EXPERIMENTAL EMBRYOLOGY

BY

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PREFACE

For the biologist there are, I conceive, in the main two problems. One is to give an account of those activities or functions by means of which an organism maintains its specific form in an environment. The other is to find the causes which determine the production of that form, whether in the race or in the individual. The solution of the first of these problems is the business of physiology, in the usual sense of the term. The second falls to morphology.

It is with the origin of form that we are here concerned, and in particular with its origin in the individual. The endeavour to discover by experiment the causes of this process—as distinct from the mere description of the process itself—is a comparatively new branch of biological science, for Experimental Embryology, or, as some prefer to call it, the Mechanics of Development (*Entwicklungsmechanik*), or the Physiology of Development, really dates from Roux's production of a half-embryo from a half-blastomere, and the consequent formulation of the 'Mosaik-Theorie' of self-differentiation. That hypothesis has been the focus of much fruitful criticism and controversy, the experiment has been followed by many others of the same kind, and the present volume is an attempt to sketch the progress of these researches and speculations on the nature and essence of differentiation, as well as of those which deal with growth, cell-division, and the external conditions of development.

In writing this review I have had the very great advantage of an excellent model in the textbook of Korschelt and Heider (*Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere*, Allgemeiner Theil, Jena, 1902). I have indeed followed the general arrangement adopted by these authors fairly closely except in one respect. I believe so strongly that the processes of growth and cell-division, though they always (in the Metazoa) accompany, are yet distinct from, differentiation, that I have felt justified in treating them in a chapter apart from the other internal factors of development. The external factors—whether of growth, cell-division, or differentiation—are discussed in Chapter III, and the ground is thus cleared for a consideration of the real problem—the differentiation of specific form.

The last chapter is devoted to the theories, scientific and philosophical, of Hans Driesch. I sincerely hope that Herr Driesch will allow my great admiration for the former to atone in some measure for my inability to accept the tenets of neo-vitalism.

It is a very great pleasure to me to acknowledge my indebtedness to the Delegates and Secretaries of the Clarendon Press, and in particular to Professor Osler, for undertaking the publication of this book, as well as for the pains which have been expended in its preparation. Dr. Osler also took the trouble to read through the whole of the manuscript, and Mr. G. W. Smith and Dr. Haldane have been kind enough to look through certain chapters.

To Dr. Ramsden I am under great obligations for his assistance in that part of Chapter II, Section 1, in which surface-tensions are discussed; to Dr. Vernon for calling my attention to Roberts's work on Anthropometry, and to Mr. Grosvenor for the information embodied in the foot-note on p. 89. Mr. A. D. Lindsay has given me invaluable assistance in those sections of Chapter V which deal with the philosophy of Kant, while, for Aristotle, I was fortunately able to attend Professor Bywater's lectures on the *De Anima*.

I can hardly express the debt I owe to Mr. J. A. Smith for much friendly counsel and criticism, although he is, of course,

in no way responsible for the philosophical speculations in which I have ventured to indulge.

The illustrations are largely borrowed from Korschelt and Heider's work, and I must thank Herr Gustav Fischer, of Jena, for his readiness in supplying the blocks. Others are from the original publications[1], and I am obliged to the proprietors for permission to make use of them. A few are my own.

In the appendices will be found an account of some recent work on the relation between the symmetry of the egg and that of the embryo in the Frog, and on the part played by the nucleus in differentiation.

[1] *Proceedings of the Boston Society of Natural History*, the *Journal of Experimental Zoology* (Williams & Wilkins, Baltimore), the *American Journal of Physiology* (Ginn & Co., Boston), *Zellen-Studien* (Fischer, Jena), *Verhandlungen der Anatomischen Gesellschaft* (Fischer, Jena), *Ergebnisse über die Konstitution der chromatischen Kernsubstanz* (Fischer, Jena), *Archiv für mikroskopische Anatomie* (Cohen, Bonn), *Archiv für Entwicklungsmechanik* (Engelmann, Leipzig), and the *Popular Science Monthly* (Appleton & Co., New York).

CONTENTS

CHAPTER I

INTRODUCTORY

THAT living creatures reproduce their kind is a fact which is familiar to us all, but it is the peculiar privilege and province of the embryologist to observe and to reflect upon that marvellous series of changes whereby, out of a germ which is comparatively structureless and unformed, a new organism is developed which is, within the limits of variation, like the parents that gave it birth.

Development is the production of specific form. From a particular kind of germ only a particular kind of individual will normally arise, though unusual conditions may lead to the formation of an abnormality or monstrosity. Thus, while the germ is the material basis, development is the mechanism of inheritance. The student of heredity seeks to express in terms which shall be as exact as possible, ultimately mathematically exact, the degree of similarity between the offspring on the one hand, and parents and more remote ancestors on the other. The embryologist has under his very eyes the process by which that similarity is brought about, and even when the resemblance shall have been stated with all possible precision, it will still remain for him to give an explanation of those changes whereby the inheritable peculiarities of the species are handed on from one generation to the next.

Used in the widest sense of the word, development includes not merely the formation of a new individual from a single cell, whether fertilized or not, but also the phenomena of budding and regeneration. In a narrower sense, however, the term is restricted to the first of these processes, and a corresponding distinction is made, however artificially, between Experimental Embryology and Experimental Morphology, when the subject is treated from a physiological point of view.

In development two factors are obviously involved. One is growth, or increase of volume, more correctly increase of mass; the other is differentiation, or increase of structure; and, in multicellular organisms, both these factors are accompanied by division of the nucleus and the cell.

Segmentation is the first sign, or almost the first sign, the developing ovum gives of its activity; and this cutting up of the egg-cell into parts, which marks the beginning, is also continued during the later stages of ontogeny, and goes on as long as the life of the organism endures.

Growth is especially characteristic of the embryonic and of the adolescent organism. It occurs at different rates in the different cells, and indeed the growth of a group of cells is in itself often an act of differentiation. Growth may depend upon the absorption of water or the assimilation of other substances, and this may lead simply to an increase in the size of internal cavities, as in the blastula of Echinoderms or the Mammalian blastocyst; to an increase in the volume of the living protoplasm; or to the secretion of intracellular or intercellular substances, either organic (for example, the notochordal vacuoles, the matrix of cartilage and bone) or inorganic (the skeletal spicules of Echinoderm larvae, Sponges, and Coelenterata). This increase of mass is not only conditioned by the presence of food in the form of substances found in the environment, but depends on such external circumstances as temperature, atmospheric and osmotic pressure, and so forth.

But while the embryo is dividing up its material—a material which is already to a certain extent heterogeneous, composed, for example, of protoplasm and deutoplasm or yolk—while it is increasing its mass, it is also undergoing a process of differentiation; and, as even a superficial acquaintance with embryology will inform us, one of the most characteristic features of differentiation is that it occurs in a series of stages which follow upon one another in regular order and with increasing complexity. When segmentation has been accomplished—sometimes, indeed, during segmentation—certain sets of cells, the germ-layers, become separated from one another. Each germ-layer contains the material for the formation of a definite set of organs—the endoderm of a Vertebrate, for instance, contains the material for the alimentary tract and its derivatives—gill-slits, lungs, liver, bladder, and the like; the germ-layers are therefore not ultimate but elementary organs, and elementary organs of the first order. In the next stage these primary organs become subdivided into secondary organs—as the archenteron of an Echinoderm becomes portioned into gut and coelom-sac, or the ectoderm of an Earthworm into epidermis, nervous system, and nephridia—and in subsequent stages these again become successively broken up into organs of the third and fourth orders and so on, until finally the ultimate organs or tissues are formed, each with special histological characters of its own. This end is, however, not necessarily reached by all the tissues at the same time. Indeed, it is no uncommon thing for certain of them to attain their final structure while the others are yet in a rudimentary condition; thus, in some Sponges the scleroblasts begin to secrete spicules in the larval period, nematocysts may be formed in the Planula of the Coelenterates, notochordal tissue is differentiated in the newly hatched tadpole of the Frog; and, speaking generally, larval characters are developed at a very early stage.

To this regular sequence of ontogenetic events Driesch has applied the term 'rhythm', the rhythm of development. The organs of the body are, however, by no means all formed of single tissues—bone, epithelium, blood, and the rest—but are compounded, frequently of very many tissues, and this 'composition', to quote a term of Driesch's again, is another of the obvious features of organogeny.

While, therefore, in the last resort all differentiation is histological, that final result, the assumption by the cells of their definitive form, is only achieved after many changes have taken place in the position of the parts relatively to one another while the organs are being compounded, and so its specific shape conferred upon the whole body.

It is possible to find a few general expressions for the manifold changes that take place in the relative positions of the parts. Several years ago, in 1874, His compared the various layers of the chick embryo to elastic plates and tubes; out of these he suggested that some of the principal organs might be moulded by mere local inequalities of growth—the ventricles of the brain, for instance, the alimentary canal, the heart—and he further succeeded in imitating the formation of these organs by folding, pinching, and cutting india-rubber tubes and plates in various ways. This analysis, however, deals only with the foldings of flat layers, and must be supplemented by a more exhaustive catalogue of the processes concerned in ontogeny, such as that more recently suggested by Davenport. Davenport resolves the changes in question into the movements of cells or cell aggregates, the latter being linear, superficial, or massive, and within the limits of these categories the phenomena are susceptible of further classification. The catalogue proceeds as follows :—

I. THE MOVEMENTS OF SINGLE CELLS.

1. Migration of nodal thickenings in a network of protoplasm: e. g. the migration of the 'cells' to the surface of the Arthropod ovum to form a blastoderm, the movements of vitellophags, and yolk-nuclei (Fig. 1).

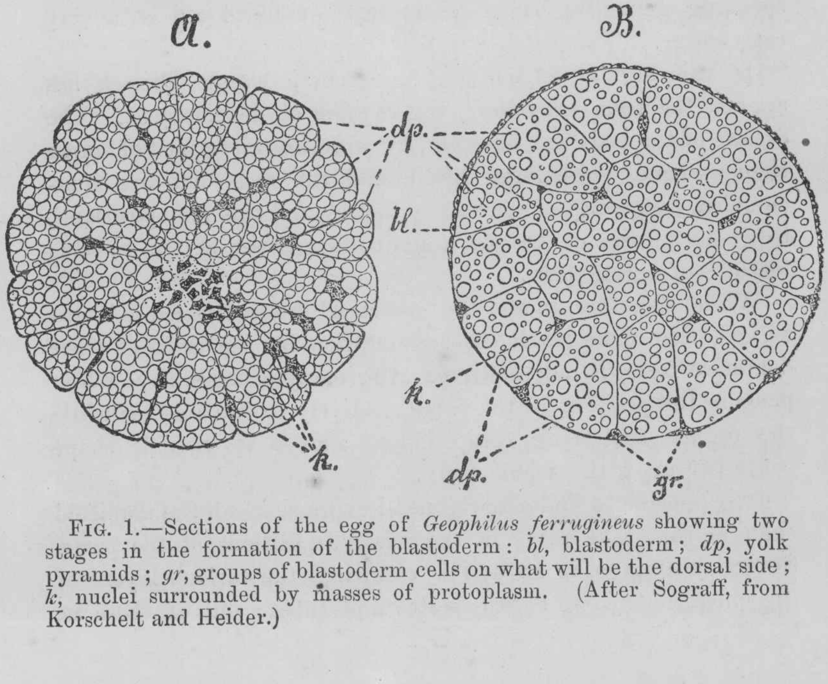

FIG. 1.—Sections of the egg of *Geophilus ferrugineus* showing two stages in the formation of the blastoderm: *bl*, blastoderm; *dp*, yolk pyramids; *gr*, groups of blastoderm cells on what will be the dorsal side; *k*, nuclei surrounded by masses of protoplasm. (After Sograff, from Korschelt and Heider.)

2. Migration of free amoeboid bodies: e.g. the mesenchyme cells in the Echinoderm gastrula, the lower layer cells of Elasmobranchs, the blastomeres amongst the yolk-cells in Triclads and Salps.

3. Aggregation of isolated cells.

a. Linear aggregates: e.g. the kidney of Lamellibranchs, the yolk-gland of Turbellaria, capillary blood-vessels.

b. Superficial aggregates: e.g. the blastoderm of Arthropods, the formation of the imaginal gut-epithelium in some Insects.

c. Massive aggregates: e.g. the gemmule of Sponges, the spleen of Vertebrates.

4. Attachment of isolated cells to another body: e.g. the union of muscles to the shell in Mollusca and Arthropoda, of tendon to bone in Vertebrates, the application of skeletal cells to the notochord.

5. Investment and penetration by isolated cells: e.g. the follicle cells between the blastomeres in Tunicata, the muscles of the gut in various animals, the septa of the corpus luteum, the formative cells of the vitreous body of the Vertebrate eye, the immigration of the nephric cells in the Earthworm.

6. Transportation of bodies by wandering cells: e.g. of the buds in Doliolidae.

7. Absorption by wandering cells: e.g. phagocytosis in Insect pupae and in the tadpole's tail.

8. We may place here the frequent alterations in the shapes of cells, which do not apparently involve growth: e.g. when flat cells become columnar.

II. The Movements of Cell Aggregates.

A. Linear Aggregates.

1. Growth in length: e.g. the growth of the roots and stems of plants, of the stolons and hydranths of Hydroids, the outgrowth of nerves, of the necks of unicellular glands, the growth of the blood-vessels from the area vasculosa into the body of the Chick embryo, of blood-vessels towards a parasite, the growth of mesoblastic and other germ-bands in Annelids, the back-growth of the Vertebrate segmental duct, and the like.

2. Splitting.

a. At the end, that is, branching: e. g. of nerves, blood-vessels, kidney tubules, glands, tentacles.

β. Throughout the length: e. g. the segmental duct of Elasmobranchs, the truncus arteriosus of Mammalia.

3. Anastomoses: e. g. of the dorsal and ventral roots of the spinal nerves, of nerve plexuses, of capillaries, of bile capillaries, of the excretory tubules of Platyhelmia.

4. Fusion with other organs: e. g. of a nerve with its end-organ, of the vasa efferentia with mesonephric tubules, of nephridia with the coelom in Annelida.

B. Superficial aggregates.

i. Increase of area.

a. Growth of a sphere.

1. Equal in all directions: e. g. the blastula of Echinoderms.

2. Unequal.

a. Unequal in different axes: e. g. the conversion of a spherical blastula into an ellipsoid Planula in Coelenterata, or into an ellipsoid Sponge larva, or of the spherical into the ellipsoid blastocyst in Mammalia.

β. Unequal at different poles: e. g. the formation of ovoid forms, such as Planulae, the club-shaped gland of *Amphioxus*, the auditory vesicle of Vertebrata.

b. Growth of a plane surface.

1. Equal in all directions: e. g. the growth of the blastoderm over the yolk in Sauropsida, or Cephalopoda.

2. Unequal.

a. When parts lying in one plane move out of that plane: e. g. invaginations and evaginations of all descriptions (Fig. 2).

β. When parts—e. g. a row of cells—lying in one plane are moved in that plane: e. g. the germ-bands of *Clepsine*, by the growth of the epiblast (Fig. 3).

ii. Alterations of thickness.

a. Increase: thickenings: e. g. the formation of the central nervous system in Teleostei, the formation of gonads from the coelomic epithelium, the development of hair follicles, the trophoblast in the Mammalian placenta (Fig. 4).

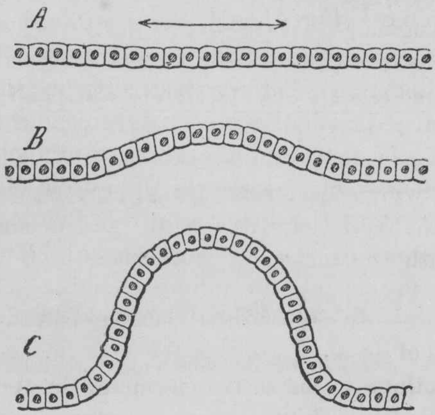

FIG. 2.—Three stages of an invagination or evagination. (After Korschelt and Heider.)

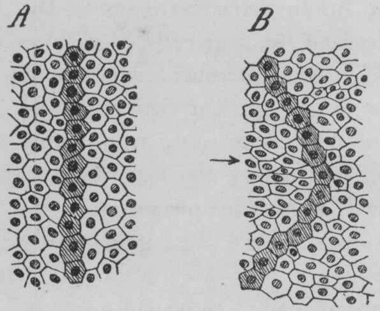

FIG. 3.—Displacement of a row of cells in an epithelium. (After Korschelt and Heider.)

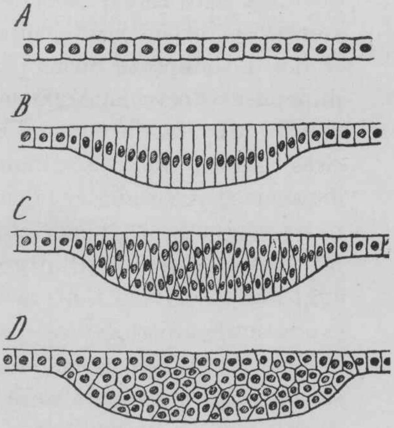

FIG. 4.—Four stages in the formation of an epithelial thickening of many layers. (After Korschelt and Heider.)

b. Decrease: thinnings: e.g. in the roof of the thalamencephalon and medulla, the outer layer of the lens, the trophoblast of the Mammalian blastocyst.

iii. Interruptions of continuity.

a. By the atrophy of part of a layer: e. g. when the floor of the archenteron together with the underlying paraderm disappears in Amniota (Fig. 5).

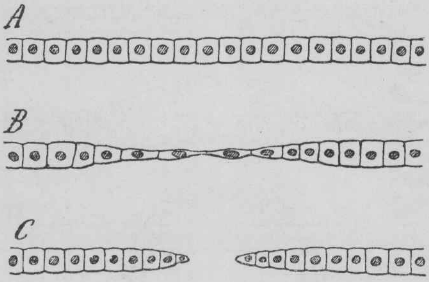

FIG. 5.—Three stages in the development of an interruption of continuity perpendicular to the surface of an epithelium. (Perforation.) (After Korschelt and Heider.)

b. By the detachment of a part: e. g. of the medullary plate from the ectoderm in *Amphioxus* (Fig. 6), of the notochord from the roof of the archenteron in Urodela and *Petromyzon*.

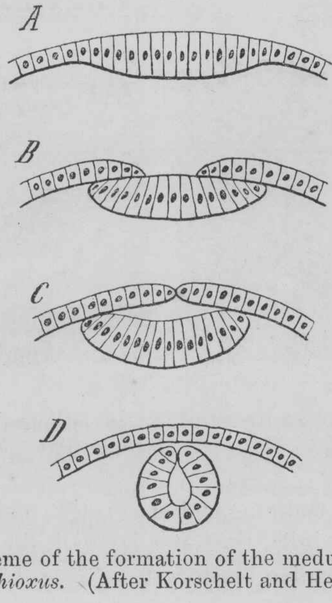

FIG. 6.—Scheme of the formation of the medullary canal in *Amphioxus*. (After Korschelt and Heider.)

iv. Concrescence of layers.

a. By their margins : e. g. the edges of the ectoderm over the medullary plate, the edges of the embryonic ectoderm inside

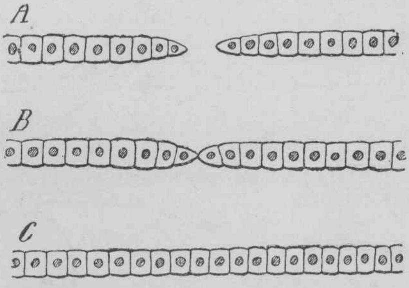

FIG. 7.—Fusion of two cell plates by their margins. (After Korschelt and Heider.)

the serosa of *Sipunculus*, the embryonic plate with the trophoblast in some Mammals (Figs. 7, 9).

b. By their surfaces (Figs. 8, 9, 10) : e. g. when the stomodaeum or proctodaeum open into the gut, when the medullary

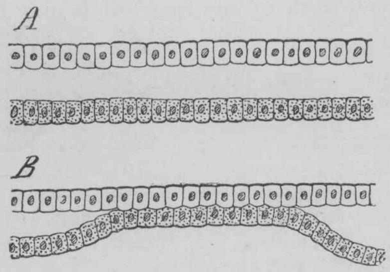

FIG. 8.—Fusion of two cell plates by their surfaces. (After Korschelt and Heider.)

folds meet, when the edges of the peritoneal groove close to form the canal of the oviduct in Amphibia and Amniota.

This concrescence is commonly followed by a communication of the cavities on opposite sides of the adherent layers, as when the stomodaeum opens into the gut, or the amnion-folds unite; but not necessarily, as when the somatopleure fuses with the trophoblast, or the allantois with the somatopleure in Mammalia.

v. Splitting of a layer into two: e. g. the inner wall of the pineal vesicle in Lacertilia (Fig. 11).

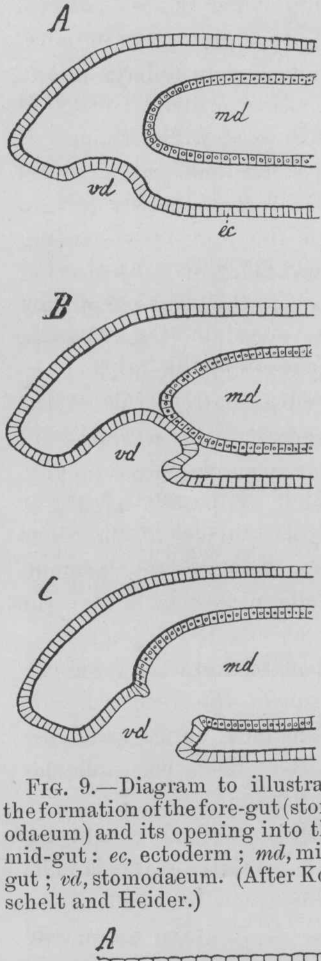

FIG. 9.—Diagram to illustrate the formation of the fore-gut (stomodaeum) and its opening into the mid-gut: *ec*, ectoderm; *md*, mid-gut; *vd*, stomodaeum. (After Korschelt and Heider.)

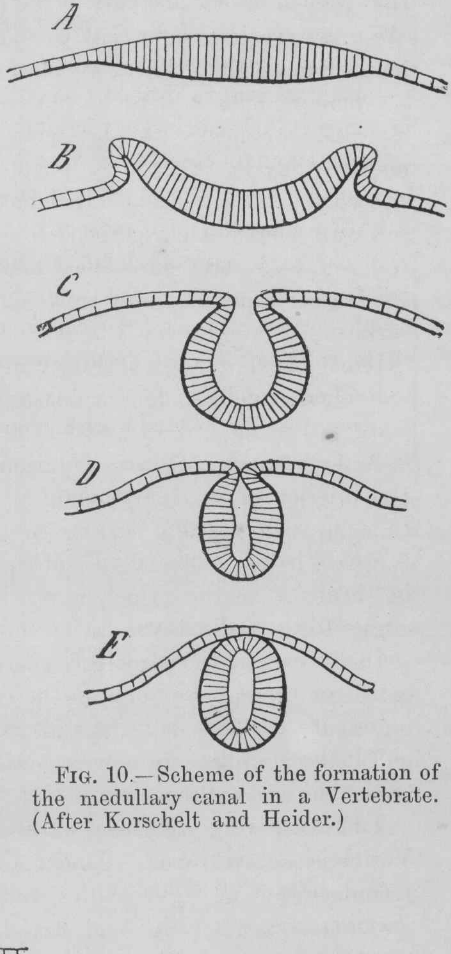

FIG. 10.—Scheme of the formation of the medullary canal in a Vertebrate. (After Korschelt and Heider.)

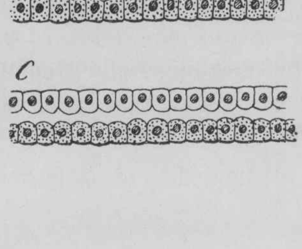

FIG 11.—Three stages in the development of an interruption of continuity parallel to the surface of an epithelium. (Delamination.) (After Korschelt and Heider.)

C. Massive aggregates.

i. Changes in volume.

α. Unequal in different axes: e. g. when the spherical larva becomes cylindrical in Dicyemidae.

β. Unequal at different points: e. g. the outgrowth of limb-buds of Vertebrates and other forms, of the buds of plants.

ii. Rearrangement of material.

a. Simple rearrangement of cells: e.g. in the formation of the concentric corpuscles of the thymus, in the development of kidney tubules in the metanephric blastema of Amniota, in the grouping of the cells to form ectoderm, gut and atrium in the Salps.

b. Development of an internal cavity: e. g. segmentation cavities, lumina of ducts and blood-vessels, of the coelom and many generative organs.

c. Dispersion of the elements of an aggregate: e. g. in gemmule formation in certain Sponges, in unipolar immigration in some Sponges and some Coelenterates, in the liberation of the germ-cells.

iii. Division of masses.

a. By constriction: e. g. the segmentation of the mesoderm and neural crest.

b. By splitting: e. g. the nervous system from the ectoderm in Teleostei and many Invertebrates, the notochord from the roof of the archenteron.

iv. Fusion of masses: e. g. of originally separate nerve ganglia (Vertebrates, Arthropods, Annelids), of myotomes, of somites in Arthropods.

v. Attachment of one mass to another: e. g. of sclerotome to notochord.

It will be seen that this *résumé* of the principal kinds of movement executed by the developing parts extends His's principle of the local inequality of growth from flat layers to linear and massive aggregates and at the same time includes the movements of isolated cells. Davenport, however, is not content merely to give a simple classification of the phenomena; he goes further, and endeavours to express them in terms of responses to stimuli, an idea due in the first instance to Herbst.