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

of the cross as such landmarks; and as long as any portion of them can be seen the cells of these quartettes can be identified, but when the ectoblast has grown around the egg so that the arms of the cross are no longer visible from the ventral side, I have found it impossible to identify individual cells. Consequently I have not traced many of the cells of this quartette directly to the organs which they form, though I have followed the lineage until there are eleven cells of the second quartette in each quadrant and six of the third, or sixty-eight cells in all. A few cells of the second quartette could be traced farther than this, owing to their relation to the anterior arm of the cross.

The derivatives of these two quartettes form all of the ectodermal covering of the body posterior to the prototroch, and in addition they give rise to the ectodermal portions of the following specific structures: a large part of the velum; the blastopore, stomodaeum, and mouth; a region of apical growth at the posterior end of the embryo, the anal cells and proctodaeum, the external excretory cells, the shell gland, foot, and otocysts, the branchial chamber, gills, and larval heart. It will thus be seen that a large part of the important organs, both of the larva and of the adult, are derived from these two quartettes.

The prototroch forms a convenient and fairly accurate boundary between the cells of the first quartette on the one side and those of the second and third quartettes on the other. A glance at Figs. 78 and 80 will show that the portion of the larva posterior to the velum is much larger than that anterior to it, and at the time when the larva changes into the adult the portion of the body anterior to the velum becomes very small and almost disappears, while the region posterior to the velum gives rise to practically the entire body.

1. *The Second Quartette.*

In the formation of the adult body this group of cells is perhaps the most important of any in the entire egg. Knowing this fact, I have done my best to trace the lineage of these cells as far as possible, but in spite of prolonged effort I have not been able to carry the lineage beyond a stage in which

forty-four cells of this quartette are present ; this has been due both to the great number of cells in the entire egg and to the lack of landmarks to which I have already referred.

The first division of the cells of the second quartette has been described (p. 63) ; by it each cell is equally divided in a dexiotropic direction into right and left halves ($2a^1$ and $2a^2$, etc.), Fig. 18 and Diagram 4.

At the second division, which was described on p. 83, the right half is unequally divided, in a laeotropic direction, into a small upper and a large lower cell ($2a^{1.1}$ and $2a^{1.2}$, etc.), Figs. 26–28 and Diagram 6. The upper cell in each quadrant forms the terminal cell in one of the arms of the cross. At the same time, Figs. 26–28 and Diagram 6, the left half ($2a^2$, etc.) divides into an upper and a lower cell ($2a^{2.1}$ and $2a^{2.2}$, etc.) by a cleavage which is slightly laeotropic, almost radial. Of these two cells the upper one is slightly the larger. There are now four cells of this quartette in each quadrant, a right upper and lower (the right upper is the tip cell) and a left upper and lower, Diagram 10 and Figs. 29–33.

Next the right lower and left upper ($2a^{1.2}$ and $2a^{2.1}$, etc.) divide simultaneously in each quadrant, though in the posterior quadrant the division is later than in the other three, Figs. 35, 38, 39, and Diagram 7. In each case the direction of the cleavage is slightly laeotropic in the right cell and dexiotropic in the left. The previous division of the right half (to form the tip cells) was laeotropic, so that here we have another violation of the law of alternating cleavages. By this division six cells in each quadrant are formed,—an upper, middle, and lower right, and an upper, middle, and lower left, Diagram 7 and Figs. 40, 43.

The first of these six cells to divide is the upper right or the tip cells in the arms of the cross. The tip cell of the posterior arm divides before the others, Fig. 42, in a slightly dexiotropic direction. The other tip cells divide a little later, Figs. 44, 45, in a direction which is more or less variable, being usually, however, dexiotropic in the left and anterior arms and laeotropic in the right. Inasmuch as all these cells were formed by laeotropic cleavage, the subsequent division of one of them

in the same direction is a violation of the rule of alternating cleavages; but to just the extent that this cleavage ceases to be perfectly spiral, it becomes bilateral. This division of the tip cells is an equal one, but the posterior tip cells are much larger than any of the others. At a later stage, Fig. 53, the two tip cells of the posterior arm again divide, and this time also in the same direction as the preceding cleavage. While the law of alternation is thereby violated, bilateral and teloblastic cleavages are established.

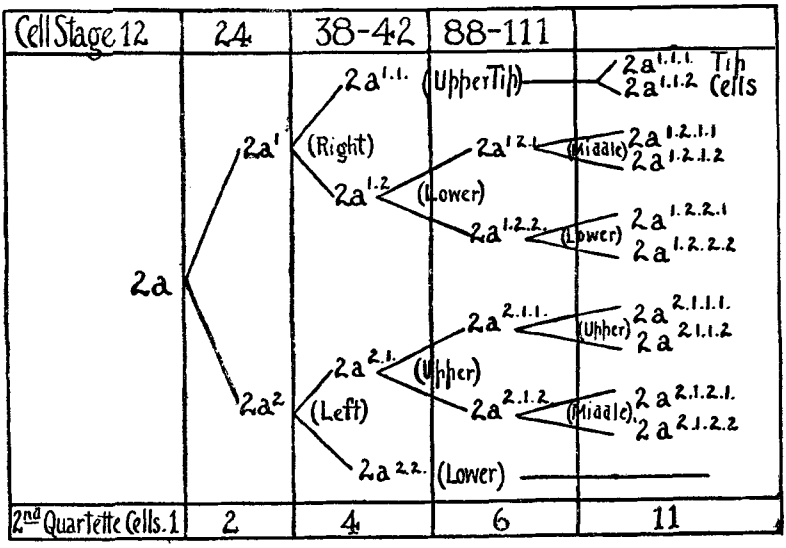
Very soon after this division of the tip cells, the lower right cell ($2a^{1.2.2}$, etc.) in each quadrant divides in a laeotropic direction into two cells ($2a^{1.2.2.1}$ and $2a^{1.2.2.2}$), of which the upper is somewhat the larger; and immediately following this division the right middle cell ($2a^{1.2.1}$, etc.) divides in the same direction into two cells ($2a^{1.2.1.1}$ and $2a^{1.2.1.2}$, etc.), of which the upper one is slightly the smaller, Figs. 46, 47. Coincident with this last division the left upper and middle cells in each quadrant ($2a^{2.1.1}$ and $2a^{2.1.2}$, etc.) divide in a horizontal direction into approximately equal products, Figs. 46, 47, and Diagram 8.

Of the six cells described on the previous page and shown in Diagram 7, all have now subdivided except the lower left one in each quadrant. There are thus formed eleven cells of the second quartette in each quadrant, or forty-four cells in all.

The divisions of this quartette have been in pairs both as to time and direction of cleavage. The table on the following page summarizes the history of this quartette.

Beyond this stage I have not traced the lineage of the entire quartette. I believe, however, that the progeny of some of these cells can be recognized at a more advanced stage, though I have not seen the spindles by which they are formed. In Fig. 56, for example, each of the two terminal cells in the right and left arms of the cross ($2a^{1.1.1.2}$ and $2c^{1.1.1.2}$, etc.) has divided in a bilateral way, forming a row of four cells running around the end of each arm. The terminal cells of the anterior arm are very small and apparently do not divide ; their peculiar history in C. plana has been described (p. 89). In Fig. 50 the cells lying just anterior to the tip cells are probably $2b^{1.2.2.1.1}$ and $2b^{1.2.2.1.2}$, and, accordingly, the large cell lying peripherally to

these ($2b^{2.2}$, Fig. 56) should be the right lower cell shown in Fig. 47. Still the whole identification of the cells of this region must be considered as more or less doubtful. It is, however,



much more certain that the large cells $2b^{1.2.2.1.1}$ and $2b^{1.2.2.1.2}$ of Figs. 62, 63, 69, 70, 71 are the same cells in each of these cases, and that they are the protoblasts of the velum in this region of the embryo.[1]

Comparisons.

Blochmann ('81) has described the divisions of the cells of this quartette in Neritina up to the stage when there are four cells in each of the quadrants, but while his figures agree perfectly with Heymons' ('93) work on Umbrella and my own on Crepidula, his interpretation of the figures is at variance with the results of all recent studies on the cell lineage of gasteropods. Reason has already been given (p. 65) for believing that Blochmann was mistaken in his derivation of some of these cells; and a correction of his interpretation has been suggested which, while finding confirmation in his figures, would bring his account into agreement with the work, particularly, of Heymons, Kofoid, and myself.

[1] See Note p. 204.

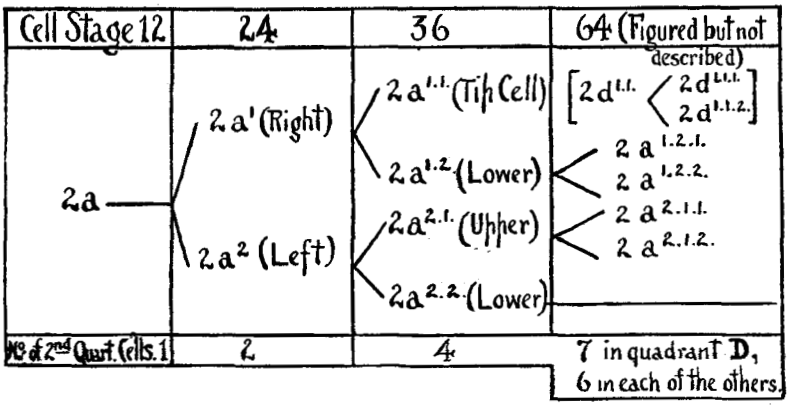
Although no description is given of the further history of these cells in Neritina, Blochmann figures a much more advanced stage (his Fig. 56), in which only the macromeres and the "Urvelarzellen" are labelled. Although he has not described the derivation of any of the twelve new micromeres in this figure, so faithfully is it drawn, that it is possible by comparing it with similar stages in Crepidula to determine the origin of each one of these new micromeres. I have reproduced this figure in Diagram 12, *b*, and inasmuch as its cells are not labelled in the original I have simply designated the cells as in Crepidula, and have indicated their origin by arrows.

It will be seen that two new cells in each quadrant lie just outside the turret cells and between adjacent arms of the cross. These cells correspond, I believe, to the ones which in Crepidula I have called the *middle right* ($2a^{1.2.1}$, etc.) and the *upper left* ($2a^{2.1.1}$, etc.). If this interpretation is correct, there are at the most advanced stage in which the cells can be identified six cells of the second quartette in each quadrant of Neritina. These cells correspond in every respect to the six cells of this quartette which are found in each quadrant in Crepidula, *viz.*, the *lower*, *middle*, and *upper right*, and the *lower*, *middle*, and *upper left*.

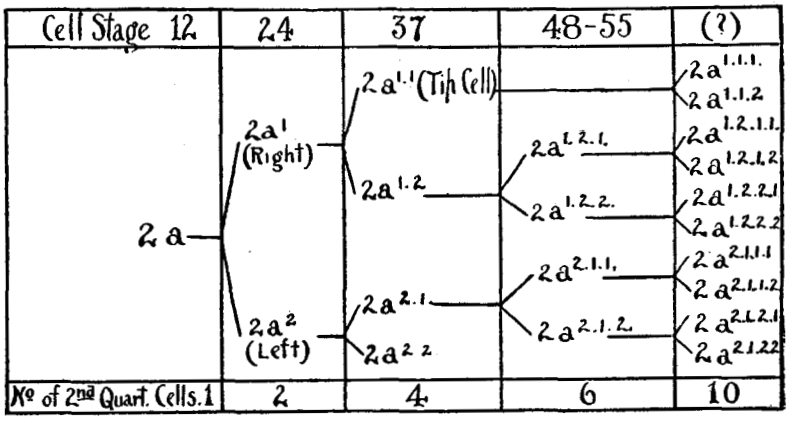
The following table shows the divisions of this quartette as given by Blochmann, and the corresponding cells in Crepidula enclosed in brackets :

Cell Stage 12	24	28	36 – 1
$a^2(2a)$	$a^I_2(2a^1)$	$a^I_2(2a^1)$	$a^I_2(2a^{1.2})$
			a^{III}_2 (2a$^{1.1}$ Tip Cell)
	$a^2(3a)$	$a^{II}_2(1a^{1.2})$	$a^2(3a^1)$
			$a^{IV}_2(3a^2)$
№ of 2nd Quart. Cells. 1	2	3	5

Adopting the amendments which have been suggested, the divisions of 2a in Neritina are as follows :



Heymons ('93) has observed every division of this quartette in Umbrella up to the formation of ten cells in each quadrant (he merely mentions the last two divisions, and does not figure or describe them). *These divisions are cell for cell exactly like those in Crepidula. Even the direction of every cleavage and the size of all the resulting cells are the same.* This wonderful and long-preserved resemblance is more particularly shown in the table of cleavages in Umbrella.

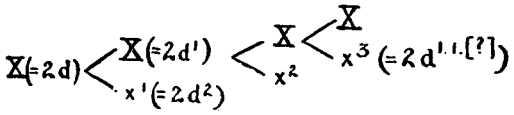


With the exception of one division of the upper left cell in each quadrant, Heymons has seen every division of this quartette which I have observed in Crepidula. Inasmuch as he merely mentions the fact that he has observed divisions of the

cells $2a^{1.1}$, etc. (the tip cells), and does not show them in his figures, I cannot determine whether the posterior arm in Umbrella differs from the other arms, as it does in Crepidula. In conclusion, the wonderful resemblance between Umbrella and Crepidula in the history of the first quartette is shown to a still greater extent in the history of the second.

In both Nereis and Unio the cells of this quadrant D are unlike those of the gasteropods described. The cell 2d is called by Wilson ('92) the "first somatoblast"; he has followed it through a great many divisions, and has established the fact that it gives rise to a large part of the ectoderm of the trunk. This cell has a remarkably similar history in Unio (Lillie, '95). It divides repeatedly, always in a bilateral way, and apparently gives rise to parts of the body corresponding to those which come from this cell in Nereis.

In our present state of knowledge it is useless to attempt to compare the bilateral cleavages of the first somatoblast in Nereis and Unio with the spiral cleavages of the cell 2d in Neritina, Umbrella, and Crepidula. A few of the earlier division products may perhaps be compared; *e.g.*, in both Nereis and Unio the first three cleavages give rise to similar cells, and at least two of these cells, possibly three, may be compared with the products of 2d in the gasteropods, as is indicated in the following table:



From its peculiar position both with regard to the somatoblast and the cells which correspond to the molluscan cross, I believe that x^3 is the equivalent of the posterior tip cell in the gasteropods.

The division of the other members of the second quartette, *i.e.*, 2a, 2b, and 2c, can be compared with the divisions in the gasteropods much more satisfactorily. In Nereis the divisions of these cells are shown by the following table giving the lineage of 2a:

Cell Stage 16	32	58
2a	2a¹	2a¹·¹·¹, 2a¹·¹·² } Post Trochal cells.
	2a²	Left Stomatoblast.
№ of 2nd Quart Cells. 1	2	3

The cell $2a^{1.1}$ is the tip cell in Crepidula, and lies in the row of velar cells, not posterior to it. This is not however a profound difference, as will be shown in the section devoted to the velum, since at most it means that at certain points the velum in Crepidula lies *one cell* farther from the apical pole than in Nereis. The cell $2a^2$, with the corresponding cells $2b^2$ and $2c^2$, forms the stomodaeum in Nereis. In Crepidula a very long time intervenes between the origin of the cell $2a^2$ and the formation of the stomodaeum, and I cannot trace the derivatives of this cell into that structure.

In general it may be said that the divisions of the cells 2a, 2b, and 2c, as far as they have been followed, are very much the same in the annelid and gasteropod.

In Unio Lillie ('93) has found that the cell $2a^1$ has a peculiar history: the right half, $2a^2$, takes part in the formation of the larval mantle; the left half, $2a^1$, which in Nereis is the left stomatoblast, moves into the cleavage cavity and there divides, giving rise to the mesoblast which enters into the larval organs. In Crepidula a similar larval mesoblast cell arises in each of the quadrants A, B, and C, and probably from the cell groups derived from 2a, 2b, and 2c (see p. 149). Because of its peculiar history the divisions of the cell $2a^1$ in Unio are unlike those of the corresponding cells in the other quadrants and also unlike the divisions of 2a in any other animal hitherto described. The divisions, however, of 2b and 2c are like those in Neritina and the other gasteropods already described, as the following table of the lineage of 2b in Unio will show:

Cell Stage 12	22	38
2b	$2b^1$	$2b^{1.1.1}$, $2b^{1.1.2}$ } Larval Mantle.
	$2b^2$	$2b^{2.1.}$, $2b^{2.2}$ } Larval Mantle.
1	2	4

In summing up the history of the second quartette attention should be called to the fact that in the gasteropods, which have been studied with reference to the cell lineage, there is no marked difference in size between the members of this quartette, and accordingly the divisions up to the time when there are eleven cells in each quadrant are almost identically the same in each of the four groups. On the other hand, in the annelids generally and in Unio, at least, among the mollusks, the posterior member, 2d, is much larger than any of the others; its divisions are bilateral and more numerous than in the corresponding cells of the other quadrants. This difference seems to be due to a shortening of the development and a consequent precocity in the segregation of materials destined to form the principal organs of the body. There is evidence, as will be shown later, that essentially the same organs develop from the cell 2d in Unio and Crepidula; the difference therefore in this case is not one of material substance or destiny but rather a time difference according to which the development of 2d in Unio is compressed into a much smaller number of cleavages than in the case of Crepidula.

2. *The Third Quartette.*

All that has been said of the difficulties of tracing the cells of the second quartette is true in still greater degree of those of the third. The early divisions of this quartette are much slower than those of the second, and there are no distinguishing marks by which the cells may be known. I have therefore been unable to trace this quartette beyond the stage in which it gives rise to six cells in each quadrant, or twenty-four cells in all.

The first division of this quartette occurs at the stage when there are twenty-nine cells present. Before the division has been completed in all the quadrants the first quartette has divided twice and the second three times. The cleavage is not simultaneous in all the quadrants, the order of division being 3d, 3c, 3b, 3a (Figs. 25–28). The direction of the cleavage is nearly radial, though after the cleavage has

occurred it is seen to be plainly laeotropic in 3a, 3b, and 3c and dexiotropic[1] in 3d, *i.e.*, the cleavage is nearly bilateral on the posterior side of the ovum ; it is not purely bilateral, because the lower division product, $3c^2$, lies nearer the mid line on the right side than does the corresponding cell, $3d^2$, on the left, Figs. 29–35.

This is but another illustration of the fact that bilaterality first appears on the posterior side of the egg, that it is due to the change in direction of the cleavage of one out of four cells, and that it is not perfect when it first appears, but is merely a deviation from the spiral type toward the bilateral. In this case also, as in every other, the oblique character of the cleavage is much more pronounced after the daughter cells are formed than during the nuclear division.

By this first cleavage of the third quartette there is formed an upper and a lower cell in each quadrant. The lower cell ($3a^2$, etc.) is a little smaller than the upper ($3a^1$, etc.).

The next division of these cells occurs at the stage shown in Figs. 36 and 38. The upper cells of this quartette on the posterior side of the egg ($3c^1$ and $3d^1$) divide before the others and in a bilateral manner, Fig. 36. A little later, Fig. 38, the corresponding cells on the anterior side of the egg ($3a^1$ and $3b^1$) divide in a dexiotropic direction. There is now one lower cell and a right ($3a^{1.1}$, etc.) and left ($3a^{1.2}$, etc.) upper cell of this quartette in each quadrant.

Next the lower cell divides into right ($3a^{2.1}$, etc.) and left ($3a^{2.2}$, etc.) halves in each quadrant, Fig. 43 and Diagram 7. This division is slightly laeotropic in the anterior quadrants but bilateral in the posterior ones.

The outer products of this division on the posterior side of the egg ($3c^{2.1}$ and $3d^{2.1}$) then divide bilaterally into upper and lower products, $3c^{2.1.1}$ and $3c^{2.1.2}$, $3d^{2.1.1}$ and $3d^{2.1.2}$, Fig. 45.

About the same time the outer upper cells in the posterior quadrants ($3c^{1.2}$ and $3d^{1.2}$) divide into upper and lower products, ($3c^{1.2.1}$ and $3c^{1.2.2}$, $3d^{1.2.1}$ and $3d^{1.2.2}$) Figs. 44 and 45.

[1] The cleavage of this cell is not always reversed, for in some cases the division of the nucleus may take place in the usual, *i.e.* laeotropic, direction, and the daughter nuclei may lie in this position relative to each other and yet the cell body may show reversal of cleavage, *e.g.*, $3d^2$ Fig. 35.

Then the upper cells of the anterior quadrants ($3a^{1.1}$, $3a^{1.2}$, $3b^{1.1}$, $3b^{1.2}$) divide in a dexiotropic direction into the cells $3a^{1.1.1}$ and $3a^{1.1.2}$, $3a^{1.2.1}$ and $3a^{1.2.2}$, etc.

There are thus formed two upper, two middle, and two lower cells in each of the quadrants A and B, and two upper, one middle, and two lower cells in each of the posterior quadrants, C and D (see Diagram 8). These facts are brought together in the following tables, giving the lineage of 3a and 3d ; 3b is precisely like 3a, 3c like 3d.

Cell Stage	34	60–77	109
3a	$3a^1$ Upper	$3a^{1.1}$ Right	$3a^{1.1.1}$, $3a^{1.1.2}$ (Middle)
		$3a^{1.2}$ Left	$3a^{1.2.1}$, $3a^{1.2.2}$ (Middle)
	$3a^2$ Lower	$3a^{2.1}$, $3a^{2.2}$	
1	2	4	6
3d	$3d^1$ Upper	$3d^{1.1}$ (Inner) (E), $3d^{1.2}$ (Outer)	$3d^{1.2.1}$
			$3d^{1.2.2}$
	$3d^2$ Lower	$3d^{2.1}$ (Outer), $3d^{2.2}$ (Inner)	
1	2	4	5

I have never seen the cells $3c^{1.1}$ and $3d^{1.1}$ divide, though they become quite large and the corresponding ones $3a^{1.1}$ and $3b^{1.1}$ do divide at the stage shown in Figs. 38 and 40. Every division of 3d and 3c is bilateral, except the first, which is transitional between the spiral and the bilateral. During this time the only other cells of the ectoblast which show bilateral cleavage are the tip cells in two of the arms of the cross, *viz.*, $2c^{1.1}$ and $2d^{1.1}$.

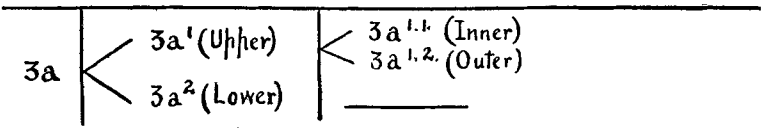
This is the history of the third quartette as far as I have followed it. It is particularly notable, in that bilateral symmetry within the ectoblast first appears in these cells, and that while all the other cells are dividing spirally the cells of this quartette in the two posterior quadrants always divide bilaterally.

Comparisons.

Blochmann ('81) has described the first division of the third quartette in Neritina (according to his designations the cells are a_2, $a^{IV}{}_2$, b_2 and $b^{IV}{}_2$, etc., but following the modification which I have suggested, they are, in the nomenclature of this paper, $3a^1$ and $3a^2$, $3b^1$ and $3b^2$, etc.). The cells lie closely pressed into the furrows between the macromeres; their first cleavage is apparently radial, and the lower cell product ($3a^2$, etc.) is smaller than the upper (Blochmann's Figs. 51 and 53). In passing, I merely call attention to the fact that this cleavage closely resembles the first division of the third quartette in Crepidula.

Blochmann gives no further history of these cells in Neritina, but his Fig. 56 shows what I believe is the second division of the third quartette. If my interpretation of this figure, which is given in Diagram 12, *b*, is correct, the upper cell in each quadrant ($3a^1$, $3b^1$, $3c^1$, $3d^1$) divides bilaterally in each case, giving off a smaller cell toward the mid line of the embryo. This division is in most regards like the corresponding one in Crepidula, but with this interesting point of difference: in Neritina all the cells of this quartette, on the anterior as well as on the posterior side, divide bilaterally. As in Crepidula, bilaterality appears most marked in the cells of the third quartette, but it is characteristic of all the cells of the quartette, and not merely of those of the two posterior quadrants.

The further history of these cells cannot be followed in Blochmann's figures. The following table presents a summary of the cleavages of the third quartette in Neritina:



The divisions of the third quartette in Umbrella are wonderfully like those in Crepidula. Heymons describes the direction of the first division as follows (p. 253): "Die Spindeln sind rechtwinkelig zur Dorsoventralachse des Eies gestellt," *i.e.*, as

his figures show, the spindles are placed radially. The lower cell ($3a^2$, etc.) in each case is smaller than the upper ($3a^1$, etc.), just as in Crepidula. After their formation, the lower derivatives move in a laeotropic direction, and the cleavage might therefore be considered as spirally dexiotropic. (The direction of this cleavage is not clearly marked in Heymons' figures, and, judging by his Figs. 8 and 12, it seems to me that the cleavage of 3c and 3d might be considered laeotropic. If this is really a dexiotropic cleavage, it is another violation of the alternation of cleavages, since the preceding cleavage was dexiotropic.)

The next division of this quartette is peculiar, and closely resembles the same cleavage in Crepidula. At the 38-cell stage, the cells $3c^1$ and $3d^1$ divide before the cells $3a^1$ and $3b^1$, and in a bilateral manner. Exactly this same thing happens in Crepidula. In Umbrella, the two products of this division lying nearest the mid line are the "Exkretzellen," or protoblasts of the larval excretory organs, and are designated E and E^1 by Heymons. The cells formed by this division ($3c^{1.1}$ (= E) and $3c^{1.2}$, $3d^{1.1}$ (= E^1) and $3d^{1.2}$), are large and clear; they have the same characteristics in Crepidula.

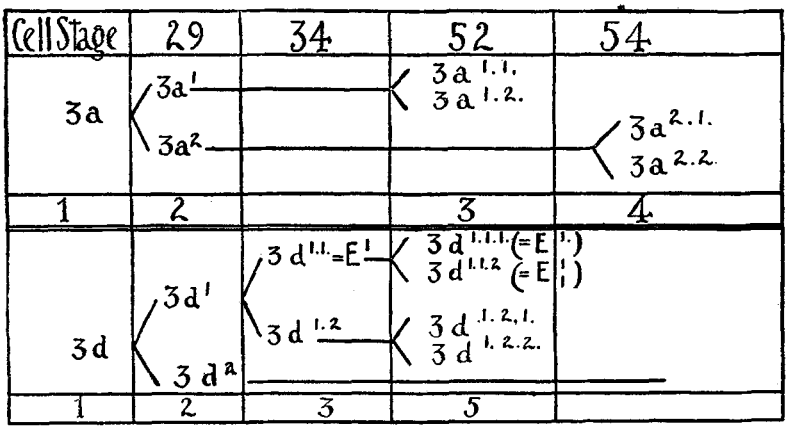
The corresponding divisions in the anterior quadrants, A and B, occur much later, *viz.*, at a stage when there are 52 cells present, and the cleavage is slightly laeotropic. In Crepidula, this cleavage occurs soon after the divisions of the posterior quadrants; and the spindles are nearly horizontal, as they are in Umbrella, but slightly dexiotropic instead of laeotropic. (From the position of the two cell products after the division, as shown in Heymons' Figs. 19 and 20, I should be inclined to consider this cleavage as slightly laeotropic, almost bilateral, in Umbrella.)

At the next cleavage there is a slight disagreement between Umbrella and Crepidula. According to Heymons the two upper cells in the posterior quadrant ($3c^{1.1}$ (= E) and $3c^{1.2}$, $3d^{1.1}$ (= E^1) and $3d^{1.2}$) divide in nearly a vertical direction, giving rise to two small cells on each side of the mid line, which lie alongside the lower cells $3c^2$ and $3d^2$. A little later the cells $3a^2$ and $3b^2$ divide as they do in Crepidula, but $3c^2$ and $3d^2$ do not divide. In Crepidula, on the other hand, all the lower

cells ($3a^2$, $3b^2$, $3c^2$, $3d^2$) divide at nearly the same time, and soon after, the outer upper cells in the quadrants C and D ($3c^{1.2}$ and $3d^{1.2}$) divide in nearly a radial direction, while $3c^{1.1}$ and $3d^{1.1}$ do not divide. In shape and position the cells resulting from these divisions are almost identically the same in Umbrella and Crepidula, though the method by which they arise is somewhat different in the two cases.

Heymons has observed two further divisions of his cells $c^{1.1.1}$ and $d^{1.1.1}$ ($\dot{E}$ and E^1), *i.e.*, of the two upper cells in the quadrants C and D; but since I have not observed these divisions in Crepidula, I need not give a detailed description of them here.

The cleavage of the third quartette in Umbrella may be compared, at a glance, with the cleavage of the same cells in Neritina and Crepidula by means of the following table, which gives the lineage of 3a and 3d in Umbrella:



When we come to sum up the resemblances between Umbrella and Crepidula in the history of the third quartette, we find the same remarkable similarity which characterizes the cells of the other quartettes. Owing to the fact that bilateral symmetry appears in the posterior cells of this quartette (3c and 3d) the division of these two cells is highly peculiar, but all these peculiarities (at least as to the cell products, if not as to the method of their formation) are point for point exactly

alike in Crepidula and Umbrella. These resemblances are so minute and so long continued that they form a fitting climax to the many similarities which have been pointed out heretofore.

The divisions of the third quartette have not been followed by Wilson, Lillie, or Kofoid.

3. *Organs formed from the Second and Third Quartettes.*

As was indicated in another place (p. 114), all the organs of ectodermal origin lying posterior to the first row of velar cells are derived from the second and third quartettes, and a portion even of the foremost row of velar cells comes from the second quartette; nevertheless I have not been able, save in a few cases, to trace individual cells of these quartettes directly to the organs which they form. However, many of the organs of this region can be derived, in great probability, from certain *groups* of cells.

As is shown in Diagram 8, which is the latest stage to which the lineage of the whole ectoblast was traced, the first quartette occupies the apical region of the egg, and is surrounded by a broad belt of cells derived from the second and third quartettes. The cells of the second quartette lie at the ends of the arms of the cross, and approximately over the first and second cleavage furrows, which are still visible between the macromeres. The cells of the third quartette alternate with those of the second, and lie approximately halfway between the first and second furrows. In each quadrant the third quartette touches the first by only a single cell, but the cell group grows broader as it extends out toward the periphery of the egg; the second quartette is as broad where it touches the first quartette as at the periphery.

Since from this stage onward there is no extensive rotation of the cells around the egg axis, it is possible to locate some of the organs within certain of these cell groups. Other organs, particularly those near the middle of the ventral surface, cannot be traced even to these different cell groups with any degree of certainty, as I do not know what part the cells of the second and third quartettes take in the closing of the blastopore.

(a) *Blastopore, Stomodaeum, and Mouth.* — The ectoblast extends over the yolk from all sides at about the same rate, in consequence of which the blastopore closes near the middle of the ventral side. However, the *growth* of the ectoblast does not take place at the same rate in all directions, as is clearly shown by the fact that the apical cells do not lie opposite the blastopore at the time when it closes, but at the anterior end of the embryo, Fig. 65. The angular distance between the apical cells and the blastopore in this figure is less than 90° on the anterior side, while it is more than 270° between the same points in the opposite direction. This greater growth of the ectoblast on the posterior side of the egg must take place entirely in the cells of the second and third quartettes, since at this stage the growth of the first quartette is greater anterior to the apical cells than posterior to them. This unequal growth does not cause the blastopore to close more rapidly at its posterior side, but it does change the position of the apical pole, though the ventral pole remains fixed until after the closure of the blastopore.

At first the blastopore is not circular in outline; in fact, from the time when the germ layers are fully segregated, Figs. 42, 43, the cells of the third quartette in each quadrant lie slightly nearer the ventral pole than those of the second. This advance is somewhat increased in Fig. 47, so that the outline of the edge of the ectoblast is notched at four points, corresponding to the second quartette cells, and protrudes at the four intermediate points, which correspond to the third-quartette cells. In a later stage, Fig. 52, when the advancing edge of ectoblast can be seen from the ventral side of the egg, its notched character is still more apparent, the four notches forming the angles of a regular quadrangle. The angles of this quadrangle lie over the first and second cleavage furrows; at the posterior angle there is a broad recess in the lip of the blastopore, and within this recess are the four enteroblasts still uncovered by the ectoblast (see also Fig. 48).[1]

[1] The quadrangular form of blastopore has been described by Wilson in Nereis; and in that animal, as in Crepidula, the angles lie within cell groups derived from the second quartette, while the sides are formed by cells of the third quartette.

From this time on the blastopore closes from the sides more rapidly than from the anterior and posterior ends, and as a consequence the quadrangular shape is lost, and the blastopore becomes an irregular oval, Figs. 54, 57, 61, and then an elongated slit-like opening, Figs. 58, 60, 63. Finally both the anterior and posterior ends of the slit close, and there is left a narrow pore, Figs. 65, 66, 71, 72. Immediately around this pore there is a depression of the ectoblast, Figs. 65, 73, which is most extensive on the anterior and lateral sides The outlines of this depression become sharply marked, forming the fundament of the mouth; and its inner edges, especially the two lateral boundaries, turn inward as shown in Fig. 68, forming the fundament of the oesophagus or stomodaeum. For a brief period the stomodaeum is closed at its inner end, Fig. 88; but it soon opens again at the very point at which it closed, Figs. 90 *et seq.*, and thereafter remains in open communication with the cavity of the mesenteron. It is at first very short, Figs. 90, 91, but later becomes a long tube, Figs. 92, 93, 95. When it first begins to elongate, it is directed anteriorly from the mouth-opening to the mesenteron, so that it opens into the anterior part of that cavity, Fig. 92. In later stages, with the growth of the foot, the expansion of the shell gland, and the enlargement of the whole region posterior to the velum, the mouth-opening is pushed farther and farther forward, the yolk cells are shifted backward, and the whole direction of the stomodaeum is reversed, so that it runs posteriorly from the mouth-opening to the mesenteron, Figs. 78, 93, 95. Finally, with the greater development of asymmetry the inner end of the stomodaeum is moved slightly to the right, as shown in Fig. 82.

Throughout its entire length the stomodaeum is composed of columnar, ciliated cells, and along its posterior wall there is a double row of large clear cells, with cilia larger than usual, which is directly continuous with some large ciliated cells covering the median surface of the foot ; by the beating of these cilia the nutrient fluid surrounding the embryo is drawn into the mesenteron, Figs. 99, 104, 105.

(b) *The Posterior Growing-Point.* — At first the cell divisions on the posterior side of the egg are less frequent than on

the anterior side, Figs. 49–55. But, though the divisions are slow, the cell growth is rapid, in consequence of which the cells posterior to the transverse arms of the cross become enormous in size. The cells on the anterior side of the egg divide rapidly, but the total growth is less than that of the cells on the posterior side ; consequently the whole apical pole is shifted forward, Figs. 49–55.

Afterwards, at the extreme posterior end of the embryo, cell divisions begin, and proceed so rapidly that in a very short time there are more ectoderm cells on the posterior than on the anterior side, Fig. 64. The region of greatest activity lies just ventral to the future shell gland, and almost immediately over the mesoblastic teloblasts. Radiating from this region are more or less regular rows of cells, Figs. 64, 65, which are particularly well marked on the ventral surface. I have not been able to identify constantly any ectoblastic teloblasts, though in many eggs there are three or four large ectoblast cells lying between the mesoblastic teloblasts, from which many of the cell rows radiate. Two of these cells are shown at the extreme end of the embryo in Fig. 65. They are large cells with clear protoplasm, and from their position and character I believe that later they become the ciliated anal cells, which are shown in Figs. 78, 95.

The cell rows mentioned are much more pronounced in some eggs than in others. In a few cases they seem to cover the whole posterior end of the embryo, though in general they could be distinguished only on the ventral side. Here they run forward almost to the mouth as a series of branching, irregular rows, Fig. 65, and include the whole region which ultimately becomes the foot.

The cells from which these rows radiate lie on the mid line between the mesoblastic teloblasts, and must therefore be descended from the cell 2d. This cell also gives rise to a posterior growing-point in the annelids and in Unio, from which, in the case of the former, the ectoblast of the trunk is largely, perhaps entirely, derived, while in the latter the shell gland and foot are formed from the derivatives of this cell. The shell gland and foot in Crepidula are evidently formed from this

same cell. I do not doubt that this posterior region of teloblastic growth has essentially the same origin and destiny in Nereis, Unio, and Crepidula; and, if so, it follows that the cell 2d in Crepidula is really like the "first somatoblast" in Nereis and Unio, although its earlier divisions are very different. This difference, as I have already explained, is probably in the main a time difference, being due to the shortening of the history of this cell in the annelid and lamellibranch.

(c) *The Velum.* — The velum can first be distinguished as a row of small polygonal cells running across the ventral surface of the embryo immediately posterior to the apical plate and some distance in front of the blastopore, V^1, Figs. 65–67. These cells can be traced out to the sides of the embryo, where they turn forward and dorsalward, and finally become wholly indistinguishable from the surrounding cells. This row can be recognized in the velum throughout all the further development. It forms the most anterior row of velar cells, and ultimately becomes the most important part of the velum.

Just posterior to this first row is a second, V^2, which is composed of larger cells and is less distinct than the first row. The median portion of this second row can be recognized in all the older stages, Figs. 76, 79, 81, 82, as two or more large cells with clear protoplasm and vesicular nuclei; its lateral portions are not clearly marked.

The cells of these two rows are not ciliated at first, and can be traced only by their form and position. The long velar flagellae which they afterward bear do not develop until a late period, but from the time when the blastopore closes until these flagellae appear the embryo swims about in the egg capsule by means of the short cilia which cover the cells of the apical, dorsal, and pedal cell plates.

The median portion of the first row arises from the cells which lie just beyond the ventral end of the apical plate. These cells are in all probability $2b^{1.2.2.1.1}$ and $2b^{1.2.2.1.2}$. One of these cells is shown dividing in Fig. 71. In Fig. 72 a transverse row is formed from these cells which is plainly the first row of velar cells. It will be remembered that the apical plate is formed

from seven cells of the anterior arm of the cross, and that the terminal cells of this arm are probably thrown away.[1] Therefore the cells lying immediately beyond the anterior arm are the ones from which this median ventral portion of the first velar row comes. These cells may be traced back to a single one, $2b^{1.2.2.1}$, Figs. 46, 47, which lies at the end of the anterior arm. In this same position two cells are found a little later, Fig. 50, which have evidently come from this single cell by equal cleavage ; these cells are therefore $2b^{1.2.2.1.1}$ and $2b^{1.2.2.1.2}$. At a later stage they increase to four, Figs. 56, 71, and finally to six in Fig. 72.

The portion of the first velar row lateral to these six cells is evidently derived from the anterior turret cells, $1a^2$ and $1b^2$. These cells are shown undivided in Fig. 49, while in Fig. 50 they have divided bilaterally into the cells $1a^{2.1}$ and $1a^{2.2}$, $1b^{2.1}$ and $1b^{2.2}$. They are characterized by having clear protoplasm and large nuclei, and can be recognized for a considerable period lying just in front of the terminal cells of the right and left arms of the cross, and on each side of the median velar cells, Figs. 50–56.

The earliest figure which shows the protoblasts of the first velar row in position is Fig. 50 ; there are here two median and four turret cells, forming a series of six cells surrounding the cross on its anterior side, and extending from tip to tip of the transverse arms. In Fig. 56 they are shown increased to eight by the bilateral division of the median cells, and in Fig. 62 to ten or twelve. The terminal cells of the transverse arms of the cross divide, forming a row of four cells across the end of each arm, Fig. 56, and it is probable that these also must be added to the velar cells already described, making in Fig. 50 ten velar cells, in Fig. 56 sixteen, and in Fig. 62 at least eighteen or twenty. These cells belong to the first velar row only, and they extend from the mid-ventral line about two-thirds of the way around toward the mid-dorsal line. During all this time the posterior turret cells remain undivided, and the velar row ends dorsally against these cells.

It is probable that the mid-ventral portion of the second velar row, V^2, is derived from the cell which I have identified

[1] See Note p. 204.

provisionally as $2b^{2.2}$, and which lies just beyond the median cells of the first row, Figs. 56, 69, 70. I have not been able to determine whether any part of the second row arises by subdivision of the cells of the first; if not, this row may include a few cells of the third quartette ($3a^{1.1.1}$ and $3b^{1.1.1}$, Fig. 56) at the points opposite the anterior turrets.

These are the only velar cells whose origin I have been able to determine with any degree of probability; even in the case of these I recognize that there is an element of uncertainty, since the lineage was not followed cell by cell to a later stage than Figs. 47 and 48. However, I hold it highly probable that my identification of the velar cells in Figs. 50 and 56 is correct, and the identification in the later stages, Figs. 65 *et seq.*, is only a little less probable.

Several irregular rows of cells intervene between the first row of velar cells and the mouth, and in the latest stages figured several rows are seen running posterior to the mouth. All of these cell rows can be traced outward to the sides of the embryo, and all of them are ultimately ciliated and form part of the velum. Most of these cell rows could not have come from the first and second velar rows, and they must therefore have been derived from cells lying still farther away from the apical pole.

Thus the preoral velum is composed of a few cells of the first quartette, many of the second, and possibly a few of the third. It consists of many rows of cells, more or less regular in arrangement, extending from the first velar row in front to the edge of the mouth behind, Figs. 79, 81, 82. Of course the postoral velum must be composed of still more remote cells of the second and perhaps even of the third quartettes.

From the time of their appearance, Fig. 65, the first and second velar rows are slightly curved forward on the ventral mid line. In later stages, Figs. 76 *et seq.*, when, with the development of the foot and shell gland, the mouth is moved forward from the middle of the ventral face, this middle portion of the velum is carried still farther forward and at the same time the lateral portions of these velar rows are elevated above the general level and finally drawn out into a pair of

lobes which curve backward and downward on each side of the mouth, Fig. 79. Because of these opposite movements of the median and lateral portion of the preoral velum, but chiefly through the backward and downward growth of the lateral portions, the velum, when seen in apical view, bears a deep sinus on the ventral mid line, Figs. 79, 82.

In these later stages, Figs. 76 *et seq.*, the first velar row forms a slight ridge across the ventral mid line just posterior to the apical cell plate, which is particularly well marked because composed of a single row of small cells with densely staining nuclei which are bounded in front by the very large cells of the apical plate and behind by the large cells of the second velar row, Figs. 78, 79. Behind the cells of the second row and on the very edge of the mouth-opening is a third well-marked row, consisting like the first of small cells with densely staining nuclei, Figs. 79, 81, 82. This row can be traced laterally to the place where it joins the first row to form the margin of the velar lobe. At this point it bears a pair of prominences which ultimately become the tentacles, Fig. 81, T ; these structures therefore are formed in the preoral velum, in fact in the second cell row of the prototroch. In later stages they lie over the cerebral ganglia.

On the mid line these rows of velar cells are raised but a little above the general level, but laterally they are borne on the margins of the very prominent velar lobes. Cross sections of these lobes show one row of large rounded cells, which forms the extreme margin of the lobe and bears the long velar flagellae. On each side of this are one or more rows of large crescentic-supporting cells, Figs. 103–105. Similar cells have been described by Patten ('86) as present in Patella.

The postoral velum is not well defined until the last stage shown in the drawings, Figs. 81, 82, though somewhat irregular rows of nuclei can be seen crossing the body posterior to the mouth in stages as early as Fig. 76. In these later stages a ridge of cells runs out from the posterior edge of the velar lobe and can be distinctly followed to the ventral mid line of the foot. This is the postoral ridge of velar cells, and it runs

around the margin of the velar lobe on the posterior side, being separated from the preoral ridge by a shallow ciliated groove. On the ventral surface these ridges are widely separated, the preoral lying some distance in front of the mouth, as the postoral is some distance behind it. As shown in Figs. 81, 82, the postoral ridge crosses the foot posterior to the large ciliated cells which lie just behind the mouth, and on the mid line the ridge from each side turns backward and ends in a median row of ciliated cells. The whole area between the anterior and posterior ridges is clothed with a coat of fine cilia.

Laterally the postoral ridge grows less prominent, and in sections of the velar lobes taken about halfway between the dorsal and ventral surfaces, the postoral velum is merely a series of columnar, ciliated cells running around the posterior margin of the velar lobes, Figs. 103–105.

Passing up toward the dorsal side, the velum divides on each side of the embryo into two branches, Figs. 78, 80. The posterior branch, which is much smaller than the anterior one, continues up over the dorsal surface posterior to the head vesicle, being incomplete, however, on the dorsal mid line. The anterior and larger branch turns forward in a sharp curve on each side of the body, and ends abruptly on each side of the apex, Figs. 80, 82. The cells lying between the two branches on the dorsal surface are the large ciliated cells of the posterior cell plate.

At the point where the branching occurs, one large cell is found directly in the angle between the two branches, Figs. 77–80. This is, I believe, the posterior turret cell of each side. I could not determine whether the turrets contribute anything to the formation of the velum on the dorsal side as they do on the ventral. In one sense they lie within the velum, as does the whole posterior cell plate, being bounded in front by the anterior and behind by the posterior branches, but in any case the foremost row of the velum lies nearer the apex on the dorsal side than it does on the ventral, since it runs on the apical side of the posterior turret cells. From its position relative to the apical organ and the large cells of the posterior plate, it is probable that this anterior branch of the

velum follows the posterior edge of the right and left arms of the cross from tip to base.

I have not observed any cilia on the posterior branch, and believe that it is not functional as a locomotor organ ; the anterior branch, on the other hand, is clothed with long velar flagellae, and in later stages grows more and more prominent, forming the dorsal part of the velar lobe.

The posterior branch seems to be a continuation of the entire velum rather than of either the preoral or postoral portions ; the velum is therefore double on the dorsal side of the embryo. The posterior branch occupies the position of the velum in Ishnochiton and of the prototroch of the annelids, and I interpret the fact that it bears no cilia as indicating that it is a phylogenetic remnant of the ancestral velum. The anterior branch, on the other hand, is a new aquisition not represented in Chiton, nor even in the more primitive gasteropods.

It is now known that there is a postoral band of cilia in quite a large number of molluscan larvae. Brooks ('76) was, I believe, the first one to discover this band. Since then Haddon ('82) has shown that it is present in some Nudibranchia; Hatschek ('80) has described it and an adoral band, together with the usual preoral band, as present in Teredo ; and McMurrich ('85) has described a postoral band of cilia as present in the veliger of Crepidula.

Judging from position and structure there can be little doubt that the anterior ciliated ridge in all these cases is homologous with the *preoral ciliated band* in annelids, the posterior ridge with the *postoral band*, and the ciliated groove with the *adoral band.*

In its fully formed condition at the beginning of larval life, the velum of Crepidula is a very large and an extremely complex structure, consisting of many rows of ciliated cells running around the margin of the wheel-like lobes which are borne on each side of the head vesicle of the larva. The locomotor flagellae are very long and powerful, and their movements indicate some kind of nervous control. The entire margin of each lobe is surrounded by many regularly arranged pigment spots, which are beautifully colored, one row being a delicate green,

another a faint red, and still another sepia or black. Each velar lobe contains many stellate mesoblast cells, and the whole structure is highly irritable and contractile.

This structure is much larger and more complex than the annelid prototroch; and perhaps nowhere, with the possible exception of the echinoderms and Enteropneusta, is there a larval locomotor organ which will compare in size and complexity with the velum of many gasteropods.

Comparisons.

Reference has already been made to the origin of the velum in Neritina (p. 94). Blochmann was able to trace the tip cells of the transverse arms ("Urvelarzellen") to this structure, but he does not indicate what other cells enter into it. Of these velar cells he says (p. 162): "Schon während das Ektoderm anfing sich nach der ventralen Seite hin auszubreiten, sind die Zellen *vz* und vz_1 an die beiden Seiten gerückt, und in einer dieselben verbindenden Zellreihe werden dieselben lichtbrechenden Körnchen bemerkbar (Fig. 66), wodurch eine weitere Ausbreitung des Velums angedeutet wird. Dasselbe erscheint jedoch noch nicht kontinuirlich, sondern von den ursprünglichen Velarzellen *vz* und vz_1 ausgerechnet sind jederseits nur zwei oder drei Velarzellen sicher zu erkennen. Auch ventral ist das Velum noch nicht geschlossen."

As I have already indicated, it is very probable that these same cells form the lateral portions of the velum in Crepidula. I was not inclined to accept this view at first, because on the anterior side the first velar row lies beyond the tip cells of the anterior arm[1] and because the tip cells of the right and left arms seemed at first sight very far removed from the velum. Accordingly, I said in my first preliminary ('91): "In Crepidula it seems that no part of the transverse arms forms the velum." However, a more prolonged and careful study of the velum shows that these terminal tip cells, increased to four on each side, very probably form the lateral portions of the first velar row. There is thus the most exact agreement between these two animals in the origin of this portion of the velum.

As to the origin of other portions, no comparisons can be drawn since Blochmann has made no further observations on this point. The turret cells in Neritina are very small, and have not divided up to the last stage in which they can be recognized, and one cannot tell from Blochmann's figures whether they form any part of the velum or not. His figures would indicate, though they would by no means establish this point, that the velum does not branch dorsally as in Crepidula.

Heymons did not observe the origin of the velum in Umbrella. However, the following statement quoted from his work (p. 278) shows that in this animal the velum is the same in its general appearance, and must occupy essentially the same position as in Crepidula: "Die vorderste Partie des Eies, die dem früheren animalen Pol entspricht, wird von hellen grossen Ektodermzellen bekleidet. Dieser ganze Theil setzt sich bald noch schärfer als in früheren Stadien von der übrigen Masse des Eies ab, und zwar geschieht dies besonders durch das Auftreten des Velums. Letzteres beginnt sich gleich nach dem Verschluss des Gastrulamundes zu zeigen und besteht anfänglich aus einigen hellen und körnchenreichen Ektodermzellen, die sich später aneinander legen und dann in einer kontinuirlichen Reihe rings um den Embryo herum ziehen. Der von ihnen umschlossene Bezirk ist als Velarfeld zu bezeichnen. Die Mitte desselben fällt mit dem früheren Centrum des animalen Poles zusammen, welches, wie oben erwähnt wurde, mitsammt den Richtungskörpern an das Vorderende des Embryonalkörpers gelangt war." Heymons observed the first division of the four turret cells, but he did not follow them to their destination.

There is no velum or prototroch in Unio, and consequently we need not be surprised to find certain cells which enter into the velum in Crepidula diverted to other uses in that animal. Thus Lillie finds that the cells $2a^{1.1}$, $2b^{1.1}$, and $2c^{1.1}$, which are velar cells in Crepidula, assist in forming the larval mantle of Unio. He records two divisions of each of the turret cells, but did not determine their destiny.

Wilson, in his work on Nereis, first established the exact cell origin of the prototroch among the annelids. In this animal it

is formed entirely from the four turret cells, or trochoblasts, as Wilson appropriately calls them. Each of these cells divides twice, forming in all sixteen cells, twelve of which compose the prototroch. By the growth and division of these cells the tip cells of the cross are forced into a position below the prototroch, and are called by Wilson "post-trochal cells." Though they take no part in forming the prototroch, they lie but one cell below it, and may perhaps be considered as having been crowded out of the trochal series by the rapid growth and early division of the trochoblasts.

Mead ('94) has found that in Amphitrite and Clymenella the same cells form the prototroch as in Nereis. Each of these trochoblasts divides twice, as in Nereis, and all sixteen of these cells enter the prototroch. "Later the prototroch is completed by the addition of nine more cells from the 'second generation of micromeres' in quadrants A, B, and C respectively." That these additional cells of the second quartette are the same, at least in part, as the velar cells of Crepidula is shown by the further statement made by Mead that "almost the entire substance of $a^{2.1}$ ($2a^1$) and $c^{2.1}$ ($2c^1$) enters into the prototroch."

Remembering the many points of difference between the fully formed velum of the gasteropod and the prototroch of the annelid, it is most interesting and instructive to find such essential agreement in origin between the two. In fact, it may be truly said that they are even more alike in origin than in final structure.

(d) *The Shell Gland.* — This characteristic molluscan organ appears late in development in the case of Crepidula, Figs. 74 *et seq.* From its position on the mid line and at the posterior end of the embryo it is probable that it comes from the group of cells derived from 2d.

It is formed in the first instance by the very rapid multiplication of cells in a limited region of the ectoblast. These cells are densely packed together, so that in surface views of the egg only the nuclei can be recognized. At the centre of this proliferating area the nuclei are smallest and most numerous, and they grow successively larger from the centre toward the

periphery, Fig. 74. This proliferating area then invaginates, forming at first a shallow depression, and later the edges of this depression arch over until they nearly meet in the centre, Figs. 75, 77, 92. A short time after this the edges begin to extend in every direction, the invagination becomes shallower and broader, and at the same time a thin cuticle, which is the first trace of the shell, appears over the surface of the invaginated cells, Figs. 78, 95, 104, 105. While the shell gland is comparatively small, these cells are columnar, Figs. 92, 95, but as it increases in size they become extremely flat and thin, so that it is scarcely possible to see them even in sections, Figs. 103, 105. The cells at the margin of the shell gland, however, are columnar, and it is from these that the growth of the shell takes place.

Owing to the shifting of the posterior end of the embryo toward the ventral side, as shown in Figs. 80, 93, 95, the shell which was at first on the postero-dorsal area comes to be located entirely at the posterior end of the embryo, which now appears truncated, Figs. 80, 93, 95. The margin of the shell gland then extends forward on the left side much more rapidly than it does on the right, and at the same time the whole posterior part of the embryo is pushed over to the right.

In both Neritina and Umbrella the shell gland forms on the postero-dorsal surface of the embryo, but in neither case has its cell origin been determined. In Unio it is derived from the cell 2d, or the "first somatoblast," and, as we have seen, it probably comes from the same cell in Crepidula.

In Fulgur the invagination of the shell gland occurs at an early period, when the ectoblast has extended but a short distance over the yolk. Its early appearance seems to have misled McMurrich ('86), who regarded it as an invagination of unknown significance, but of very general occurrence. Except for its early appearance it is in all respects similar in origin and development to the shell gland of other gasteropods.

(e) *The Foot.* — Immediately after the formation of the shell gland the foot appears as a single median protuberance on the ventral surface, Figs. 76, 77. At first the prominence is about as long in the antero-posterior diameter as it is wide, but

in later stages it is much broader than long. On the median surface of the foot there are several large ciliated cells which resemble the apical and dorsal cells, and which I have therefore called the pedal cell plate. All the rest of the foot is covered by a columnar epithelium of ectoderm cells. When it first appears it is about equally prominent over its whole surface, Figs. 76, 77, but in the course of further development the posterior part becomes much more prominent than the anterior. The foot is, as it were, tipped up on its anterior edge by being crowded forward from behind. This forward tilting continues, as shown in Figs. 80–82, until the foot, instead of lying posterior to the mouth as it did at first, lies ventral to it. At an early stage the ectoderm forming the foot separates from the yolk beneath, and the cavity thus formed becomes traversed in every direction by mesoderm cells.

About the time that the supraoesophageal ganglia first appear the otocysts arise as small invaginations of the ectoderm on each side of the foot. They are at first open pits, which gradually close, forming vesicles the outer walls of which lie in the layer of ectoderm covering the foot, Fig. 100. At first the vesicle is quite small, and the cells surrounding it are cuboidal, but in later stages it increases in size and its walls grow thinner, Figs. 80–82, 105; at the same time its outer wall separates entirely from the ectoderm covering the foot and the vesicle comes to lie entirely within the cavity of the foot. The cerebro-pedal connectives end directly against the otocysts, and a small strand of cells, the origin of which I have not determined, connects the otocysts of the two sides.

In the oldest embryo figured the foot bears a thin cuticular operculum over its posterior surface. At a still later stage it becomes much more prominent and is triangular in outline, the apex being directed ventralward and forward. A very great number of cells which stain deeply and are probably gland cells are distributed quite uniformly in its epithelium.

As has been mentioned (p. 131), Lillie has found that the foot in Unio is formed from a portion of the ventral plate, which is derived from the first somatoblast, X (2d). I have called attention to the fact that in Crepidula the cell rows

which are formed on the ventral side anterior to the growing-point probably correspond to the ventral plate of Unio, and also, as in that animal, give rise to the foot. There is good reason to believe that these cell rows ultimately come from the cell 2d.

The cell origin of the foot is not given by either Blochmann or Heymons. From the latter's figures, however, it is evident that its place of origin and early history in Umbrella is essentially the same as in Unio and Crepidula.

In Patella (Patten, '86) and Fulgur (McMurrich, '86) the foot is said to arise as two lateral swellings which subsequently fuse together on the ventral mid line. Although it is single in its origin in Crepidula, the row of large transparent cells along its median surface gives it the appearance of being double, especially in the large embryos of C. convexa and C. adunca ; however, careful study of profile views and of sections shows that it is not double, but is a single median protuberance.

(f) *The External Excretory Cells.* — On each side of the embryo, just posterior to the velum and dorsal to the foot, several of the ectoderm cells swell up and gradually lose their nuclei and cell boundaries, Fig. 78 ; the cells become vacuolated, and the vacuoles are filled with small granules which stain deeply. Later the several vacuoles seem to flow together into one or more large ones, Figs. 80, 81. In the early stages these cells form a part of the ectodermic layer, but as the embryo grows older they grow more prominent, and the whole mass is constricted at the base, so that it becomes pear-shaped, the narrower end being attached to the embryo and the larger end being distal, Figs. 81, 104. The surrounding ectoderm cells crowd in at the neck of this constriction, and work their way entirely beneath these excretory cells. About the beginning of the free larval life many of the vacuoles with their granular contents disappear, and there is left on each side a clear, pear-shaped mass, which is attached for a time in the deep constriction posterior to the velum. Ultimately these structures appear to be pinched off completely. I have not observed them in the process of being cast off, but they suddenly disappear and leave no trace behind, except that one

sometimes finds one of these masses lying near an embryo, but wholly free from it ; I conclude, therefore, that they are thrown away.

When the embryos are stained with haematoxylin, the granular contents of the excretory cells stain dark carmine, while all the remainder of the embryo stains a royal purple, or dark blue. This carmine color, as is well known, can be produced by treating haematoxylin with weak acids, and the fact that these excretory cells stain a carmine color may indicate that they contain some acid secretion.

Heymons has traced with great care the history of the external excretory cells in Umbrella. They are derived from the cells $3c^{1.1}$ and $3d^{1.1}$. These cells divide, and then sink into the interior of the body and are overgrown by ectoderm cells. They are afterwards filled with brown concrement particles. Generally the right excretory cells develop, while the left do not.

These cells lie near the anal cells, at the posterior end of the embryo, and far removed from the velum and foot. I cannot, therefore, believe that they correspond in cell origin to the excretory cells of Crepidula, although $3c^{1.1}$ and $3d^{1.1}$ in Crepidula repeat in a most remarkable way all the peculiarities of the same cells in Umbrella, having been formed by bilateral cleavage, and being large, clear cells with vesicular nuclei. I have not been able to trace the cell origin of the excretory cells in Crepidula, and the possibility remains that they are derived from $3c^{1.1}$ and $3d^{1.1}$, as in Umbrella. If this be the case these cells must be displaced much farther forward than in Umbrella, possibly by the more active division of the ectoderm cells near the growing-point. But on the other hand it is possible, as is evidenced by the dissimilarity in their later history, that the excretory cells in Umbrella and Crepidula are not homologous, and that they do not have the same cell origin.

Heymons does not consider the differences between these external excretory cells of prosobranchs and opisthobranchs to be any serious objection to their homology. He says (p. 293): "Der Umstand, dass die äusseren Urnieren der Prosobranchier

paarig sind, wird keine Schwierigkeit machen, da die Entwicklungsgeschichte von Umbrella für eine ursprünglich paarige Anlage spricht. Auch die Lage des Organs am hinteren Körperende braucht noch kein Grund dagegen zu sein. Durch die Untersuchungen von McMurrich wissen wir, dass die äusseren Exkretionszellen der Prosobranchier ebenfalls bald etwas weiter vorn, bald etwas weiter hinten sich befinden." This difference in position seems to me, however, to be a very considerable one. In all prosobranchs these cells lie close behind the velum, while in Umbrella they are removed from that structure by almost the whole diameter of the embryo. Further, the fact that they sink into the interior in Umbrella would indicate that they are different from the excretory cells of prosobranchs.

Rabl ('79) believes that the so-called "primitive excretory cells" have no excretory function at all, but are merely a part of the velum. The fact, however, that in very many forms they are found to contain granules or crystals which have been seen to be extruded from the cells lends support to Bobretzky's ('77) idea that these cells really have an excretory function, and the fact that they are completely cast off in Crepidula would still more strongly support that view. That they are any portion of the velum, as has been maintained by Rabl and McMurrich, seems to me to be distinctly negatived by their general position behind that organ and their complete separation from it.

Bobretzky ('77) says that the ectoderm passes unbroken beneath these cells, while McMurrich ('86) believes that the excretory cells form a part of the layer of ectoderm covering the embryo, and that therefore they are not underlaid by ectoderm. In Crepidula, as we have seen, these excretory cells at first form a part of the general ectodermal layer, and are not underlaid by ectoderm; in later stages, however, the ectoderm forms a layer beneath them very nearly if not quite complete. If the conditions which prevail in Crepidula are general, it is probable that McMurrich based his conclusions on the study of younger stages, while Bobretzky was guided by the study of older ones.

In closing this section on the history of the ectomeres, I append a table, giving the number of cells in the various quar-

NUMBER OF DIVISIONS IN DIFFERENT QUARTETTES.

	Cell Stage	8	12	16	20	24	28	32	36	40		44
	1. Quart.	4	—	8	—	—	—	16	16	20		24
Discocoelis	2. Quart.	0	—	4	—	—	—	8	8	8		8
	3. Quart.	0	—	0	—	—	—	4	4	4		4
	4. Quart.	0	—	0	—	—	—	0	4	4		4
	Cell Stage	8	12	16	20	23	29	32	36	38	42	
	1. Quart.	4	—	8	—	12	16	16	20	20	22	
Nereis	2. Quart.	0	—	4	—	5	5	8	8	9	10	
	3. Quart.	0	—	0	—	2	4	4	4	4	4	
	4. Quart.	0	—	0	—	0	0	0	0	1	2	
	Cell Stage	8	12	17	20	22 24	27	32	36	38	39	46
	1. Quart.	4	4	8	—	8 —	9	10	—	10	10	16
Unio	2. Quart.	0	4	5	—	9 —	10	13	—	18	19	19
	3. Quart.	0	0	0	—	1 —	4	4	—	5	5	5
	4. Quart.	0	0	0	—	0 —	0	1	—	1	1	2
	Cell Stage	8	12	16	20	24	25 29	33	37	38	40	44
	1. Quart.	4	4	4	8	8	8 8	8	8	8	8	12
Umbrella	2. Quart.	0	4	4	4	8	8 8	12	16	16	16	16
	3. Quart.	0	0	4	4	4	4 8	8	8	8	10	10
	4. Quart.	0	0	0	0	0	1 1	1	1	2	2	2
	Cell Stage	8	12	16	20	24	25 29	30	34	38	42	44
	1. Quart.	4	4	8	8	8	8 12	12	12	12	12	12
Crepidula	2. Quart.	0	4	4	4	8	8 8	8	8	12	16	16
	3. Quart.	0	0	0	4	4	4 4	4	8	8	8	8
	4. Quart.	0	0	0	0	0	1 1	2	2	2	2	4
	Cell Stage	8	12	16	20	24	28	32	36	41	45	46
	1. Quart.	4	4	8	8	8	12	—	11	12	16	16
Neritina	2. Quart.	0	4	4	4	8	8	—	16	16	16	16
	3. Quart.	0	0	0	4	4	4	—	4	8	8	8
	4. Quart.	0	0	0	0	0	0	—	0	1	1	2
	Cell Stage	8	12	16	20	24	25					
	1. Quart.	4	4	—	—	8	8					
Planorbis	2. Quart.	0	4	—	—	8	8					
	3. Quart.	0	0	—	—	4	4					
	4. Quart.	0	0	—	—	0	1					
	Cell Stage	8	12	16	20	24	28	32	36	40		44
	1. Quart.	4	4	8	8	8	8	12	12	12		16
Limax	2. Quart.	0	4	4	4	8	8	8	8	12		12
	3. Quart.	0	0	0	4	4	8	8	8	8		8
	4. Quart.	0	0	0	0	0	0	0	4	4		4

COMPARISON OF LATER STAGES IN NEREIS, UMBRELLA, AND CREPIDULA.

	Cell Stage	48	52	56	58					
Nereis	1. Quart.	—	—	—	36					
	2. Quart.	—	—	—	12					
	3. Quart.	—	—	—	4					
	4. Quart.	—	—	—	2					
	Cell Stage	47	51	55	59	65	69	75	83 93	101
Umbrella	1. Quart.	12	12	12	12	12	16	20	20 24	28
	2. Quart.	16	20	24	24	24	24	24	32 36	36
	3. Quart.	10	10	10	12	18	18	20	20 20	20
	4. Quart.	5	5	5	7	7	7	7	7 9	9
	Cell Stage	47	52		58 60	64	68	77	88	111
Crepidula	1. Quart.	15	15		15 15	15	15	19	23	26
	2. Quart.	16	16		22 22	24	24	25	32	44
	3. Quart.	8	8		8 10	12	14	16	16	24
	4. Quart.	4	9		9 9	9	11	13	13	13

tettes at different stages for all forms with spiral cleavage which have been sufficiently studied. It will be seen that up to the 44-cell stage, beyond which it is impossible to carry the comparison in most cases, the first quartette divides most frequently in the annelid and the polyclade, the second and third quartettes in the mollusk, and the fourth quartette in the polyclade and mollusk. A comparison of Nereis, Umbrella, and Crepidula at the 58-cell stage shows still more plainly that the divisions of the first quartette are very rapid in the annelid, while those of the second and third quartettes are much more rapid in the mollusk.

While in general the number of cell divisions may be taken as a measure of the development, precocity in cell division does not always indicate precocity in differentiation ; *e.g.*, in the case of the first somatoblast (2d) the differentiation is much slower in the gasteropod than in the annelid, and yet the cell divisions are more numerous in the former than in the latter. Cell division is not always associated with differentiation, and therefore the measure of differentiation cannot always be determined by the number of divisions. In the cases compared above, however, there is no doubt that the more rapid

divisions of the first quartette in the annelid are associated with the more rapid differentiation of the upper hemisphere in that animal.

VI. HISTORY OF THE MESOMERES.

The origin of the mesoblast was treated in a previous part of this paper, and its history was traced up to the time when it is completely separated from the other germinal layers. The primary mesentoblast (4d) is formed at the 24-cell stage, but the complete segregation of its mesoblastic and entoblastic constituents does not occur until there are 65 cells present, of which eight are the descendants of 4d. Of these eight cells, four lie on each side of the mid line; the two posterior ones on each side are the enteroblast or intestinal cells, the two anterior ones are mesoblast cells, Figs. 42, 44, 46. These mesoblast cells, four in all, form the beginning of two bands, which ultimately extend about halfway around the egg.

1. *The Mesoblastic Bands.*

The posterior mesoblast cell is the teloblast, or "pole cell," of the bands. It is a large rounded cell, free from yolk granules, and, when stained, is rather darker than any of the surrounding cells. It is frequently seen dividing, and always so as to add new cells to the posterior ends of the bands. The anterior cell on each side (primary mesoblast) is the first purely mesoblastic cell formed. It is much smaller than the teloblasts, and has less affinity for stains. These two anterior cells divide soon after the teloblasts are formed, Fig. 42, usually across the long axis of the bands, but sometimes in the direction of that axis, Fig. 46.

The bands grow in length both by the addition of new cells at their posterior ends and by the subdivision of the cells already formed. They ultimately extend around the periphery of the egg from near the mid line behind to the first, or transverse, furrow on each side. In all the figures up to and including Fig. 53 these bands lie nearer the dorsal than the ventral side, but in all stages older than Fig. 53, they are nearer the ven-