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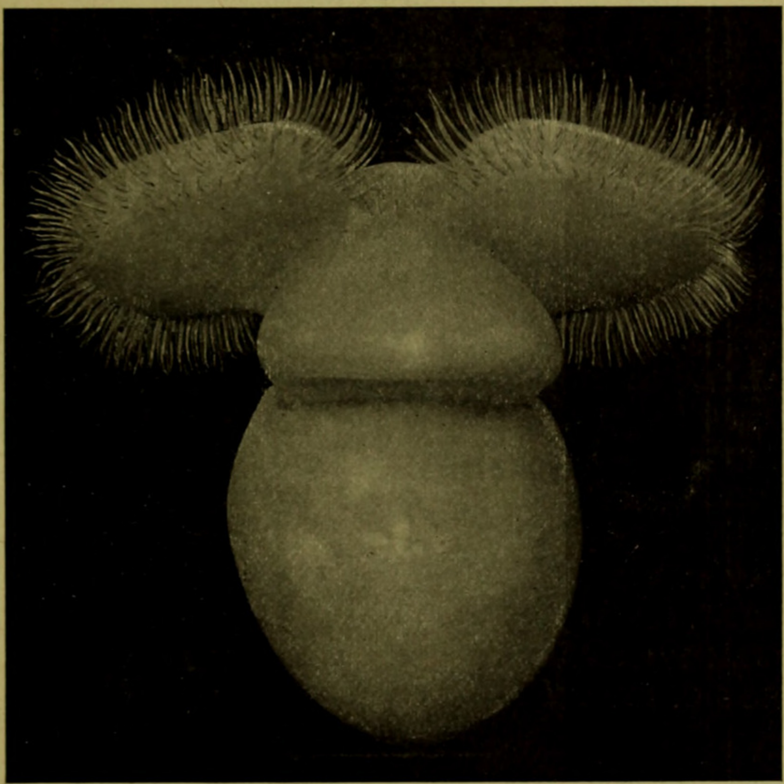
The Development of a Mollusk



By B. E. Dahlgren, D.M.D.

American Museum of Natural History

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Guide Leaflet No. 21

American Museum of Natural History

Seventy-seventh Street and Central Park West, New York City

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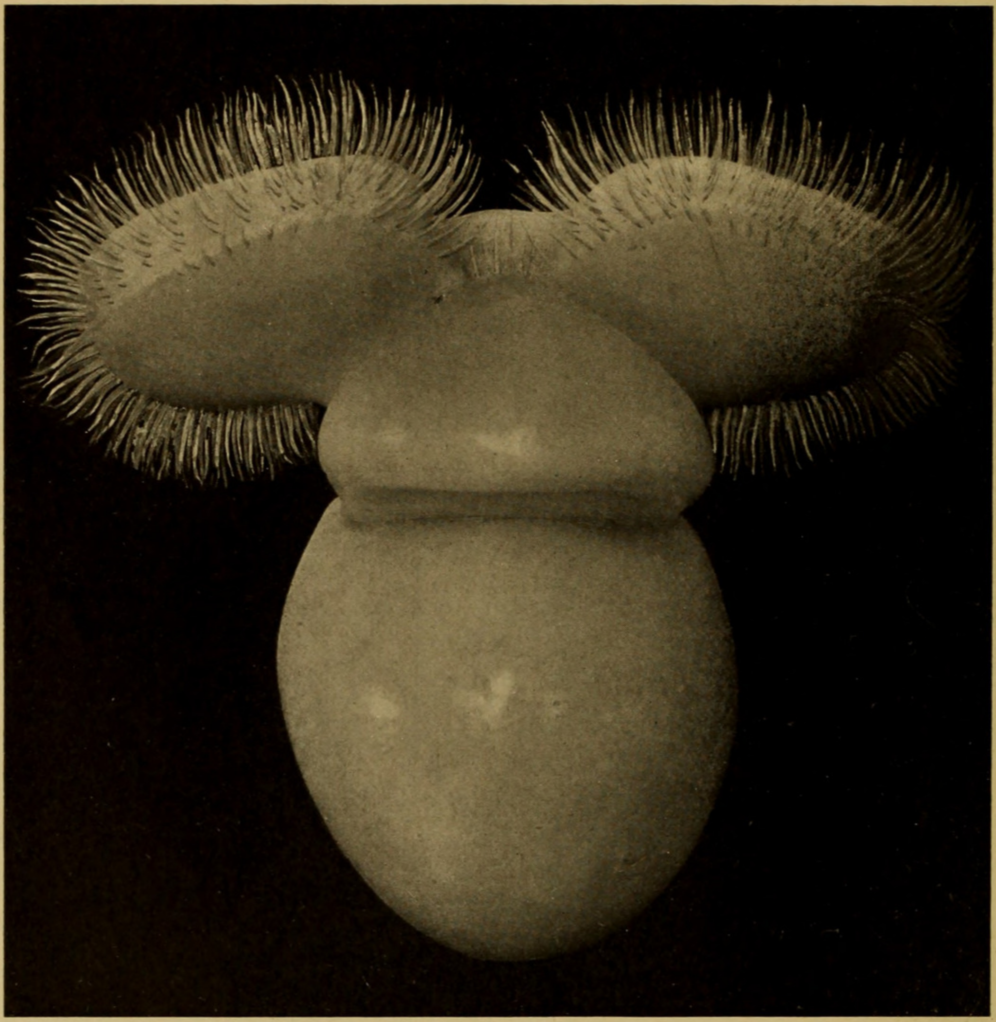

MODEL 21. FRONT VIEW

The fully formed mollusk larva, or veliger.

The Development

of a

Mollusk

A Guide to the Series of Models Illustrating the Development of Crepidula in the Department of Invertebrate Zoölogy

By

B. E. DAHLGREN, D. M. D.

American Museum of Natural History

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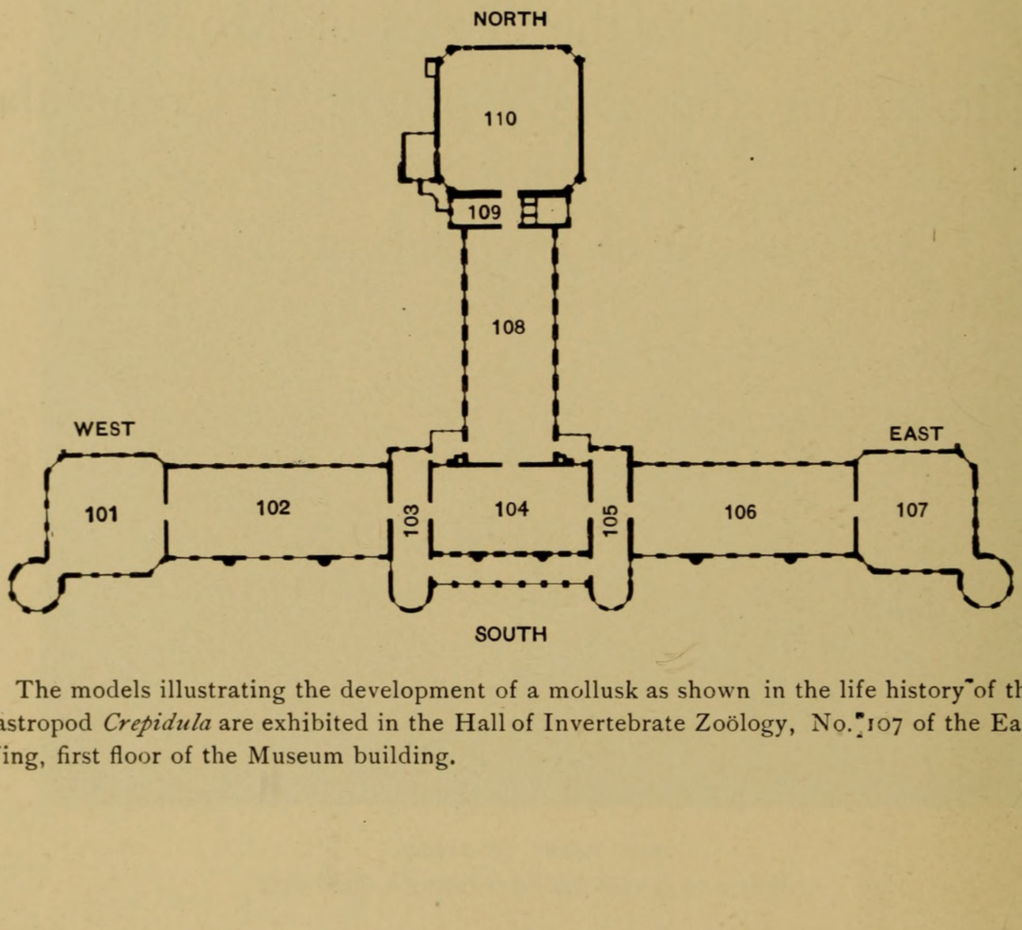
FIRST FLOOR



The models illustrating the development of a mollusk as shown in the life history of the Gastropod *Crepidula* are exhibited in the Hall of Invertebrate Zoölogy, No. 107 of the East Wing, first floor of the Museum building.

THE DEVELOPMENT OF A MOLLUSK.[1]

A GUIDE TO THE SERIES OF MODELS ILLUSTRATING THE DEVELOPMENT OF CREPIDULA.

By B. E. Dahlgren, D.M.D.,
American Museum of Natural History.

Introduction.

THE problem of how living organisms arise must have ever presented itself to the questioning mind. The processes involved in the origin of new individuals nevertheless remained for ages an unsolved mystery. The most familiar example, the origin of the young bird from an egg, cannot have failed to arouse the interest even of primitive man. It must also have furnished the first suggestion towards an explanation. Although undoubtedly long unsuspected, in time it became known that every animal which does not multiply by simple division into two like the very lowest arises from an egg, which is either hatched or developed within the body of the parent. Until a century and a half ago it was generally believed that the egg contained a miniature animal, which became perfected during incubation. Not until the substance called protoplasm had been recognized as the universal "physical basis of life," and, by the aid of the microscope, all living bodies had been found to be composed of cells, was anything like a correct understanding of the nature of the egg and its development attained. The egg was found to be a cell derived like all other cells by the division of a preëxisting cell. Its development, resulting in the formation of the myriad cells of a new individual, was found to proceed by a process of cell-division, essentially similar to that by which growth takes place in the adult.

[1]Reprinted from *The American Museum Journal*, Vol. VI, pp. 28-53. Jan., 1906.

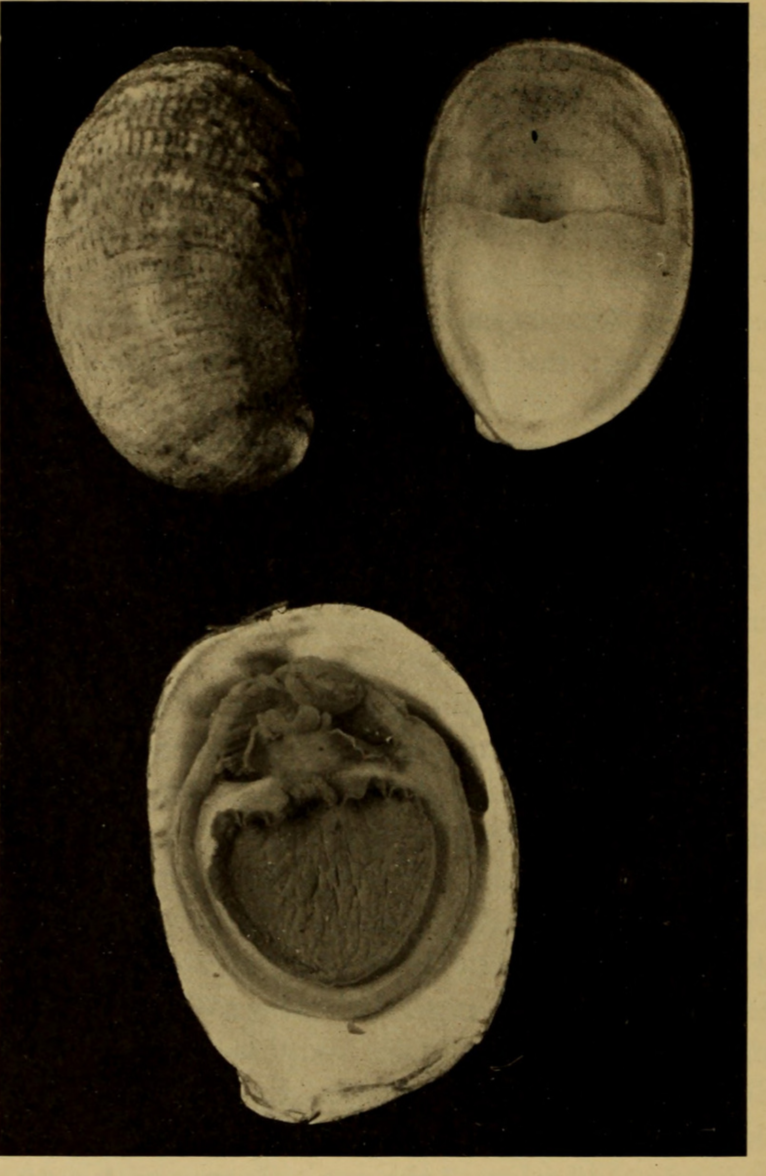
Out of the discovery of the character of the egg, of its origin from a parent cell and of its processes of development grew numerous other problems demanding the attention of investigators. Thus the science of embryology came into existence. This science seeks to discover every step in the development of an organism and to trace resemblances and differences of structure and form from their very earliest beginnings. It investigates the conditions which influence development and seeks to discover the factors which determine each step in the formation of an organism, to what extent development is dependent upon external causes and to what extent it is predetermined by the internal organization of the egg. It seeks to determine precisely what this internal organization is and to explain the manner in which the reproductive cell becomes the bearer of the characters of the parents and by what process it is able to transmit these to the offspring.

The comparison of the development of different animals soon revealed striking similarities at certain stages. It was found that after cell-division had proceeded to a certain extent the developing egg assumed a form resembling a mulberry (the morula); that later the cells invariably became arranged in the form of a hollow sphere (the blastula), this in turn giving rise to a somewhat more complicated flask-shaped form (the gastrula). It was seen that these various stages presented remarkable correspondences to certain lower forms of life. The analogy of the undivided egg to a simple unicellular protozoan; of the mulberry, or morula, stage to simple aggregations of unicellular animals such as are found among the lowest forms of life; of the blastula to certain Flagellates which occur in the form of hollow, free-swimming, multicellular spheres, and the apparent analogy of the gastrula to certain polyps led to the theory that the developing animal, in the course of its formation from the egg, passes successively through the forms of a whole series of lower organisms which may be considered as its ancestral types.

Formulated at a time when the evolution theory had been recently advanced, this corroborative theory aroused the liveliest interest. Although the original theory has been largely modified since the developmental history of a greater number of forms has become known, comparisons such as these have thrown much light on the connections existing between various classes of animals, the extent to which developmental histories correspond being, in a degree, an index of relationships.

With a view primarily to increase the embryological evidences of evolution and at the same time to gain a clearer conception of relationships, the development of all the various types began to be traced from the original germ layers. Naturally the conditions which might influence development were considered, and explanations of how the mechanical action of simple physical factors, such as pressure, cohesion and gravity, might tend to cause a dividing egg of a given character to assume successively the various forms through which it passes during development, were soon advanced and received with great enthusiasm. To determine exactly how important a rôle these extrinsic factors play, and the extent to which the future form of an organism is predetermined by the intrinsic character of the egg is evidently of the greatest importance in the solution of the problem of heredity and constitutes at present one of the main problems of embryology.

Although the earlier embryologists were satisfied with simply tracing the origin of the various organs of the body from their primary germ layers which begin to be defined with the gastrula stage, nowadays the solution of the origin of every organ or feature of the body and the significance and factors of every step in development are sought by the most painstaking tracing of the history of every single cell arising by every succeeding division of the egg. It was with a purpose such as this that an elaborate and careful study of the development of *Crepidula* was undertaken by Prof. E. G. Conklin, of the University of Pennsylvania. This study has been followed by the author in constructing for the American Museum of Natural History the series of models described in the present paper.



THE SLIPPER LIMPET OR BOAT SHELL
Crepidula fornicata Lamarck

The Development of Crepidula.

The models represent on a greatly enlarged scale (about 400 diameters) the more important stages in the development of the egg of a gasteropod mollusk of the genus *Crepidula*—the Slipper Limpet, or Boat Shell—common on the coast of the United States. The exceedingly minute eggs (.182 mm. in diameter) are laid in great numbers in capsules secreted by the mollusk. These capsules, to the number of 50 or 60, each containing about 250 eggs, are united into a grape-like cluster generally found under the shell of the Crepidula attached to the stone or other object upon which it lives its sedentary life. The total number of eggs laid at one time by an animal is about 13,000.

The unfertilized egg (Fig. *a*) is a nearly spherical single cell consisting of a very small amount of protoplasm surrounded by a relatively larger amount of yolk material, mostly in the form of small globules. Within the protoplasm, in a nearly central position, is found the nucleus of the cell. The whole egg is enveloped by a cell membrane.

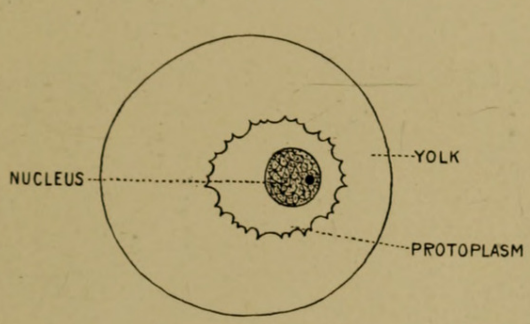


FIG. *a*

The first change which takes place in the egg, preparatory to development, is a migration of the nucleus and protoplasm from a central position toward the upper surface of the egg, the yolk, or deutoplasm, taking its position below it. The egg thus becomes distinctly symmetrical about a vertical axis (Fig. *b*). The upper pole, at which the protoplasm is found, is known as the *animal* pole; the opposite, or lower, as the *vegetative* pole, since

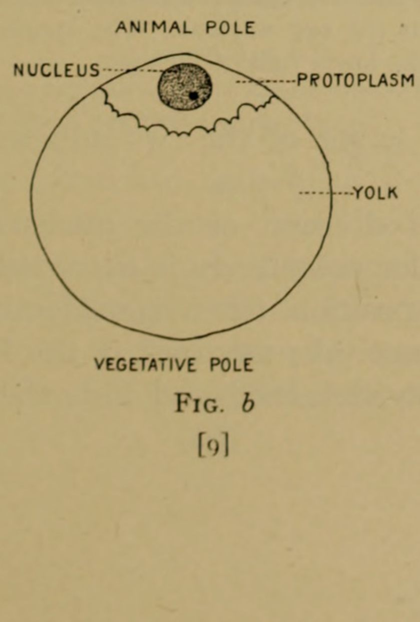
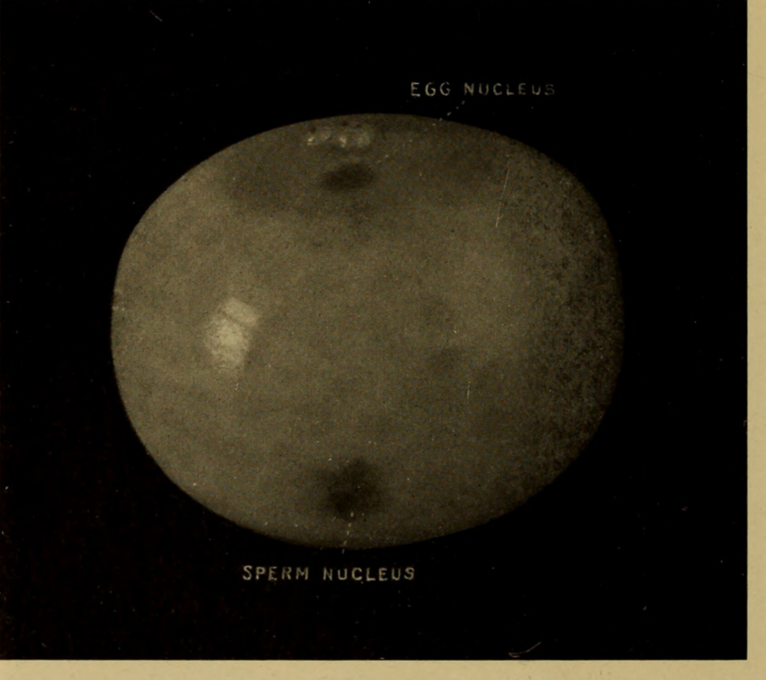


FIG. *b*

about this is collected the yolk or food material contained in the egg. This axis may be followed throughout the development and has been found to correspond to the dorso-ventral axis of the future larva.

About the time of the change in the position of the nucleus and protoplasm, a division of the former takes place. One of the portions resulting from this division, surrounded by a small amount of protoplasm, is extruded at the animal pole, where it remains for a time as a minute body. This is the "first polar



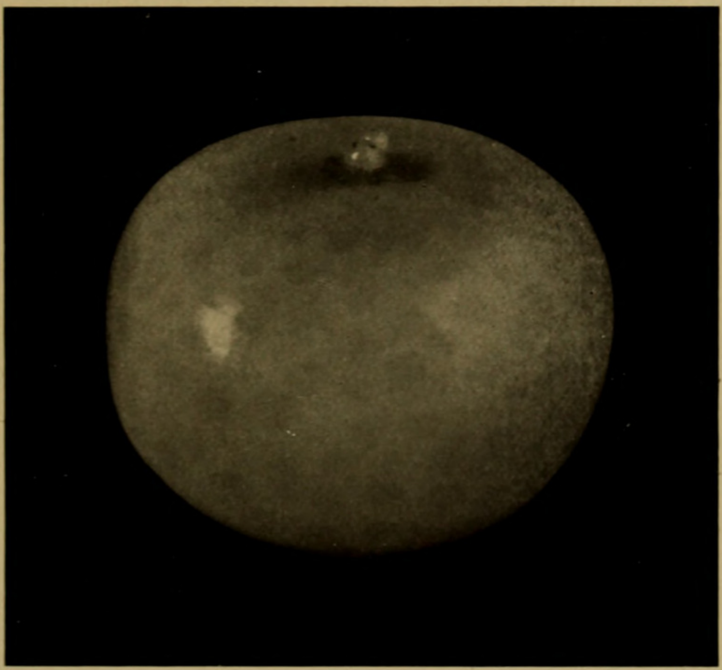
MODEL 1, A

The individual egg showing the clear protoplasmic area above, under the two polar bodies; the yolk with the yolk globules below. In the protoplasm at the animal pole is seen the egg nucleus. The sperm nucleus is represented shortly after entering the lower half of the egg.

body" and is the larger of the two adherent bodies shown in Model 1,B.

This process of division of the nucleus is soon repeated, and a second smaller polar body is extruded. These two polar bodies remain in position for a considerable length of time. Although they do not take any part in the future development, becoming ultimately detached and lost, their elimination is of particular significance in the preparation of the eggs for fertilization. The process is known as the "maturation" of the egg.

The sperm cells are inclosed with the ova in the capsules. They consist chiefly of a nucleus with a very insignificant amount of protoplasmic substance. A single sperm cell enters the ovum somewhere about the vegetative pole, at the time of the beginning of the maturation process, and its nucleus gradually makes its way upward toward the egg nucleus, until the two nuclei are in contact. These nuclei, known as the "pronuclei" of the egg, may be seen in Model 1,B lying close together in the protoplasm at the animal pole. The egg is now fertilized and capable of developing into a new organism.



MODEL 1, B

The fertilized egg, showing the egg and sperm nuclei in contact at the animal pole. On either side of them are the centrospheres.

Each nucleus is composed largely of a peculiar substance, which has been given the name "chromatin," because of the readiness with which it assumes the stains used for coloring microscopic objects. Though little is known about the definite function and properties of chromatin, its importance is evidently very great, for it is found in the nuclei of all cells. Generally it is seen as small particles in the form of loops or bands, more or less compactly arranged, and of a definite number in any given species. To these the name "chromosomes" has been given. The division of a nucleus seems to consist mainly in a careful separation of the chromosomes into two equal parts.

There is also present in connection with each nucleus a small body which seems to be the center of all nuclear changes, the "centrosome." Whenever any activity of the nucleus such as a division takes place, the centrosome is in evidence.

Centrosomes are to be observed in both of the pronuclei of the undivided egg, and radiations apparently extend from them to each separate chromosome. The arrangement of the chromatin now becomes looser, and the chromosomes are more widely separated. The centrosomes come to lie in diametrically

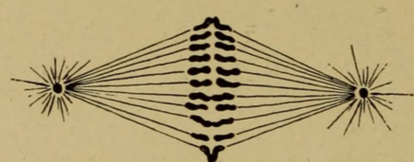
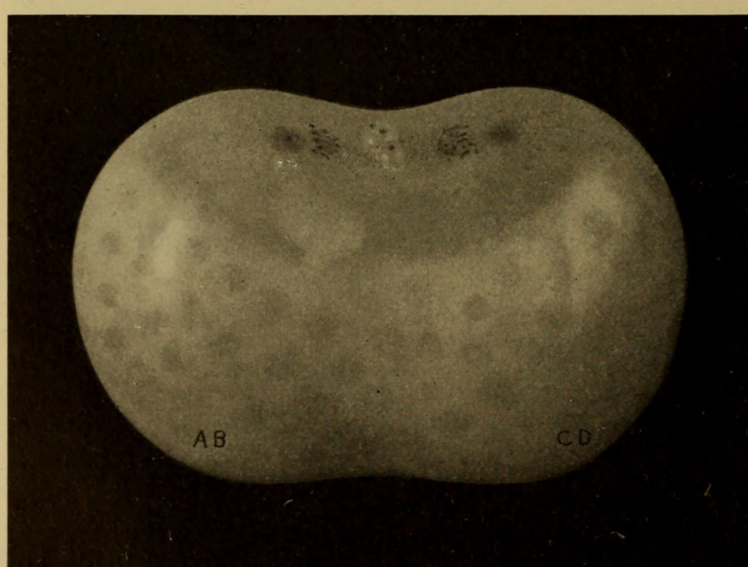


FIG. *c*

opposite positions with the two pronuclei between them. The nuclear boundaries next disappear, the chromosomes become



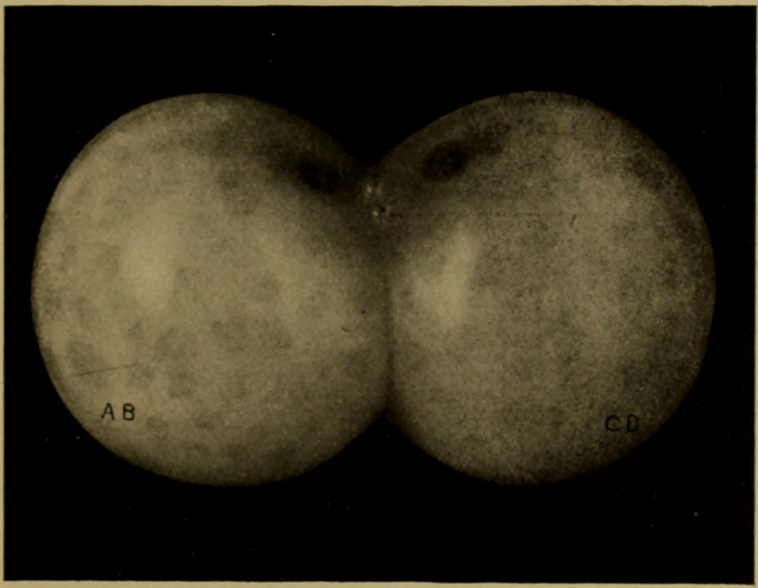
MODEL 2

First cleavage. Separation of chromosomes. Elongation and constriction of the egg preceding its complete division into two cells.

still farther separated, the radiations become more distinct, and soon seem to act on the chromosomes as two sets of fibers. The next step is a separation of every chromosome into two parts, which seem to be drawn in opposite directions toward the two centrosomes. These changes are shown in Model 2 and Fig. C.

In this manner two new nuclei are formed from the pronuclei, each new nucleus being composed of one-half of the chromatin of the male and female pronuclei, and each nucleus having a centrosome.

At the same time that the division of the pronuclei takes place a corresponding division of the whole egg occurs. The egg elongates (Model 2), a constriction takes place, and finally, coincident with the formation of the two new nuclei, there is

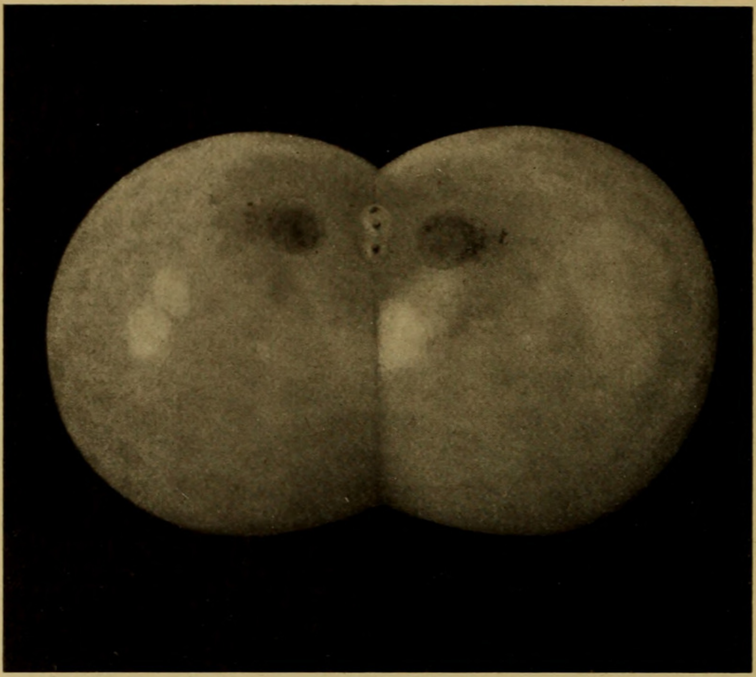


MODEL 3

Completion of first cleavage. Two cells. Polar bodies in the furrow between them. Daughter nuclei and centrospheres in each cell.

a complete separation of the egg into two halves, forming two new cells, each made up of protoplasm and yolk, like the single undivided egg, and each having a nucleus with its centrosome (Model 3). One of these two new cells gives rise to the anterior portion of the embryo, the other to the posterior.

Beginning with this, the first cleavage, up to the time when the larva is capable of taking in new food, the whole process of



MODEL 4

Resting stage after first cleavage. The two cells flattened against each other.

MODEL 5

Beginning of second cleavage. Nuclei resolved into division spindles. This model shows plainly two centrosomes, radiations and the two sets of chromosomes in each cell.

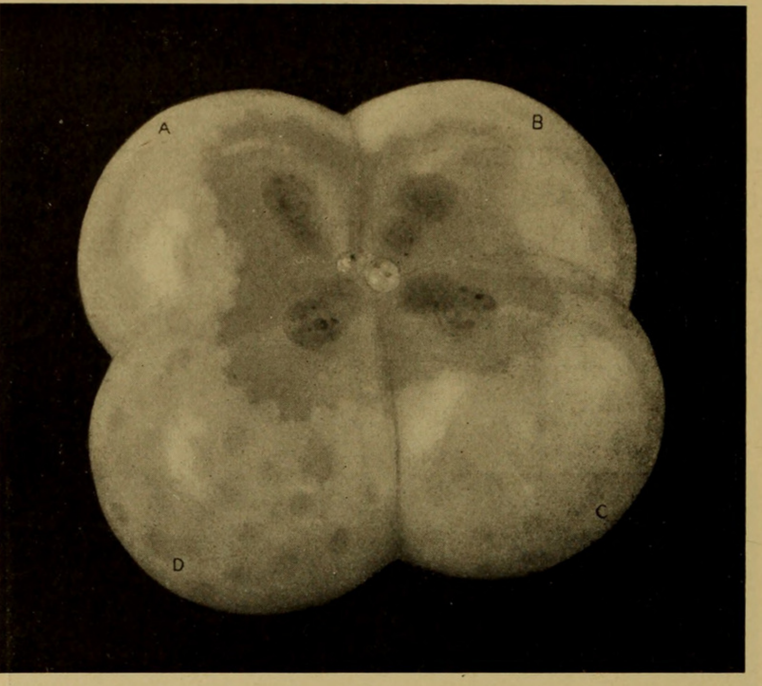
development proceeds through the repeated subdivision of these cells.

The second cleavage, which occurs at right angles to the first, divides the egg and the body of the future larva into right and left halves. This cleavage, initiated by a division of the centrosome, takes place by the changes in each nucleus, followed by an elongation and constriction of the cell. Finally a complete division of each nucleus and each cell into two parts takes place (Models 5 and 6). This gives four new cells, Model 7, each

MODEL 6
Second cleavage. Further separation of chromosomes. The two cells elongated and showing a constriction.

destined to form a definite part of the future organism, but each constituted as far as we can see in a precisely similar manner.

In the next, the third, cleavage the division takes place in a new direction. This, as indicated by the nuclear figures on Model 8, is oblique. Instead of a division into two equal parts, only a portion of the protoplasmic substance at the animal pole separates off, giving rise to four small cells which eventually lie above and slightly to the right of the four lower larger cells. (Model 9 shows the eight cells resulting from this cleavage.)

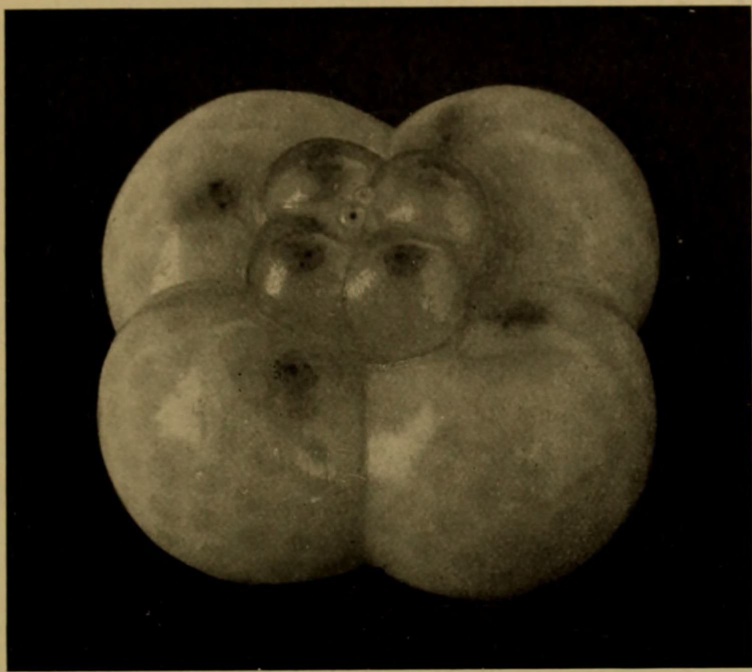


MODEL 7

Second cleavage complete, so that four cells are formed.

MODEL 8

Third cleavage. Division spindles radial. The raised surface at the inner end of each spindle indicates the point at which four new cells will be separated off.



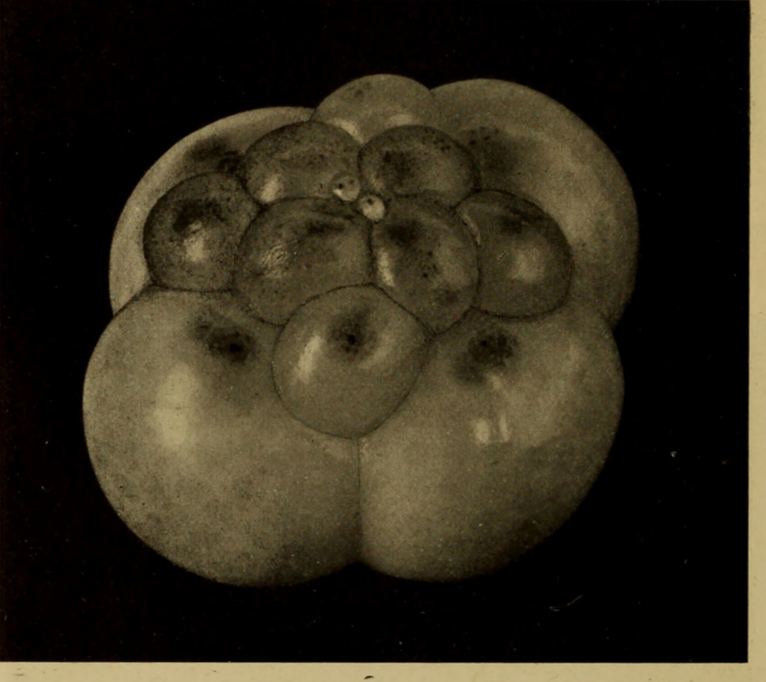
MODEL 9
Third cleavage completed. First quartet of small cells or ectoblasts formed.

MODEL 10
Fourth cleavage begun.

The fourth cleavage (Model 10) is also oblique. It results in the separation of another quartet of small protoplasmic cells slightly to the left of the large yolk-laden cells and also at the animal pole (Model 11).

The fifth cleavage is simply a division of the first quartet of small cells (Model 12).

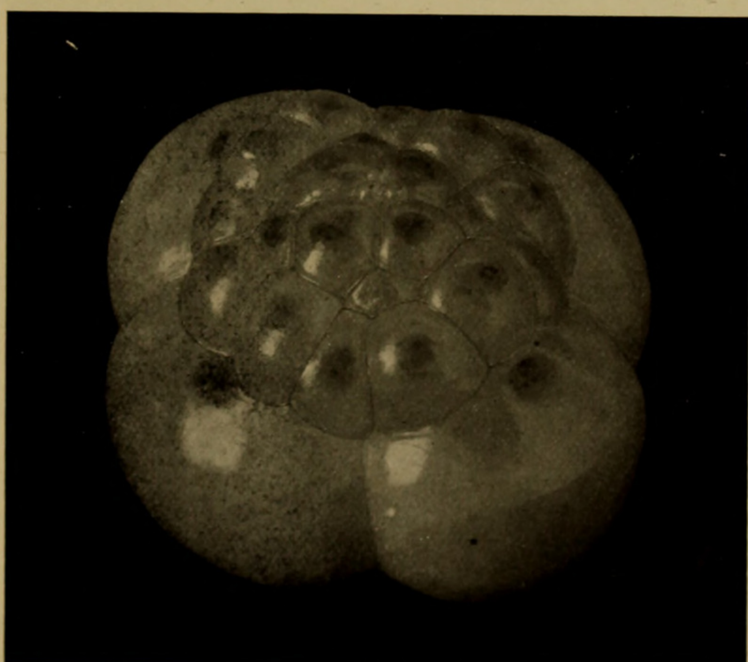
By the sixth cleavage, the beginning of which is shown in Model 12, a third and last quartet of similar small cells is given off at the animal pole. This cleavage also is oblique, but to the right. By this alternation in the direction of each cleavage



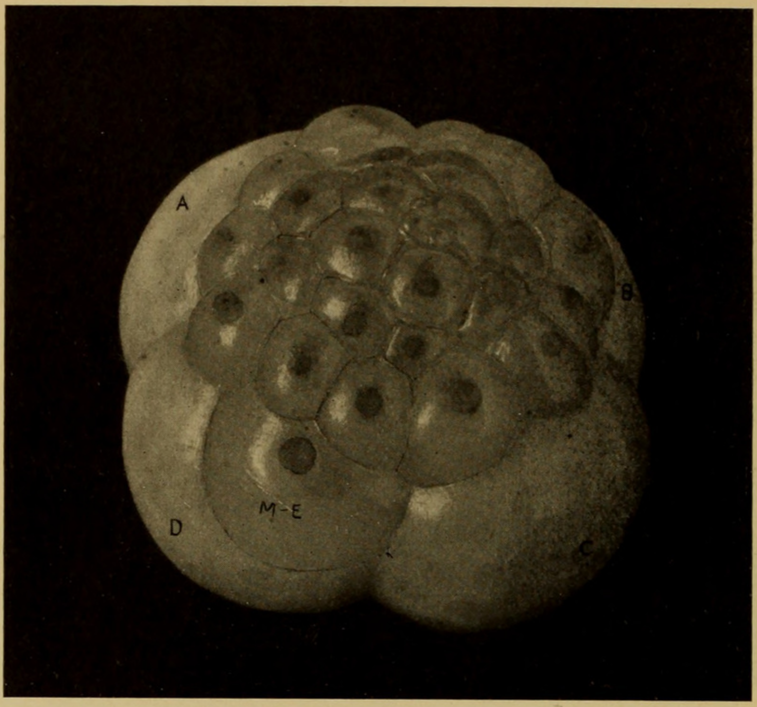
MODEL 11
Fourth cleavage completed. A second quartet of ectoblasts formed. Division beginning in cells of first quartet. Fifth cleavage begun.

plane, which began with first cleavage as indicated by the rotation of nuclei to the right, or in a clockwise direction on Model 4, the symmetrical arrangement of the cells is maintained. Lying at the animal pole of the egg, these three quartets of small cells form the so-called dorsal plate, which, by rapid multiplication of cells by division, is destined to grow until it completely covers the egg and forms the outer layer or ectoderm of the embryo. These cells are therefore known as "ectoblasts."

MODEL 12
Fifth cleavage completed. Sixth cleavage begun. Formation of third quartet of ectoblasts.

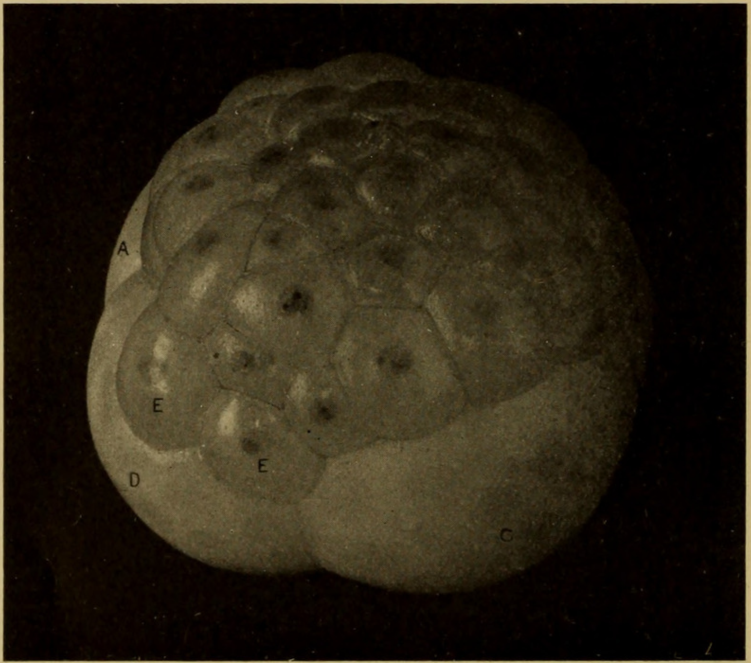


MODEL 13
Sixth cleavage completed. Second quartet has also divided; separation of ectoblasts completed.



MODEL 14

Separation from the left posterior large cell (D) of a single cell, the mesentoblast (M–E).



MODEL 15

Division of mesentoblast. The number of ectoblast cells has increased by further division of the three quartets.

The seventh cleavage (Model 12) divides the second quartet of ectoblasts.

The eighth cleavage (Model 13) consists of a second division of the first quartet of ectoblasts.

The ninth cleavage is unique, only one rather large cell, the "mesentoblast," M.-E. being separated off from the left posterior of the larger cells (D, Model 14). This new cell divides into two (Model 15) and again into four parts (Model 16). The upper two of these four cells, concealed on the model by the rim of the dorsal plate, multiply rapidly by division, and the cells which are formed from them make their way between the dorsal plate of the ectoblasts and the large yolk-laden cells below. They will form the future middle layer or mesoderm of the embryo, and

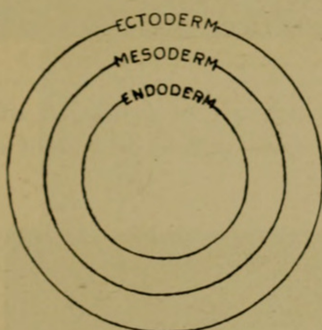


FIG. *d*

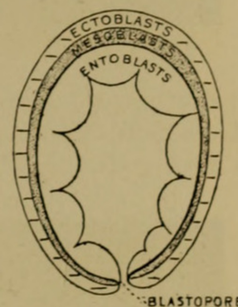
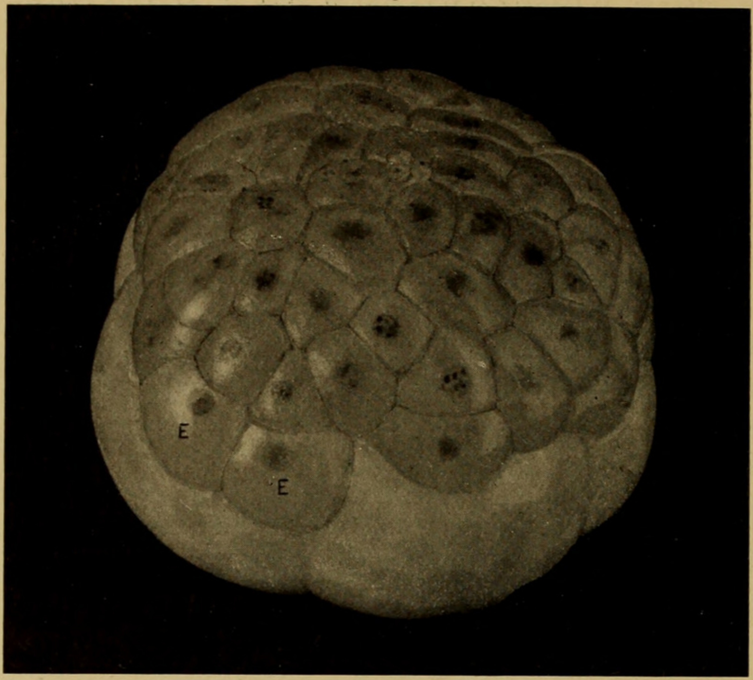


FIG. *e*

are known as the "mesoblasts." After the separation of the mesoblasts the remaining three large cells finally divide, giving in all eight or nine large inferior cells, the "entoblasts," which in time will form the inner layer of the embryo.

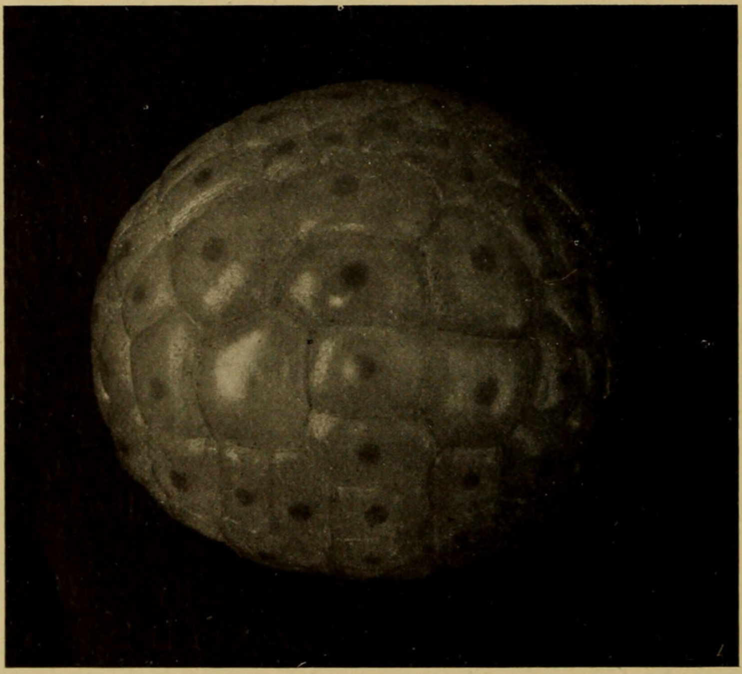
At an early stage there are thus separated in the egg the rudiments of the three layers distinguishable in the development of all higher animal organisms : ectoderm, mesoderm and endoderm. These may be diagrammatically represented as in Fig. *d*.

The ectoblasts by multiplication of cells soon extend over the entire ovum until only a narrow pore is left on the lower or ventral pole (Models 17, 18). Owing to the unequal rate of this growth, the upper or animal pole is at the same time shifted anteriorly till its angular distance from the lower vegetative pole becomes on this side only 90° (Model 18).



MODEL 16

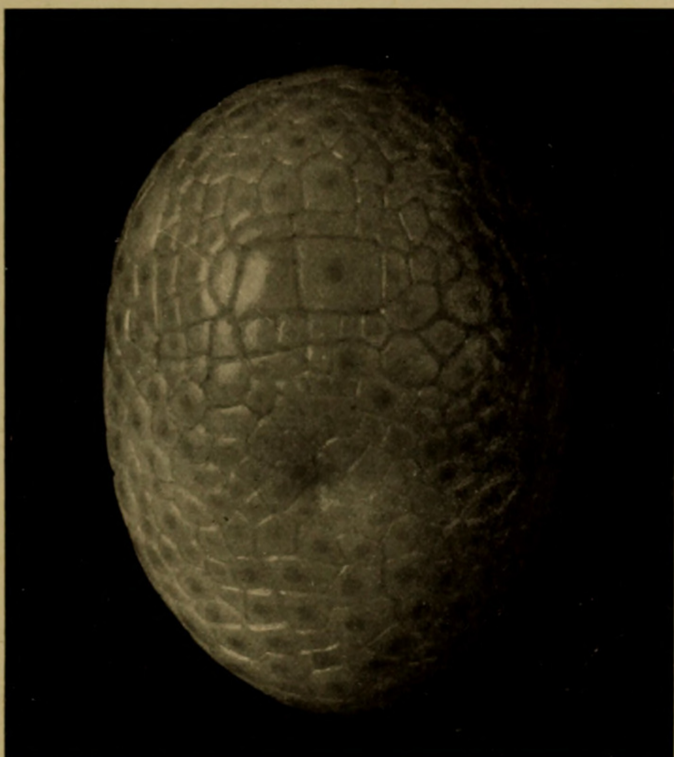
Second division of mesentoblast, resulting in the formation of two meso-blasts and two entoblasts, which are concealed under the rim of the plate of ectoblasts, further divisions of ectoblast cell.



MODEL 17

Continued spreading of ectoblasts over the surface of the egg. Their origin from the three quartets is indicated in the model by colors: first quartet, red; second, blue; third, uncolored.

Immediately around the pore left by the closing of the edge of the ectoblasts is seen on this model the depression which indicates the beginning of the future mouth of the embryo. For a short time the pore itself is closed, but soon opens again and communication is thus established between the exterior and the internal cavity of the embryo. The structure of the embryo at this time may be represented diagrammatically as in Fig. *e*.



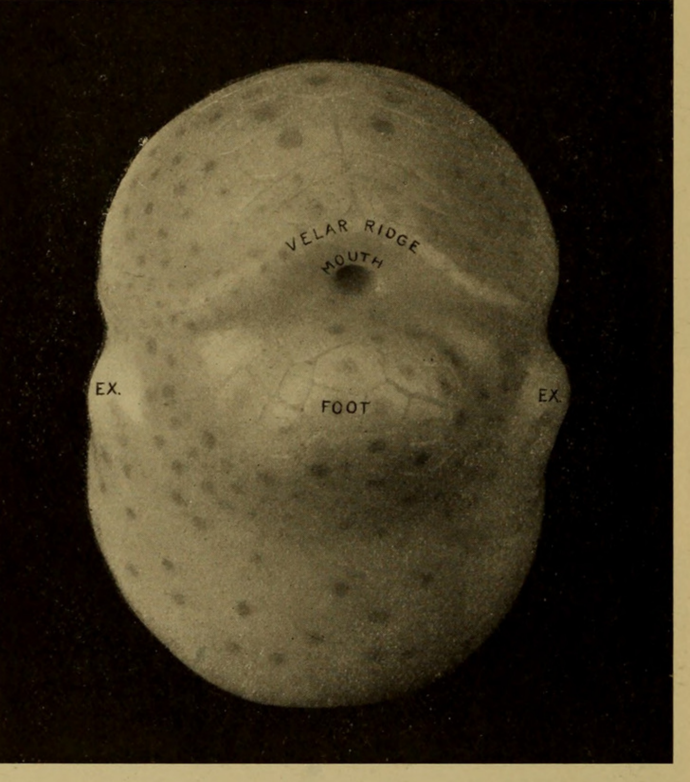
MODEL 18

The ectoblasts completely enclose the egg, leaving only a narrow pore (blastopore), about which is seen a depression. The derivation of ectoblasts from the three quartets indicated on the models by the coloring. The various regions of the future larva are becoming more sharply defined.

From this time on, the development consists of the differentiation by growth of the multiplying cells of these three separate layers into the specialized organs of the body.

The ectoderm cells which, as shown by the number of nuclei, are already very numerous, multiply rapidly in certain areas indicated by the slight outgrowths on the surface. These soon become more pronounced and form the beginning of the ectodermic organs of the embryo.

Above the mouth opening, which by this time is clearly defined, a ridge marks the beginning of the velum, or swimming organ, of the larva; below the mouth there is a large protuberance which will form the foot; at the sides of this two smaller knob-like outgrowths form the larval kidneys. At a point directly op-



MODEL 19

The larva begins to assume its definitive form. The mouth opening is formed; above it the curved edge of the velum is defined; below it the foot begins to protrude; on either side of this the first appearance of the larva kidney (EX) is indicated. At the lower pole of the model the shell gland is shown.

posite the apical, or head, end the shell gland develops (Model 18). Model 19 shows the shell beginning to be secreted by the shell gland.

The entoblast cells of the cavity of the gastrula by a process of unequal growth rapidly go to form the various parts of the digestive tube: stomach, liver, intestine etc. The œsophagus is formed by an invagination of the ectoderm from the exterior.

The middle layer, the mesoblastic layer, forms the muscles, the circulatory system, heart and blood-vessels and the supporting tissues of the body.

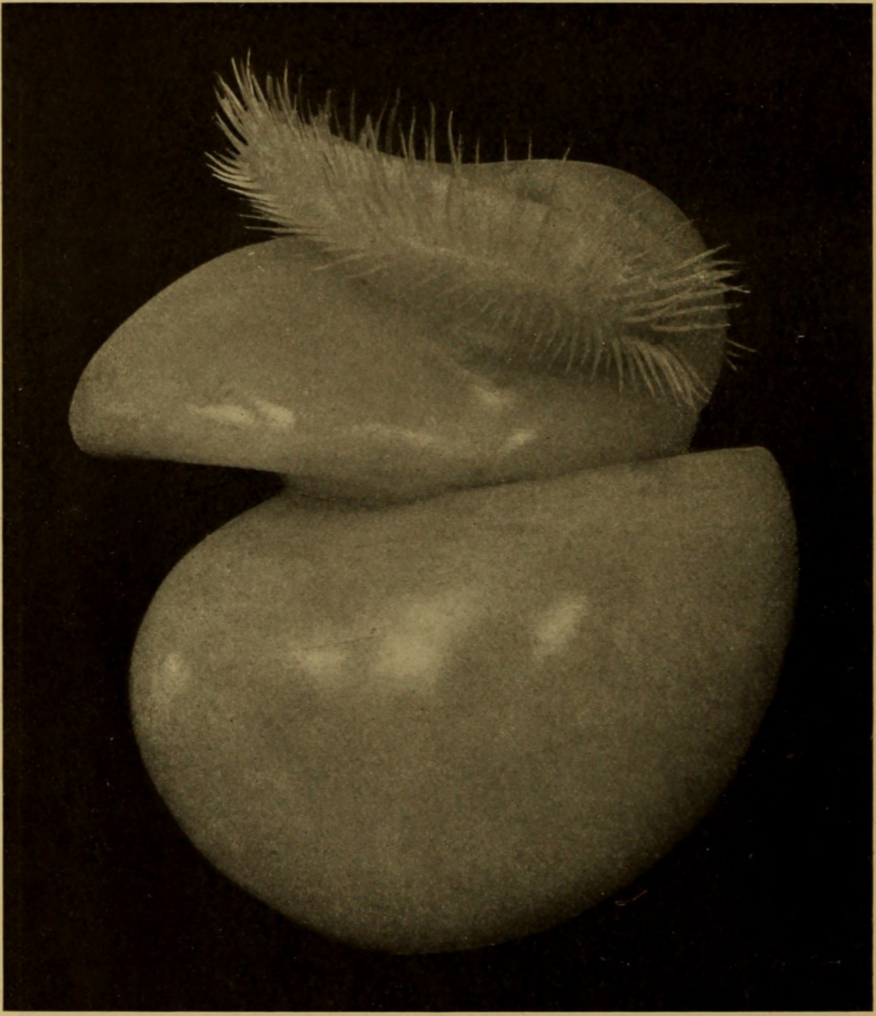
Coincident with this differentiation of the regions of the body into organs, a change in the direction of the antero-posterior axis of the embryo takes place. The whole posterior portion is

MODEL 20

The formation of the veliger larva has proceeded farther. The various external organs are well defined. Below is seen the shell secreted by the underlying cells of the shell gland.

pushed ventrally: the mouth opening and the whole apical pole are shifted forward, and there is a twisting of the entire axis, plainly seen in the bending of the intestine. This organ, which originally lay in the mid-ventral line, assumes the form of an almost complete loop (Model 22). The asymmetry of the mollusk larva is thus established and the definitive asymmetry of the adult is foreshadowed.

Models 21 and 22 show the completed larva, the free-swim-

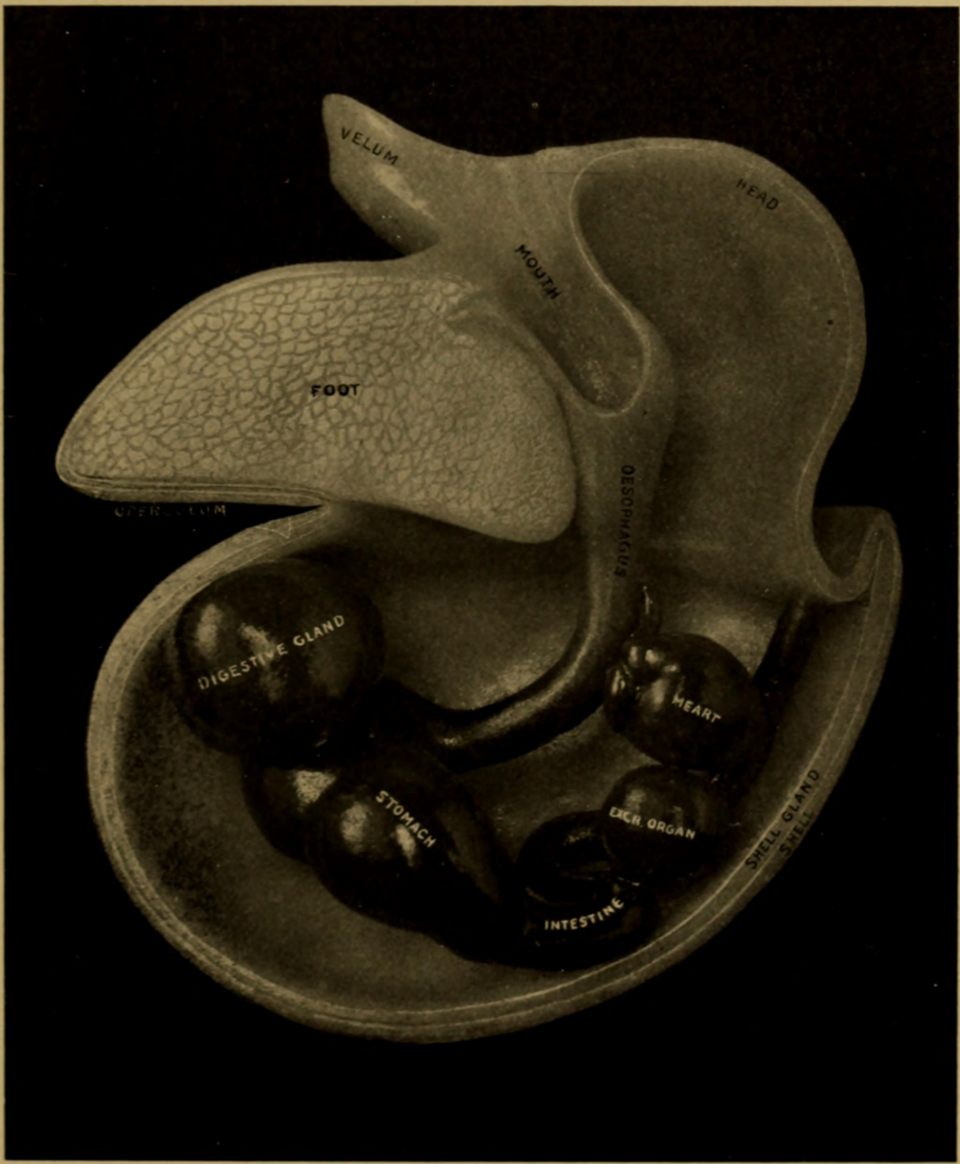


MODEL 21. SIDE VIEW

The mollusk larva, or the veliger, completed. The velum, or swimming organ, about the anterior end bears two rows of cilia. The foot is large and prominent and bears on its under surface the lid, or operculum, by which the opening of the shell is closed when the animal withdraws into it. On the head are seen the two eyes. The two raised points near these mark the position of the feelers or tentacles.

ming veliger with its fully formed ciliated velum, or swimming organ, the shell and the large foot, bearing on its lower surface the operculum, or lid, by means of which the shell is closed when the animal withdraws into it. On the head are seen the two eyes and near them the tentacles.

The veliger stage, though more or less suppressed in land mollusks, is common to all gastropods. By an additional series of changes, consisting in a continued growth and development in certain directions, this larva is ultimately metamorphosed into the adult form of its species.



MODEL 22

A section of the veliger showing the internal anatomy.

APPENDIX.

TECHNICAL DESCRIPTION OF THE MODELS.[1]

1. A. The ovum of *Crepidula* at the time of fertilization.

1. B. The fertilized ovum showing pronuclei lying in the cytoplasm at the animal pole. On either side of them the centrospheres. At the vegetative poles is seen the yolk-stalk. Jour. Morph., Vol. XIII, 1897, fig. 1.

2. First cleavage—appearance of first cleavage furrow. Jour. Morph., Vol. XIII, figs. 3, 4.

3. Completion of first cleavage furrow. Nuclei and asters opposite each other in the two blastomeres. Between the blastomeres are the polar bodies. Jour. Morph., Vol. XIII, fig. 5.

4. Resting stage after first cleavage. Flattening of blastomeres against each other. Dexiotropic turning of nuclei, asters and protoplasmic areas. Jour. Morph., Vol. XIII, fig. 7.

5. Beginning of second cleavage. Læotropic turning of spindles and protoplasmic areas. The centrospheres of preceding cleavage lie near the cleavage furrow. Jour. Morph., Vol. XIII, fig. 7.

6. Second cleavage. Beginning of second cleavage furrow. Læotropic rotation of spindles. Polar furrow being formed. Jour. Morph., Vol. XIII, fig. 9.

7. Completion of second cleavage. Asters nearly in position of poles of preceding spindles. Polar furrow well formed. Jour. Morph., Vol. XIII, fig. 10.

8. Third cleavage. Spindles almost radial, but showing slight dexiotropic rotation. Jour. Morph., Vol. XIII, fig. 12.

9. Third cleavage. Completion of first quartet. Position of asters shows that division was dexiotropic. Jour. Morph., Vol. XIII, fig. 13.

10. Fourth cleavage. Læotropic. First quartet has rotated into furrows between macromeres. Jour. Morph., Vol. XIII, fig. 14.

11. Fourth cleavage complete. Fifth cleavage, læotropic division of first quartet of micromeres and formation of "turret cells" (trochoblasts). Jour. Morph., Vol. XIII, fig. 16.

12. Fifth cleavage complete. Sixth cleavage dexiotropic. Formation of third and last quartet of ectomeres. Sixteen cells. Jour. Morph., Vol. XIII, fig. 17.

[1] The models correspond to the figures in "The Development of Crepidula," by Dr. E. G. Conklin, Jour. Morph., Vol. XIII, 1897, and "Karyokinesis and Cytokinesis," Jour. Acad. Nat. Sci., 2d Ser., Vol. XII, Phila., 1902.

13. Sixth cleavage complete. Division of second quartet complete. Quadrangular plate of ectomeres with angles of plate in furrows between macromeres. Twenty ectomeres (4 apical, 4 turret and 12 belt cells) and 4 macromeres. Jour. Morph., Vol. XIII, figs. 19, 20.

14. Formation of first member of fourth quartet, the mesentoblast, from the left posterior macromere; formation of basal cells of cross by the second division of first quartet. Jour. Morph., Vol. XIII, figs. 22, 23.

15. Division of the mesentoblast completed, dexiotropic. Second and third quartets. Turret cells formed. Forty-two cells: 4 apicals 8 cross, 4 turret, 20 belt cells, 2 mesentoblasts, 4 macromeres. Jour. Morph., Vol. XIII, fig. 29.

16. Fourth quartet completed by læotropic cleavage of macromeres, A, B and C. The two mesentoblasts of the preceding stage have divided, forming the two enteroblasts and two primary mesoblasts which lie immediately above the latter, but concealed by the plate of ectoblasts. Jour. Morph., Vol. XIII, fig. 31.

17. Further division of ectoblasts. Expansion of arms a, b and c of ectoblastic cross into a cell plate. Anterior shifting of apical cells. Posterior turret cells undivided. Formation of quadrangular blastopores, the enteroblasts in posterior angle. Jour. Morph., Vol. XIII, figs. 51, 52.

18. Later stage. Apex on ventral side, slightly to the right. Cells of ectoblastic cross, first quartet, cover the whole anterior end of embryo. Large cells of posterior arm, dorsal. The closing of the blastopore and a depression about it indicating the formation of the stomodæum. The superior rows of ectoblast cells of second quartet, directly above the blastopore, form the first and second velar rows. The shell gland is forming at the postero-dorsal and somewhat to the left. Jour. Morph., Vol. XIII, figs. 65, 74, 75.

19. Older embryo, showing apical, posterior and pedal cell plates. On either side to the anterior and posterior of the dorsal cell plate, the velar rows are branching. Mouth and the external kidneys are formed, the shell gland expanding. Jour. Morph., Vol. XIII, figs. 76 to 79.

20. Older stage-formation of velum and foot. The shell gland greatly expanded and forming the shell of the veliger. Jour. Morph., Vol. XIII, figs. 80–82.

21. The fully formed veliger.

22. Section of the preceding.

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