

I. THE PRIMARY CLEAVAGES.

1. *The First Cleavage. Figs. 2-6.*

I cannot state exactly the length of time which intervenes between fertilization and the first cleavage, nor between the latter and the following cleavages. However, not less than four hours elapse after the entrance of the sperm into the ovum before the first cleavage begins, and the interval is probably longer. I have frequently found *Crepidulas* in the process of egg-laying, and after carrying the newly laid eggs several miles to the laboratory and there fixing and staining them, have found on examination that the male and female pronuclei were still far apart.

No "segmentation nucleus" is formed, *i.e.*, the male and female pronuclei do not fuse before the appearance of the karyokinetic spindle which introduces the first cleavage. In fact, the male and female chromatin loops remain separate until the equatorial plate stage of the first spindle. About the stage shown in Fig. 2, however, the chromatin loops form a continuous plate; though the part of the plate lying beneath the polar bodies (the upper side in the figure) probably came from the female pronucleus, while the other portion (the lower half) came from the male pronucleus. The axis of the spindle lies in the long diameter of the protoplasmic area, or rather the protoplasmic area continually enlarges its diameter in the direction of the axis of the spindle from the time the spindle first appears until the first cleavage is completed. The radiations of the archoplasmic bodies at the poles of the spindle are plainly visible in all the surface views, and a large central corpuscle or centrosome can be seen in the most favorable preparations. After the chromatin is distributed equally to the two poles of the spindle the division of the cell body begins. A furrow first appears at the formative pole, and gradually extends until it forms a constriction all around the ovum, but deeper at the formative pole than elsewhere, Figs. 3 and 4. The cell body then divides into two equal portions *AB* and *CD*, Figs. 5 and 6. These blastomeres are at first nearly spherical,

and touch each other only by a comparatively small surface ; later they become much more closely pressed together, and the surface by which they are in contact becomes much larger, so that each of the blastomeres is almost a hemisphere, Fig. 7.

Immediately after the division of the nucleus the archoplasmic bodies, Figs. 5 and 6, begin to increase in size and to become much more definite in outline. Each one lies close beside the nucleus in the position of the pole of the preceding spindle, and in surface preparations looks as if it might be the shadow of the nucleus. My attention was first called to these bodies by finding what I supposed to be two nuclei in each cell, one of which was fainter in color and outline than the other and looked as if it might be at a lower level in the egg, and it was some time before I could bring myself to believe that these bodies, which are so plainly visible even in preparations of the whole egg, and which in many cases are fully as large as the nuclei themselves, were nothing other than the "archoplasmic bodies" of Boveri or the "spheres attractive" of van Beneden.¹

A careful study of one of these bodies in its resting stage shows that it is a clear vesicular structure, containing apparently a finely granular fluid and having a fairly definite outline from which radiations proceed in every direction, Figs. 5, 6, 8, 10, etc. As it begins to divide, however, preparatory to the formation of the karyokinetic spindle, the definite outline of the body grows fainter and fainter until it cannot be recognized, while the radiations extend much further through the protoplasm of the cell.

At the close of the first cleavage, the nuclei, asters, and protoplasmic areas lie directly opposite each other in the two blastomeres, Fig. 5, but as soon as the blastomeres begin to flatten against each other and the whole egg assumes a more compact form all these structures move in the direction of a clock's hands, as shown in Fig. 6. *This movement of the nuclei, asters, and protoplasm takes place invariably in the same direc-*

¹ I shall throughout this paper call these bodies the *asters*, a name first used in this connection by Fol ('73) to signify the radiating cytoplasmic structure within the cell.

tion, and it must therefore have been predetermined during, and perhaps before, the first cleavage.

I have not been able thus far to discover by what means or in what manner this movement is predetermined. In *Crepidula* the first spindle does not seem to indicate any such rotation, though it is exceedingly suggestive to note that Warneck ('50) in the case of *Limax* and Fol ('75) in *Cymbulia* found that the first cleavage was oblique to the axis of elongation of the egg. Kofoid ('95) however, in his recent careful work on *Limax*, found no evidence in favor of Warneck's account. In some cases in which the first cleavage is very unequal, as *e.g.*, in *Urosalpinx*, the plane of the first cleavage is oblique to the axis of elongation, and it may be that it is also oblique to the polar axis of the egg.

But however the direction of these movements may be predetermined, the fact that they are predetermined, at least during the period of the first cleavage, is a profoundly significant one, indicating as it does that *the first cleavage of the egg belongs to a series of "spiral" cleavages which for at least nine successive generations of cells are alternately dextrotropic and laeotropic.*

Strictly speaking the first cleavage could scarcely be called a *spiral* one, since there is but a single spindle which intersects the chief axis of the egg; and besides there is no definite cross axis to which the direction of this spindle can be referred. It is certain, however, that the dextrotropic turning of the nuclei and protoplasmic areas after the first cleavage is, on the one hand, causally related to their laeotropic turning during the second cleavage, and on the other hand it seems to be predetermined at least as early as the preceding cleavage. It is therefore highly probable that the first cleavage belongs in the same category with the succeeding spiral cleavages, though perhaps it would be more exact and less paradoxical to speak of it as *prospectively spiral and dextrotropic.*

These so-called "spiral" cleavages are always radially symmetrical.¹ A glance at Fig. 6 or 7 will show that the two blastomeres are not mirrored representatives of each other, *i.e.*,

¹ This subject is treated at length in the concluding section of this paper.

the egg is not bilaterally symmetrical with reference to the first cleavage plane, but it is radially symmetrical; the blastomeres are congruent antimeres, and the egg at this stage is a "one-rayed radiate," as Chun ('80) calls the Ctenophores. The radial symmetry of the egg prevails undisturbed from the time polarity is first established (p.39) until the primary mesoblast is formed (p.67). After this event the posterior half of the egg becomes more or less bilateral, while the anterior half remains radially symmetrical. Finally, at a relatively late stage the entire egg becomes bilateral.

The rotation of blastomeres in some of the later stages of cleavage has long been known and commented upon. So far as I can find Selenka ('81) first used the term *spiral* in this connection. He described in the polyclades a "laetropen oder λ -Spirale" in the formation of the first quartette of micromeres, and a "dextiotropen oder δ -Spirale" in the formation of the second quartette, but he did not apply either of these terms to the earlier or later cleavages. Lang ('84) first called attention to the fact that the *second cleavage* in *Discocoelis* takes place in a "left-wound spiral." Since then this same fact has been observed in the case of many other animals (cf. Conklin ('91), Wilson ('92), Heymons ('93), Lillie ('95), *et al.*), and, with one or two exceptions which will be described later, the direction of this cleavage is invariably the same.

Up to the present, however, no one has shown that the *first cleavage* also is a spiral one. In all other works on this subject, so far as I am aware, it is asserted that the position of the spindles during the second cleavage is the first indication of spiral cleavages (see Wilson ('92), pp. 387, 453, Heymons ('93), p. 249, Lillie ('95), pp. 14, 15).

I believe, however, it may be safely asserted that in all cases in which the second cleavage is laetotropic the first is dextiotropic, and that the initial cause of the spiral cleavages is not to be found in the direction of the nuclear spindles, but rather in the structure of the unsegmented egg itself.

2. *The Second Cleavage. Figs. 7-10.*

The spindles usually appear simultaneously in the two blastomeres, Figs. 7, 9, though occasionally earlier in one than the other, as shown in Fig. 8. The axes of the two spindles are almost parallel to each other, and at right angles to that of the preceding spindle. The two spindles are not quite parallel, however, as is shown in Fig. 7, where the spindles are laeotropic, the left pole in each case being at a higher level in the egg than the right one. Thus the axes of the spindles, when viewed from the side, cross each other at a slight angle. It will also be noticed in Fig. 7 that the entire spindle in each blastomere lies somewhat to the left of the median plane of the blastomere. The position and direction of the spindles in this case indicate, before the division occurs, that the cleavage will be laeotropic. The spiral character of the preceding cleavage could be observed only after the division had occurred.

The first cleavage furrow is at first a straight line as seen from the animal pole, Fig. 6, but as the second cleavage comes on, this line becomes bent slightly to the right when placed in the line of vision, Figs. 7, 9. From the angles where this bent portion joins the rest of the first furrow, the two halves of the second cleavage run outward toward the periphery, Figs. 9, 10. The second cleavage really consists of two quite independent furrows; their ends never meet at the centre, and one of them may appear somewhat earlier than the other, Fig. 8. These furrows begin to form near the animal pole and run out around and through the blastomeres until they reach the vegetal pole, completely dividing the two blastomeres into four, which are approximately equal in size.

3. *The Origin and Significance of the Polar Furrows. Figs. 7-12, Diagram 2.*

The bent portion of the first furrow included between the central ends of the second cleavage is a feature of considerable practical as well as theoretical importance. It is a well-known fact that there is, in the eggs of many animals, a furrow at the intersection of the first and second cleavage planes, which does

not lie in either of these planes, but is oblique to both of them. Rabl ('79) calls this in Planorbis the "cross" or transverse furrow ("Querfurche"), indicating thereby that it lies transverse to the long axis of the embryo. Blochmann ('81) also mentions this furrow as being present in the egg of Neritina, and describes the method of its origin. He calls attention to the fact that it lies in the transverse plane of the embryo; and he considers that it is caused by the difference in the time of division of the two cells. But that this is not generally the case, is shown by the fact that it is present in many eggs in which the division of the first two blastomeres occurs simultaneously. Rauber ('82) has described at some length a similar furrow, which is found in the frog's ovum, as well as in Petromyzon and Gobius. He calls it the breaking line ("Brechungslinie"), and says that it may be formed in two ways: (1) the second furrow really consists of two furrows, one of which divides one of the first two blastomeres, the other the other one; these two furrows may or may not meet in the centre; in the latter case the breaking line is formed; (2) if a breaking line is not formed at first, it may appear later by the shifting of the blastomeres. While Rauber considers that the position of the breaking line has an influence on the subsequent cleavage, he regards its position relative to the other furrows or to the embryonic axes as purely a matter of chance. As he points out, it is particularly well marked in the four-cell stage of many ova; at this stage there are often two "cross furrows" on opposite sides of the egg; these are at right angles to each other, so that each of the four cells is acute at one pole and truncated at the other. O. Hertwig ('80) has also called attention to this furrow in the egg of Sagitta. He says of it: "An dem animalen Pole des Eies, welcher gerade abgebildet ist, stossen nicht alle vier Zellen, wie es bei regelmässiger Furchung der Fall sein sollte, in einem Punkte zusammen, sondern nur zwei derselben berühren sich mit verbreiterten Enden und bedingen eine kurze gerade Furche, welcher wir ihrer Lage nach als *Polarfurche* benennen wollen; die beiden anderen Zellen, welche von der gegenseitigen Berührung ausgeschlossen sind, enden zugespitzt an den beiden

Enden der Polarfurche. Ganz dieselben Verhältnisse wiederholen sich am vegetativen Pole; nur treffen sich hier die beiden Zellen, welche den animalen Pol nicht erreichten, mit verbreiterten Enden. Sie bilden eine *vegetative Polarfurche*, welche die animale, wenn wir beide auf dieselbe Ebene projiciren, unter rechtem Winkel kreuzt, wie man beim Wechseln der Einstellung an dem durchsichtigen Object leicht feststellen kann. . . . Eine ähnliche Anordnung der vier ersten Furchungszellen wie bei *Sagitta* hat soeben auch Rabl an den Eiern von *Planorbis* genau beschrieben, er nennt die Polarfurche Querfurche und bemerkt hierzu, dass sie einen wichtigen Anhaltspunkt für die Orientirung des Keimes abgiebt."

In all holoblastic eggs which are laden with yolk the polar furrow at the vegetal pole is much longer than the one at the animal pole, — in fact, the latter may be absent altogether, as is the case with *Crepidula*. In using the expression "polar furrow" in connection with this animal, it must be understood to refer only to that structure which Hertwig calls "vegetative Polarfurche." As just remarked, the name "Querfurche" seems to have been given in the belief that this furrow is always transverse to the antero-posterior axis of the embryo, as it is in *Planorbis* and *Neritina*, and as I have found is the case in *Urosalpinx* and *Tritia*. If one may judge from the figures alone this seems to be its position in *Nassa* and *Fusus*, as described by Bobretzky ('77), and in *Vermetus*, studied by Salensky ('87). In all forms, however, in which the first cleavage coincides with the antero-posterior axis, or is at right angles to it, the furrow in question could not be transverse to that axis, but would necessarily be oblique to it; this is its position in *Nereis*, *Umbrella*, and *Crepidula*. In such cases the name "cross furrow" is evidently a misnomer. The furrow bears no constant relation to the axes of the embryo, being at one time transverse and at another oblique to the longitudinal axis; and it is just as illogical to name this furrow from its relation to the axes of the embryo as it would be to name the first cleavage from such a relation, which in some animals coincides with the antero-posterior axis, in others is at right angles to it, and in still others is oblique to it.

There are also objections to the word "Brechungslinie," proposed by Rauber; it is not a breaking line, nor a broken portion of a line, and the name indicates nothing with regard to its position. Moreover the fact that the "Brechungslinie" is not constant in position indicates that it is not the result of a determinate series of spiral cleavages, as is the case among annelids and mollusks, but that it is merely a "pressure surface," the result of surface tension, and it therefore has no reference to the character of the cleavage, which might be radial or bilateral or neither. This term, therefore, even if unobjectionable for the purpose for which it was employed by Rauber, ought not to be applied to the furrow in question.

The expression "polar furrow," however, is open to none of the objections mentioned; this furrow is found only at the two poles of the egg, and so far as the name is descriptive at all, it is quite accurate. I shall, therefore, use it exclusively hereafter to designate that portion of the first furrow which lies between the central ends of the second furrow, both at the animal and vegetal poles. Although always and entirely a part of the first furrow, it seems to lie in, and form a part of, both the first and second furrows.

Although in different animals the polar furrow may bear no constant relation to the embryonal axes, it does in all known cases of spiral cleavage bear a very constant relation to the first and second cleavages. In *Crepidula*, for example, if the first furrow be placed in the line of vision, the polar furrow always bends to the right, in the second furrow it bends to the left, and this is true whichever end of the furrow is nearer the observer. These relations are true only when the egg is viewed from the animal pole; obviously they would be reversed if seen from the vegetal pole, *i.e.*, the polar furrow would bend to the left when in the first furrow and to the right when in the second. This relation is of great practical importance, since it enables one to distinguish at a glance the first furrow from the second, even up to an advanced stage, and it thus forms a ready means of orientation. In Fig. 10 and all succeeding stages it is impossible to distinguish between the first and second furrows except in this way; in Figs. 8 and 9, how-

ever, the second cleavage is not yet complete, and can, therefore, be easily distinguished from the first, and in the ova which are there figured, as well as in hundreds of others which I have studied, the relation of the polar furrows to the first and second cleavages is always the same.

Similar furrows are shown and described in the works of very many authors, and indeed in the ova of almost every group of animals; but in most cases no mention is made of any definite relation between these furrows and the first and second cleavage planes. In the frog, according to Rauber ('82), this furrow bears no constant relation to the first two cleavages, and Eycleshymer ('95) seems to have found the same thing true of *Amblystoma*, *Petromyzon*, and *Corregonus*. But in a very large number of animals, belonging to groups as far removed from each other as mollusks, annelids, and polyclades, the relation between the polar furrow and the first and second cleavages is a constant one. In Blochmann's figures of the egg of *Neritina*, and in Lang's figures of *Discocoelis*, the polar furrow is shown bending to the right in the first cleavage (the position which it has in *Crepidula*), though neither of these investigators calls attention to this fact in the text or description of figures.¹ The same fact is further shown and commented on by Wilson ('92) in the case of *Nereis*, Heymons ('93) in *Umbrella*, and Lillie ('95) in *Unio*. A very striking exception to this rule has been discovered by Crampton ('94) in the case of *Physa*, a sinistral gasteropod, in which the direction of the polar furrow is reversed, and he points out the fact that the figures which Rabl ('79) gives for *Planorbis*, and a figure given by Haddon ('82) for *Janthina*, seem to show a similar reversal. So far as I know these are the only cases on record in which the polar furrow constantly turns to the left when seen in the first furrow, whereas in *many* cases, as I have indicated, it constantly turns to the right.²

¹ One figure which Blochmann gives, Fig. 40, corresponds very closely with my Figs. 9 and 10; the second furrow is still incomplete, and two of the macromeres are much more obtuse at the centre than the other two. The polar furrow thus formed bends to the right in the first furrow just as it does in *Crepidula*.

² Since this was written Kofoid's final paper on *Limax* ('95) has appeared, in which he thoroughly discusses the "cross furrows," especially the relation of the

A phenomenon so widespread and so striking cannot be wholly adventitious and without significance. As we have seen, Blochmann explains the formation of the polar furrow in *Neritina* by the fact that one of the first two blastomeres divides before the other one. This would not explain the constant relation of the polar furrow to the first and second cleavages unless in all the groups mentioned one blastomere divided earlier than the other one, and this of course is not the case.

Rauber ('82) attributes the formation of the "Brechungslinie" to a tendency on the part of all the furrows to avoid the pole. This, of course, is not true of the first furrow, and in any case it is no explanation of the phenomenon. Jordan and Eycleshymer ('94) are right when they say (p. 412), "The furrows do not *avoid* the pole; but the mechanical cell-stresses are rarely so adjusted that the furrows intersect at the pole. There seems no need for a special term—'Polflucht'—to express this fact, since the 'shunning' of the pole can hardly be a matter of primary significance." But while surface tension is a sufficient causal explanation of such pressure surfaces as the "Brechungslinie," this principle alone is not able to explain the *constant* position of the polar furrow with reference to the first two cleavages, and this constant position is a matter of primary significance.

In his classical work on *Nereis*, Wilson ('92) has carefully described the polar furrows, and has pointed out the fact that they are of great value in the orientation of the egg and embryo.¹ The position of these furrows is precisely the same in *Nereis* and *Crepidula*, except that there is a short polar furrow at the upper pole in *Nereis* which is generally wanting in *Crepidula*. In the last section of his paper Wilson points out the significance of the "cross furrow," and although he does not directly explain the cause of its constant relation to

ones on the dorsal and ventral sides of the egg. As my account is in substantial agreement with Kofoid's, and as it touches upon a few points not mentioned by him, I have allowed it to stand as first written.

¹ I had earlier ('91) called attention to the fact that the polar furrow bears a constant relation to the first two cleavages, but had attempted no explanation of this fact.

the first two cleavages, yet that explanation lies so near the surface that I should not take the trouble to enter upon that subject here were it not for the fact that I have a few suggestions to make which are not found in his work.

The polar furrows are in all cases the result of spiral cleavages, and the direction of the polar furrows relative to the first and second cleavages is always dependent upon the direction of the spirals. Because the second cleavage is laeotropic, the vegetative polar furrow bends to the right in the first cleavage and to the left in the second; in *Physa*, in which the direction of the spirals is reversed, the direction of the polar furrows is reversed.

The cause of these relations can be made plain by means of the accompanying diagram. In Diagram 2, *a*, the macromeres B and D lie at a slightly lower level than A and C, and have given off A and C by a laeotropic division. It is seen in this figure that there is but one polar furrow, and that it turns to the right when seen in the first furrow, and to the left when seen in the second. This is the state of affairs which prevails in *Crepidula*, *Neritina*, *Umbrella*, *Urosalpinx*, etc. Let us suppose, however, that the passage from the two to the four-cell stage had taken place in the reverse direction as it does in *Physa*, and as is shown in Diagram 2, *b*, where A and C lie at a somewhat lower level than B and D, and have given off the latter by a dexiotropic division. There is here but one polar furrow, and when seen in the first furrow it turns to the *left*; when in the second furrow, to the *right*. It is evident, therefore, in all those cases where there is but one polar furrow which turns to the right when seen in the first furrow, and to the left when seen in the second, that the second cleavage was laeotropic.

As a rule when there is but one polar furrow, it is somewhat shorter at the formative than at the vegetative pole, Diagram 2, *c*. Yet as an extreme case there are found ova in which the single polar furrow is almost equal in length at the two poles; this is admirably illustrated by the egg of *C. convexa*, Diagram 2, *a*, which is laden with a large quantity of yolk, and in which the macromeres A and C, while lying at a slightly higher level than

B and D, are somewhat smaller in size, while the single polar furrow remains almost as long at the animal as at the vegetal pole. In the egg of *C. fornicata*, which contains less yolk,

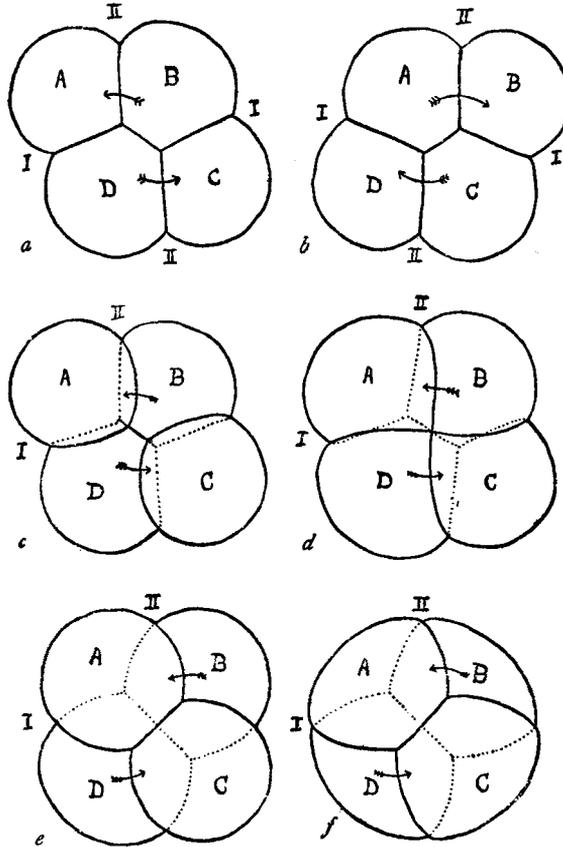


DIAGRAM 2.—Polar furrows of spiral cleavage.—*a*, The condition in eggs with much yolk (*C. adunca*), in which the polar furrow is as long at one pole as at the other.—*b*, The position of the polar furrow in reversed cleavage.—*c*, The condition in eggs with a smaller amount of yolk (*C. fornicata*), in which the cells A and C lie at a higher level than B and D, and the polar furrow is shorter at the animal than at the vegetal pole.—*d*, Egg with a still smaller amount of yolk (*C. plana*), in which the four macromeres meet in a point at the animal pole; there is but one polar furrow, the vegetal.—*e*, Egg of *Discocoelis* (Lang), in which there are two polar furrows of nearly the same length.—*f*, Egg of *Botryllus*; polar furrows similar to the last, but whole egg more compact.

and which is represented in Diagram 2, *c*, the relation of the blastomeres to each other is in the main the same as in Diagram 2, *a*, still the macromeres A and C overlie B and D to a greater extent than in the preceding diagram, and there-

fore the polar furrow, while running in the same direction at both poles, is distinctly shorter at the animal than at the vegetal pole. Diagram 2, *d*, represents the condition of the polar furrow in *C. plana*; it shows that in this egg, which has less yolk than that of *C. fornicata*, the blastomeres A and C overlie B and D still more than in the case last mentioned, and that they meet in a *point* at the animal pole. There is here no polar furrow at all at the animal pole, though the one at the vegetal pole is well developed. In Diagram 2, *e*, which is a diagrammatic representation of the egg of *Discocoelis* as described by Lang, the macromeres A and C not only overlie B and D, but they meet in a line, which forms a polar furrow at the animal pole lying at right angles to the one at the vegetal pole. These furrows may or may not be equal in length; generally the one at the animal pole is the shorter, though Lillie has found that it is the longer in *Unio*, which is due to the fact that in this case the cells at the animal pole are larger than those at the vegetal. Finally, in Diagram 2, *f*, which represents the egg of *Botryllus*, we find the greatest degree of compactness of the blastomeres; the polar furrows at the upper and lower poles are nearly equal in length, and the individual blastomeres no longer preserve independence of outline, but are rounded into a nearly perfect sphere. Two or more of these different forms may be found at different stages in the cleavage of the same egg. At the moment of cleavage the blastomeres are generally more independent and less compact than during the "resting stages" between cleavages. Thus in many ova the blastomeres at the moment of cleavage are like those represented in Diagram 2, *e*, while during the "resting period" they become much more compact, like those shown in Diagram 2, *f*.

Two types of ova are represented in the diagram given above, one in which there is scarcely any polar differentiation, the other in which it is well pronounced. The former is represented by figures *e* and *f*, and in such cleavage forms polar concentration of protoplasm and nuclei is impossible, the nuclei in fact lie near the centres of the blastomeres and the yolk is uniformly distributed throughout the protoplasm; the latter type is represented

by figures *a* to *d* in which the polar concentration of protoplasm and nuclei is very marked. In all eggs in which there is but one polar furrow there is decided polar differentiation of the yolk and protoplasm; where two polar furrows are present this segregation is less pronounced.

The statement that the polar furrow turns to the right when seen in the plane of the first cleavage is true only when there is one polar furrow, and that the one at the lower pole. When there are two polar furrows, as in Diagram 2, *e* and *f*, the lower one still preserves this same relation when seen from the animal pole, while the upper one bends to the *left* when seen in the first furrow, and to the *right* when seen in the second. Of course, if these were viewed from the vegetal pole, the relations would be reversed.

The fact that in very many cases the first cleavage is dextrotropic and the second cleavage laeotropic is a profoundly important and significant one, determining as it does, not only the direction and relation of the polar furrows, but *also influencing more or less the character and direction of every succeeding cleavage. They are the first of a long series of spiral cleavages which take place alternately to the right and to the left, each of which, except the first, finds the sufficient cause of its direction in the direction of the preceding cleavage.*

4. *The Axial Relations of the First Two Cleavages.*

Throughout the course of segmentation the four macromeres remain very much larger than the cells to which they give rise, and as they do not change their relative position, at least until about the time of the closure of the blastopore, it becomes very easy to orient all the future furrows and cells with reference to the first two cleavages. If we examine one of the later stages, such as Figs. 61 and 64, in which the antero-posterior axis of the embryo is well marked by the elongated blastopore, we find that the four macromeres and the polar furrow are still recognizable, and that the cleavage line in which the polar furrow bends to the right, *i.e.*, the first cleavage, is transverse to the antero-posterior axis of the

embryo, and therefore when first formed divided the ovum into an anterior and a posterior half; while the second furrow, the one in which the polar furrow bends to the left, coincides with the median plane of the embryo, and hence divided the first two blastomeres into two right and two left macromeres.¹ While it is thus easy to determine from the earliest appearance of the first cleavage what the antero-posterior axis of the future embryo is to be, it is not possible to distinguish the anterior end from the posterior until the stage with twenty ectoderm cells, Fig. 22, when the mesentoblast is formed. A similar relation of the first cleavage plane to the embryonic axes is also found in *Teredo* (Hatschek, '80), *Umbrella* (Heymons, '93), and *Nereis* (Wilson, '92). In *Crepidula* I believe it has no causal relation to the bilateral symmetry of the embryo. The egg itself is not bilateral with respect to the first or second cleavage plane, as has been pointed out (p.), but is from the first up to the time when the mesentoblast is formed radially symmetrical. So far as the entoderm cells are concerned, the second furrow lies nearly in the median plane of the bilateral embryo, and the first furrow nearly at right angles to this; but among the ectoderm and mesoderm cells such shiftings of position occur that the final plane of bilateral symmetry in no way corresponds with either of the first two cleavage planes. This conclusion will be treated more fully after the facts upon which it is based have been taken up in their regular order.

II. THE SEGREGATION OF THE ECTOBLAST.

I. *Formation of the First Quartette of Micromeres.* Figs. 12, 13, Diagram 3 (p. 60).

The third cleavage separates four protoplasmic micromeres from the four yolk-containing macromeres. The karyokinetic

¹ It will be seen that in all the figures except those of the first plate the first furrow runs from right to left on the plate; for the sake of appearance merely, the figures of the first plate are arranged so that the first furrow runs up and down. In the first plate, therefore, the antero-posterior axis runs from right to left as the figures are arranged on the page, while in all the other plates it runs up and down.