Pressure Experiments on the Egg of Cerebratulus lacteus.

By

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With 7 figures in text.

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The following is a record of the results obtained by compressing the eggs of *Cerebratulus lacteus* during maturation and early cleavage stages. The material is excellent for this purpose, since division is regular, and the egg may be oriented both by means of the polar bodies, and the stalk of the egg membrane at the vegetative pole. The experiments were undertaken with a view to determining how the maturation and early cleavage stages might be modified by pressure, and to discover if possible whether any modifications so produced would have any permanent effect upon later development.

I am indebted to Professor T. H. MORGAN for the suggestion of the problem, and for assistance in the course of the work, which was carried out at the Biological Laboratory of Tufts College at Harpswell Maine, where the privileges of the Laboratory were accorded me by Prof. J. S. KINGSLEY and Prof. H. V. NEAL.

A brief review of normal cleavage is necessary, in order to make clear how the compressed eggs differ in their development. For this I have referred to the papers of C. B. WILSON, and E. B. WILSON, in connection with my study of the living eggs.

Normal Cleavage of Cerebratulus.

When the eggs are freed from the body, each one within its egg membrane, the large conspicuous germinal vesicle is still intact and lies eccentrically between the center of the egg and the animal

pole. After about fifteen minutes the vesicle breaks down, and the nuclear area, which is much lighter than the surrounding protoplasm, migrates toward the periphery, where it broadens slightly (Fig. V, *2*).

Fig. I.

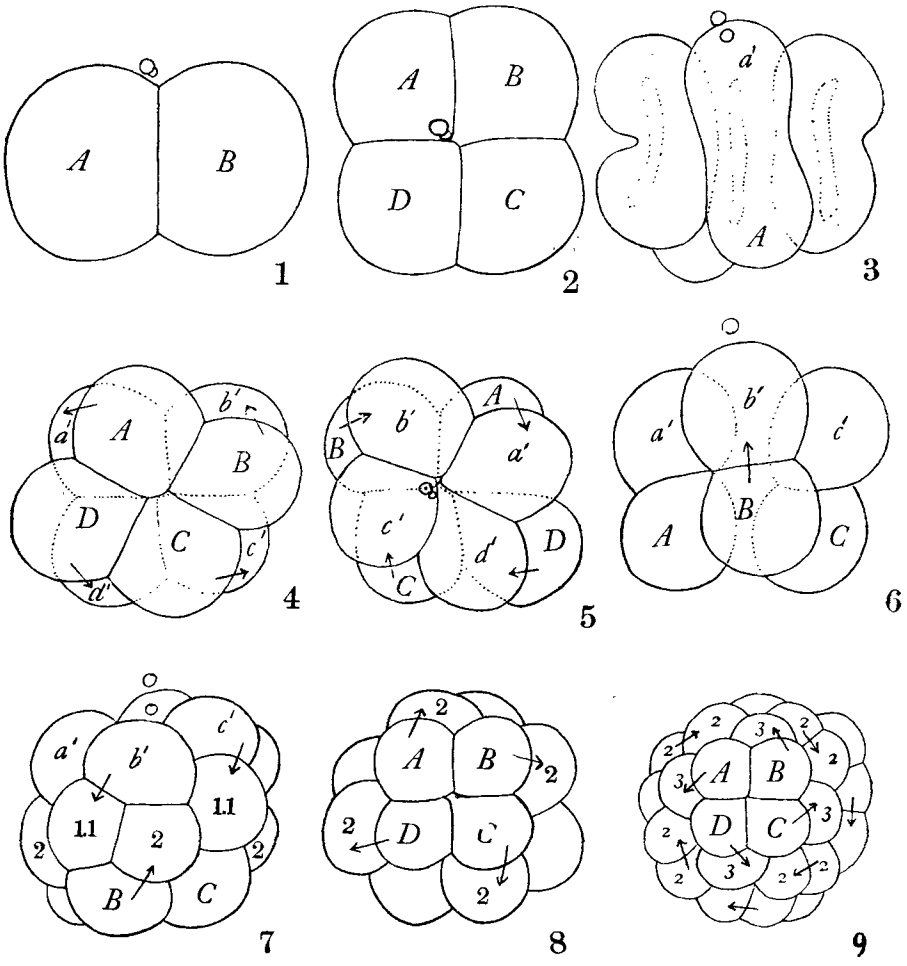

Fig. I, *1—9*, normal development of *Cerebratulus lacteus*. X 170.
1, 2-cell stage, side view; *2*, 4-cell stage, polar view; *3*, 4-cell stage, side view, at beginning of third cleavage; *4*, 8-cell stage, lower pole view; *5*, same stage, from upper pole; *6*, side view 8-cell stage; *7*, 16-cell stage, side view; *8*, same stage from lower pole; *9*, 32-cell stage, from lower pole.

Here the nucleus remains, at the first polar metaphase, proceeding no further until fertilization. The second polar body is formed about one and a half hours later.

At the first cleavage, the spherical egg is divided into two equal

blastomeres (Fig. I, *1*), the cleavage plane being meridional, and coinciding with a line drawn between the polar bodies and the stalk of the egg membrane at the vegetative pole. The egg membrane is shown in Fig. V, *3*. The second division is also meridional at right angles to the first, Fig. I, *2*; the four resulting blastomeres are equal. Fig. 1, *3* is a side view of this stage, showing the spindle areas lengthened out preparatory to the third division. At the completion of this division, Fig. I, *6*, the four upper cells, lettered *a'—d'*, are seen to be turned somewhat to the left of the corresponding lower cells *A—D*, a tendency which can be observed even in Fig. I, *3*, in the cells *A—a'*. The position of the arrows in Fig. I, *6* indicates a dexiotropic cleavage. In many cases the four upper cells are slightly larger than the lower, as described by E. B. WILSON. In other eggs there was no observable difference in size. This coincides with the fact stated by C. B. WILSON that the third division gives rise to eight equal blastomeres. I made numerous drawings of these apparently equal cells, and found in some cases that the upper and lower cells were exactly equal in size; in other cases the difference could be detected only by a measurement of the cells. In the majority of eggs, however, the four upper cells were larger. Fig. I, *4* is a lower pole view of the 8-cell stage, showing how the upper cells *a'—d'* are rotated to the left of the lower ones.

In the fourth cleavage, as shown in Fig. I, *7*, a side view of this stage, the cells *A—D* give rise to a second quartet of cells, numbered 2, while *a'—d'* also give rise to four cells, numbered 1,1. In both cases the arrows indicate a laeotropic direction. Fig. I, *8* is the same stage viewed from the lower pole. Each of the sixteen cells divides again to form the 32-cell stage, Fig. I, *9*.

Development of Compressed Eggs.

1. Eggs Laterally Compressed at the 2-cell Stage until after the 4-cell Stage.

The method employed was as follows: The eggs were artificially freed from the body and placed in glass dishes with sea water, where they were kept before fertilization, until they became rounded out. A small quantity of sperm was then added, and development was allowed to proceed normally until the completion of the first cleavage, Fig. I, *1*, about two hours after fertilization.

A quantity of eggs was then transferred to a glass slide, which

had been smeared with albumen fixative, so that the eggs floated in a thin film of water. A cover glass was placed over the eggs, supported by paper strips of such thickness that the glass was in light contact with the surface of the eggs. The slide was then put

Fig. II.

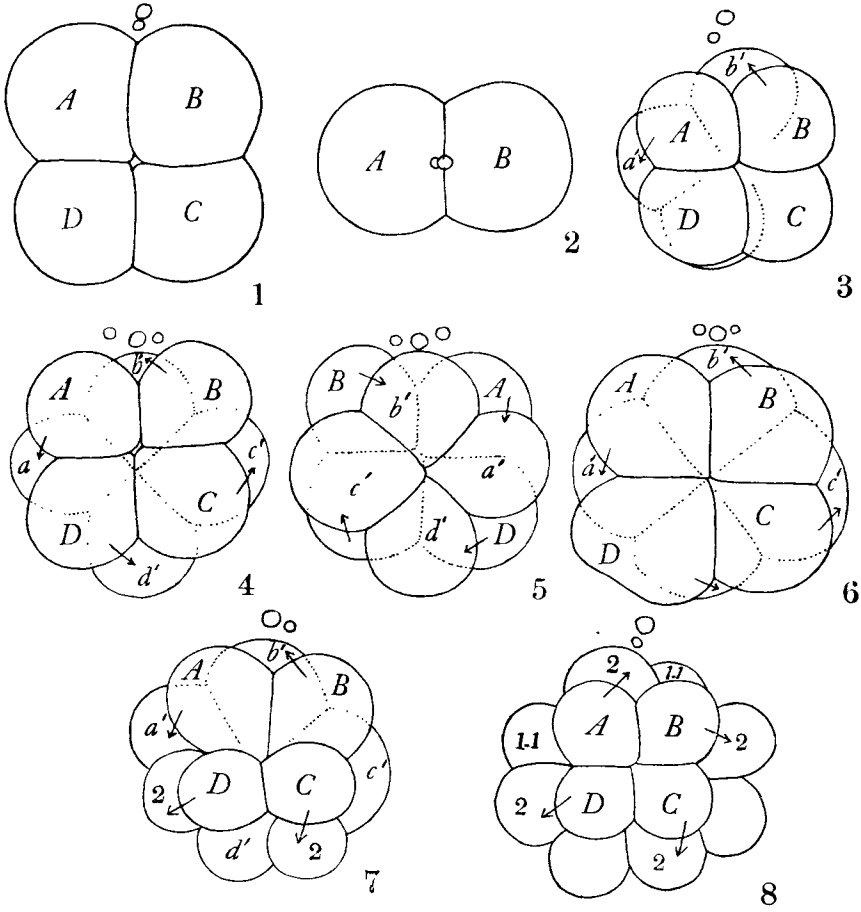

Fig. II, *1—8*, development of eggs compressed up to 4-cell stage. X 170.
1, 4-cell plate, derived by a second, equatorial, cleavage from a normal 2-cell stage; *2*, 4-cell plate, from upper pole; *3*, *4* and *6*, early and late 8-cell stages, side view; *5*, view of 8-cell stage from other side, cell $a'-d'$ nearest the observer; *7*, *8*, early and late 16-cell stages, side view.

under a bell jar, in order to obviate any increase in pressure due to the evaporation of water.

When the eggs of the control series had reached the 4-cell stage, about one hour later, the eggs on the slide were examined, and 4-cell stages were found, but unlike the normal. The second

cleavage plane had come in equatorially (Fig. II, *1*), instead of meridionally, as in the controls (Fig. I, *2*). On account of the lateral pressure in Fig. II, *1*, division could not take place either above or below the first two cells, and the result was a flat plate of four cells, which all lay in the same plane on the slide. The polar bodies lay near the edge of the cells *A*, *B*; and the stalk of the egg membrane, below the junction of the cells *C*, *D*. (The first four cells are here lettered *A*—*D* although not identical with the first four *A*—*D* of normal division, since they have not the same relation to the polar bodies.) In this figure the cells *A B* are slightly larger, but this condition was by no means constant. Some eggs showed cells *C D* larger, others, *A* and *D*; still others, *B* and *C*; occasionally, only one cell was larger than the others: in fact every combination possible. Eggs with the two upper blastomeres larger were however more frequent than any other single type, for, of thirty-five 4-cell stages counted, seventeen eggs showed the upper cells larger, eighteen eggs included all the other combinations together. In polar view of this stage, Fig. II, *2*, only two cells were seen, with the polar bodies between them.

Not all eggs upon the same slide showed the 4-cell stage as just described. The pressure varied in different regions, and some eggs were found, where there appeared to be no pressure, which had segmented normally. This made it necessary to isolate the compressed eggs when pressure was removed just after the 4-cell stage. They were placed singly upon depression slides and covered. At short intervals drawings were made, up to the 8- and 16-cell stages, and less frequently of the blastula stage.

The third cleavage appeared at the same time as in normal eggs (Fig. II, *3*). Each cell of the original four, *A*—*D*, gave rise, obliquely and to the left, to four other cells *a'*—*d'*, which lay at the same level with each other, and below the first four. In this figure, *C* had not yet divided to form *c'*. (The lettering here employed is the same as in drawings of normal development, i. e. *A*—*D* indicate the first four cells; *a'*—*d'*, the first quartet derived from them. The cells *A*—*D* are shown nearest the observer.) Fig. II, *4* is in the same position as the preceding figure, and the first quartet *a'*—*d'* is shown fully formed.

When this stage is compared with the normal 8-cell stage in Fig. I, *4*, the two are seen to be practically identical, except as regards the position of the polar bodies. Fig. II, *4* however, is a side

view of the compressed egg, while Fig. I, *4* is a lower pole view of the normal egg. Except for the position of the polar bodies then, the lower pole view of the normal is similar to the side view of the compressed egg. If the egg as figured in Fig. II, *4* should be turned over to the other side so as to show the cells $a'—d'$ nearest the observer (Fig. II, *5*) it will be seen that the direction of the arrows is now toward the right, and the figure is therefore not identical with the lower pole view of the normal, Fig. I, *4*. It coincides, however, with the upper pole view of the normal, Fig. I, *5*. Thus the egg from one side is similar to the upper pole of the normal; on the other side, to the lower pole. This comparison has no significance other than simply to make clear the cell contour of the compressed egg at this stage.

After the third cleavage was completed (Fig. II, *6*), the blastomeres appeared somewhat flatter, with broader surfaces of contact, and one cell *D* showed the beginning of a fourth division. In Fig. II, *7*, from the same egg a little later, *D* is seen to have divided, giving rise by an oblique division to cell 2. Later *C* divided in the same manner. Very soon after, *A* and *B* each divided similarly completing a second quartet of cells numbered 2, the first quartet being $a'—d'$ (Fig. II, *8*). At the same time, the cells $a'—d'$, on the other side of the egg, divided to form the quartet 1.1. This completed the 16-cell stage.

When this side view is compared with the lower pole view of the normal 16-cell stage in Fig. I, *8*, it will be seen that here, as well as in the 8-cell stage, the results are identical, both in regard to position of the cells and their origin, as indicated by the arrows. The only difference between the two is, as before, the position of the polar bodies, which in the compressed egg lie between the cells 2 and 1.1.

To return to the 4-cell stage, and compare Fig. II, *1* with Fig. I, *2*, it will be seen that, disregarding the polar bodies, the side view of the compressed egg here also is similar to the normal polar view. We may say then, that the compressed eggs, from the 4-cell stage on, developed, so far as concerned the external form, as if the side of the egg were the pole. As before stated, this comparison does not imply that the first four cells in the two cases are equivalent in any way, but that, given four cells, which in one case form the polar view of an egg, in the other, the side view, the same mechanical factors cause a similar cell configuration. After these

four cells were formed in the compressed egg, there was thus no mechanical difficulty to overcome in the way of readjusting cells to new positions, such as will be seen later in the development of eggs compressed for a longer period. In the blastula stage of the eggs just described, the cells were all approximately equal and regularly arranged, so that there was no observable difference between the cells at the sides and at the poles. Normal pilidia resulted from these eggs.

2. Eggs Compressed up to the 8-cell Stage.

In the second series of experiments, the eggs were allowed to remain under pressure until the 8-cell stage, which was reached at the same time as in the normal, about four hours and a half after fertilization. The eggs were isolated as before upon depression slides, and frequent drawings were made. Fig. III, *1—4*, were drawn from the same egg within an interval of fifty minutes.

By observation of the eggs under pressure at the time of the third cleavage, it was found that the 4-cell plates, similar to Fig. II, *1*, gave rise in the third division to 8-cell plates, the pressure of the cover glass upon the eggs preventing cells from forming above or below the first four (Fig. III, *1*). There was often observed a tendency of these third division lines, which started radially toward the center, to change their direction somewhat, and run equatorially in the center of the egg. In Fig. III, *1*, the result of this was the formation of four larger cells *B*, *C*, *F*, *G*. Fifteen minutes later, these four cells gave rise to four smaller cells lying above them (Fig. III, *2*). There is a general correspondence between this view, and Fig. II, *8*, a 16-cell stage in the first experiment, but it is probable that division on the other side of the 8-cell plate was not so regular. Twenty minutes later *D* gave rise to *d'* (Fig. III, *3*), and *G* divided for the second time. Fig. III, *4*, a little later, showed *A* giving rise to *a'*. This egg did not develop beyond a fairly regular 32-cell stage. That this was not due primarily to the disturbance of cleavage, is probable from results obtained with other eggs.

The development of a slightly different 8-cell plate is shown in Fig. III, *5*. Here the cleavage lines all converge toward the center, forming a rosette of eight cells. The cells *A*, *C*, *E*, *G* overlapped the other cells a trifle, and these four were the first to give rise to four central cells, *a' c' e' g'*, shown in Fig. III, *6*. This form of egg appears to coincide in the main with Fig. III, *2* and Fig. II, *8*,

namely, four central and eight peripheral cells. Fig. III, 7 and 8, drawn from two to three hours later, showed a fairly rounded blastula, with irregularities in the size and position of the cells. Next day

Fig. III.

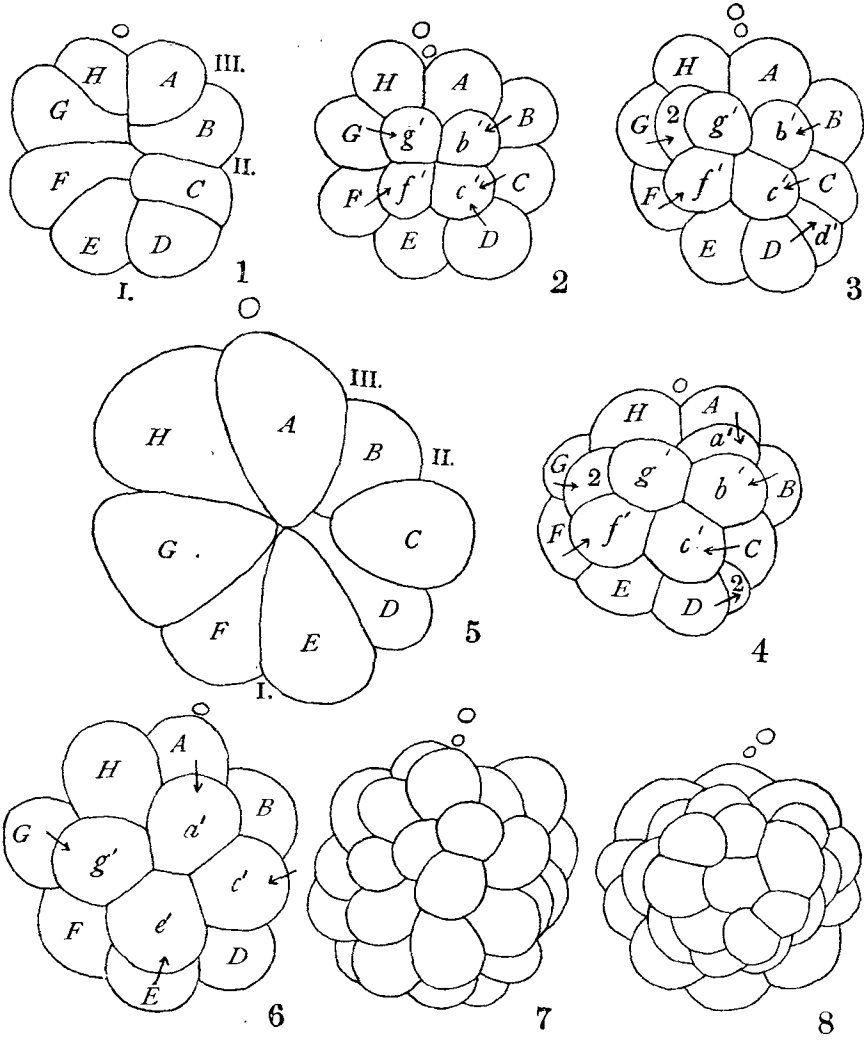

Fig. III, *1—8*, development of eggs compressed up to the 8-cell stage. X 170. (All in side view.) *1*, 8-cell stage, in form of flat plate; *2*, *3*, *4*, later stages of same egg; *5*, another 8-cell plate; *6*, *7*, *8*, later stages of same egg; *I.*, *II.*, *III.*, first, second, and third cleavage planes.

the cells had all separated, and lay as isolated spheres within the egg membrane. No other eggs of this lot developed beyond the blastula stage. In a second lot of 8-cell plates, many reached a

pilidium stage, but the majority of pilidia were abnormal, several showing only one lappet.

Fig. IV.

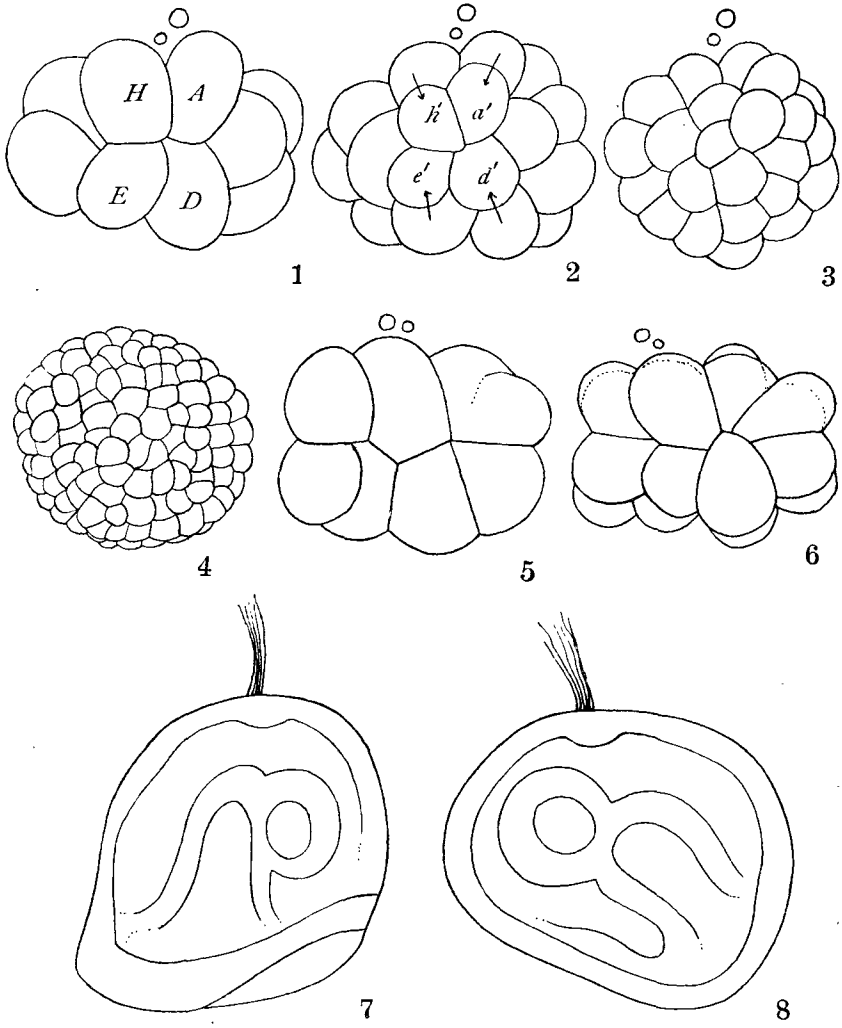

Fig. IV, *1—8*, development of eggs compressed up to the 8-cell stage. X 170.
1, irregular 8-cell plate; *2*, *3*, later stages from same egg; *4*, late blastula stage from same egg; *5*, another 8-cell plate; *6*, 16-cell stage from same egg, in two 8-cell layers; *7*, *8*, normal pilidia from 8-cell plates, about 48 hours.

Fig. IV, *1—4* are taken from an individual of a successful series, in which several 8-cell plates gave rise to normal pilidia. Fig. IV, *1* is an irregular plate, four central cells lying a little above

the others, and an extra cell appearing at the right. In the next stage, Fig. IV, *2*, the four central cells gave rise to four other centrally placed cells *a' d' e' h'*. The remaining cells divided irregularly. Owing to these irregularities in division, there was no definite 16-cell stage in this egg. It developed however into an early blastula of fairly regular form (Fig. IV, *3*). Fig. IV, *4* is a later stage of the same egg. Two days later, the pilidium stage was reached, shown in Fig. IV, *7*. This appeared to be perfectly normal.

Fig. IV, *5* and *6* are from another individual, which shows the transition from an 8-cell plate to a two-layered plate form of sixteen cells. While the later development of this egg was not followed, it is known that it reached a normal pilidium stage.

From the different types of 8-cell plates figured, it is clear that soon after release from pressure, the cleavages varied more or less in regard to time, to the form and position of the cells. Later, blastulas, from even the more irregular plates, attained a fairly normal contour, and gave rise to normal pilidia.

In this class of experiments, some reconstruction of form was necessary to convert the flat 8-cell plate into the normal blastula form. While this was accomplished in some cases by a comparatively regular method, as in Fig. III, *1—4*, the transformation was, in the main, quite irregular, and varied in almost every egg examined.

I compressed some eggs up to the 16-cell stage, and obtained several apparent blastulae, but development proceeded no further, and the cells separated, lying isolated within the egg membrane until they disintegrated.

In the preceding experiments the amount of pressure upon the eggs was small, the cover glass being only in light contact with the egg so that no upward division of cells was possible. In other experiments, the eggs were subjected to varying amounts of actual compression, so that the two blastomeres were abnormally flattened. These eggs developed into 4- and 8-cell plates similar to those before described. Later development, upon release of pressure, was however extremely irregular. In some cases, the eggs divided irregularly about as far as a 32-cell stage, when the cells separated, rounded up, and lay isolated within the egg membrane until they disintegrated. It frequently happened that the 8-cell plate segmented no further, the blastomeres separating as in the former case. In these eggs there was nothing to indicate that the nuclei had segmented

irregularly. DRIESCH, in his pressure experiments on sea-urchin eggs, figured a separation of blastomeres forming 8-cell plates, but in his material they united again, returning to the plate form. This was not observed in *Cerebratulus*.

When pressure was extreme, the cleavage furrows which started at the periphery were not completed at the center and on release of pressure the egg shriveled up and disintegrated. In most cases of this kind, the nuclei appeared to segment abnormally.

The relation of the results of the foregoing experiments upon the question of localization may be stated as follows: Since the normal position of the cells may be altered in the egg of *Cerebratulus* in a variety of ways without affecting the end result, it would appear that the cells up to and including the 8-cell stage, are of equal and similar value in development. This coincides with the results obtained by DRIESCH in his pressure experiments upon sea-urchin eggs. It is also in harmony with the fact observed by E. B. WILSON for *Cerebratulus*, that an isolated blastomere of the 8-cell stage will develop into a normal pilidium.

3. Eggs Compressed during Maturation and Fertilization.

Another series of experiments was undertaken with a view to determining the effect upon development of compression during maturation and fertilization. In these experiments, as soon as the eggs had rounded out in sea water after being freed from the body, a small quantity of sperm was added while the germinal vesicle was still intact. The eggs were then placed upon a slide, and covered with a glass supported by thin strips of paper so that the eggs were thus under a certain amount of actual pressure as in the last described experiment with 8-cell plates. An eye-piece micrometer was used to determine the extent of pressure. The normal diameter measured .7 mm. This was increased usually to .9 or 1.0 mm. under compression.

The eggs in the first series were kept under pressure for about three hours, until the second cleavage in the control eggs. When examined, the eggs were found to be compressed in various axes, but only those were chosen for study which had been subjected to pressure directly from the side. Fig. V, *1* shows an egg compressed from the side, as indicated by the eccentric position of the nucleus, and the stalk of the egg membrane. The diameter under pressure measured .9 mm. Under these conditions, the germinal vesicle broke

down after a short time, and the nuclear area appeared as a light streak, broader at the periphery, as in the normal eggs (Fig. V, *2*). When not fertilized, the normal egg halts at this stage, the first polar metaphase. The sperm had been added to this lot just before compression, but the time of entrance of the sperm was not observed.

Fig. V.

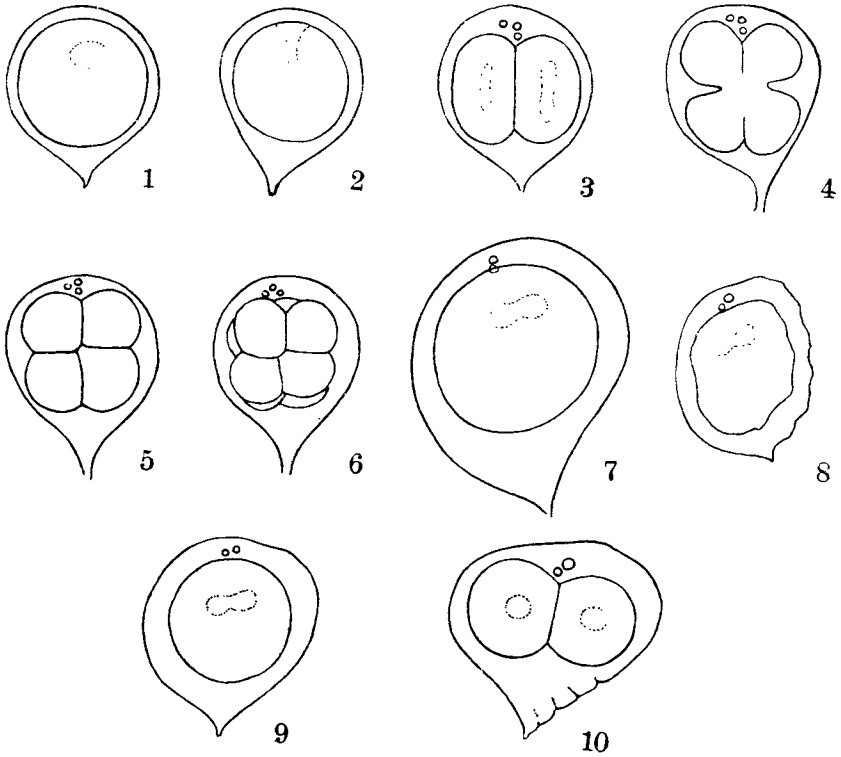

Fig. V, *1—10*, development of eggs compressed laterally during maturation and fertilization. X 85.
1—6, egg compressed to .9 mm. from before dissolution of germinal vesicle, up to 4-cell stage.
2, formation of first maturation spindle; *3*, 2-cell stage; *4*, *5*, early and late 4-cell stage under pressure; *6*, 8-cell stage, pressure removed, typical for egg compressed up to 4-cell stage.
7—10, egg compressed to 1.1 mm. from before dissolution of germinal vesicle to formation of second polar body.
7, egg after fertilization, formation of first division spindle; *8*, shrinking of egg and membrane on release from pressure, followed by *9*, return to normal contour; *10*, normal 2-cell stage.

After about two and a half hours compression, the polar bodies were found to be extruded, and the egg had reached the normal 2-cell stage, Fig. V, *3*. The eggs were kept a little longer under pressure until the second cleavage furrow began to appear (Fig. V, *4*), which was equatorial here on account of pressure, as in the first

experiments described. The egg was then freed, and isolated. The resulting 4-cell plate, Fig. V, *5*, gave rise to four other cells, in Fig. V, *6*, forming an 8-cell stage similar to II, *4* of the first experiment. No eggs of this lot, or of any similarly treated, developed beyond the 8-cell stage. The time of formation of polar bodies and cells was apparently not retarded by compression.

At another time, eggs were compressed to 1.1 mm. for two hours (Fig. V, *7*) from fertilization while the germinal vesicle was intact, until after the formation of the second polar body in the controls. When pressure was released, the cell wall appeared very irregular Fig. V, *8* but rounded out again in about fifteen minutes (Fig. V, *9*). Half an hour later, a 2-cell stage with slightly unequal blastomeres resulted, and the egg ceased to divide beyond an irregular 4-cell

Fig. VI.

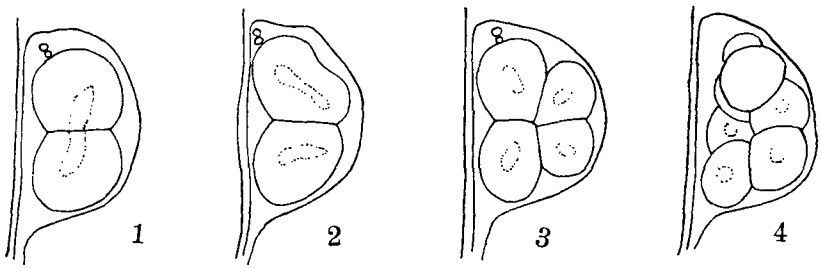

Fig. VI, *1—4*, egg compressed from before dissolution of germinal vesicle up to 4-cell stage. *1*, egg greatly compressed from sides, causing polar elongation and equatorial first division; *2*, *3*, *4*, later development.

stage. So far as could be superficially determined, the nuclear divisions appeared regular.

Several cases were observed similar to Fig. VI, *1* in which the egg had been compressed not only on two sides, by contact with the slide and cover glass, but on the remaining sides, by contact with the paper support of the cover glass and the egg membrane. The egg was thus greatly elongated in the polar axis, and the first cleavage spindle took up its position in the long axis of the protoplasmic mass. The first cleavage plane, in Fig. VI, *2*, thus cut the egg approximately at right angles to the egg axis and to the normal first cleavage plane. A second cleavage came in at right angles to the first, giving rise to four unequal cells (Fig. VI, *3*). Further division was irregular (Fig. VI, *4*), and soon ceased.

I was unable to find any eggs compressed during maturation and fertilization which developed beyond the 8-cell stage. By far

the majority of the compressed eggs proceeded no further than the extrusion of the polar bodies, — in many cases not so far. I tried subjecting eggs to shorter periods of pressure, but with no better success.

The question suggests itself whether the failure to develop further is due to the disarranging of the spindle and chromosomes by compression, or to abnormal conditions acting upon the cytoplasm. In all the eggs figured, there was nothing to indicate any disturbance of the spindle region, which could be easily located as a clear light area in the egg. In some eggs subjected to extreme compression, the nuclear region was also involved, and in these cases the nuclear material probably fragmented, since numerous small clear areas were observed. Such eggs were obviously too abnormal for further study. In Fig. V, *1*, the egg was moderately compressed and the nucleus was free to move in its normal path toward the periphery to form the polar bodies; the nuclear conditions in Fig. V, *2—5* were apparently regular, and the same as in the eggs described in the first experiment, which developed into normal embryos from 4-cell plates.

In eggs subjected to greater pressure, as in Fig. V, *7*, the nucleus segmented in a regular manner, but the cytoplasm appeared more vacuolated under pressure, and the wrinkling of the egg surface, and subsequent rounding out indicated an abnormal strain upon the cytoplasm. Even if compression is sufficient not only to affect the cytoplasm, but also to place the nucleus in an abnormal position within the cell, as in Fig. VI, *1*, it will still segment normally.

In all these cases it seems clear that the nucleus may segment regularly during the early stages, although the cytoplasm may be more or less compressed, but when compression is extreme, it involves both nucleus and cytoplasm, and the nucleus fragments irregularly. Since the nucleus does segment regularly during early development, while the cytoplasm is subjected to strain, it seems reasonable to conclude that the cause of later non-development lies not in any abnormality of the nucleus but in the impairing of the cytoplasm in some way. The same explanation would appear to hold true in the case of the 4- and 8-cell plates which were formed under considerable pressure; the abnormal pressure upon the cytoplasm was here responsible for the separation of the blastomeres after compression, and their failure to segment further.

4. Polar Compression during Maturation and Fertilization.

The method was the same as in the preceding experiments. Slides were examined to find eggs which had been compressed from the upper pole. When found in this position, the nucleus appeared at the centre, and the egg membrane appeared spherical, its stalk being hidden below the egg as in Fig. VII, *1*. The egg here figured measured .9 mm. under compression, and was kept in this condition until the second polar bodies formed in the controls. None were found then in this egg. The pressure was released; and the egg later divided regularly into two equal blastomeres (Fig. VII, *2*). After

Fig. VII.

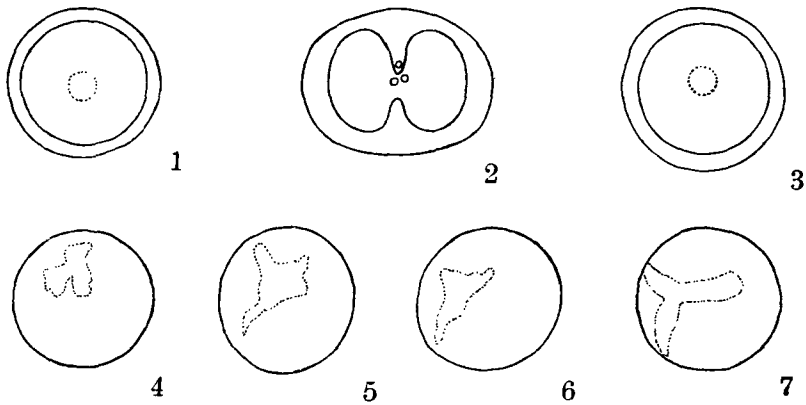

Fig. VII, *1—7*, development of eggs under polar compression during maturation and fertilization. X 85. *1*, egg compressed to .9 mm., germinal vesicle intact; *2*, 2-cell stage developed after release from pressure; *3*, egg compressed to 1.0 mm., germinal vesicle intact; *4—7*, abnormal positions taken by germinal vesicle after its dissolution.

reaching a normal 4-cell stage, division ceased. Six other eggs were observed which behaved in the same manner. The formation of the polar bodies in all seemed to be somewhat delayed, apparently being prevented by the pressure of the cover glass upon the upper pole of the egg. There were no irregular clear areas to indicate abnormality in the nuclear region.

When eggs were compressed to 1.0 mm. or more, abnormalities appeared in the region of the spindle, and no polar bodies were formed after release from pressure. In Fig. VII, *3*, the egg measured 1.0 mm. in diameter when first compressed, and the germinal vesicle was intact. Later the nuclear wall broke down. The nuclear area under normal conditions would have moved toward the upper pole

to give off the polar bodies (Fig. V, *2*), or, as in Fig. VII, *1*, *2*, halt here until release of pressure made possible the formation of the polar bodies. The nuclear area however assumed the positions indicated in Fig. VII, *4*—*7*, showing an apparent attempt to reach the periphery at some point other than normal.

It would thus appear that polar compression up to 1.0 mm. is great enough to act upon the germinal vesicle at the time of its dissolution, and cause it to take abnormal positions. Polar compression to .9 mm. while acting on the cytoplasm, is not great enough to reach the nucleus, which in this case therefore is free to move toward the upper pole, where the pressure of the cover glass prevents the formation of the polar bodies. This is only a check on development, and when pressure is released, development continues, at least as far as the 4-cell stage.

The same general conclusion is reached here, as in the case of laterally compressed eggs, namely, that moderate pressure affects the cytoplasm, but extreme pressure affects the nucleus as well, immediately arresting development. The laterally compressed egg is capable of withstanding greater pressure than the polar compressed, since pressure in the former case does not interfere with the path of the nucleus in maturation toward the periphery. In polar compressed eggs, as in the first case, we find that the nucleus segments regularly during early development after the cytoplasm has been compressed, so that here too we may attribute failure to develop further to injury of the cytoplasm rather than of the nucleus.

Summary.

1) In eggs of *Cerebratulus lacteus* subjected to slight compression at the 2-cell stage until after the 4-cell stage, the second cleavage, under pressure, is equatorial; the third, after release, is meridional. In the normal the second is meridional, and the third equatorial. Thus compression causes a transposition of the second and third cleavage planes. Normal pilidia result from these forms.

2) When eggs are compressed up to the 8-cell stage, flat plates of eight cells result, which also may give rise to normal pilidia.

3) Since the normal position of the cells in the egg of *Cerebratulus* may be altered without affecting the end result, it would appear that the cells up to and including the 8-cell stage are of equal and similar value in development.

4) In eggs subjected to greater pressure at the 2-cell stage up to the 8-cell stage, the blastomeres frequently segment no further when released, but become separated, and lie isolated within the egg membrane. In several cases an irregular 16- or 32-cell stage may be reached before separation of the cells.

5) Since the nuclei are apparently not rendered abnormal by this amount of pressure, failure to develop further seems due to the effect of compression upon the cytoplasm.

6) Eggs laterally compressed to a great extent during maturation and fertilization and then set free may segment regularly as far as the 8-cell stage. Beyond this none were observed to develop.

7) Eggs compressed from the poles during maturation and fertilization may develop regularly as far as the 4-cell stage. The maximum of pressure which permits development thus far, is less than the maximum for the laterally compressed eggs.

8) The failure to develop further in these last two cases of moderate pressure is probably due to some impairing of the cytoplasm, and not to a disturbance of the nuclear elements.

Columbia University, Jan. 3, 1910.

Zusammenfassung.

1) Werden die Eier von *Cerebratulus lacteus* im Zwei- bis nach dem Vier-Zellenstadium geringer Kompression unterworfen, so verläuft die zweite Furche unter Druck äquatorial; die dritte, nach dessen Aufhören, liegt meridional. Normalerweise ist die zweite meridional und die dritte äquatorial. Also veranlaßt die Kompression eine Vertauschung der zweiten und dritten Furche. Von diesen Formen stammen normale Pilidia.

2) Die Kompression der Eier bis zum 8-Zellenstadium ergibt flache Platten von 8 Zellen, welche gleichfalls normalen Pilidien zum Ursprung dienen können.

3) Da die normale Stellung der Zellen im Ei von *Cerebratulus* ohne Einfluß auf das Endergebnis verändert werden kann, so scheinen wohl die Zellen bis inklusive zum 8-Zellenstadium von gleich großem und ähnlichem Wert bei der Entwicklung.

4) Werden Eier im 2-Zellenstadium bis hinauf zum 8-Zellenstadium einem stärkeren Druck unterworfen, so furchen sich die Blastomeren nach dem Aufhören des Druckes häufig nicht weiter, sondern trennen sich und liegen isoliert innerhalb der Eimembram. In manchen Fällen kommt es noch zu einem irregulären 16- oder 32-Zellenstadium vor dem Auseinanderweichen der Zellen.

5) Da die Kerne durch den angewandten Druck anscheinend nicht abnorm gemacht werden, so scheint die Wirkung der Kompression auf das Protoplasma schuld an dem Scheitern der Weiterentwicklung.

6) Während der Reifung und Befruchtung von den Seiten her in größerer Ausdehnung komprimierte Eier vermögen sich, danach vom Drucke befreit, bis

zum 8-Zellenstadium regulär zu entwickeln. Darüber hinaus wurde bei keinem eine Entwicklung beobachtet.

7) Während der Reifung und Befruchtung von den Polen her komprimierte Eier können sich regulär bis zum 4-Zellenstadium entwickeln. Das für eine Entwicklung bis zu diesem noch zulässige Druckmaximum ist geringer als das Maximum für die von den Seiten her komprimierten Eier.

8) Das Scheitern der Weiterentwicklung in diesen letzten zwei Fällen bei der Anwendung mäßigen Druckes rührt wahrscheinlich von einer irgendwie schwächenden Einwirkung auf das Protoplasma her, nicht von einer Störung der Kernelemente.

(**W. Gebhardt,** Übersetzer.)

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