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C. B. DAVENPORT

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STUDIES IN MORPHOGENESIS.

IV.

A PRELIMINARY CATALOGUE OF THE PROCESSES CONCERNED IN ONTOGENY.

BY C. B. DAVENPORT.

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No. 6. — Studies in Morphogenesis. — IV. A Preliminary Catalogue of the Processes concerned in Ontogeny.[1] By C. B. Davenport.

CONTENTS.

Most important perhaps of all the problems which the biologist sees lying unsolved before him is that of the development of the individual, — a problem to which, from the time of Aristotle, zoölogists have repeatedly turned, although scarcely hoping for its eventual solution.

Without attempting to consider the various theories of Ontomorphogenesis which have at different times been offered, it is sufficient to state that it is now generally agreed that ontogenesis is a process, or rather a complex of processes, taking place in the protoplasm of the developing individual.

Now it is a highly probable belief that no movement takes place in protoplasm except as a response to stimuli. The very fact that ontogenesis is a complex of actions indicates that there must be a large number of stimuli raining in upon the different parts of the developing protoplasm to which they respond.

In order to gain some idea of what the stimuli are, it is first necessary to analyze the ontogenetic complex of processes into its simple elementary ones.

It is the aim of this paper to make such an analysis into the elementary ontogenetic processes as a basis for determining the nature of the exciting stimuli.

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, E. L. Mark, Director, No. L.

Other authors have devoted chapters to "Developmental Processes," but none of these can be considered as at all complete.

Thus O. Hertwig, in his "Text-Book of the Embryology of Man and Mammals" (English Translation by E. L. Mark, 1892, p. 76), has a "General Discussion of the Principles of Development." He recognized two main ones: (1) the principle of unequal growth (producing folds which are either invaginations or evaginations, and which may unite along their edges); and (2) the principle of histological differentiation.

Minot, in his Human Embryology, in a chapter on "Differentiation," seems to think also that these two processes are sufficient to explain the differentiation of organs.

More important in this connection than either of the preceding is the recent paper of Herbst in the "Biologisches Centralblatt" (Vol. XIV. Nos. 18–22). This author, after reviewing the literature upom taxism and tropism, explains as phenomena of the same order certain ontogenetic processes. He has not, however, attempted to catalogue all the ontogenetic processes.

Before beginning the present catalogue, I may state that I distinguish between ontogenetic *principles* and ontogenetic *processes*. Under the first head I include such laws of development as terminal growth, repetition of parts and bilateral symmetry in development. These I have not attempted to catalogue. The present paper is concerned only with the latter group, which comprises the different elementary operations or actions exhibited in ontogeny.

These may be divided into two classes: 1. the grosser ontogenetic processes; and 2. histogenic processes. This paper deals with the first class only.

In discussing the grosser ontogenetic processes we may distinguish (A) those of a more general nature from (B) the more special ones.

A. The *general ontogenetic processes* comprise those of a general physiological character. Of these, at least three are commonly recognized: —

1. Growth (including both the results of assimilation and of imbibition of water).
2. Nuclear division.
3. Secretion.

B. The *special* ontogenetic processes are differential in character, i. e. the differentiation of the body is effected by them.

These processes may be classified, first of all, according to the form of

the protoplasmic bodies in which they occur. These exist either as (I.) isolated cells, or as larger multinucleated bodies. Of the latter we may recognize three classes: (II.) bodies extended chiefly in one direction, — threads, fibres, tubules; (III.) those which extend as a layer; and (IV.) those in which the three dimensions are more nearly equal, forming solid masses.

I propose now to discuss the processes occurring in each of these four classes.[1]

I. Ontogenetic Processes occurring in Migratory Protoplasmic Bodies — Mesenchyme.[2]

1. *Migration of Nodal Thickenings in a Protoplasmic Mesh-work.* This process is found, for example, in many Arthropod eggs before the formation of the peripheral blastoderm. (Figure 1.) No one can doubt that protoplasm extends throughout the whole egg in the form of a mesh- or foam-work, whose interspaces are filled with yolk. The protoplasm is aggregated around the nuclei at certain nodal points, which later migrate to the surface or through the yolk as vitellophags. Cf. K. & H.,[3] Figs. 7, 363, 417, 448, 472, 473, 771.

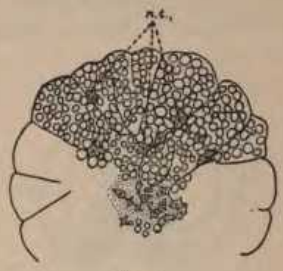

Fig. 1.

[1] It may be a cause of dissatisfaction to some that this classification is not "strictly dichotomous"; it is still more serious that the different heads are not of co-ordinate rank or mutually exclusive. Of course, the classification employed in this list cannot be regarded as a final one. I hope, however, that I have succeeded in an attempt roughly to arrange the different items in a logical fashion.

[2] In the present paper the word "mesenchyme" is used as a name for all amœboid, migrating cells, of whatever origin.

[3] Throughout this paper certain abbreviations are used in referring to the books from which the figures are copied. These are: K. & H. for Korschelt und Heider's "Entwicklungsgeschichte"; M. for Minot's "Human Embryology"; and H.-M. for Hertwig's "Text-Book of Embryology of Man and Mammals," translated by Mark.

Fig. 1. Section through an egg of a Myriapod (Geophilus), showing the nodal thickenings (*n. t.*) in the act of migrating towards the periphery of the egg. See K. & H., Fig. 449.

2. *Free Migration of Amœboid Bodies.* This process differs from the preceding in that the migrating bodies are not connected together. It is characteristic of mesenchyme. I know that Dreyer ('92, Jena. Zeitschr., XXVI. 359) and Sedgwick ('94, Quart. Jour. Micr. Sci., XXXVII.) insist that the cells of mesenchyme, which are usually considered unconnected like so many amœbæ, are really nodal thickenings in an extensive mesh-work or foam-work, the intervening fluids being the, in some places confluent, vacuoles. Wherever mesenchyme has this structure, its migrations belong to the preceding class. But I believe there still remains a considerable residuum of cases falling under this head.

This process is capable of division into two subprocesses; viz. (*a*) migrating of mesenchyme out of a protoplasmic layer in order to become free, and (*b*) migrating through fluid-filled spaces. Both these processes are illustrated in Figure 2. Further illustrations will be found in K. & H., Figs. 102, 103, 170, 175–180, 182, 186, 188–190, 207, 285, 559, 596–598, 628, 698, 733, 809, and M., Figs. 121, 234, 239.

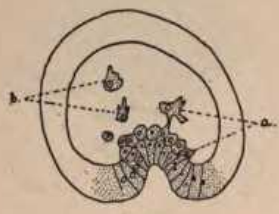

FIG. 2.

The migratory processes named below are of subordinate rank to Nos. 1 and 2. But, being fairly well marked and of considerable importance, it is convenient to treat them as co-ordinate.

We may distinguish, first, movements of mesenchymatous elements towards and from each other, and, secondly, movements with reference to other protoplasmic masses.

3. First among the former we recognize the *aggregation of migratory protoplasmic bodies*, and here we may distinguish three sub-classes according to the form of the resulting body.

a. First we have the *aggregation of mesenchyme into a body with a chiefly linear dimension*, — the formation of a thread, cord, or tubule.

Examples of this process in Invertebrates are seen in the formation of the kidney of Lamellibranchs, which seems to be laid down as a cord-like aggregation of mesenchyme, and in that of the thread of the yolk glands

Fig. 2. Section of Holothurian larva showing mesenchyme migrating out of a layer at *a*, and through a fluid-filled space at *b*. From H.-M., Fig. 109.

of Turbellaria according to Iijima (Zeitschr. f. wiss. Zool., XL. 455). Among Vertebrates, we have the observations of Paterson, (Figure 3,) according to which the sympathetic nerve arises by the aggregation of mesenchymatous elements into a strand; of His, who affirms the origin of the spinal and the olfactory ganglia from migrating cells; and of various authors, who make blood capillaries and lymph vessels arise by this process (cf. M., pp. 217, 413).

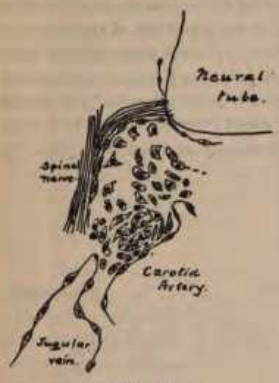

FIG. 3.

FIG. 4.

FIG. 5.

b. Next we must consider the *aggregation of mesenchyme into a superficially extended body,* — the formation of a layer. This process does not seem to be very common; one example is seen in Figure 4.

c. As the last of these processes of aggregation we have the case of *aggregation into a mass.* This wide-spread ontogenetic process may be illustrated by the formation of gemmules in a marine sponge (Figure 5). Other examples are found in the formation of the adductor muscles of

Fig. 3. Cross section of a rat embryo in the upper thoracic region, showing the development of the sympathetic nerve (between spinal nerve and carotid artery). From A. M. Paterson, '91, Trans. Roy. Soc. Lond., Pl. XXII. Fig. 4.

Fig. 4. Later stage of the embryo shown in Figure 1. The migrating protoplasm has aggregated itself into a layer at the surface of the embryo. See K. & H., Fig. 449.

Fig. 5. Section of a marine sponge (Esperella), showing a gemmule, a mass of aggregated mesenchyme which is about to produce a gemmule (1'), and migrating, not yet aggregated mesenchyme (1). After H. V. Wilson ('94, Jour. of Morph., IX. Pl. XIV.).