

THE NUTRITION OF THE OVUM OF *HYDRA VIRIDIS*.

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UNIVERSITY OF VIRGINIA.

The incipient ovary of *Hydra viridis* is represented by a mass of proliferated interstitial cells. At a very early stage in the development of the ovary some of its cells become much larger than the others. There seems to be a struggle on between these cells; for, as development of the ovary proceeds, but one of the larger ones remains whole, and the smaller ones perish. The cells, that are directly involved in this struggle, are enclosed in a thin wall of slightly chromatic, modified epithelio-muscular cells. Kleinenberg (72), Brauer (91), Downing (08) and Tannreuther (08) agree in the statement that one of the enlarged interstitial cells gets the ascendancy over the others and grows at their expense. If there be in the incipient ovary more than one greatly enlarged interstitial cell, these may fuse to form the oögonium as over against the cells of what Tannreuther (08) designates "the cells of the peripheral region which contribute to the formation of the yolk," p. 274. These peripheral cells are not taken into the growing oögonium's cytoplasm bodily as Brauer (91) described. They disintegrate at the periphery of the oögonium and are then resorbed. The relation of these disintegrating cells to the cytoplasm of the final oögonium are shown in Fig. 1. Figs. 3 and 4 show phases of disintegration in these neighboring enlarged interstitial cells. As their cytoplasm breaks down, the nuclei display disintegration features. Eventually the entire cell disintegrates. The substance of these disintegrated cells is absorbed by the oögonium, as Kleinenberg (72) described. The material thus obtained results in the oögonium growing greatly to become a conspicuously large amœboid cell (Text-figure 2). This cell, by means of radiating stout pseudopods, spreads out over one third or more of the mesoglea's outer surface. This amœboid gamete was first figured by Fewkes and Mark in 1884. This pseudopodial cell has now attained its maximum size and is, therefore,

the primary oöcyte. The feeding of the oögonium, of the final oögonial generation, upon the neighboring, enlarged interstitial cells represents the first phase of the nutrition of the ovum of *Hydra viridis*. Nutrition, in this phase, is referred to the growth of the final oögonium into the primary oöcyte.

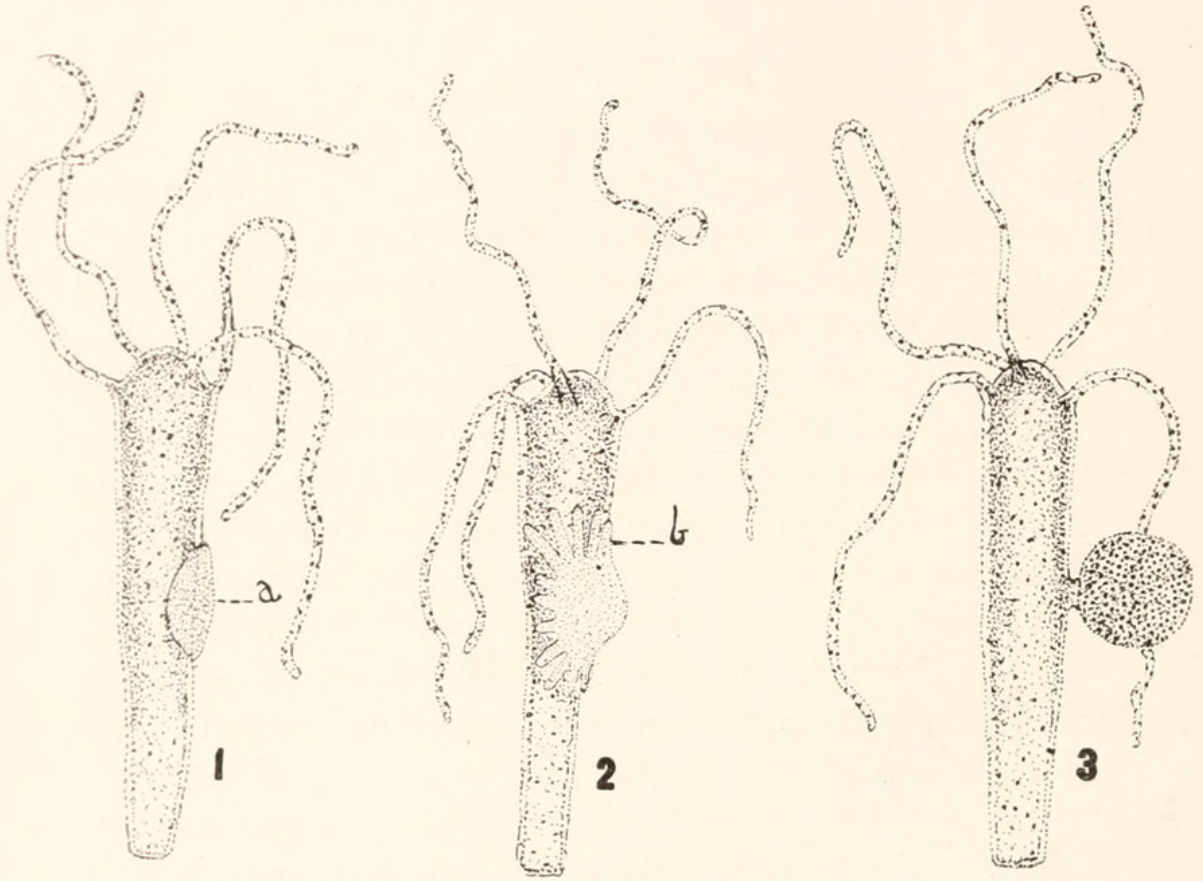


FIG. 1. Oögonium before pseudopodia are thrown off. *a* shows plane through which section, shown in figure 1 of plate, was taken.

FIG. 2. Oöcyte with maximum number of pseudopodia. *b* shows plane through which section, shown in figure 5 of plate, was taken.

FIG. 3. Advanced primary oöcyte with a full complement of deutoplasm.

Previous investigators have failed to recognize that there are two phases in the nutrition of *Hydra's* ovum. Perhaps failure, on their part, to recognize the dual nature of the nutrition of the ovum of *Hydra* arises out of the resemblance of the disintegrating interstitial nuclei to deutoplasmic granules (Fig. 3). Brauer (91) held that the nuclei of the cells, that were being ingested by the egg, became the yolk granules or his "Pseudozellen." Downing (08) says the "interstitial cells adjacent to the egg in the fairly mature ovary have their walls in contact with the egg resorbed and the content of the cell becomes part of the egg (Nusbaum).

The greatly enlarged nuclei, gorged with lecithin, also become yolk granules or "Pseudozellen," p. 66. Tannreuther (08) also looks upon the yolk granules as arising from the nuclei of the interstitial cells. He says: "When the pseudopodia are completely formed, the nuclei of the interstitial cells forming the ovary are taken up by the amœboid egg and become changed into the yolk or pseudo-cells of the egg. . . . After the yolk or pseudo-cells are formed they divide amitotically" (p. 264).

We have been unable to bring the details of *Hydra viridis* ovary in line with the above interpretations and facts.

To begin with, up until the time that the growing, amœboid oögonium has made maximum contact with the mesoglea—thus placing it in relation to the endoderm—there has been no yolk formation. In the meantime, however, many of the attending, peripherally disposed cells have disintegrated and have been resorbed. Sometimes this disintegration and resorption has gone so far that, before the oögonium has well advanced in growth, the attending cells lie only at its margin (Fig. 1). In a typical example, by the time the oögonium has reached its maximum growth, there is but a thin tissue of highly modified epidermis covering its general surface (Fig. 5). In such example, there may yet be disintegrating cells at the tips of the pseudopods or even beyond them. Thus it is to be emphasized that many of the enlarged interstitial cells have disintegrated (perhaps most of them) and have been resorbed during the oögonium's growth. And yet, up until maximum surface contact with the mesoglea has been established, no yolk formation has resulted. It should be further indicated that we have found no enlarged interstitial cells to be taken up bodily by the amœboid egg-cell. These two features of the nutrition of ovum of *Hydra* stand in contrast with what Tannreuther (08) describes. He says: "When the egg has reached its growth, it is amœboid in form with the nucleus near the center. The egg at this stage of development contains no yolk, . . . but when pseudopodia are completely formed, the nuclei of the interstitial cells forming the ovary, are taken up by the amœboid egg and become changed into yolk or pseudo-cells of the egg. Fig. 6 represents a cross-section of several pseudopodia into which the nuclei of the interstitial cells of the ovary

are passing" (p. 263-264). The contrast between what Tannreuther herein describes and our observations appears in two ways. In the first place, if yolk formation depends upon the disappearance of the interstitial cells of the ovary, then yolk should appear when these cells disappear. They are clearly seen to disappear throughout the growth of the oögonium and yet until the latter has reached its full growth no yolk has appeared. In the second place, we find that no interstitial cells have been bodily taken up or ingested as shown by Tannreuther in his Fig. 6. His Fig. 6, however, is not, in itself, convincing; for he shows the so-called nuclei leaving only two interstitial cells. Moreover, the cells from which these nuclei are migrating show no marked cytoplasmic change. Likewise, his written observations are not convincing with reference to the manner in which yolk arises. He makes the significant statement that "The pseudopodia do not grow out between the cells of the ovary, but rather between the ovary as a whole and the mesoglea" (p. 263). If, now, the pseudopodia were sent out with reference to yolk formation, dependent upon the interstitial cells of the ovary, they would "grow out between the cells of the ovary" and not "between the ovary as a whole and the mesoglea."

There is no meaning in the extensive application of the primary oöcyte's pseudopodia to the mesoglea, if the yolk granules are derived from the interstitial cells. On the other hand, we see in this spreading out of the primary oöcyte over the mesoglea a method of making maximum contact with a source of food material upon which to draw for the elaboration of deutoplasm.

In *Hydra*, the endoderm is the source of food supply. Kepner and Hopkins (24) observed that, as a diploblastic animal, *Hydra* cannot transport widely material absorbed by the endoderm. For example, chloretone injected into the enteric cavity of *Hydra* effects only the adjacent ectoderm of the body proper. The sphincters at the bases of the tentacles prevented the injected chloretone entering the latter and the compression of the walls of the peristome prevented chloretone entering its lumen. It was thus of interest to observe that the tentacles and peristome received none of the chloretone that had been absorbed by the general endoderm, for they became unusually active in contrast

to the quieted body proper. Just as chloretone could not be sent to the closed tentacles, so it appears the endoderm of *Hydra* cannot send food-material along a narrow channel to its oögonium. The growing oögonium must, therefore, come to the endoderm. As a result of this imposition, by the time the final oögonium has become, through growth, a primary oöcyte, an extended relation between the latter and the endoderm has been established. This relation established marks the inception of the second phase of the nutrition of the ovum of *Hydra viridis*. At the beginning of this second nutritional phase, there are no deutoplasmic inclusions within the cytoplasm. Soon, however, yolk is formed within the cytoplasm of the oöcyte (Fig. 5). This deutoplasm is elaborated by the oöcyte out of material taken over in solution from the endoderm and assimilated by the female gamete. Thus the deutoplasm may be looked upon as material elaborated by the oöcyte. The deutoplasmic granules are not to be considered the lineal descendants of original nuclei of neighboring interstitial cells that have come to be more and more numerous through amitosis. This position seems logical when we bear in mind the fact that, though many interstitial cells have disintegrated (perhaps most of them) and have been resorbed during the egg's growth, yet, up until maximum surface exposure to the endoderm has been made, no yolk-formation has resulted. Our interpretation is further strengthened by the observation that so long as yolk is making its appearance within the primary oöcyte a maximum surface relation to the endoderm is maintained; but when the maximum amount of yolk has been formed the egg retreats from the endoderm as Tannreuther (08) indicates: "After the amœboid egg becomes filled with yolk, the pseudopodia are drawn in and the egg becomes nearly spherical" (p. 264), (Text-figure, 3). The second phase of the nutrition of *Hydra viridis*, therefore, ends with the retreat of the primary oöcyte from the mesoglea after it has become filled with deutoplasm. No deutoplasm is formed thereafter. This phase of nutrition is referred to the development of the zygote.

SUMMARY.

The nutrition of *Hydra viridis* is a dual process, there being two phases.

The first phase has reference to the nutrition of an oögonium of the final generation. This oögonium is nourished through the disintegration and resorption of adjacent interstitial cells. Through the nourishment, thus obtained, the final oögonium grows into a large pseudopodial cell, the primary oöcyte. The first nutritional phase is referred to the growth of the final oögonium into a primary oöcyte. It does not involve yolk-formation.

The second phase of nutrition begins with the primary oöcyte lying, as a pseudopodial cell, in extended relation to the endoderm. Yolk is elaborated by the oöcyte from material handed over by the endoderm and the protoplasm of interstitial cells is not involved. The second nutritional phase is referred to the development of the zygote.

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EXPLANATION OF PLATE.

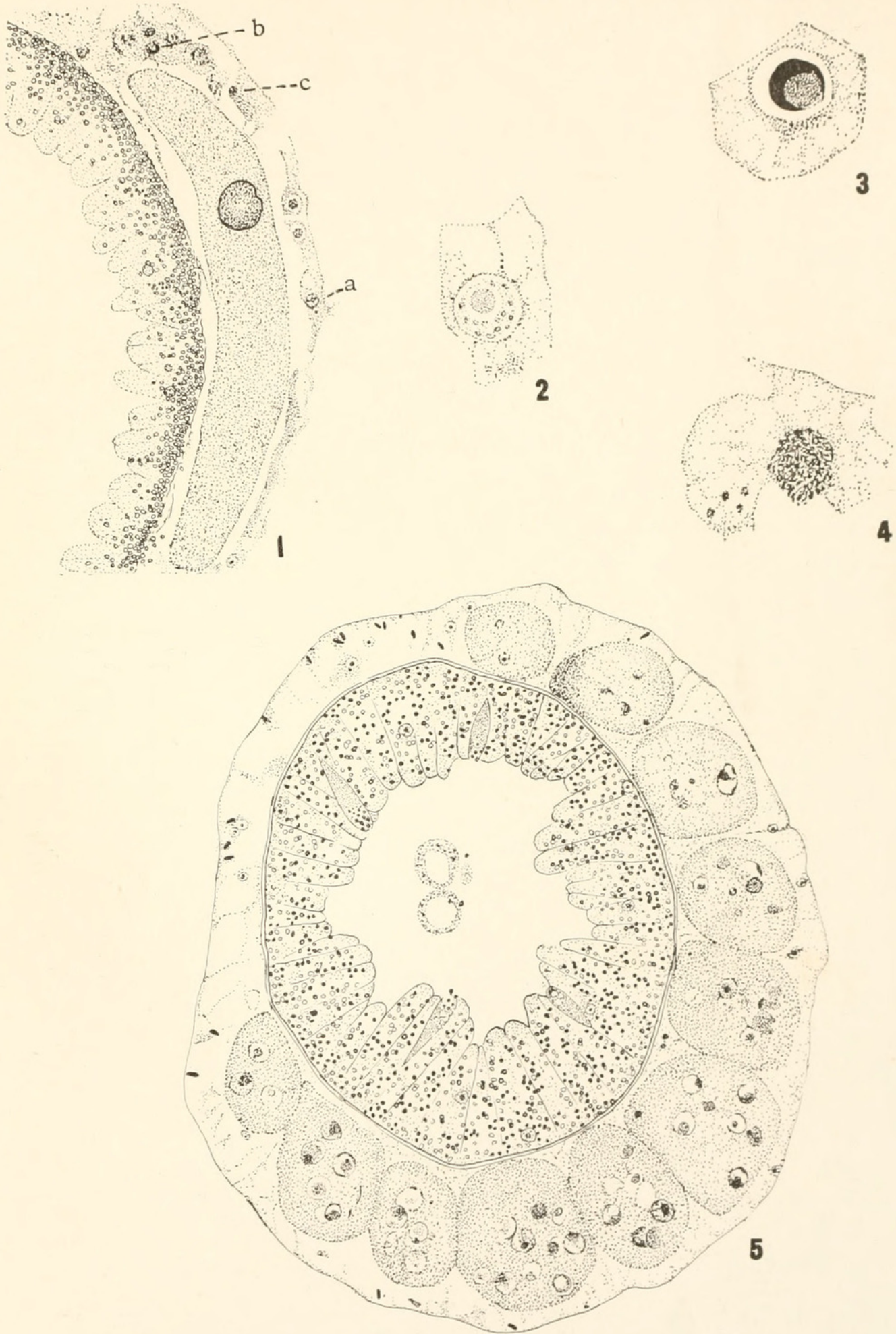
FIG. 1. Part of a section taken through plane indicated at *a* in text-figure. A group of disintegrating interstitial cells is shown at *b*, *c*. *a* shows that already, in this particular example, the superimposed ectoderm was but a single layer thick. $\times 250$.

FIG. 2. Cell *a* of Fig. 1, magnified to indicate the character of cell that forms ovarian wall. $\times 1,250$.

FIG. 3. Cell *b* in Fig. 1. Shows a disintegrating interstitial cell in which the nucleus resembles a deutoplasmic granule. $\times 1,250$.

FIG. 4. Cell *c* in Fig. 1. An attending interstitial cell in a more advanced phase of disintegration than cell shown in Fig. 3. The nucleus no longer resembles a deutoplasmic granule. $\times 1,250$.

FIG. 5. Section taken through plane indicated at *b* in text-figure. Shows eleven pseudopodia closely applied to mesoglea. Yolk-formation has begun; it is not, however, completed though all enlarged interstitial cells have disappeared. $\times 250$.



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PUBLISHED MONTHLY BY THE
MARINE BIOLOGICAL LABORATORY

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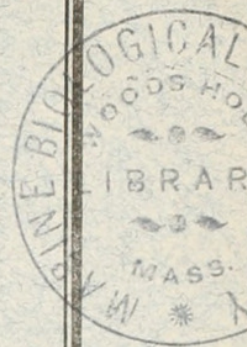
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