ds} \cdot \left( \frac{dy}{dx} \right) \right]$$

$$= \frac{1}{2} \frac{p\lambda}{\lambda^2 - \mu^2} \cdot y^2 \cdot \frac{dx}{ds} \left[ y \cdot \frac{d}{dx} \left( \frac{dy}{dx} \right) + \left( 2 + \frac{\mu}{\lambda} \right) \left( \frac{ds}{dx} \right)^2 \right]$$

$$= \frac{1}{2} \frac{p\lambda}{\lambda^2 - \mu^2} \cdot y^2 \cdot \frac{dx}{ds} \left[ y \cdot \frac{d^2 y}{dx^2} + \left( 2 + \frac{\mu}{\lambda} \right) \left( 1 + \left( \frac{dy}{dx} \right)^2 \right) \right].$$

Now if the radius of curvature be  $\rho$ ,

$$-\frac{1}{\rho} = \frac{d^2 y/dx^2}{[1 + (dy/dx)^2]^{3/2}},$$



and as the curve of the balloon we are considering is concave downwards we take the negative sign, we have

$$\begin{aligned}\eta &= \frac{1}{2} \frac{p\lambda}{\lambda^2 - \mu^2} y^2 \cdot \frac{dx}{ds} \left[ -\frac{y}{\rho} \left( 1 + \left( \frac{dy}{dx} \right)^2 \right)^{\frac{3}{2}} + \left( 2 + \frac{\mu}{\lambda} \right) \left( 1 + \left( \frac{dy}{dx} \right)^2 \right) \right] \\ &= \frac{1}{2} \frac{p\lambda}{\lambda^2 - \mu^2} y^2 \cdot \frac{ds}{dx} \left[ \left( 2 + \frac{\mu}{\lambda} \right) - \frac{y \sqrt{1 + \left( \frac{dy}{dx} \right)^2}}{\rho} \right].\end{aligned}$$

But the normal at the point  $x, y$  has the equation

$$PG = y \sqrt{1 + (dy/dx)^2},$$

so that the condition for a contraction to occur at any point is that

$$PC/PG > 2 + \mu/\lambda,$$

PG being the normal at the point, and PC the radius of curvature. But  $\mu/\lambda$  is Poisson's ratio, and equals about 0.3 for most substances. Now if we apply this result to the axes of the spheroid, we find that the condition for shrinkage of the equatorial axis is

$$a^2/b^2 > 2 + \mu/\lambda,$$

since the normal at the equator  $= a$ , and the radius of curvature  $= b^2/a$ .

Thus if the ratio  $\frac{(\text{equatorial axis})}{(\text{polar axis})}$  be greater than about 1.6, a slight distension of the spheroidal balloon will be accompanied by a diminution in the length of the equatorial axis. The diminution will continue till the ratio of the axes is approximately 1.6, after which point both axes will increase with further increase in volume. The figure, 1.6, depends to some extent on the value of Poisson's ratio. As we have to deal with membranes for which this ratio is not known, it may be convenient to show in tabular form the effects of variations of Poisson's ratio upon the figure given for the ratio of the axes necessary to give a diminution in the length of one of them.

The following table shows the minimum value for the ratio  $\frac{\text{equatorial axis}}{\text{polar axis}}$ , which will give a contraction of the equatorial axis if any distension occurs, together with the value of Poisson's ratio upon which the particular value of the minimum depends.

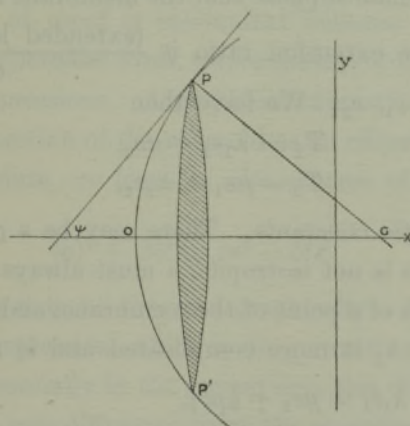
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Poisson's Ratio.	Minimum value for $a/b$ for contraction of $a$ .
0.1	1.449
0.2	1.484
0.3	1.517
0.4	1.549
0.5	1.581
0.6	1.613
0.7	1.644
0.8	1.673
0.9	1.703

The part played by Poisson's ratio in determining the minimum value for which a shortening of the equatorial axis will occur is accordingly not a very great one.

While the above is a rigorous method of proof, it is rather complicated, as it involves calculus of variation. The same result may be reached in a very much more simple way, which will now be described, as an alternative proof.

Consider a portion of the spheroidal balloon shown in the figure. There will



be at every point two principal surface forces,  $T_1$  along the meridian, and  $T_2$  transverse to it. Consider the forces on the whole surface  $PO P'$  in the direction  $x$ . The surface tension will be, taking the deformed surface as  $x, y$ ,

$$T^1 \cdot 2\pi y \cdot \cos \psi,$$

and the pressure inside will be  $y^2\pi \cdot p$ , because the volume  $OPP'$  must be in equilibrium under the pressure forces alone, and so the  $x$  force on the curved surface must balance that on the circle  $PP'$ .



Therefore

$$T_1 \cdot 2\pi y \cdot \cos \psi = p \cdot \pi y^2$$

or

$$T_1 = \frac{1}{2}py \cdot \sec \psi = \frac{1}{2}p \cdot PG = \frac{1}{2}p \cdot \rho_2,$$

where  $\rho_2$  is the radius of curvature of the transverse section of the spheroid at P.

Again consider the forces round the surface, and normal to it. Take an element of it,  $ds \cdot ds'$ , where  $ds$  is in the meridian. The force  $T_1 ds'$  has a component downwards equal to  $T_1 ds' \cdot d\psi$ , which is equal to  $T_1 ds' \cdot ds/\rho_1$  where  $\rho_1$  is the radius of curvature of the meridian section. Similarly, considering the transverse section, we get  $T_2 ds \cdot ds'/\rho_2$ . Now the pressure gives an upward force  $p \cdot ds \cdot ds'$ .

Therefore

$$T_1/\rho_1 + T_2/\rho_2 = p.$$

We have now obtained equations which are exact for the curvature of the membrane in the deformed state of the surface. To go further with the problem we must relate the tensions to the extensions of the membrane, and so shall take them small.

Without difficulty we shall suppose that the membrane has different strengths in two directions. The extension ratio is  $\frac{(\text{extended length} - \text{old length})}{\text{old length}}$ ; let the two lengths be  $s_1, s_2$ . We have then

$$T_1 = \lambda_1 s_1 - \mu s_2,$$

$$T_2 = \mu s_1 + \lambda_2 s_2,$$

where  $\lambda$  and  $\mu$  are elastic constants. There may be a difference between  $\lambda_1$  and  $\lambda_2$  if the membrane is not isotropic;  $\mu$  must always be the same. If  $y$  is the undeformed radius of a point of the membrane, and  $y + \eta$  is its extended radius, then  $s_2 = \eta/y$ .  $s_1$  is more complicated and is not required. Then,

$$\lambda_1 s_1 = \mu s_2 + \frac{1}{2}p\rho_2,$$

therefore

$$T_2 = \lambda_2 s_2 - \frac{\mu}{\gamma_1} (\mu s_2 + \frac{1}{2}p\rho_2),$$

and

$$p = \frac{\frac{1}{2}p\rho_2}{\rho_1} + \frac{1}{\rho_2} \left[ \frac{\lambda_1 \lambda_2 - \mu^2 \cdot s_2}{\lambda_1} - \frac{1}{2} \frac{\mu}{\lambda_1} p\rho_2 \right].$$

So

$$s_2 = \frac{\frac{1}{2}p\lambda}{\lambda_1 \lambda_2 - \mu^2} \cdot \rho_2 \left[ 2 + \frac{\mu}{\lambda_1} - \frac{\rho_2}{\rho_1} \right],$$

and

$$\eta = \frac{\frac{1}{2}p\lambda}{\lambda_1 \lambda_2 - \mu^2} y \cdot \rho_2 \left[ 2 + \frac{\mu}{\lambda_1} - \frac{\rho_2}{\rho_1} \right].$$

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We can express this in terms of simpler properties of the membrane. Take a strip along the meridian and stretch it. Let  $k$  be the modulus of elasticity and let  $\sigma$  be the ratio of lateral contraction to elongation. Then in the stretching,  $T_1 = ks_1$ , and  $T_2 = 0$ , and  $s_2/s_1 = \sigma$ .

But  $T_1 = \lambda_1 s_1 - \mu s_2$ , and  $-\mu s_1 + \lambda_2 s_2 = 0$ . Hence  $\sigma = \mu/\lambda_2$ .

We do not want this, but  $\sigma'$ , the lateral contraction when the tension is transverse. We have the meridian stretching

$$k = \frac{\lambda_1 \lambda_2 - \mu^2}{\lambda_1}.$$

Therefore

$$\eta = \frac{\frac{1}{2}p}{k} \cdot y \cdot \rho_2 \left[ (2 + \sigma') - \frac{\rho_2}{\rho_1} \right].$$

The contents of the bracket, upon the sign of which depends the contraction or extension of the point of membrane, is the same as obtained before by the other method of proof, for  $\rho_2$  is a normal. Taking the axes as before,  $a$  and  $b$ , of the spheroid, we see that the condition for a contraction of the equatorial axis is that the ratio  $\frac{\text{equatorial axis}}{\text{polar axis}}$  shall be greater than  $\sqrt{(2 + \sigma')}$  as above.

This second method of proof is convenient because it can be applied to balloons of other than spheroidal form, where the use of the first method results in awkward integral expressions. A graphical expression of the result can be obtained by plotting a section of the spheroid as an ellipse referred to its centre as origin, and the evolute, or locus of the centres of curvature, from the equation

$$(a)^{\frac{2}{3}} + (b)^{\frac{2}{3}} = (a^2 - b^2)^{\frac{2}{3}}.$$

The ratio PG/PC can then be obtained graphically. It is of importance to note, in the graphical expression, which is the generating axis of the spheroid. In the formal proofs, especially in the second one, this difficulty does not arise to the same extent, the only difference being the co-ordinates of  $x$  and  $y$ , which must be taken in such a way as to give the correct expression according to the direction of the generating axis.

(iii) We now pass to the third consideration, and shall show that the mammalian erythrocyte behaves, when increased in volume, like a balloon, and not like a solid body, the changes met with being precisely what we should expect from the result in (ii). The erythrocyte may be very easily distended by immersing it in a saline solution of less than the osmotic pressure of the plasma. Water enters the cell under these circumstances, and increases its volume. Now the erythrocyte is in form a spheroid, except that it has two



little concavities in its sides. Let us apply what we know regarding the alteration in shape of such bodies when their volume is increased, assuming for the moment that the erythrocyte is a balloon-like body, and that its membrane is homogeneous. As the volume increases, the first thing which will happen is that the little biconcavities will turn inside out, for at these places the curvature is positive, and, therefore, the pressure is applied there principally. The result will be the formation of a typical spheroid. The volume continuing to increase, this spheroid will alter in shape, the alteration depending on the ratio of the axes. In the erythrocyte the ratio of the axes is about 3, so there will be a steady diminution in the length of the equatorial axis, accompanied by an increase in the length of the polar axis, and an increase in volume. This condition will continue till the ratio  $\frac{\text{equatorial axis}}{\text{polar axis}}$  is about 1.6.

Thereafter the axes will both increase.

If the erythrocyte is not a balloon-like body, as the volume increases the axes will both increase.

It will thus be seen that the type of change which the erythrocyte undergoes will be different according to its structure. The matter is one which can easily be tested, and which, moreover, will form a crucial test. We accordingly have to consider whether (a) the equatorial axis of the erythrocyte decreases in length when the cell increases in volume, and (b) whether the minimum value through which it passes is such as to give a ratio of the two axes of about 1.6. If both these conditions are fulfilled, we may with certainty say that the erythrocyte is a balloon-like body. In the mathematical investigation above we have considered the behaviour of an ideal spheroidal body, with an isotropic membrane. No red cell fulfils these conditions, but we can obtain a knowledge of how the ideal red cell behaves by taking averages of a large number of cells. Thus the defects in one cell are compensated by lack of the same defects in others, so that, by dealing with averages, we may expect the final results to be the same as those obtained from the consideration of an ideal body. We shall now consider the evidence on the point.

In a paper published in 1922 the behaviour of erythrocytes when placed in hypotonic saline is dealt with. It was found that the cells, which had an average diameter (equatorial axis) of  $8.6\mu$ , become less in diameter as the volume increases, passing from  $8.6\mu$ , the size in the blood stream, to about  $7.1\mu$ , a minimum value, and thereafter increasing again. Now consider the ratio of the axes when the equatorial axis is at its minimum. We know the length of the equatorial axis, but, because of experimental difficulties, it

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is impossible to measure the polar axis. We can arrive at an idea of the ratio, however, in the following way. We know that the volume of the cell before its form is altered is expressed by  $\frac{4}{3}\pi a^2b$ , when the little concavities have been turned out. Now, if the equatorial axis,  $2a$  be  $8.6\mu$ , and the semi-polar axis be  $b = 0.3a$ , the volume will be  $102\mu^3$  approximately. When the cell has altered in form, we do not know the length of the polar axis but we do know that the volume of the cell cannot be less than  $102\mu^3$ , and that the semi-axis major (equatorial) is from the above measurement of the minimum,  $3.55\mu$ . The necessary length of  $b$ , in order to make the volume equal to  $102\mu^3$ , will be found to be  $1.94\mu$ , so that the polar axis of the cell in its distended condition will be  $3.88\mu$ . The ratio  $\frac{\text{equatorial axis}}{\text{polar axis}}$  therefore is 1.83. This

is the ratio which will exist if the volume is unaltered; but the volume has increased, so that the ratio of the axes must be  $< 1.83$ . The figure we expect from theoretical considerations is 1.5 approximately. Even if the ratio found in the above experiment, which must be less than 1.83, be as great as 1.7, the divergence from the expected figure will be so small as to lie within the range of experimental error. When it is remembered that this experiment is merely representative of a considerable number, there will be no doubt that the evidence is strong that the erythrocyte behaves as if it were a balloon-like body, possessing a membrane for which Poisson's ratio is about the same as for other known substances.

Further experiments on the same point will be found in a recently published paper (2). In this paper the experiments are open to less experimental error. They show that the equatorial axis of the cell undergoes shrinkage as the volume of the cell increases—the increase being brought about by immersion in plasma diluted by water—but, the tonicities dealt with being greater than in the communication referred to (1), the minimum value of the equatorial axis is not so nearly approached. It is shown that the ratio of the axes must be smaller than 2.3, and, by extrapolation, smaller than 1.8, when the equatorial axis is at its minimum. This last figure agrees with the result just discussed.

It ought to be pointed out that several observers have stated that the diameter of the erythrocyte becomes less as the volume increases (3, 4, 5). Careful measurements are not, however, given. Hamburger and Pijper both state that this shortening of the diameter is to be expected in a balloon-like body, but give no proof, nor do they deal with the minimum value through which the equatorial axis should pass. Certain other observers state that they



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observe no shortening of the equatorial axis with increased volume, and that both axes increase (6, 7). The reason for this statement being made by the observers quoted is at once revealed by an examination of their methods, which we have criticised elsewhere (2). There appears to be no observation which shows that there is not a shortening of the equatorial axis when the cell volume increases, and which thus supports Rollett's view, which is conducted in such a manner as to merit any consideration.

It is to be concluded that the suggestion that the erythrocyte of man behaves as if it were a body of dense sponge-like structure is not tenable in the face of the facts, and that the view that the red cell is a balloon-like structure filled with fluid, or with a semi-fluid substance, is the only one which will explain the changes in form observed in it. A study of the behaviour of spheroidal balloons thus furnishes a most convincing proof of the correctness of this view of the structure of the mammalian erythrocyte.

*Summary.*

The changes in form which occur in a balloon of spherical shape when distended are discussed. Two proofs are given that with an increase of volume the equatorial axis must decrease if the ratio  $\frac{\text{equatorial axis}}{\text{polar axis}}$  is greater than  $\sqrt{2 + \sigma}$ ,  $\sigma$  being Poisson's ratio for the membrane. The extent of the shortening is also dealt with. It is shown that in the case of the human erythrocyte the experimentally obtained figures agree in a striking manner with the figures deduced by considering the cell as a balloon-like body with a membrane for which Poisson's ratio is about the same as for most known substances. From this result it may be deduced that Rollett's view of the structure of the erythrocyte is at variance with the facts, and therefore untenable.

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## LITERATURE.

- (1) Ponder, 'Roy. Soc. Proc.,' B, vol. 94, p. 103 (1922).
  - (2) Ponder and Millar, 'Quart. Jour. Exper. Physiol.' vol. 14 (1924).
  - (3) Hamburger, 'Zeitschr. f. Biol.,' vol. 35, p. 252 (1897).
  - (4) Pijper, 'South African Med. Jour.' (1919).
  - (5) Lewis, 'Journal Med. Research,' vol. 10, p. 513 (1904).
  - (6) Price-Jones, 'Jour. Path. and Bact.,' vol. 23, p. 371 (1920).
  - (7) Fischer, 'Oedema and Nephritis' (1915).
-