

It will be seen at once that both Blochmann and Kofoid fail to identify the cells of the third quartette with the corners of the ectoblastic plate, and consequently mislabel the whole of the belt, carrying the proper designations one cell too far to the right in the one case, and one cell too far to the left in the other. This proposed correction of Blochmann's account and of Kofoid's modification is further supported by a figure of the egg of *Neritina* of this same stage, given by Bütschli ('77), Pl. XVII, Fig. 3a, in which the position of the cells plainly shows that the angles of the ectoblastic plate are formed by the third quartette, while the two cells on each side between the angles have evidently come by division from a single cell.

With this slight modification of Blochmann's account *Neritina* is made to agree in the matter of the belt cells with *Nereis*, *Umbrella*, *Limax*, *Unio*, four species of *Crepidula*, *Urosalpinx*, *Fulgur*, *Sycotypus*, and *Illyonassa*, and at the same time Blochmann's statement as to the derivation of the "Urvelarzellen" is confirmed, and Kofoid's contention for the alternation of cleavages is satisfied.

III. THE SEGREGATION OF THE MESOBLAST AND ENTOBLAST.

1. *Formation of the Mesentoblast. Figs. 21, 22, Diagram 4 (p. 60).*

At the stage just described, with twenty micromeres and four macromeres, the left posterior macromere divides in a laeotropic direction, as shown in Fig. 21. The cell thus formed is very much larger than any of the micromeres, and, unlike them, contains a considerable quantity of yolk. This cell, although formed by a laeotropic division, remains in nearly the same position in which it was first separated from the macromere until a much later stage, Fig. 33. Like the belt cells it is partly overlapped by the micromeres which lie nearer the apical pole, but a considerable part of it is exposed on the surface. In a strict use of the term, therefore, it cannot be said at this stage to form the *middle layer* any more than the belt cells form a middle layer. In fact, it is neither a "layer" nor is it "middle," and yet from a part of this cell most of the

mesoblast is developed. Since this cell gives rise to the posterior part of the alimentary canal as well as to the mesoblast, I shall call it the *mesentoblast*, ME (= 4d).

Soon after its formation it divides, as shown in Fig. 25, into right and left halves, ME¹ and ME²; this division is dextro-tropic, as is shown by the fact that the right half overlaps the left, Figs. 26 and 27. These cells remain for some time in the position in which they are formed; they lie to the right of the future median plane, which is marked by the second cleavage furrow, and are more nearly symmetrical with reference to the ectoblastic plate than to the macromeres, Figs. 26, 29, 30. The next cleavage of these cells, Fig. 30, leads to the formation of

2. *The Primary Enteroblasts. Figs. 30, 31.*

The spindles which introduce this division are bilaterally symmetrical with reference to the line along which the two cells are in contact; anteriorly the spindles diverge from this line and at the same time slant upward, so that the cells which are given off anteriorly lie at a higher level than the posterior moieties, Fig. 31. These anterior cells are about equal in size to the posterior ones, but contain less yolk. The posterior cells are the *primary enteroblasts*, and together with two other cells, to be described in a moment, give rise to the posterior or distal end of the intestine. They are purely entoblastic, and do not divide again until about the time of the closure of the blastopore. The anterior cells are still of mixed character, containing both mesoblast and entoblast.

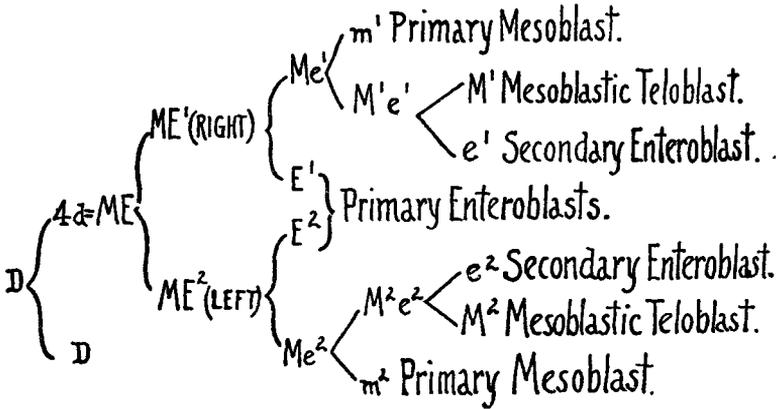
Up to the last cleavage there had not been a single bilateral division; even in the formation of the mesentoblast and its division into right and left halves, all the cleavages were spiral. But with the division of the right and left mesentoblasts, by which the primary enteroblasts are cut off posteriorly, bilateral cleavages suddenly appear. All subsequent divisions of the mesoblast, as far as I have been able to follow them, are bilateral. In the ectoblast and entoblast, however, bilaterality appears very gradually, and is not prominent until a very late period.

3. *The Primary Mesoblasts. Figs. 32-39.*

The two anterior cells resulting from the preceding division are still mesentoblasts, and the mesoblastic and entoblastic substances in these cells are not completely separated until after two more purely bilateral divisions. The first of these divisions, Fig. 32, occurs immediately after the formation of the primary enteroblasts, and gives rise to two small cells, m^1 and m^2 , Figs. 33, 35, 36, which are the *primary mesoblasts*, *i.e.*, they are the first purely mesoblastic cells formed. They are not, however, strange as it may seem, the "pole cells" of the mesoblast; they or their derivatives form the *anterior* or distal end of the mesoblastic bands, and not the *posterior*, growing end. The two posterior products of this division, M^1e^1 and M^2e^2 , still contain both mesoblast and entoblast. Finally, by another division of these two cells, Fig. 41, the mesoblast and entoblast are completely separated. This division is also purely bilateral, and results in the formation of the *mesoblastic teloblasts*, M^1 and M^2 , Figs. 42 *et seq.*, and the *secondary enteroblasts*, e^1 and e^2 . The latter cells lie in front of and overlap the primary enteroblasts, E^1 and E^2 , and like these they are in contact with each other along the mid line. The mesoblastic teloblasts lie laterally to the secondary enteroblasts, and are far removed from each other, Figs. 42 *et seq.* Counting from the formation of the mesentoblast, 4d (the primary mesoblast of most authors), it has taken eight cell divisions to bring about the complete segregation of the mesoblast and entoblast in this region of the egg. This can be seen at a glance in the table of the lineage of 4d on the following page.

It is at once apparent from this table that there is a very intimate connection, at least in origin, between the mesoblast and the entoblast. The cell 4d seems to contain all the mesoblastic substance which was originally present in the macromere D; but it also contains a considerable amount of entoblastic substance, less than half the cell being destined to form mesoblast. The separation of the mesoblastic and entoblastic substances in this cell begins by the formation of the primary enteroblasts, E^1 and E^2 , on the posterior side of the

two cells into which 4d divides, and is further continued by the separation of the primary mesoblasts, m^1 and m^2 , on the anterior side. At this stage there are three cells on each side derived from 4d: the primary enteroblast behind, the primary mesoblast in front, and a mesentoblast cell in the middle, Figs. 33-41. Finally the segregation is completed by the division of the middle cell of the three into a secondary enteroblast behind, and a mesoblastic teloblast in front, Fig. 41. This final separation of the mesoblast from the enteroblast does not occur until there are sixty-five cells present, of which eight cells are the progeny of 4d. Of these eight cells four are entero-



blasts and four are mesoblasts, and the latter are almost immediately increased to six by the division of the two primary mesoblasts, m^1 and m^2 , Fig. 42. The mesoblast cells form a short band, one on each side, which extends forward almost parallel with the edge of the ectoblastic plate, but entirely covered by ectoblast cells; the enteroblasts are but partially covered by ectoblast until a relatively late stage. The mesoblast cells are further characterized by containing no yolk, while both pairs of enteroblasts contain a considerable number of yolk spherules.

This method of the separation of the mesoblast is, I believe, unique, and I should be inclined on that account to doubt the correctness of the description here given were it not for the fact that I have followed the lineage of the cell 4d with the

greatest care throughout the stages shown in the table above, and in Figs. 22-41 in the plates; and beyond this stage I have traced the enteroblasts and the mesoblastic teloblasts step by step, until the latter give rise to the mesoblastic bands extending half way around the egg, Figs. 49, 51, 53, and the former apparently become the distal portion of the intestine, Figs. 61, 65, 68.

Owing to difficulty in tracing these cells I was not able to work out their history satisfactorily for a long time. Consequently in both of my previous papers on this subject ('91 and '92) I described the cell 4d as the primary mesoblast, feeling assured that it was this because it gave rise to mesoblastic bands. It was not until I had taken up the later history of the entoblast and the formation of the alimentary canal, that I found that the two proximal (originally posterior) cells in each band were the first intestinal cells, and that therefore the cell 4d contained both mesoblast and entoblast.

So far as I know, but two other cases at all similar to this are said to occur among Mollusca. In *Patella*, Patten ('86) has described two "entomesoblast" cells, which lie one on each side of the four large cells at the vegetal pole. These large cells are entoblastic, and probably correspond to the four macromeres present in many other forms. The entomesoblasts appear at the blastula stage, and after elongating into the cavity of the blastula, each cuts off a large cell at its inner end, which is the mesoblastic teloblast; the outer part of each cell is entoblast.

The other case is given by Stauffacher ('93) for *Cyclas cornea*. In this animal the formation of the mesoblast is similar to the process in *Patella*, except that the two mesentoblasts are in contact along the mid line as they are in *Crepidula*, whereas they are said to be separated by the four macromeres in *Patella*. In both these cases, however, the resemblance to *Crepidula* extends no farther than the formation of paired mesentoblast cells, and even in this regard the resemblance is more apparent than real.

In the formation and subsequent divisions of the cell 4d, *Umbrella* is strikingly like *Crepidula*. This resemblance is

of 4d up to a very late stage, and with such accuracy of detail that one can scarcely doubt the soundness of his conclusions. In fact, his results have led me seriously to doubt the correctness of my own interpretations; but after a careful reëxamination of my preparations and drawings, I am unable to reach any other conclusion than that already given. I cannot say that I have actually observed the cells which I have called the enteroblasts going into the formation of the intestine. The last stage in which they could be identified beyond any doubt is shown in Fig. 65, and between this stage and those shown in Figs. 68 and 76 there is more or less discontinuity. Still I believe that the evidence is clearly in favor of the view which I have advanced. The enteroblasts E^1, E^2, e^1, e^2 are not only in exactly the right position to form the distal end of the intestine, but they differ in histological character from the mesoblast cells, and closely resemble the entoblasts in that they contain a number of yolk spherules; besides in all the later stages the large cells which I have called the mesoblastic teloblasts, M^1 and M^2 , are plainly visible lying at the posterior ends of the rather indistinct mesoblastic bands. These cells are frequently seen dividing, but during all the time that the mesoblastic bands are forming, the enteroblasts never divide, which is, I think, pretty good evidence that they are not the mesoblastic teloblasts.

In Heymons' figures of the later stages (see his Figs. 29 and 30), the position and appearance of the mesoblastic teloblasts is so similar to the corresponding cells in *Crepidula*, that one can scarcely doubt that they are homologous cells. However, between the two teloblasts in *Umbrella* is a group of small cells, which, from their position, should correspond to the enteroblasts of *Crepidula*, but which seem to be very different in origin and history from these cells. Of this group of cells Heymons says, p. 281: "Zwischen den beiden aus einander gewichenen Urmesodermzellen befindet sich eine Anzahl von 4-6 kleineren Mesodermzellen. Dieselben entsprechen der Zellgruppe, an deren Bildung die zuerst entstandenen kleinen Mesodermzellen *m m* Antheil nahmen. Letztere sind jetzt allerdings nicht mehr als solche herauszufinden.

Die erwähnte Zellgruppe liegt in der Medianlinie am Hinterende der Schalendrüseneinstülpung." In short, this group of cells lying between the teloblasts in *Umbrella*, corresponds in origin to the most anterior derivatives of 4d in *Crepidula*, which ultimately lie at the anterior ends of the mesoblastic bands; the cells which lie between the teloblasts in *Crepidula* are the most posterior derivatives of 4d.

Von Wistinghausen ('91), Wilson ('92), and Lillie have observed that a number of small cells are budded off on the surface of the primary mesoblasts in *Nereis* and *Unio*. Wilson says that these small cells later wander into the cleavage cavity and form "secondary mesoblast," and Lillie believes that the same thing happens in *Unio*. It is to be observed that the enteroblasts of *Crepidula* are, for a long time, uncovered by the ectoblast cells, and that they apparently lie in the layer of ectoblast, and in this regard resemble the small cells described by the authors just mentioned. It is scarcely possible that those small cells are homologous with the enteroblasts in *Crepidula*, but it is sufficiently obvious that in many cases the history of the so-called "primary mesoblast" has not been followed far enough to determine whether it gives rise to anything else besides mesoblast. If a cell arises in the proper place on the posterior side of an egg, and gives rise to a row or band of cells, it is generally supposed to be sufficient ground for calling it the primary mesoblast. I believe that the so-called "primary mesoblast" of many other gasteropods would be found to contain both entoblast and mesoblast if its later history were carefully followed.¹

In *Planorbis* and *Umbrella* the cell 4d arises at the 24-cell stage, as it does in *Crepidula*; in *Unio* it appears when 32 cells are present; in *Neritina* at the 36-cell stage; in *Nereis* at the 38-cell stage; while in *Limax* it is not separated until the 64-cell stage. This apparent difference in the time of its formation is due chiefly to the fact that in some cases the ecto-

¹Blochmann's Figs. 62 and 63 for *Neritina* show two mesoblast bands of two cells each, and between them anteriorly a number of small entoblast cells, some of them closely connected with the mesoblast. These entoblast cells are of doubtful origin, and it may be that they correspond to the enteroblast cells of *Crepidula*.

meres divide more rapidly than in others. But in all these cases the cell 4d is formed in the fourth quartette of cells separated from the macromeres. The essential likeness in origin of this cell in all these forms is thus clearly shown, though it arises at apparently different times in different eggs.

In addition to the mesoblast thus formed, which is bilateral and teloblastic in growth, three other mesoblast cells arise from the ectoblast in *Crepidula* at a much later stage. These cells, which correspond to the "larval mesoblast" of Unio (Lillie ('93), p. 570), appear in the quadrants A, C, and B, and give rise to the scattered mesoblast cells in the region of the blastopore, and at the anterior end of the embryo. The origin of these cells cannot be described satisfactorily until the later history of the ectoblast has been considered (see p. 149).

Although I do not propose in this section to take up the history of the different layers, yet it seems best here to describe the complete separation of the fourth quartette of cells to which 4d belongs.

4. *Completion of the Fourth Quartette and Rotation of the Ectoblast. Figs. 33, 34.*

A laeotropic division in the 24-cell stage separated the mesentoblast from the left posterior macromere; the corresponding divisions in the other macromeres are delayed until the stage with 49 cells, Figs. 33, 34. At this stage each of the macromeres, except the left posterior one, gives rise to a large yolk cell, 4a, 4b, and 4c, by a laeotropic division. The cells thus formed are a little larger and contain much more yolk than the mesentoblast 4d. They move around into the furrows between the macromeres, and ultimately take part in forming the ventral wall of the mesenteron.

No divisions corresponding to this are given for *Nereis* or *Unio*.¹ In *Limax* and *Planorbis* the cells 4a, 4b, 4c are separated at the same time with 4d; in *Umbrella* at about the same stage as in *Crepidula*; in *Neritina* two cells which seem to cor-

¹ Mead ('94) briefly mentions the fact that these divisions occur in *Amphitrite*, *Clymenella*, and *Lepidonotus*.

respond to 4a and 4c are formed almost immediately after 4d, and before the latter divides into right and left halves. At a later stage two other cells, designated by Blochmann en_a and en_a^1 , are supposed to have come from the macromere a (B of our system). In Blochmann's figures they are shown in the segmentation cavity, half way between the animal and vegetal poles. All of these cells, together with en_x , a small entoblast cell whose origin was not known, are shown in the figures¹ moving up through the space between the macromeres into the segmentation cavity on the upper side of the egg. It seems a very remarkable thing that entoblast cells should travel through the segmentation cavity in this way. So far as I know, nothing like it occurs in any other animal, and I find it hard to believe that Blochmann is right on this point. There are too many points of agreement between *Crepidula* and *Neritina* throughout the entire development to make probable the view that they are so wholly unlike in this one regard. Only one figure of the small entoblast cells given by Blochmann has a familiar appearance, and that is his Fig. 64, in which three small entoblast cells are shown at the vegetal pole in the positions occupied by 4a, 4b, and 4c in *Crepidula*.

These fourth-quartette entomeres were observed and figured by McMurrich ('86) for *Fulgur*, though he did not suspect their real nature. He says of them (p. 413): "On surface view three elongated elevations (Plate XXIV, Fig. 8) are seen radiating toward the centre of the blastodermic area, but not extending centrally farther than the edge of the area, and lying rather alternate with the macromeres than opposite them. What the significance of these elevations may be it is not easy to say, but sections through ova of this stage show them to be coincident with the first formation of the *mesoderm*. . . . If this interpretation of the sections be correct, it would seem that the macromere which does not show an elevation on surface view is the one which gives rise to the mesoderm, but what may be the cause of the formation of the elevations on the macro-

¹ In interpreting Blochmann's account of these smaller entoblast cells I have been compelled to rely largely upon his figures, since little mention is made of them in the text.

meres is to me quite uncertain. I think it safe to conclude that the mesoderm arises by a separation of protoplasm from *one* of the macromeres." I find that these elevations are the small yolk cells 4a, 4b, and 4c. They appear somewhat later than the cell 4d, just as is the case in *Crepidula*.

That these cells really belong to the same quartette as 4d is shown not only by their position and method of origin, but also by the fact that the macromere D does not divide again until a very late stage, and then in a series of divisions which affects each of the other macromeres and leads to the separation of a fifth quartette (5a-5d) from the macromeres. And that all the cells of the fourth quartette, like those of every other quartette, are really homodynamous, is strongly suggested by the fact that they are all yolk cells of about the same size, that they are chiefly entoblastic (4a, 4b, 4c entirely so, and 4d more than half), and that the points in which 4d differs from the other members of this quartette are probably due to the posterior elongation of the body and the origin of bilateral symmetry.¹

Since these fourth-quartette entomeres are smaller than any other cells of the inner layer except the enteroblasts, I shall call them the *smaller enteroblasts*. Like the mesentoblast, 4d, they are formed by a laeotropic division, and immediately after they are separated they begin to rotate in an anti-clockwise direction, until they come to lie in the furrows between the macromeres, and in this position they are carried around to the ventral side with the growth of the ectoblastic cap. At the same time that these cells rotate to the left all the derivatives of 4d also rotate in the same direction, and thus come to lie at the posterior end of the second furrow; and what is more remarkable, the whole ectoblastic cap is rotated with these cells through almost 45°. There is here furnished another evidence

¹ In a previous paper ('92) I called attention to the fact that the cell 4d is homodynamous with the other cells, 4a, 4b, and 4c of the fourth quartette. Heymons ('93), who reached the same conclusions in his work on *Umbrella*, curiously misinterprets me on this point. He says (p. 270): "Nach Conklin sollen dagegen die primären Darmzellen (the macromeres A, B, C, and D) in Ursprung und Lage den beiden Urmesodermzellen entsprechen, eine Ansicht, die ich für *Umbrella* entschieden zurückweisen muss." A reference to my paper will show that I there advanced exactly the view which was afterwards advocated by Heymons, and is still further elaborated in this paper.

that the micromeres are more firmly bound to each other than to the macromeres, and the explanation of this fact cannot be found in this case in the presence of a segmentation cavity, since this cavity has long before completely disappeared. Although it has not been mentioned before, it will be seen by consulting the figures that before this general rotation of the upper pole takes place (Fig. 33) the ectoblast on the posterior side of the egg has become bilaterally symmetrical. There is formed at the upper pole, as will be described later, a cross of ectoblast cells, the four arms of which lie nearly half way between the first and second furrows, and hence in the median planes of the macromeres. These arms at first consist of two cells each, Figs. 29, 30, but in the stage represented in Fig. 31, in all the arms except one the number of cells is increased to three; this one, which lies over the left posterior macomere, contains for a very considerable period only two cells. This is one of the first traces of a bilateral arrangement of the micromeres, though it soon becomes very well marked. In *C. adunca* bilateral symmetry does not appear in the ectoblast until still later, three cells being formed in the posterior arm of the cross as in each of the others. In the egg of this species, in which the larval history is most completely suppressed, and which might, therefore, be supposed to have adult characters impressed upon it at an earlier period than in eggs with a larval development, bilaterality appears later than in either of the other species.

Almost from the earliest appearance of the mesentoblast it is in itself bilaterally symmetrical. The divisions which lead to the formation of the primary enteroblasts and the primary mesoblasts are, as we have seen, typically bilateral, and their plane of symmetry very nearly coincides with that of the ectoblast cells.

Although the macromeres have from the first been radially symmetrical, as is shown by the presence of the polar furrow, yet the future plane of bilateral symmetry is well marked in them, since the first and second cleavage planes which separate them lie respectively in the transverse and median planes of the embryo; the plane of bilateral symmetry in the entoblast lies at an angle of nearly 45° with that of the ectoblast and

mesoblast, and it is not until the three smaller entoblasts are formed and the whole of the ectoblast has been rotated in an anti-clockwise direction that the planes of symmetry in the three layers come to coincide in the median plane of the future animal.¹ The bilateral symmetry which is to characterize the adult appears at different times and in different directions in each of the layers, and at a later period these planes, which have been diversely established, come to coincide in the chief axis of the developing organism. No better evidence could be desired to show that such forms of cleavage are coenogenetic, and that at the same time they are not the result of merely mechanical causes. *In cleavage, as in the entire ontogeny, one is impressed with the evident purposefulness of every event; the end seems to be in view from the beginning, and the building materials are sorted and arranged with reference to this end result.*

In this connection it is interesting to inquire into the causes which produced this rotation. There can be little doubt that it is due to the three smaller entoblasts, since at this time there is no apparent activity in any other part of the ovum. These cells are given off in a left spiral cleavage, and they lift the overlying ectoblast cells and turn them in an anti-clockwise direction until these three entoblasts lie in the furrows between the macromeres, and so the egg is left in as compact a form as possible.

Heymons ('93) has shown that an exactly similar rotation of the ectoblast takes place in Umbrella. The rotation occurs at the same time, in the same direction, and to the same extent as in Crepidula. Heymons also assigns the same cause which I have attributed both here and in my former paper ('92), *viz.*, the rotation of the small entoblasts into the furrows between the macromeres.

Fig. 33 seems to indicate that the primary enteroblasts, E' and E², were prevented from rotating into the furrow between D and C by the pressure of the overlying cells, for as soon as the latter are lifted by the formation of the smaller entoblasts

¹ It is not strictly true that the planes of symmetry in the three layers coincide after the rotation of the fourth quartette, though they are brought much nearer together by that rotation. Even in the stages immediately preceding the formation of the larva, Figs. 65-76, it can be seen that the apical cells of the ectoderm, *Ap.*, still lie to the right of the median plane in the entoderm.

the enteroblasts rotate into this position in advance of the ectoblastic cap. In such eggs as the one shown in Fig. 34 it is seen that the entoblastic derivatives of the cell 4d have rotated farther in an anti-clockwise direction than the overlying mesoblast and ectoblast. Although the cell 4d was formed at a much earlier period than the corresponding cells 4a, 4b, and 4c, it does not rotate until the latter cells are formed, when all rotate together, but at first only the lower or entoblastic derivatives of 4d join in this rotation. In this process the ectoblast is wholly passive, and the rotation of the smaller entoblasts seems to be the result of purely mechanical causes (*e.g.*, surface tension and consequent intercellular pressure); and yet these mechanical causes are governed and directed by the higher coördinating forces which are at work in the building of the organism. For example, the mechanical conditions would have been perfectly satisfied if the smaller entoblasts had rotated in the opposite direction and had carried the ectoblastic cap with them, so that as a result the planes of symmetry in the ectoblast and entoblast would not have coincided, but would have crossed each other at right angles. *We must find the ultimate cause of this anti-clockwise rotation not in such external mechanical conditions, which are, however, incidentally fulfilled, but in those more complex internal conditions, which direct the course of ontogeny, and which in our ignorance we call the coördinating force, or hereditary tendency.*

5. *The Four Macromeres, or Basal Quartette. Figs. 34, 37, 42, 52.*

At the time when the layers are all segregated the macromeres still form much the largest part of the egg. They are composed almost entirely of yolk, and their nuclei and protoplasmic portions lie near the surface just in advance of the ectoblastic cap. The four cells are nearly equal in size, and they are from this stage onward closely pressed together, so that the egg is nearly spherical in form and never again assumes the quatrefoil shape. The polar furrow extends between these cells from the vegetal to the animal pole, though on the upper side of the egg it is covered by the cap of ecto-

blast cells. After the formation of the fourth quartette the macromeres do not divide again until a little before the closure of the blastopore, Fig. 54, and consequently the first and second cleavage planes and the polar furrow serve as excellent landmarks throughout a period when the egg is becoming confusingly complex.

In closing this section on the segregation of the layers it may be well to summarize the number and position of the cells in the three layers at the stage shown in Fig. 33.

1st Quartette, Ectoblast Cells	15	
2d " " " "	16	
3d " " " "	8	
	39	
4th " {	Primary Mesoblasts	2
	Mesentoblasts	2
	Primary Enteroblasts	2
	Smaller Entoblasts	3
	9	
Macromeres, Larger Entoblasts	4	
	52	

But for the lack of one cell in the posterior arm of the cross there would be ten ectoblast cells in each quadrant, and this layer would be radially symmetrical. In *C. adunca*, as

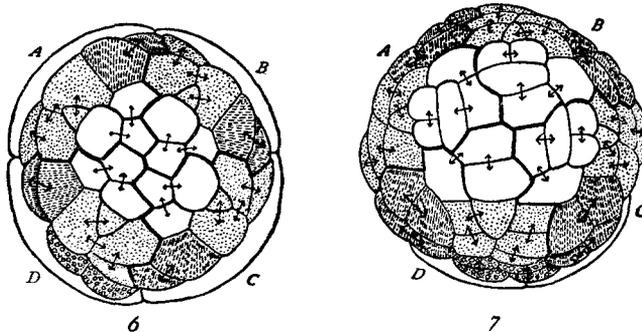


DIAGRAM 6. — Forty-two cell stage of *Crepidula*. Shading as in Diagrams 3 and 4. The cross (shown in strong outline) lies in the position in which it was first formed. The heavy, radiating lines separate the cells of the different quadrants.

DIAGRAM 7. — Sixty-cell stage of *Crepidula*. Shading and heavy lines as in the preceding. The whole of the ectoblast has rotated to the left, due to the rotation of the fourth-quartette cells. The "middle cells" in three arms of the cross have divided transversely. The third-quartette cells on the posterior side have divided bilaterally.

has been said, this cell, which is lacking at this stage in the other species, is present, and the ectoblast is radially symmetrical. The four macromeres may still be considered radially symmetrical. The cells of the fourth quartette lie on the sides of the egg in the furrows between the four macromeres, but the radial symmetry of the egg is destroyed by the behavior of the posterior member of this quartette, 4d. All the divisions of this cell except the first one are purely bilateral in position.

IV. HISTORY OF THE FIRST QUARTETTE OF ECTOMERES.

DIAGRAMS 6-11.

Owing to the presence of certain peculiar landmarks, I have been able to follow the cell lineage of the first quartette farther than that of the others. The derivatives of this first quartette give rise to the whole apical region of the embryo, *viz.*, all the ectodermal cells of the head vesicle, an apical plate of ciliated cells, the posterior cell plate, the dorsal portion of the functional velum and a portion of the first velar row on the ventral side, the supraoesophageal ganglia and commissure, the cerebro-pedal connectives, and, possibly, the pedal ganglia, an apical sense organ, and the paired eyes.

Wilson ('92) has shown that in *Nereis limbata* and *N. megalops* this quartette gives rise not only to the entire upper hemisphere of the trochophore, but also to the head kidneys and all the cells of the prototroch. This is not the case in *Crepidula*; all that portion of the velum which lies at the ends of the right, the left, and the anterior arms of the cross being derived from the second quartette, while only the intermediate portions come from the first quartette. The anterior branch of the velum on the dorsal side of the body is also derived from the first quartette. As to the head kidney,¹ it is not present in marine prosobranchs, as is well known.

The first division of the cells composing this first quartette gives rise to the *turret cells*, as has been described (p. 58). Their second division occurs immediately after the formation of the mesentoblast 4d, as shown in Fig. 23; each of the four

¹ Wilson has lately suggested that this structure may be a mucous gland as Mead found to be the case in *Amphitrite*.