

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*.

cells divides in a dextrotropic direction, and in a plane at right angles to that of the previous cleavage. When the division is completed it can be seen that the outer daughter cells are largely overlapped by the apical or stem ($1a^{1.1}-1d^{1.1}$) cells. The outer cells ($1a^{1.2}-1d^{1.2}$) become the *basal cells* in the arms of a cross, the origin, history, and significance of which will now be considered.

1. *The Ectoblastic Cross.*

In the history of this ectoblastic cross, and of the four turret cells which lie between its arms, is comprised the history of the whole upper hemisphere of the larva. It is the one landmark which has made it possible to follow the cell lineage in some cases to the formation of definitive organs. In treating, then, the history of the first quartette, I shall first deal with the cross, and then take up the turret cells.

(a) *Formation.* — Although two-thirds of all the cells entering into the cross are present and in position at the stages shown in Figs. 23–25, the cross itself does not become apparent until the four small cells have been formed which become the *tip cells* of its arms, Fig. 29, $2a^{1.1}-2d^{1.1}$, and Diagram 6. These tip cells come from the second quartette, though all the other cells of the cross belong to the first; for convenience, however, I shall here treat of the cross as a whole, though its tip cells would properly come under the section on the history of the second quartette of ectomeres. The tip cells are formed by an oblique and unequal division of four of the *belt cells*, $2a^1-2d^1$, the cleavage being distinctly laeotropic. The upper and smaller moiety becomes the terminal or tip cell ($2a^{1.1}-2d^{1.1}$) in each arm of the cross, though its relation to the other cross cells is so close that I doubt whether any one who had not watched its formation would suspect that it was not derived from the basal cells of that structure. The cross then contains all the cells of the first quartette except the turret cells, and in addition the tip cells, which come from the second quartette. When it first appears it consists of twelve cells; the four apical cells form its centre, while there are two cells in each arm, one basal, the other

terminal ; the basal cells were produced by the second division of the apical cells (the turret cells were formed at their first division), and, as just explained, the terminal cells are derived from the second group of micromeres. (See Diagram 6.)

(b) *Axial Relations.* — When first formed the centre of the cross lies exactly at the animal pole of the egg, and the polar bodies are attached at the point where the four apical cells meet. The arms of the cross lie between the first and second cleavage furrows, about 30° or 40° to their right, *i.e.*, in a clockwise direction from those furrows, Figs. 29–32.

At the period when the three smaller entoblasts are formed, Fig. 33 and Diagram 7, the whole ectoblastic cap is rotated to the left until the arms of the cross come to lie nearly over those furrows, so that one arm is approximately anterior, one posterior, one right, and one left. This is not strictly true, since it can be seen by consulting the figures that even after the general rotation of the ectoblast shown in Fig. 33 the arms of the cross do not lie in the furrows between the macromeres, but slightly to the right of them. This continues to be true up to a late period in the cleavage, *e.g.*, in Figs. 51 and 53, the left arm of the cross is distinctly farther forward than the right, while in these figures and a great many others, *e.g.*, Figs. 64, 65, 68, 71, 72, 75, and 76, the anterior arm, which has now grown around to the ventral side, lies to the right of the mid line of the embryo. Ultimately, however, the anterior arm, which can be much more easily followed than the others, comes to lie precisely in the median plane, Figs. 79, 81, 82.

By another and much greater shifting of the ectoblast, which will be described in another section, the entire cap of ectoblast is carried forward through an angle of about 90° . This forward shifting goes on at the same time that the ectoblast is rotating in an anti-clockwise direction, so that by the time that the anterior and posterior arms lie in the median or second furrow, which can still be plainly seen between the yolk cells, the transverse arms lie anterior to the transverse or first furrow.

From its earliest formation up to a late stage in its history the cross in itself is distinctly dextrotropic ; *i.e.*, each arm taken in connection with the apical cell from which it is chiefly

derived forms a linear series of cells, the apical one of which lies to the right of the apical pole. The four arms thus form a right-wound spiral around the apical pole. This arrangement is especially noticeable in the nuclei of these cells, and can here be recognized at the first glance. After the longitudinal splitting of the arms and the division of the apical cells to form the "rosette," this dexiotropic arrangement of the arms of the cross can no longer be recognized.

(c) *Later History.* — Starting from the earliest appearance of the cross, when it contains twelve cells, the cell lineage of the entire structure has been followed to a stage when it contains sixty-six cells, Figs. 53, 56, and Diagram 11. The first cells of the cross to divide are the basal cells in the anterior, the right and the left arms ($1a^{1.2}$, $1b^{1.2}$, $1c^{1.2}$) in the 44-cell stage, Fig. 31. In all the species save *C. adunca* the division in the basal cell of the posterior arm is delayed until a considerably later period, Fig. 42. By this division, which is slightly dexiotropic, the basal cells are divided into a larger peripheral moiety, the *middle cell* ($1a^{1.2.2}$ — $1d^{1.2.2}$), and a smaller apical one, still called the *basal cell* ($1a^{1.2.1}$ — $1d^{1.2.1}$). Each arm save the posterior contains at this stage (Figs. 32, 35, 36) three cells, — a basal, middle, and terminal.

When there are 66 cells present, Fig. 42, the basal and terminal cells of the posterior arm divide, the spindle in each case being parallel to the long axis of the arm. In this way the posterior arm comes to be composed of four cells arranged in a linear series, the two proximal ($1d^{1.2.1}$ and $1d^{1.2.2}$) derived from the basal cell and the two distal ($2d^{1.1.1}$ and $2d^{1.1.2}$) from the terminal one, Diagram 8.

About the same time that the cells of the posterior arm divide radially, the middle cell in each of the other arms divides in a plane nearly transverse to its long axis into two equal portions, the *left and right middle cells*, $1a^{1.2.2.1}$ and $1a^{1.2.2.2}$, $1b^{1.2.2.1}$ and $1b^{1.2.2.2}$, etc., Fig. 42 and Diagram 7. The left moiety in each arm is a little nearer the apical pole than the right, and the cleavage is therefore laeotropic. This division of the middle cell in the anterior, the right, and the left arms is the beginning of a longitudinal cleavage of each of these arms,

which is continued until, as shown in Fig. 49, they are split from base to tip.

Before this longitudinal division of these three arms is completed, the four central or apical cells divide in a laeotropic direction; by this division four central and four peripheral cells are formed. The former ($1a^{1.1.1}$ – $1d^{1.1.1}$) are the *apical rosettes* (Wilson ('92), p. 392); the latter are the *peripheral rosettes* ($1a^{1.1.2}$ – $1d^{1.1.2}$). The peripheral rosettes are slightly larger than the apical cells, and lie just central to the turret cells and between the basal cells of adjacent arms, Figs. 44, 45. The division of the four apical cells ($1a^{1.1.1}$ – $1d^{1.1.1}$) is rarely simultaneous, and yet the sequence of cleavage follows no invariable order. In the ova figured the cells of the second and fourth quadrant have divided, while those of the first and third are just dividing.

At the same time that the apical cells are dividing, the terminal cell of each arm, except the posterior, divides into two small cells. This division is frequently very irregular; in Figs. 44 and 45 it is dextrotropic in the right and anterior arms, and laeotropic in the left; in other words, the cleavage is bilateral in the transverse arms. This is, I think, the most frequent condition, but there are many deviations from this form. The products of this division are the *right* and *left tip cells*. Finally, the longitudinal splitting of all the arms, except the posterior, is completed by the equal division of the basal cells (Figs. 46, 47, and Diagram 8) into right and left portions, the *right* and *left basals* ($1a^{1.2.1.1}$ and $1a^{1.2.1.2}$, $1b^{1.2.1.1}$ and $1b^{1.2.1.2}$, etc.). This division is very nearly meridional, but subsequent stages, e.g., Fig. 50, show that the left moiety is a little nearer the apical pole than the right; the division is, therefore, laeotropic.

The cross now consists of 30 cells, as follows:

Apical cells	4
Peripheral rosettes	4
Post. arm — 1 basal, 1 middle, 2 terminal	4
Ant. right and left arms, each 2 basal, 2 middle, 2 terminal cells, 6	18
in each arm. In 3 arms	18
Total	30

These cells all belong to the first quartette except the two terminal cells of each arm, which were derived from the second quartette, Diagram 8. The cells in three of the arms, the ante-

rior, the right, and the left, continue to divide in the same way and at nearly the same time, though the cells of the anterior arm become larger than those of the others, and this entire arm becomes broader, though scarcely as long as either of the others.

After the stage shown in Diagram 8 the right and left middle cells in each of the three arms just mentioned divide in a purely bilateral manner. These cleavages are not only symmetrical with reference to the median plane of the embryo, but the time at which the cells divide shows that the cleavage

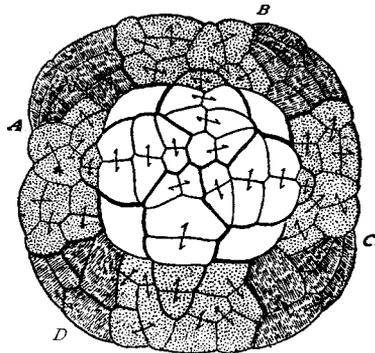


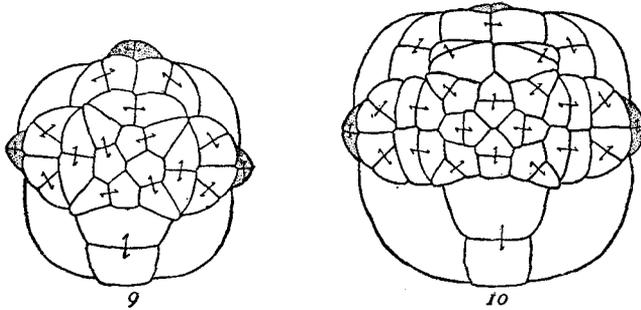
DIAGRAM 8. — Crepidula: 92 ectoblast cells (109-cell stage). Shading and heavy lines as in preceding diagrams. The egg is represented as if all the ectoblast cells could be seen from the apical pole, though actually many of the peripheral cells lie far down on the sides, or even on the ventral face of the egg.

is bilateral and not radial, the middle cell on the posterior side of the transverse arms dividing before any of the others, Fig. 49. The right middle cell in each case divides in a dextrotropic direction, the left middle cell in a laeotropic, Figs. 49, 50, and Diagram 9. In this way a *right* and *left intermediate cell*, $1a^{1.2.2.1.1}$ and $1a^{1.2.2.2.1}$, etc., is formed in each of these three arms.

Fig. 50, which is a view from the apical pole, shows the cross after the intermediate cells have been formed. This figure and the next one, Fig. 51, are particularly interesting, since they show a polar body attached at the point where the four apical cells come together. This is the last stage in which I have found the polar bodies attached to the egg, though they are found still later free in the egg capsules and sometimes within the alimentary canal of the embryos.

Very soon after the formation of the intermediate cells the peripheral rosette cells divide almost in a radial direction into central and peripheral portions, $1a^{1.1.2.1}$ and $1a^{1.1.2.2}$, etc., Fig. 51, which are almost equal in size. The division is purely bilateral, and the two posterior cells divide a little before the two anterior ones, as was the case with the middle cells.

After this stage the cleavage at the apical pole becomes more or less irregular, and is especially difficult to follow, because the shape and position of the cells is so variable. In fact, at about the stage shown in Figs. 53–56, the whole egg becomes irregular in outline, and every part seems to be undergoing contraction or expansion. This, like the previous period of irregularity mentioned on p. 75, and shown in Figs. 33, 34, is due to divisions and changes of position which are taking



DIAGRAMS 9 and 10. — First quartette in *Crepidula*, showing the later history of the cross and turret cells.

place in the entoblasts. The result of these changes is the formation of the archenteric cavity; and as soon as this is formed, Figs. 63, 64, the egg comes back to a regular form again, and many landmarks which were lost for a time reappear. Some marks, however, especially the cells of the anterior and posterior arms of the cross, can be followed right through this period. Soon after the division of the peripheral rosette cells the apicals divide in a radial direction into two cells about equal in size, Fig. 53 and Diagram 10. These we shall call the *inner* and *outer apicals*, $1a^{1.1.1.1}$ and $1a^{1.1.1.2}$, etc. In this case, as in the two preceding cleavages, the posterior cell of this quartette divides first, the anterior one last.

About the same time that the apicals are dividing, the right and left basals in the transverse arms divide in a direction parallel to the long axis of the arm into the *inner* and *outer basals*, Fig. 53, $1a^{1.1.2.1}$ and $1a^{1.1.2.2}$, etc., and a little later the corresponding cells in the anterior arm divide obliquely and unequally, giving off a thin, wedge-shaped *outer basal*, which lies between

the basal and middle cells of the arm, Figs. 65-68, 70, and Diagram 10. At nearly the same time the anterior intermediate cells divide into upper and lower portions, which lie on each side of the anterior arm, Fig. 56 and Diagram 10.

Next, as shown in Fig. 53, the two cells (proximal and distal tip cells) derived from the tip cell of the posterior arm divide in the direction of the long axis of the arm, forming four cells which have come from the single original tip cell. These four cells lie in line with the two proximal cells of the posterior arm, so that now the entire arm consists of a linear series of six cells.

Finally, the last stage in which I have been able to recognize the entire cross is shown in Fig. 56 and Diagram 11. At this stage the two tip cells which lie at the ends of the right and the left arms divide across the axis of the arms, so that there are four tip cells at the end of each arm. Unlike the four tip cells of the posterior arm, these do not lie in the long axis of the arm, but across it. About the same time all the middle and intermediate cells of the transverse arms divide radially, so that there come to be two right and two left middle cells, and two right and two left intermediate cells in each arm, one of the two being proximal, the other distal in each case.

The fate of the tip cells of the anterior arm is very uncertain. I have not been able to trace them satisfactorily beyond the stage shown in Fig. 56, when they are still very small and insignificant. *However, I believe that in C. plana they are crowded entirely out of the layer of ectoblast cells, and that they are thrown wholly away.*¹ Fig. 71, 2b^{1,2} shows the two anterior tip cells very plainly. Even here, however, they show important changes in position and structure; they project above the level of the surrounding ectoblast cells, and their nuclei have no definite boundaries, while the chromatin seems to be dissolving and

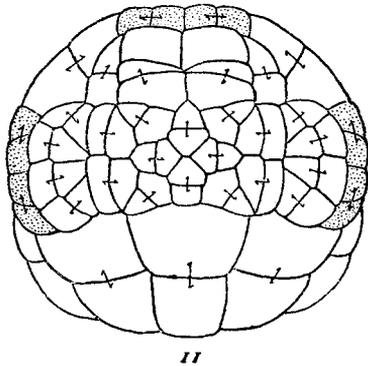


DIAGRAM 11. — The first quartette in Crepidula, showing the later history of the cross and turret cells.

¹ See Note p. 204.

spreading throughout the cell. The whole cell stains very much more uniformly than does a normal cell, and in this regard these tip cells resemble the polar bodies in the stages where they are last seen and where they are undoubtedly degenerating. Further stages in the degeneration of the tip cells are shown in Figs. 69, 70; in the former the two tip cells are pushed still further above the level of the surrounding cells, while in Fig. 70 they are separated from each other and practically detached from the egg. I have observed this process in only a few eggs of the species *C. plana* and am not wholly convinced that it is a constant feature. Such a phenomenon is certainly very remarkable and unusual, and I am not prepared to draw any conclusions as to its significance.

In this last stage, then, in which the cross can be recognized as a whole, it is composed of the following cells :

Apical	{	Inner	4	
		Outer	4	
Peripheral Rosette	{	Inner	4	
		Outer	4	16
				16
	{	Basal {	Inner	2
			Outer	2
		Middle {	Inner	2
			Outer	2
Transverse Arms	{	Intermediate {	Inner	2
			Outer	2
		Tip (Terminal)	4
			Right Arm	16
			Left Arm	16
				32
				32
	{	Basal {	Inner	2
			Outer	2
Anterior Arm	{	Middle	2	
		Intermediate {	Inner	2
			Outer	2
		Tip (Terminal)	2
				12
				12
	{	Basal	1	
		Middle	1	
Posterior Arm	{	Intermediate	0	
		Tip (Terminal)	4
				6
				6
				6
		Total		66
				66

I have found it impossible to trace the cell lineage of certain parts of the cross, especially the transverse arms, farther than the stage shown in Figs. 54, 56, and Diagram 11. The cells become so numerous beyond this stage that I can only point out the general outlines of these arms, *e.g.*, their posterior boundary and terminal cells are for a long time clearly marked by the large ciliated cells which lie just behind them, Figs. 53, 55, 64, *et seq.* The anterior borders of the transverse arms become confused with the lateral extensions of the anterior arm, but even in this case it is possible for a considerable time to distinguish between the anterior and transverse arms by means of the large anterior turret cells or their derivatives which lie in the angles between these arms. But while there is a degree of uncertainty about the exact outline of the transverse arms, there are other portions of the cross which remain perfectly distinct until a period much later than any shown in the figures, in fact until the larval life is practically at an end. In all the later figures which show an apical view of the egg, *e.g.*, Figs. 50, 56, 79, the four characteristically arranged apical cells can be plainly seen, while the two proximal cells in the posterior arm and the median portion of the anterior arm can be recognized throughout the greater part of the larval life. The cells of the anterior arm which remain recognizable throughout this period are, counting from the apical cells :

Apical, outer (anterior)	1
Basals { Inner	2
{ Outer	2
Median	2
Total	<hr style="width: 100px; margin: 0;"/> 7

The two proximal cells of the posterior arm ($1d^{1.2.1}$ and $1d^{1.2.2}$) are recognizable for a very long period, *e.g.* Fig. 64. They become very large, and, together with the two posterior turret cells, form a large part of the head vesicle or umbrella.

(d) *Significance of the Cross.* — In seeking to learn the significance of this peculiar structure, it will be well first of all to compare it with similar structures found in the segmenting eggs of other animals, then to inquire into the mechanical principles involved in its formation, and finally to seek for its significance in the ontogeny.

Blochmann ('81) has given a most interesting and complete account of the cross in *Neritina*. He did not recognize that the four apical cells are in any way connected with this structure, and hence he speaks of it as four cell series ("Zellreihen"), an anterior, posterior, right, and left. He followed the history of these cell series until there were three cells in each one except the posterior, which contained four. Owing to the presence of peculiar shining granules in the terminal cells of the transverse arms, Blochmann was able to trace these cells to a very late stage in the cleavage. He believed that they entered into the formation of the velum, and hence called them "Urvelarzellen."

In spite of the many minute and wonderful resemblances between the cross in *Neritina* and *Crepidula*, the derivation of the cells composing it is very different in the two animals if Blochmann's account is to be trusted. In *Neritina*, as in *Crepidula*, the cross is first recognizable when there are two cells, one basal and one terminal, in each arm. The following scheme shows Blochmann's derivation of the cells of the cross in *Neritina*, as compared with my account of *Crepidula*:

NERITINA.	CROSS CELLS.	CREPIDULA.
1a ¹ -1d ¹	Apical	1a ^{1,1} -1d ^{1,1}
2a ^{1,1} -2d ^{1,1}	Basal	1a ^{1,2} -1d ^{1,2}
2a ^{1,2,1} -2d ^{1,2,1}	Terminal	2a ^{1,1} -2d ^{1,1}

As has been mentioned already (p. 65), Blochmann is certainly wrong in the designations given the outer-belt cells, and consequently wrong in the designation of all cells derived from them. Making allowance for this error, we find that the terminal cells are derived from exactly the same source in *Neritina* and *Crepidula*. The only other difference concerns the basal cells. In the derivation of these cells Blochmann is certainly in error. Although he expressly states that the basal cells arise from the second quartette, he shows no stages in which the spindles are present, and his figures indicate that the basal cells have arisen exactly as they do in *Crepidula* and *Umbrella*, *viz.*, from the apical cells. The position of the cells is the same, and it is highly improbable that their origin is different. As opposed to Blochmann's view, I urge Heymons' careful

observations on Umbrella, and my own results on four species of Crepidula.

Kofoïd ('94) also has expressed the view that Blochmann was wrong in the derivation of the basal cells, and as he presents other evidence in favor of the position here taken, I quote his words: "There are indications, however, that they (the basal cells) were really derived from the apical quartette a_1-d_1 ; for (1) their nuclei are nearer those of the apical quartette; (2) the cells of the apical quartette are much smaller after the cells $a''_2-d''_2$ appear than before; (3) $a'_2-d'_2$ have just arisen by a recent division, whereas some time has elapsed since the first division of the apical quartette."

The subsequent division of the basal cells is identical with their division in Crepidula, not only in the direction of the cleavage and the size of the resulting cells, but also in the time of its occurrence. This is the more remarkable when it is considered, as will be done in a moment, that *in both Crepidula and Neritina the direction of this cleavage really determines the continued existence of the cross, and further, that it violates the "law of alternating cleavages."*

In its later history the identity of the cross in Neritina and Crepidula is still further emphasized. At a stage with 49 ectoderm cells (Blochmann's Fig. 56, corresponding approximately to my Fig. 36 or 38), the cells of the posterior arm of the cross divide so as to form a series of four cells, while each of the other arms contains but three. This is such a remarkable agreement with what takes place in Crepidula, that I think it worth while to quote Blochmann's words on this point (p. 158): "Besonders bemerkenswerth erscheint bei diesem Stadium das Auftreten einer vierten Zelle in der aus drei Zellen bestehenden Reihe, die in der Mitte der hinteren Hälfte der Ektoderm-scheibe verläuft, während in den drei anderen entsprechenden Zellreihen die Dreizahl erhalten bleibt. Das Auftreten dieser Zelle ist ein ganz Konstantes und wurde an fünf Präparaten beobachtet. Man kann wohl sagen, dass in der Ektodermanlage an und für sich erst durch das Auftreten dieser Zelle vorn und hinten unterscheidbar wird, während vorher nur die Richtung der Sagittalachse durch das Vorhandensein der Körnchen-

zellen vz und vz_1 , in den seitlichen Reihen erkennbar war." Truly such a fact is "especially noteworthy" when it is found reproduced in another very different animal; and, standing as it does in direct relation to the origin of bilateral symmetry, it is a fact of profound significance.

The further history of the cross in *Neritina* is not given in detail. An ectodermal invagination is described as occurring at the apical pole, and Blochmann's Fig. 59 shows that this invagination includes the four apical cells and all the cells of the transverse arms, except the terminal ones. Judging by the figures the transverse arms seem to have been drawn into this invagination, while the turret cells and the anterior and posterior arms lie outside of it. If such a thing really happens, the transverse arms of the cross must first be wholly separated from all their connections with surrounding cells, and then drawn into the invagination; in fact, the figures mentioned show that this has happened, for the terminal cells of the transverse arms (the "Urvelarzellen") have been drawn inward until they immediately adjoin the turret cells. Concerning this invagination I have already spoken (p. 31), and I need only repeat here that I believe it is not a normal formation.

The two granular tip cells are the only ones which Blochmann was able to trace farther than the stage already mentioned (his Fig. 59). These cells he calls the *Urvelarzellen*, and he states that the velar cells first appear between them, on the dorsal side of the embryo, and then, apparently by the division of the *Urvelarzellen*, they extend ventrally around the anterior end of the embryo. It is almost certain that these same cells form part of the velum in *Crepidula* (see p. 132).

Heymons ('93) figures the cross plainly enough in *Umbrella*, as is shown by Diagram 12, *c* and *d*, taken from his Figs. 14 and 20, and yet he does not appear to have recognized this structure. To be sure, he speaks of a cross of ectoblast cells being present, and refers repeatedly to the cross in *Neritina* and *Crepidula*, but the cross which he points out in *Umbrella* is a wholly different thing from that in either of the other forms. It is composed entirely of cells of the second quartette (a'' , b'' , c'' , d''), does not reach the centre of the ectodermal field, and has

wholly different axial relations; besides, the arms are never more than two cells long, though they may become three cells broad. The real cross, *i.e.*, the structure homologous with the cross in *Neritina* and *Crepidula*, is plainly present in his figures, and its close resemblance to the same structure described by Blochmann and myself is all the more striking, since apparently Heymons did not recognize its presence.

It is composed of cells of exactly the same derivation and of relatively the same size and position. Thus the terminal cells are, using my nomenclature, $2a^{1,1}-2d^{1,1}$, and they arise by laeotropic division; the basal cells are $1a^{1,2}-1d^{1,2}$, and they arise by dextrotropic cleavage. The two cells of each arm, and especially their nuclei, lie in line with one of the apical cells, and a line drawn through the nuclei of these three cells forms a curved radius, the four radii being dextrotropic. Heymons especially says of the terminal cells (of course he does not use this designation): "Es sind dies die kleinsten Ektodermzellen welche bisher gebildet wurden." To all of these facts I have already called attention in *Crepidula*, and in general they seem to be true of *Neritina*.

In the time of its formation the cross in *Umbrella* shows some interesting differences from the cross in *Neritina* and *Crepidula*, *e.g.*, the terminal cells are first formed and the basal cells are not formed until a considerably later period. The arms are more curved in a dextrotropic direction than in either of the other gasteropods, and the whole cross is less clearly marked off from the surrounding cells. *But most important of all the differences is the fact that the first division of the basal cells is laeotropic in Umbrella, Diagram 12, d, while it is invariably dextrotropic in Crepidula and Neritina.* Upon this difference the future recognizability of the cross in the last-mentioned cases depends. If these basal cells should divide in *Neritina* and *Crepidula*, as they do in *Umbrella*, there would be no cross after the stage in which there are two cells in each arm. The existence of the cross in the later stages depends upon the direction of this one division. It is therefore all the more interesting to note that this division in *Umbrella* follows the usual rule of alternation of direction, whereas in *Neritina* and *Crepidula* it violates that rule.

The cross in Umbrella develops more slowly than in either of the other forms, — thus the basal cells are formed at the 24-cell stage in Neritina, the 25-cell stage in Crepidula, and the 39-cell stage in Umbrella. The first division of the basal cells occurs at the 37-cell stage in Neritina, the 44-cell stage in Crepidula, and the 83-cell stage in Umbrella. On the other hand, the terminal cells are formed when 25 cells are present in Umbrella, 28 in Neritina, and 30 in Crepidula. Likewise the division of the turret cells, which occurs at the 63-cell stage in Umbrella, does not occur until long after the 111-cell stage in Crepidula, at which point I ceased to follow the lineage of the entire egg. But in spite of these two cases in which Umbrella outstrips Crepidula, the division of the cells of the first quartette is much slower in the former than in the latter. Thus there are in Umbrella at the 91-cell stage 16 cells of the first quartette; in Crepidula, at a corresponding stage, 23 cells. In both cases the greatest activity is in the second quartette. Heymons says of Umbrella: "The micromeres of the first generation are smallest, those of the last largest" (*generation* is used in the sense of quartette). In Crepidula the differences are not marked, though I think the second is somewhat larger, when formed, than either the first or third. The larger size and more rapid division of the cells of any quartette are probably connected with the larger size or more rapid development of the organs to which they give rise, as Lillie ('95) has established in the case of Unio. The velar field (derived from the first quartette) is certainly larger and develops more rapidly in Crepidula than in Umbrella, and corresponding to this we have the larger size of the cells when first formed and their more rapid divisions subsequently. The smaller size of the velar field in Umbrella may account for the relative unimportance of the cross in that animal. Concerning the fate of the cross cells in Umbrella nothing is known.

Heymons has observed, but does not figure, the division of the terminal cells and a second division of the basal cells; the direction of these divisions is not given. He has also observed the rosette division by which four small cells are formed at the apical pole, "strikingly like the apical rosette of Wilson"; as

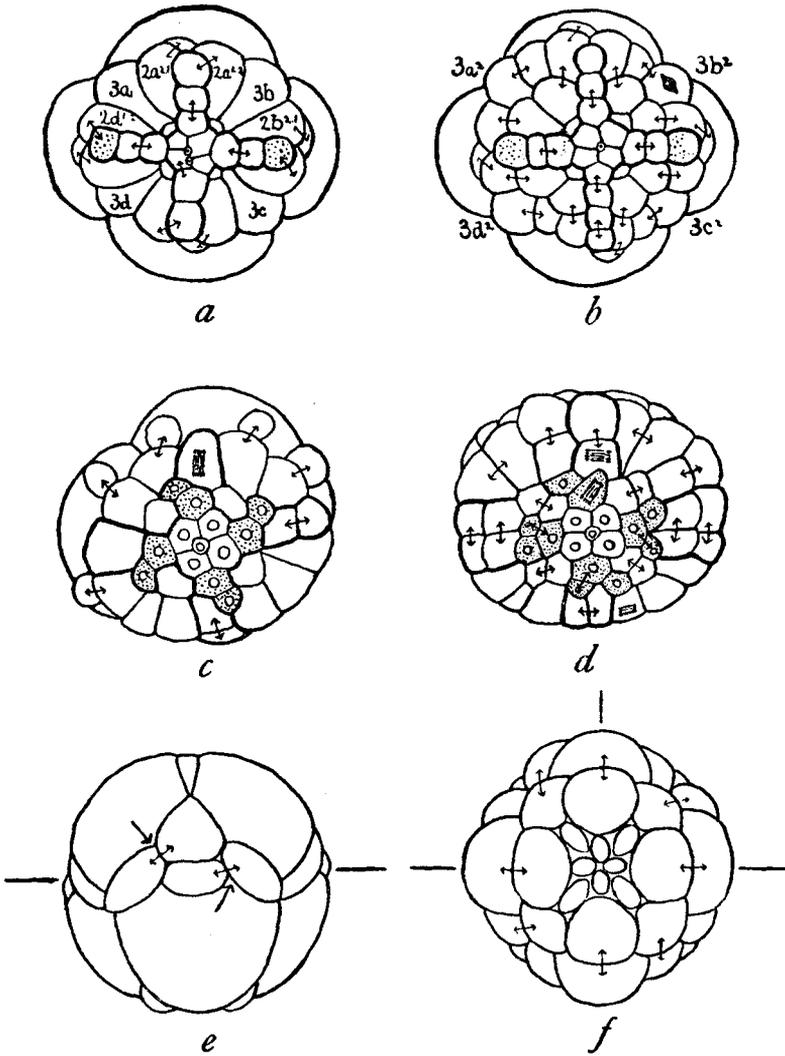


DIAGRAM 12.—The cross in Neritina, Umbrella, and Chiton.—*a*, Neritina: three cells in each arm except the posterior; the granular tip cells of the transverse arms are the "Urvelarzellen." (Blochmann's Fig. 53.)—*b*, Neritina: four cells in the posterior arm, three in each of the others. The probable origin of the outer belt cells is indicated by arrows, and the designation of the cells in this and in the preceding figure are given as in Crepidula. (Blochmann's Fig. 56.)—*c*, Umbrella: the arms of the cross are stippled; Heymons' so-called "cross" is shown in heavy outline. (Heymons' Fig. 14.)—*d*, Umbrella: stippling and outlines as in *c*. The basal cells in the arms of the cross have divided laotropically, the turret cells bilaterally. (Heymons' Fig. 20.)—*e*, Chiton: lateral view of the 32-cell stage. The small cells around the equator of the egg correspond in origin and position to the turret cells and the tip cells of the gasteropod; they should form the prototroch if they have the same destiny in the two cases. (Metcalf's Fig. XIV.)—*f*, Chiton: apical view of the 48-cell stage, showing the cross, the rosette, and the turret cells. (Metcalf's Fig. XXIV.)

in *Nereis* and *Crepidula*, this is the third division of the apical quartette.

It is very interesting to note that in so primitive a form as *Chiton*, in which the cleavage in general appears to be very different from the ordinary molluscan type, the cross is present, at least in some species. In Metcalf's ('93) figures of *Chiton marmoratus* and *C. squamosus* the cross is found as in the gasteropods just mentioned, being composed of cells of exactly the same cell origin and position, except that the tip cell is shown displaced a little to the right. These facts and several others which will be referred to later are shown in Diagram 12, *e* and *f*, which are copies of Metcalf's Figs. XIV and XXIV.¹

Wilson ('92) has shown that in the polychaetous annelid *Nereis*, a cross of ectoblast cells is present which in many respects resembles the cross in *Neritina*, *Umbrella*, and *Crepidula*. This annelidan cross, like the molluscan one, contains two cells in each arm when first formed, and these later increase to three. The centre of the cross, too, is formed by the four apical cells. In its later history each arm of the cross undergoes longitudinal splitting (*cf.* Wilson, Fig. 41), as is the case in *Crepidula*; but here the resemblances end. Professor Wilson has shown that the cross in *Nereis* differs both in origin and destiny from the cross in *Neritina*, and that both differ from *Crepidula*. This conclusion as to the difference between the mollusk and the annelid I can only more fully confirm, though, as I have already pointed out, it is almost certain that Blochmann's derivation of the cross in *Neritina* is wrong, and that it has the same origin, structure, and destiny in *Neritina* and *Crepidula*; the same thing is true of the origin and structure of the cross, at least in the early stages, in *Umbrella*. But in neither origin, structure, nor destiny does the molluscan cross resemble the annelidan. Wilson seems to consider them alike in structure, for he says (p. 442): "It is certain that,

¹ The cross is beautifully shown in *Ishnochiton* from the California coast, which is being studied at present by Mr. Harold Heath in the Zoölogical Laboratory of the University of Pennsylvania. This work, which is far the most complete yet done on *Chiton*, shows that the cleavage in that animal not only belongs to the gasteropod type, but that it is, for a considerable period, cell by cell the same.

although the two crosses have exactly the same structure, they have a completely different origin." From this statement I should be compelled to dissent, for I do not believe that they are alike even in structure. The cross in *Nereis* is purely radial in position, dextrotropic in the gasteropods. It ultimately lies in the median and transverse planes in the mollusk, midway between these planes in the annelid. It is formed almost entirely from the apical cells in the mollusk, from the terminal cells in *Nereis*, and corresponding with this difference the terminal cells are much the largest ones in the cross in *Nereis*, while they are the smallest ones in the gasteropods. And again, the posterior arm in *Nereis* is like each of the others, whereas in *Crepidula* and *Neritina* it becomes very different in structure. The cells composing the cross in *Nereis* and *Crepidula* are shown in the following scheme :

NEREIS.	CROSS CHLLS.	CREPIDULA.
$1a^{1.1.1} - 1d^{1.1.1}$	Apical	$1a^{1.1} - 1d^{1.1}$
$1a^{1.1.2.1} - 1d^{1.1.2.1}$	Basal	$1a^{1.2} - 1d^{1.2}$
$1a^{1.1.2.2} - 1d^{1.1.2.2}$	Terminal	$2a^{1.1} - 2d^{1.1}$

The cross forms relatively much later in *Nereis* than in *Crepidula*, as is shown by the exponents used in designating the cells.

In *Nereis* the arms of the cross are formed entirely from the cells $1a^{1.1.2} - 1d^{1.1.2}$, which in *Crepidula* I have called the peripheral rosette. These cells are formed at exactly the same division of the apical quartette in *Crepidula* and *Nereis*, *viz.*, the third ; in exactly the same direction, *viz.*, slightly laeotropic, almost radial (Figs. 44 *et seq.*, and Wilson's Fig. 27); and they lie in exactly the same position, *viz.*, between the turret cells (Wilson's trochoblasts) peripherally and the apical cells centrally. In *Crepidula* the two anterior peripheral rosette cells are secondarily separated from the turret cells by the lateral extension and consequent junction of the arms of the cross ; the two posterior peripheral rosette cells remain in contact with the turret cells, Figs. 49 *et seq.* In both *Crepidula* and *Nereis* the peripheral rosette cells, $1a^{1.1.2} - 1d^{1.1.2}$, divide in nearly the same direction (radial in *Nereis*; slightly bilateral, almost radial, in *Crepidula*), forming a cell series in each quadrant which radiates from the apex, Figs. 51, 53, 62, and Diagram 13. These radiat-

ing rows of cells I shall call the *rosette series*, a name suggested by the word *rosette*, first used in this connection by Wilson to designate the small apical cells formed by the third division of the first quartette. The following table will show the cells in Crepidula which correspond to the cross cells of Nereis :

NEREIS.		CREPIDULA.
Rosette		Apicals
Basals		Inner Peripheral Rosette
Middles }		Outer Peripheral Rosette
Terminals }		

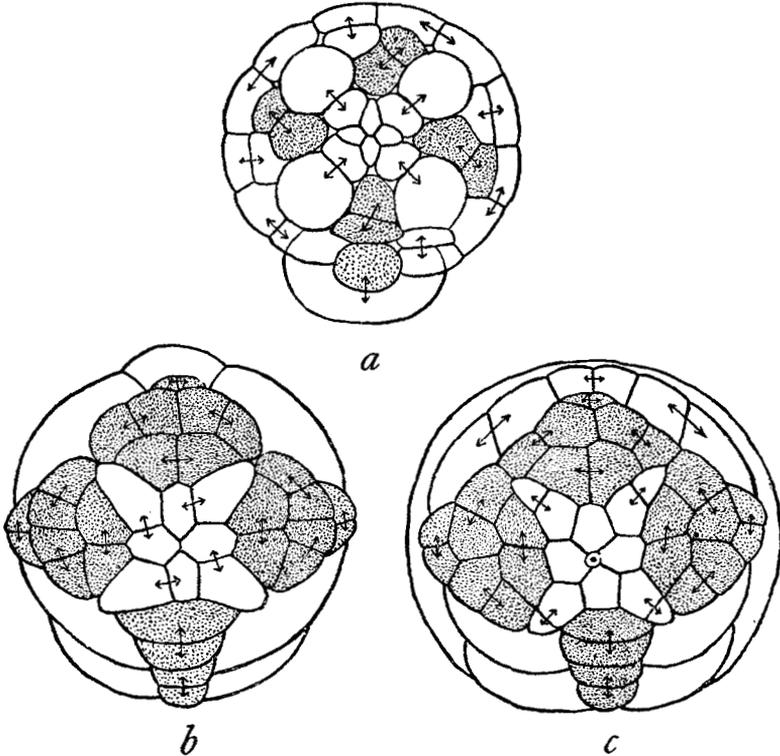


DIAGRAM 13. — The cross in Nereis and Crepidula. — *a*, Nereis : the stippled cells are the *intermediate girdle cells* (molluscan cross) excepting the posterior one (x^3) which corresponds to the "tip cell" in the gasteropod. The trochoblasts lie at the margin of the egg. (Wilson's Diagram II. B.) — *b*, Crepidula : cross cells (intermediate girdle cells of Nereis) are stippled. Apical and rosette cells unshaded as in *a*. Trochoblasts around margin. — *c*, Crepidula : shading as in *b*; rosette cells and anterior trochoblasts divided.

Inasmuch as the formation of the peripheral rosette cells occurs late in the cleavage, I have not been able to find the further division of the outer cells of the rosette series in Crepid-

ula which corresponds to the division of the terminals in Nereis, by which the middle cells are formed.

If now we attempt to compare the cells of the molluscan cross with the corresponding cells in Nereis, we find that the basal cells correspond to the *intermediate girdle cells* ($1a^{1,2}$ — $1d^{1,2}$) in Nereis, while the terminal cells are represented by cells which lie outside the prototroch, and, except in the case of the posterior arm, are secondarily separated from the intermediate girdle cells by the products of the trochoblasts, which shove in between the terminals and the intermediate girdle cells. About the time that these cells, $2a^{1,1}$ — $2d^{1,1}$, are formed in Nereis the intermediate girdle cells divide into an inner and an outer part which correspond to the basal and middle cells in the cross of Crepidula. There are thus formed four radiating rows of cells which run out to the prototroch, and correspond, at least in origin, to the arms of the molluscan cross. In the case of the posterior row there is a plain cell series, with basal, middle, and terminal cells exactly as in Crepidula (*cf.* Diagram 13, *a*, also Wilson's Fig. 38). The terminal cell (x^3) in this case is a product of the first somatoblast and is not separated from the middle cell by the prototroch, as is the case in each of the other cell series. The following table indicates what cells in Nereis correspond to the cross cells in Crepidula :

CREPIDULA.	NEREIS.
Apicals	Rosette
Basals	Intermediate Girdle, Inner
Middles	Intermediate Girdle, Outer
Terminals	Post-trochals and x^3

Every cell of the annelidan cross can be identified with the molluscan, and conversely every cell of the molluscan cross can be identified with that of the annelid. Yet on the other hand, with the exception of the apicals, not a single cell of the annelidan cross is found in the molluscan, nor a single cell of the molluscan cross in that of the annelid. In fact, the arms of the molluscan cross lie midway between the arms of the annelidan cross and *vice versa*. The fact is, there are two distinct systems of radiating cell series at the animal pole in both annelids and mollusks, the one lying in the median and transverse

axes, the other midway between these axes. The former is the well-developed cross of the gasteropods, but is not prominent in annelids (the intermediate girdle cells of *Nereis*); the latter is the conspicuous cross of the annelids, but the relatively inconspicuous rosette series of the gasteropods. We have to do, therefore, with two totally different crosses — different in position, structure, origin, and destiny. Wilson says (p. 443): “There is every reason to believe that the annelidan and molluscan crosses are analogous, but not homologous structures, whose origin is in some way connected with the mechanical conditions of cleavage. What these conditions are I am unable to conjecture.” However, if my interpretation of these structures is correct, the crosses as heretofore defined are not even analogous, and ought not to be compared at all.

In conclusion then, the cross observed by Wilson in *Nereis* is not to be compared with the molluscan cross, but rather with the rosette series of *Crepidula*, and conversely the molluscan cross is to be compared with the intermediate girdle cells of *Nereis*, and not with the cross in that animal. To call things which are not to be compared by the same name, and things which are to be compared by different names, would certainly be confusing, and the word *cross* ought therefore to be changed in either the annelid or the mollusk. Since this word was first used in describing the radiating structure in the molluscan egg, and since it has been found in several genera and species of gasteropods, and is, moreover, such a definite structure that its history can be followed very far through the embryology, I shall retain the word *cross* as heretofore used in the case of molluscan eggs, and shall take the liberty of changing the designation of the so-called “annelidan cross,” calling it the *rosette series*.

The cross, as thus defined, is present in the annelid, but is not a prominent structure, as it is in the case of the gasteropods; on the other hand, the rosette series is present in *Crepidula* as well as in *Nereis*, but it divides more slowly than in the annelid, and is therefore composed of fewer cells.¹

¹ In early stages of the cleavage of *Ishnochiton*, Heath finds that the molluscan cross is typically developed and is very prominent, while in later stages it becomes less marked and the rosette series (annelidan cross) becomes as fully developed and almost as prominent as it is in *Nereis*.

The annelidan cross (rosette series) has also been described by Mead ('94) in *Amphitrite*, *Lepodonotus*, and *Clymenella*; and in the case of the first two, the division of the "four cells which form the cross is bilateral," as it is in *Crepidula*, whereas in *Nereis* it is radial.

We find, therefore, in a large number of annelids and mollusks, representing very widely different orders, that there is a peculiar arrangement of cells at the apical pole which takes the form of two crosses whose cells have in the different animals the same origin, the same axial relations, and (as will be shown later), in many cases at least, the same destiny.

What is the significance of these crosses? Are they the necessary result of alternating cleavages, surface tension, and the like, or must we seek their cause in more remote and obscure phenomena? As was just mentioned, Wilson finds that their "origin is in some way connected with the mechanical conditions of cleavage." This conclusion is unquestionable, but that their characteristic and peculiar features are entirely *caused* by such conditions, as such a statement might seem to imply, is very questionable indeed.

In the first place it may be well to call attention to the fact that these radiating structures are not caused by the crowding of cells into the furrows between the macromeres. This is well shown in *Neritina*, *Paludina*, *Crepidula*, and *Nereis*, in which the cross is first formed midway between those furrows. In *Umbrella*, indeed, it is first seen lying over the furrows between the macromeres, — a position which it ultimately takes in *Crepidula*, owing to the rotation of the entire cap of ectoblast, — but there is no probability that even in *Umbrella* the cross is caused by those furrows.

The cross and the rosette series are the direct result of the *position, size, and shape* of their constituent cells. Anything that will satisfactorily explain these three things will afford a satisfactory answer as to the significance of these structures.

The position of cells in general is due to the direction of the cleavages, and to the subsequent rotations of the division products. The shape of cells also may be explained in general as the result of their size and position. The size of cells, however,

is not so easily explained. No phenomenon is more common than the unequal division of apparently homogeneous cells, but none is more difficult of explanation on the grounds of a purely mechanical theory of development. All these general phenomena might be perhaps the result of known mechanical conditions; and yet the combinations, modifications, and coördinations of these processes, which appear in the formation of almost any structure, ultimately require some explanation other than mechanics can as yet supply. This is abundantly illustrated in the whole history of the cleavage of such an egg as that which we are considering, and nowhere better than in the formation of the cross.

Up to the time when there are two cells in each arm of the cross, the position of each cell may be attributed, at least in part, to the regular alternation in direction of successive cleavages. The next step in the formation of the cross is highly peculiar; the basal cells, which were formed by dextrotropic cleavage, divide in a dextrotropic direction in both *Neritina* and *Crepidula*. In *Umbrella*, on the other hand, this division is laetotropic, as it should be, according to the rule that successive cleavages are in opposite directions. Associated with this regular alternation of cleavage in *Umbrella* is the fact that immediately before the division of the basal cells, the turrets divide almost bilaterally; whereas they remain undivided in *Neritina* and *Crepidula*, in which the cleavage of the basals is reversed. I was therefore inclined, at first, to attribute this reversal to the lateral pressure of the undivided turrets upon the basals, but several considerations have convinced me that this cannot be the case; in the first place the basals show no signs of such pressure, being full, well-rounded cells; again the turret cells in *Neritina* are not large enough to exert any considerable lateral pressure upon the arms of the cross; and, finally, even if such pressure were exerted, it would deflect the spindles only a few degrees from the normal position, and would still leave them laetotropic, whereas they are distinctly dextrotropic.

The same considerations are applicable to the history of the posterior arm, where repeated divisions are always in the same direction, as is true of teloblastic growth in general, and also to many of the later cleavages where reversals occur again and

again, especially with the appearance of bilateral symmetry. In all such cases, the direction of cleavage and the consequent position of cells is due to something other than the alternation of cleavage, surface tension, or intercellular pressure. For the present, therefore, one is justified in assuming that these peculiarities in the direction of cleavage, and in the *position* of resulting cells, is the result of intrinsic rather than of extrinsic causes.

This conclusion holds true with especial force in the study of the relative *sizes* of the cells composing the cross, and other adjacent structures. The very small size of the tip cells has been emphasized by Heymons and myself; upon their size depend in part the shape and structure of the entire cross. The more rapid divisions and consequent smaller size of the cells of the anterior, the right, and the left arms, as compared with those of the posterior arm, the great size of the turret cells and of the anterior cell plate, — all these contribute to the most characteristic features of the cross; and yet the known mechanical conditions of cleavage are wholly unable to explain them.

On the other hand, it is certain that the size of many of these blastomeres can be directly correlated with their prospective functions (*e.g.*, the cells of the posterior arm, the turret cells, the apical cells, the anterior cell plate), and while it is not possible at present to explain all the characters of the cross and the rosette series in this way, a strong presumption is created that these structures, like teloblastic rows of cells, are to be explained as a precocious development of certain parts. The cells of the right and left arms and their derivatives have apparently the same fate, while the destiny of the cells of the anterior and posterior arms differs from that of the transverse arms and from each other. The most obvious significance of the cross is that its cells represent the protoblasts of certain structures which are ultimately to lie in the median and transverse axes of the larva. The identity of the right and left arms is correlated with the fact that the organs are identical on the right and left sides. For a long time the anterior arm is identical with the right and left arms; in its later stages, however, it becomes slightly different, and in the end gives rise to somewhat different organs. From an early stage the posterior arm

differs from the other three, and correspondingly we find it gives rise to parts of the embryo wholly unlike those which arise from either of the other arms.

The significance of the cross, therefore, as indeed of all the most important features of the cleavage, is prospective; its cause is to be sought in some peculiarity of protoplasmic structure rather than in any extrinsic mechanical factors.

2. *The Turret Cells (Trochoblasts).*

The turret cells were formed by the first division of the first quartette of micromeres. Until the tip cells of the cross are formed they are much the smallest cells in the entire egg. Gradually, however, they increase in size, until they become much the largest cells of the egg, excepting the yolk cells. This remarkable increase in size is not due to the fact that they grow so much more rapidly than other cells, for this they do not do, but to the fact that their growth is continuous, and not interrupted by any divisions until a very late stage.

The turret cells lie in the angles between the arms of the cross. Until a late stage they are in contact with the apical cells from which they sprung; but with the longitudinal splitting of the arms of the cross and the formation of the rosette series they are pushed away from the apical cells, though they continue to lie in the angles between the arms. The two posterior turrets hold this position as long as they can be recognized at all. The anterior ones are crowded farther and farther outward and downward by the cells derived from the anterior and transverse arms.

I have never seen the turret cells in process of division, but believe that the anterior ones divide at about the stage shown in Figs. 49, 50, Diagrams 9 and 10; in the earlier figures the division has not taken place, in the later ones it has. The posterior turret cells divide very seldom, if at all. They remain very large, much larger than the anterior ones, and lie on each side in the angle between the anterior and posterior branches of the velum; they ultimately assist in forming the walls of the head vesicle. Certain large cells adjoining the posterior turrets appear to have come from the latter by division, but I do not know that this is true.

These cells, which are altogether characteristic in appearance among the gasteropods, have been found in Neritina, Umbrella, four species of Crepidula, Urosalpinx, and Fulgur. In all these cases they are particularly notable because of their small size. Cells of the same origin and position are found in Chiton, Unio, Nereis, Amphitrite, Lepidonotus, and Clymenella. In all the annelids mentioned it has been found that they form either the whole or a part of the prototroch. In four species of Crepidula, at least the two anterior ones form a portion of the preoral velum, and this is probably true of the two posterior ones also. In no other mollusk has their destiny been determined, but it is highly probable that it is the same in all the gasteropods mentioned, since these cells are wonderfully alike in origin, position, size, and general appearance in all these cases. *Considered in the light of their origin, history, and destiny, it is almost certain that the turret cells of the gasteropods are homologous with the trochoblasts of the annelids.*

In all the annelids named these cells divide twice, and then, according to Mead ('94), in Amphitrite, Lepidonotus, and Clymenella, "stop dividing forever." In Umbrella, Unio, and Chiton they have been seen to divide once only.¹ In Crepidula I have never seen them divide, though I believe the anterior ones do divide at a late stage (Fig. 50). In the other forms their divisions have never been seen.

This is certainly a very remarkable history. Here are four cells which divide at most two or three times, and then probably never divide again, while adjoining cells divide many times and continue this process for a long period. In Nereis while these trochoblasts are producing sixteen cells, the apical cells produce twenty-eight; in Crepidula, during the time that they are producing six or at most eight cells, the apical cells give rise to forty-two.

These cells are smaller when formed, and divide much more slowly in the gasteropods than among the annelids. This, I believe, is due to the fact that the velum is established relatively much later among the gasteropods than is the prototroch among the annelids.

¹ In *Ishnochiton* Heath has observed that they divide several times, before entering into the formation of the velum.

The repeated division of small cells like the apical and tip cells, when others like the turrets, ten or twenty times as large, remain undivided, suggests an inquiry into the cause or stimulus of cleavage in a normal egg. The difference between the turret and apical cells, for example, is not to be found in the fact that one is laden with yolk or food material, while the other is not. Both are protoplasmic cells derived from the first quartette of ectomeres, lying on the same side of the egg, for a long time in close contact, with apparently the same conditions of nutrition, growth, and external environment, the differences of size in the early stages being the reverse of those in the later; and yet the smaller cell grows continually and does not divide at all, and the larger cell, while growing no more than the other, divides repeatedly, producing, at the stage shown in Diagram 15, twelve cells, whose total mass scarcely exceeds that of a single posterior turret. What the normal stimulus to cleavage may be is not definitely known, but to any one who will attentively study any definite and regular cleavage it will be abundantly evident, I think, that the stimulus is not to be found in external environment alone, but rather in internal conditions. How any one can follow the history of the blastomeres of an ovum like that of *Crepidula*, and still maintain that the peculiarities of each cell are due entirely to external conditions or to intercellular relations, is more than I can understand. To me it seems absolutely necessary to believe that *between cells with such different histories there must be some internal or constitutional difference.*

The cause of the small number of divisions of these cells and of their large size in both annelids and mollusk is correlated with their prospective destiny. And, at least among the mollusks, I believe that a law might be formulated to the effect that *the size of cells in general, the frequency and direction of their divisions, and the size of the resulting cell products are all correlated with the ultimate uses to which these cells are put.*¹

¹ Lillie ('95) has advanced a similar view in the case of *Unio*, and supports it by a number of observations in which he shows conclusively that there is a close relation between the size of a blastomere and the size of the part to which it gives rise. The ground here taken is merely an extension of Lillie's proposition. It is not always true that the size of a blastomere when first formed is proportional

3. *Organs formed from the First Quartette.*

The following organs, which I have studied with more or less care, are formed from the first quartette: the umbrella, or "head vesicle," an apical plate of ciliated cells, the posterior cell plate, a portion of the velum, the supraoesophageal ganglia, an apical sense organ, a commissure connecting the ganglia with each other and with the apical organ, the cerebro-pedal connectives, and the eyes.

(a) *The Head Vesicle* reaches its maximum development before the veligers escape from the egg capsules; in fact it decreases in size as the velum increases, the walls of the vesicle being drawn out into the velar lobes. In its fully formed condition it is a large bladder-like structure, filled with a transparent fluid. The walls of the vesicle are but one cell thick in early stages, though in later stages a few scattering cells, probably mesoderm, are found on its inner surface. As the head vesicle is formed the apical cells are pushed farther and farther forward, and the vesicle is composed almost entirely of the large ciliated cells which lie posterior to the transverse arms, *viz.*, the posterior turrets and the basal and middle cells of the posterior arm. These cells form a more or less definite structure, lying posterior to the apex, which I have designated the posterior cell plate (P-C., Figs. 74-82).

(b) *The Apical Sense Organ.*—The four apical cells can be still recognized in Fig. 79. In this figure, and also Figs. 78 and 96, it can be seen that these cells are somewhat indented over their outer surface, and have proliferated a few cells inward into the cavity of the head vesicle. This mass of cells, together with the four apical cells from which it arose, forms an organ which soon comes into relation with the supraoesophageal ganglia by means of a strand of cells which grows out from those ganglia. This structure is, I believe, an apical sense organ, and it is located exactly at the point at which the polar

to the size of the part to which it gives rise, as is shown by the case of the trochoblasts cited above, but it is frequently true that the initial size of a blastomere is directly related to the size of the part to which it gives rise *and to the time of its formation.*

bodies were extruded. The apical cells, like many of the surrounding cells, are covered by a coat of fine cilia, but there is no bunch of very large cilia at this point, as in many of the trochophore larvae. An apical sense organ has not hitherto been found in molluscan larvae, I believe.

(c) *The Cerebral Ganglia and Eyes.*—These ganglia are formed on each side of the upper hemisphere, just apical to the row of velar cells and about midway between the anterior and transverse arm, Figs. 78 and 79. Before they begin to form, the cells in this region become quite small by repeated divisions. The method in which the ganglia are formed is shown in section in Figs. 94 and 96, where it is seen that the cells proliferate inward from the surface, and thus form a solid aggregate of cells. Over the area where the ganglia are being formed the ectoderm is slightly depressed, but there is no invagination.

From the position of these ganglia on each side of the anterior cell plate, and in front of the cells derived from the transverse arms of the cross (Fig. 79), it is very probable that they arise from the two anterior rosette series and perhaps in part from the lateral extensions of the anterior arm. In the larva they lie on the ventral side of the coronal plane, and it is therefore probable that they are formed from cells lying originally on the anterior side of the apex.

There are scarcely any data for determining the cell origin of these ganglia in other animals. Von Wistinghausen ('91) states that they are the only derivatives of the first quartette of ectomeres, but Wilson ('92) has shown that this is altogether improbable. In *Nereis*, Wilson derives these ganglia from a broad cell plate (see his Fig. 86 and Diagram 5) running across the apical pole in a coronal direction and extending as far down on each side as the prototroch. The position of this plate is strikingly like that of the ganglia, commissures, and apical organ in *Crepidula* as shown in apical view, Fig. 79; there is scarcely a doubt that these three organs in *Crepidula* are homologous with the "cephalic neural plate" in *Nereis*.

The eyes are formed in connection with the cerebral ganglia as independent involutions of the ectoblast. They lie, as shown in Fig. 104, on the outer side of the cerebral ganglia

and some distance below the surface. The cells of the optic cup which lie farthest to the right and left are the clear lens cells. The cells at the bottom of the cup contain a black pigment which is laid down at their inner ends.

(d) *The Cerebral Commissure.* Figs. 76, 79-82, 96.—The commissure between the two ganglia is formed by an outgrowth of elongated cells from the ganglia themselves. These outgrowths meet at the apical organ, forming a V-shaped structure, the apical organ lying at the apex of the V. Later the two limbs of the V fuse farther and farther away from the organ, forming a Y, and finally a T. The bar of the T is the cerebral commissure, and its stem represents the fused processes which run from the middle of the commissure to the apical organ. The fused character of this process is clearly seen in all the later stages, where its double nature is plainly visible; each half is composed of only a single row of elongated fusiform cells. Still later, with the degeneration of the apical organ, the stem of the T disappears completely, leaving only the commissure.

Similar strands of cells are found in other trochophore larvae, *e.g.*, in *Teredo* ('80) and *Eupomatus* ('86), according to Hatschek, but they are said to be muscles, and not nerves. The fact that in *Crepidula* these strands of cells arise from the cerebral ganglia, and form, in part, the cerebral commissure, is sufficient to prove that they are not muscles. I have, besides, carefully studied the living embryos with regard to this point, and have never seen any evidence of contraction in these cell strands. I am therefore convinced that they are nervous structures, and am consequently inclined to assign to the apical organ, to which these cell strands run, a sensory function.

(e) *The Cerebro-pedal Connectives.* Figs. 76, 80-82, 97, 104.—A process of cells, similar to that which forms the cerebral commissure, grows out from the ventral side of each cerebral ganglion, and extends on each side of the oesophagus into the foot, where it comes into close contact with the ectoderm at the sides of the foot. This is the cerebro-pedal connective. It is formed before there are any pedal ganglia, and it is possible that those structures arise from cells which have come down from the cerebral ganglia with the connective cells.

Even in the oldest stages which I have drawn, Fig. 104, there is no indication of a pedal ganglion, except a few cells which lie between the ectoderm and the otocysts, and which have evidently come from the connectives.

(f) *The Apical Cell Plate.*—The origin of the apical plate from seven cells of the anterior arm of the cross has already been described (p. 91). These cells become covered with a coat of fine cilia, and form a very definite plate, extending from the apical organ to the velum. They are especially notable in that they remain very large, and do not divide during a period when all the surrounding cells are dividing rapidly, and are relatively quite small. In later stages, Figs. 65 and 67, the anterior apical cell is crowded forward between the basal cells of the anterior arm, and in still later stages, Fig. 79, the inner basal cells divide, and two other large cells (probably derived from the outer apicals) are found on each side of the four apicals. I have followed this plate of cells through to the free veliger stage, but have not determined its ultimate destination in the post-larval period.

A plate of such definite and peculiar structure must have, I think, some special significance, and I believe it deserves to rank as a larval organ, though I do not know what function it subserves. I have called it the "apical plate" because of its position and structure, and have not intended thereby to assert its homology with the "Scheitelplatte" of the annelid trochophore. Its resemblance to the "Scheitelplatte" is suggested by its position, by its being covered with cilia, and by its relation to the apical thickening, which forms the apical organ. It is unlike the "Scheitelplatte," as described by Hatschek ('78), in that it lies chiefly in front of the apical pole, and does not form the supraoesophageal ganglia. On the other hand, as has been pointed out (p. 110), there is no doubt that the "cephalic neural plate" of *Nereis* corresponds in position, in destiny, and probably in cell origin, to the cerebral ganglia, commissures, and apical organ in *Crepidula*.

(g) *The Preoral Velum (Prototroch).*—The velum is first plainly recognizable at a comparatively late stage, Figs. 65 *et seq.*, and at a time when there are several hundred cells present.

Consequently I have found it impossible to trace with certainty its entire cell origin. Nevertheless the derivation of some of the velar cells can be established with great probability because of their relation to the arms of the cross. I shall describe here merely the preoral portion of the velum, or the prototroch, which is derived in part from the first quartette.

The first velar row, or prototroch, is derived on the anterior side from the cells immediately surrounding the cross. These cells are: (1) the anterior turrets between the arms of the cross, and (2) some of the second quartette cells at the ends of the arms. These cells are shown in position in Fig. 50, forming a single row of cells surrounding the cross on its anterior side. The turret cells, which, as we have seen, correspond in origin to the trochoblasts of the annelids, form the portions of the prototroch between the arms, while the portions at the ends of the arms are derived from the second quartette (see p. 132).

In Figs. 77, 78, and all the later stages, it can be plainly seen that the velum is divided on the dorsal side of the embryo into a posterior branch, P-B, and an anterior one, A-B. The former runs around the edge of the umbrella, and surrounds all of the first-quartette cells; the latter runs up on each side from the edge of the umbrella nearly to the apical organ. This anterior branch, therefore, is composed of cells derived from the first quartette. The position of the cells which form this branch of the velum, relative to the large ciliated cells of the posterior cell plate, P-C, Figs. 77, 78, *et seq.*, shows that they are derived chiefly, if not entirely, from cells of the transverse arms of the cross. As the velum belongs largely to the second quartette, we shall consider its origin, structure, and relationships more fully in the section devoted to those cells (p. 132).

V. HISTORY OF THE SECOND AND THIRD QUARTETTES OF ECTOMERES.

In *Crepidula* there are no prominent landmarks among the cells of these quartettes, as there are in *Nereis*, *Umbrella*, and *Unio*, and on this account it is difficult to follow the lineage of these cells very far. I have been compelled to use the arms