

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-

tral side; this is due to the fact that they are carried down over the yolk cells with the overgrowing ectoblast. When first seen on the dorsal side, Fig. 42, etc., the teloblasts and their bands lie anterior to the enteroblasts. After they have moved around to the ventral side of the egg, with the general overgrowth of the ectoblast, the teloblasts lie posterior to the enteroblasts, Figs. 57 *et seq.*, although preserving the same position relative to the bands as before. This apparent change of position can be readily understood by comparing Figs. 51-54, in which an intermediate condition is shown.

Even in the later stages the nuclei of these mesoblast cells can be plainly seen just beneath the ectoblast, but it soon becomes impossible to recognize the cell boundaries, especially at the anterior ends of the bands. At the last stage in which the entire bands can be seen, Fig. 53, there are eight or nine cells in each. In older embryos the teloblasts and posterior ends of the bands may remain distinct, while only scattered nuclei can be recognized at the anterior ends, Figs. 57 *et seq.*; but ultimately the teloblasts and all traces of the bands disappear, Figs. 74 *et seq.*

2. *The Scattered Mesoblast Cells. (Larval Mesoblast.)*

In no case can the cells derived from the bands be traced anterior to the first, or transverse, cleavage furrow, nor over the ventral face into the lips of the blastopore. Yet in all stages from Fig. 60 onwards scattered mesoblast cells are abundant at the anterior end of the embryo and over the whole ventral surface, but particularly in the region of the blastopore. It seemed impossible that so many cells so widely scattered could have come in so short a time from the mesoblastic bands, and I was therefore led to look for another source of this scattered mesoblast, especially after the publication of Lillie's ('93) beautiful results on the double origin of the mesoblast in *Unio*. I was not able, however, to trace these scattered cells to their source in the relatively small eggs of *C. plana* and *C. fornicata*; but since the plates of this article were sent to the lithographer I have found in the large eggs of *C. convexa* and *C. adunca*, of

about the stage shown in Fig. 52, one additional mesoblast cell in each of the quadrants A, B, and C, lying immediately below the ectoblast cells at the angles of the quadrangular blastopore. As was shown on page 129, these ectoblast cells are derivatives of the second quartette; and since the additional mesoblast cells are derived from the overlying ectomeres, it follows that they have come from the cell groups 2a, 2b, and 2c, though I cannot give their exact cell origin. In the few cases which I have been able to examine, the additional mesoblast cell is formed first in quadrant A, and afterward one is formed in each of the quadrants C and B. In C and B they lie on the right (as seen from the vegetal pole) of the cells 4c and 4b, while in quadrant A the mesomere lies to the left of the cell 4a. In other words, these additional mesoblast cells are bilaterally placed in the quadrants A and C. There is no doubt that the scattered mesoblast above described comes from these additional cells.

These additional mesoblast cells forcibly recall the "larval mesoblast" of *Unio*. Like the latter, they are formed from the second quartette of ectomeres, they are not teloblastic in growth, but give rise to scattered mesoblast cells, and they seem to be concerned chiefly in the formation of unicellular muscle fibres, or myocytes,¹ which appear in the foot and in those larval organs, the head vesicle and velum. On the other hand, these cells differ from the larval mesoblast described by Lillie in the fact that they arise in three quadrants instead of in one only as in *Unio*, they appear at a much later stage, and they probably give rise to adult as well as to larval structures. These differences, however, are of secondary importance as compared with the resemblances mentioned, and I do not doubt that these cells correspond to the larval mesoblast of *Unio*.

The origin of larval mesoblast in three quadrants is most suggestive, since it points, as I believe, to a primitively *radial* origin of the mesoblast. From every point of view it seems probable that *Crepidula* represents a more primitive condition in this regard than *Unio*. The radial symmetry of the other layers is more complete in *Crepidula* than in *Unio* and is pre-

¹ I follow Lillie ('95), p. 38, in the use of this term.

served much longer. The asymmetrical origin of the larval mesoblast in *Unio* is probably associated with the extreme precocity of development which is shown in the very early differentiation of this and of so many other fundamentals in that animal. In all cases which I have observed, the larval mesoblast cell in quadrant A, which is the only one found in *Unio*, is the first one formed in *Crepidula*.

It is a most interesting fact that the larval mesoblast in *Crepidula* arises in the three quadrants which have produced no other mesoblast, *viz.*, A, B, and C; the quadrant D, which gives rise to the paired mesoblast, produces no larval mesoblast.¹

Mesoblast is therefore produced in each of the four quadrants. In A, B, and C it is derived from the ectomeres of the second quartette; in D, from the fourth quartette. In all cases the segregation of mesoblast in the cell 4d is associated with elongation of the body and teloblastic growth, even in such animals as lamellibranchs and gasteropods, which are not generally considered elongated animals. In more primitive forms there is probably no teloblastic growth, and consequently the mesoblast may arise in the same way in each quadrant, as is said to be the case among polyclades and ctenophores.

From these facts it is probable that the radial origin of mesoblast is to be considered a primitive character; its bilateral origin, a secondary one. In other words, the larval mesoblast is the more ancestral, and it might properly be called the *primary* or *radial mesoblast*, while that formed from 4d might be known as *secondary* or *bilateral mesoblast*.

Throughout embryonic life all the mesoblast is but scantily developed and exists for the most part as fusiform cells. These cells are most numerous in the foot, where they form the myocytes which traverse the cavity of the foot in every direction; they are also found in considerable numbers in the velar lobes and in the head vesicle.

¹ Of course it is possible that this quadrant does give rise to larval mesoblast at a stage *much later* than that at which it arises in the other quadrants. The most diligent search, however, has so far failed to reveal it, and if larval mesoblast is ever produced in quadrant D, it must be so much later than its origin in the other quadrants as to deserve to belong to another series of phenomena.

Comparisons.

In *Neritina* well-marked bands of mesoblast are formed which have the same axial relations and general appearance as in *Crepidula*. In the latest stage shown by Blochmann in which these cells appear, Fig. 66, there are four cells in each band and the teloblasts are some distance removed from each other. As has been remarked in another place (p. 74), these cells are connected with each other by several small entoblast cells, Figs. 62, 65, which probably correspond to the enteroblasts of *Crepidula*, since they are said to form the intestine. As development proceeds the bands move farther down on the sides of the egg and are separated from the small entoblast cells. There is no suggestion in Blochmann's work of scattered mesoblast such as is found in *Crepidula*.

The formation and early history of the mesoblast bands in *Umbrella* were described on page 72. In the later stages Heymons has observed the dissolution of the bands and the nearly uniform scattering of their cells; at the same time the teloblasts disappear.

The group of small cells which lies between the teloblasts and corresponds in position, though not in origin, to the enteroblasts of *Crepidula* "probably gives rise to mesoblast cells which later are found on the outer surface of the intestine." A similar layer of mesoblast cells is found surrounding the intestine in *Crepidula*, Figs. 80, 81, though I have not supposed that it was derived from the cells lying between the teloblasts, *viz.*, E^1 , E^2 , e^1 , e^2 . The fact, however, that there is an exactly similar group of cells (the "secondary mesoblast") in *Nereis* which has exactly the same fate, and that in *Unio* also there is a similar group which, as Lillie believes, has the same destiny, is strong corroborative proof of the accuracy of Heymons' observations. In *Nereis* these cells lie uncovered at the posterior lip of the blastopore; they afterwards become pigmented and migrate inward, where they spread out upon the wall of the mesenteron. Lillie believes that essentially the same thing happens in *Unio*. In *Crepidula* this group of cells, four in number, which lies between the teloblasts gives rise, as I

believe, not to the mesoblast covering the intestine, but to the distal portion of the intestine itself.

Heymons did not observe a secondary origin of mesoblast in Umbrella, though he suggests that possibly in stages later than he has examined, ectoderm cells may migrate into the interior to form mesoderm.

VII. HISTORY OF THE ENTOMERES.

At the time when the mesoblast is completely separated from the entoblast the latter consists of the following cells :

Macromeres (Basal Quartette)	4
Smaller Entoblasts (Fourth Quartette)	3
Enteroblasts (Fourth Quartette)	4
Total	11

We will now take up the further history of each of these groups.

I. *The Four Macromeres.*

After the formation of the fourth quartette there is a long interval before the macromeres again divide; during this time the nuclei of these cells become very large and vesicular, and contain one or more large nucleoli, Figs. 52, 86, 87. These cells are composed almost entirely of yolk, and their nuclei and protoplasmic portions lie near the surface just in advance of the edge of ectoblast, and in this position they move around to the ventral pole.

What force is it which carries these nuclei around the egg just in advance of the ectoblast cells? If, as is sometimes assumed, the initial polarity of the egg is due to the fact that the yolk granules have a greater specific gravity than the protoplasm, must it be supposed that the specific gravity of these substances changes in the later stages of cleavage so that the nuclei and protoplasm sink to the lower part of the cell while the yolk rises to the upper part? The progressive movement of the nuclei and surrounding protoplasm over the yolk coincident with the extension of the ectoblast would go against any such conclusion, and would favor the view that this movement