

Surface Tension and Cell-Division.

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With 9 Text-figures.

THE series of changes which a dividing cell exhibits has long suggested to biologists that surface tension plays a dominating rôle in the process of cleavage. Without exception, theories based on this suggestion have postulated regions of differential tension on the cell-surface; the surface tension at the equator of the cell has been held to be either higher or lower than that at the polar regions of the cell. Such theories have proved of but little value as a means of further investigation, since there is no apparent means of determining how such a state of affairs could arise, nor is there any apparent differentiation in the microscopical structure near the equator of the cell-surface.

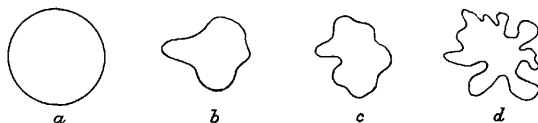
The evidence here presented suggests that regions of differential surface tension are unnecessary assumptions, and that cell-division does not take place owing to a change in surface tension at the cell-surface, but owing to a force inside the cell which operates against the surface tension. It is the equilibrium between this force and the normal surface tension which determines the shape of the dividing cell.

The fertilized eggs of *Echinus miliaris* form very satisfactory material for a study of cell-division, since the protoplasmic surface of the egg is in direct contact with an aqueous medium and because the actual process of cell-division can readily be followed under the low powers of the microscope. The normal egg is spherical, and if it be crushed or broken the resultant portions show no tendency to mix with the water, but rapidly acquire a more or less spherical shape. From this we may infer that the protoplasm of the egg resembles that

of many other cells, in that it is essentially a liquid which is immiscible with water. Further, an overwhelming body of evidence is available to show that the protoplasmic surface contains a lipid or oily phase. To what extent is the form of the egg dependent upon those conditions which determine the form of inert drops of oil surrounded by water?

Consider the simple case of oil-drops in water. The drops are all spherical owing to the existence of a force—usually called surface tension—acting at the oil/water interface. In any such system the amount of free energy will tend to reach a minimum, and since the volume of oil presents a minimum amount of surface when the drop is spherical it is obvious that

TEXT-FIG. 1.



Form of oil-drops in (a) acid water (b-d) increasing amounts of alkali in water.

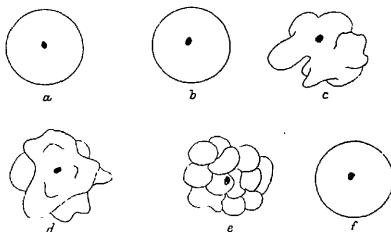
the position of stability is reached when the drops are round. The higher the surface tension the more rapidly is the spherical form assumed, and the more resistant is the form of the drop to external or internal disturbance. Now, it has been shown that the surface tension at an oil/water interface is materially affected by the hydrogen-ion concentration of the water. Hydrogen ions raise the surface tension; hydroxyl ions lower it. The effect of such changes is a marked alteration in the form of the oil.

In an acid solution the oil-drop remains perfectly spherical and is not readily deformed by external forces. In an alkaline solution, however, the drop becomes very irregular in shape and is readily deformed. In highly alkaline solutions the surface tension may actually become 'negative', and the condition of stability is reached by the splitting up of the drop to form an emulsion.

To what extent the drop of protoplasm responds to similar changes in its environment is seen from the following figures.

It will be seen that in an alkaline medium the capacity of the egg (like that of an oil-drop), to retain a spherical form is lost. The outline of the egg becomes distorted by the production of numerous blunt irregular processes, just as is the surface of the oil. On returning such eggs to normal sea-water the spherical form is gradually reformed; in acid sea-water the spherical form is quickly regained. In some cases the recovery

TEXT-FIG. 2.



a, Egg in normal sea-water, P_H 7.9; *b*, egg in acid sea-water, P_H 6.0; *c-e*, successive stages in alkaline sea-water, P_H 9.6; *f*, same egg transferred from alkaline to acid water.

of the spherical form causes the protoplasm to divide completely into two or more parts. These parts are always spherical or elliptical. The nucleated fragment alone divides to form normal blastomeres. Saponin possesses the power of lowering the surface tension at an oil/water interface, and produces similar changes in the form of the egg to those produced by alkalis.

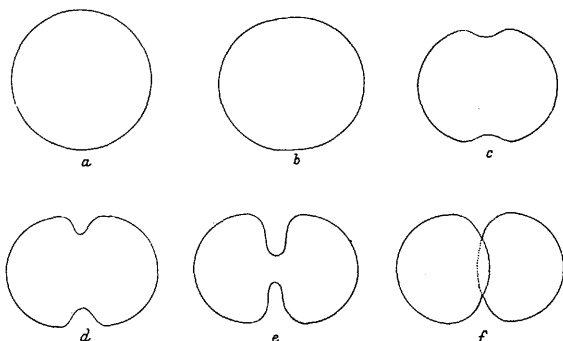
It seems reasonable to conclude that the form of the undivided egg is determined, at least in part, by the surface tension at the egg-surface.

Before proceeding to consider the part played by surface tension during the process of division, it is necessary to draw attention to certain facts in connexion with normal cleavage. The first division in the egg of *Echinus miliaris* takes

place (at 15° C.) about fifty minutes after fertilization, and takes roughly three minutes. The process of cleavage is shown diagrammatically below.

It is important to note that during cleavage there is a progressive increase in the length of the main axis of the egg; this is just as distinctive as the production of the shorter axis which is brought about by the development of the cleavage furrow.

TEXT-FIG. 3.

Stages in normal cell-division of egg of *Echinus miliaris*.

As the egg elongates so the polar regions become more and more convex, while the equatorial region becomes more and more concave.

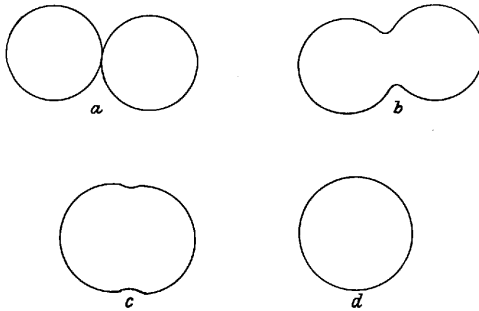
In making a comparison between the dividing egg and an oil/water system it is convenient to consider the fusion of two oil-drops rather than the division of a single drop into two equal parts. When two oil-drops fuse it is obvious (Text-fig. 4) that a reversal of the process would approximate very closely to the process of cell-division.

Now, in fusing together the amount of free energy at the surface of the oil is reduced in the ratio of 5 : 4, so that when the single drop is mechanically shaken into two equal parts,

or when the egg divides into two equal blastomeres, it is necessary to provide the surface of the two systems with free energy. Hence, during cell-division the egg must do work in order to provide free surface energy.

Before proceeding further with this argument, let us consider the effect of altering the surface tension at the protoplasmic/water interface during the actual process of cleavage. In order to do this, eggs at different stages of cleavage are transferred

TEXT-FIG. 4.



Stages in the fusion of two oil-drops.

to acid and alkaline sea-water. In the latter case division occurs quite normally; in the former case striking effects are produced.

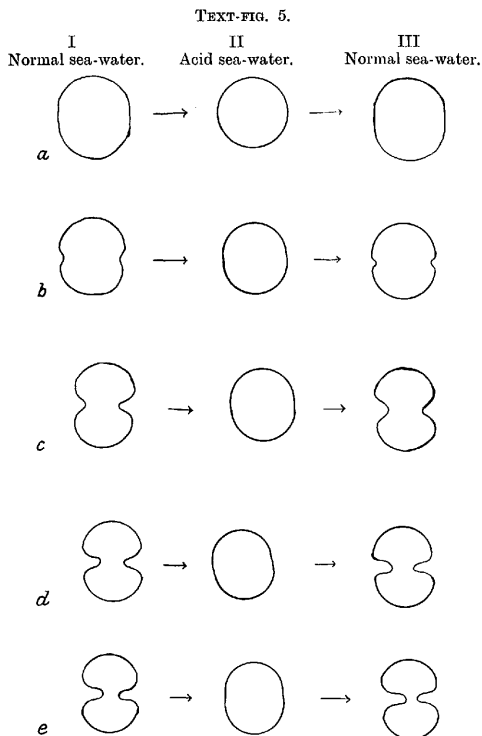
The effects of acid sea-water may be summarized as follows :

(i) The cleavage furrow is entirely lost, and in the early stages of cleavage the egg tends to become spherical in form.

(ii) In the total abolition of the cleavage furrow there is distinct evidence that the egg is elongated along the main axis of the astral figure, so that in the latter stages of cleavage the form of the egg is that of a well-marked cylinder with hemispherical ends.

(iii) The effect of acid sea-water is entirely reversible. If an egg which has been taken from normal to acid sea-water be

replaced in normal sea-water, it very rapidly returns to the stage of cleavage which it had reached prior to being placed in



Effect of acid sea-water on the form of a dividing egg.

acid sea-water: it then proceeds to complete the division at the normal—relatively slow—rate. The distinction between the two phases of recovery from the acid is most marked.

There can be but little doubt that the explanation of these facts is as follows: the acid sea-water raises the surface tension at the egg-surface, and tends to make the egg regain its spherical shape. Owing, however, to some force, which elongates the main axis of the egg, equilibrium is reached (during the latter stages of cleavage) when the egg is cylindrical and not spherical.¹ It will be noted that the increase in length of the main axis, which was noticed in normal cleavage, is much more obvious in acid sea-water owing to the abolition of the cleavage furrow.

It has been shown that when the egg is removed from acid to normal sea-water the cleavage furrow reappears at once. The amount to which the cleavage furrow develops depends entirely on the equilibrium between (a) the surface tension at the egg-surface and (b) some other force within the egg. In acid sea-water the surface tension is high and equilibrium is reached when the egg is a cylinder with hemispherical ends; in normal sea-water equilibrium is reached with a well-marked cleavage furrow. Whereas the effect of a change in surface tension is very rapidly reflected in the form of the cleavage furrow, it is also clear that the elongation of the main axis is the active process whereby free energy is supplied to the egg-surface and allows the furrow to form under normal conditions. This process is stopped in an acid solution (like so many other physiological processes) and is resumed on return to normal sea-water. The rate at which this force acts is entirely independent of the experimental rate of change of the surface tension of the egg-surface.

That the elongation of the egg axis is the active process involved is shown from the experiment of Plateau.²

If a drop of oil be placed between two metal rings A and B so as to form a complete cylinder (Text-fig 6, a), and if the rings be now moved apart, then when the distance of A to B becomes

¹ The relative surfaces which enclose an equal volume of protoplasm are

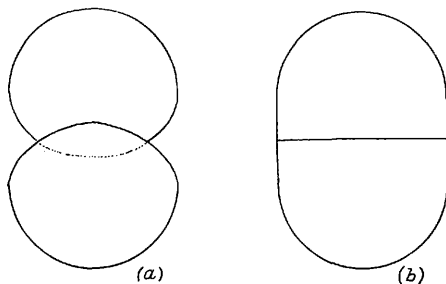
(i) Sphere	100
(ii) Cylinder with hemispherical ends	105
(iii) Two spheres (each half vol. of i)	126

² 'Statique des liquides', vol. ii.

greater than $\frac{2}{3}$ of the diameter of the rings (Text-fig 6, *b*), the form of the drop changes in the same way as that of a dividing egg. The further A is moved away from B the more convex do the ends of the cylinder become, and the more marked is the development of the 'cleavage' furrow; finally the drop is resolved into two separate parts.

There is, however, one respect in which the protoplasmic system differs from that of an oil-drop. When a drop of oil is divided into two—as in Plateau's experiment—it is a simple matter to reverse the process and reform a single drop of oil.

TEXT-FIG. 6.



Form of completely divided egg in (a) normal sea-water. (b) Acid sea-water.

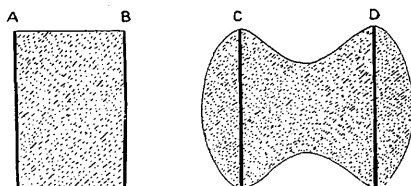
In the case of the living cell this does not occur. It would seem that this is due to the existence of a surface layer (Traube membrane) which is automatically formed when protoplasm comes into contact with water, and that the blastomeres fail to fuse with each other just as oil-drops fail to fuse together if they are shaken in smaller drops in the presence of a soap or any similar substance which can form a condensation layer at the surface of the oil.

The conclusion reached is that division of the cell is brought about by the elongation of one axis of the cell, and that the cleavage furrow results as an equilibrium between this process and the normal surface tension at the cell-surface. It need

hardly be mentioned that the existence of any form of mechanical membrane, or the presence of elements (e.g. other cells) capable of exerting a pressure in any particular direction will materially alter the system which is under discussion.

It can hardly be doubted that the elongation of the cell-axis is associated in some way with the elongation of the astral

TEXT-FIG. 7.



TEXT-FIG. 8.

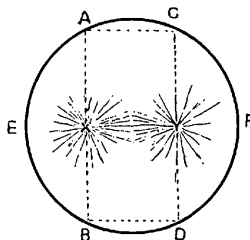


figure. Since the latter process goes on continuously during mitosis and does not begin with the elongation of the whole cell, it follows that the elongation of the cell is probably the result and not the cause of the elongation of the astral figure.

If this conclusion is correct the cell can be divided into three parts; a central cylindrical portion $ABDC$ (Text-fig. 8) which is tending to increase the length of its shorter axis, and two convex ends to this cylinder AEB and CFD . Until the ratio $\frac{AC}{AB}$ approaches $\frac{2}{3}$ the form of the cell will not change, but as

this figure is approached the sides AC and BD will begin to flatten; as soon as $\frac{AC}{AB}$ is $> \frac{2}{3}$, a definite cleavage furrow will result between A and C and between B and D. At the same time the convexity of the surfaces AEB and CFD will increase.

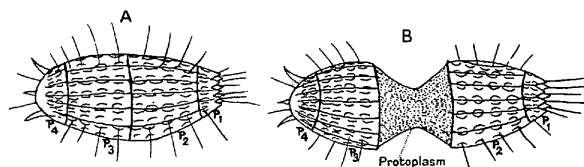
If the change in length of the axis AC is dependent upon a change in the distance of one centrosome from the other, then one would expect to find a similar relationship between this latter distance and the sector AB. The following measurements appear to show that in a variety of cells the cell begins to be deformed in appearance at the equatorial region when the distance between the asters is about .67 of the sector of that part of the cell lying between the asters, and that the cleavage furrow becomes well marked when the ratio has reached the value .8 or .9.

Type.	Authority.	Stage of Division.	Length of Axes.		Ratio $\frac{XY}{AB}$	
			XY	AB		
Multicilia lacustris	Lauterborn	Stage immediately before development of concave cleavage furrow.	1.15	2.0	.58	Average $\frac{XY}{AB} = .65$
Diplogaster longicauda (2 celled)	Ziegler		1.15	1.9	.60	
Diplogaster longicauda (4 celled)	Ziegler		1.7	2.65	.64	
Acanthocystis	Schaudinn		1.45	2.10	.69	
Ascaris	Boveri		2.2	2.9	.76	
Multicilia lacustris	Lauterborn	Definite concave cleavage furrow.	1.85	2.15	.86	Average $\frac{XY}{AB} = .85$
Diplogaster longicauda	Ziegler		1.27	1.64	.77	
Diplogaster longicauda	Ziegler		1.35	1.70	.80	
Diplogaster longicauda (4 celled)	Ziegler		1.15	1.38	.83	
Acanthocystis	Schaudinn		1.80	2.00	.90	
Ascaris	Boveri		2.65	2.9	.91	

Prior to any visible change in the appearance of the cell the ratio $\frac{XY}{AB}$ is progressively increasing from the beginning of the formation of the astral figure; it then passes through the critical value at which the furrow appears and continues to increase until complete cell-division is effected.

It is somewhat rash, perhaps, to press too far the analogy of the astral figure to the rings in Plateau's experiment. It is obvious that the mechanical model is a limited one, and that subsequent work may show that regions of differential viscosity such as are suggested by Chambers's¹ work may be found to be involved. Yet in the particular case of a cell which possesses a structure curiously fitted to play the part of Plateau's rings, division is found to proceed on just those lines demanded by the above analysis. Text-fig. 9 shows the division

TEXT-FIG. 9.



Division of *Coleps hirtus* (after Doflein). The undivided form *a* gives rise to two daughter individuals by passing through stage *b*.

of the protozoon *Coleps hirtus*. The body is covered by four hard skeletal plates P_1 - P_4 . When division occurs the distal ends of the cell remain fixed in form owing to the existing plates, and between plates P_3 and P_4 the cell becomes elongated in exactly the form demanded by the hypothesis put forward. In the stage of division illustrated a well-marked cleavage furrow has formed and the 'Plateau' ratio is about .8.

SUMMARY.

Cell-division may be accounted for by the movement of the two asters away from each other. The appearance of the cleavage furrow is due to an equilibrium between the effect of this movement on the protoplasm and the surface tension at the cell-surface. The behaviour of the cell under these forces is precisely similar to a drop of oil subjected to similar conditions. There is no necessity to postulate regions of differential surface tension at the poles or equator of the cell.

¹ 'Journ. Exp. Zool.', vol. 23, p. 483, 1917.