Schwann's Cell-Theory.

The Basis of One Hundred Years Investigation of Vital Processes.

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THE cell-theory, which Theodore Schwann gave us one hundred years ago, has been followed by such a wealth of confirmation that we are justified to-day in rating it as the most fundamental concept in the whole science of modern biology. Botanist, zoologist, physiologist and pathologist study the cell in their search for the vital phenomena which take place there during health and disease.

The cell-theory has brought us, over the course of time, to some tremendous implications, involving the mechanism, the chemistry and the physiology of reproduction; further studies on the origin and evolution of species, and on those forces—both internal and external—which affect the rise and fall of racial stocks. Since evolution is essentially a change in the hereditary endowment of succeeding generations, the units of heredity are the only ones that are likely to prove useful as units of evolution.

Dobzhansky says:—

"By far the greatest achievement of genetics to date is the establishment of the fact that the hereditary materials transmitted from parents to offspring are composed of discrete particles known as genes," "Genes have their physical abode in the microscopical cellular elements known as chromosomes."

The great scope of present investigations on the cell may be traced to the work of Schleiden and Schwann, whose names have been euphoniously associated, since 1839, with the development of the cell-theory. Schwann overshadows all others, practically to exclusion, when the history of the cell concept is under consideration. Since he was a great man, however, it is not surprising to find that he acknowledges a debt to a number of men in many fields. His contribution was one of synthesis; of weaving the mass of indigestible material into a stimulating generalization.

Various candidates appear to have had just claims to having first seen the cell. To Robert Hooke, mathematician, astronomer, physicist, chemist and physiologist, is credited the first published account of the cell. This appeared in his Micrographia in 1665, a volume which ranged

over the entire field of natural objects animate and inanimate and which, incidentally, contains the first illustration of a compound microscope, although it was invented eighty years before Hooke's observations. He might have advanced the cell concept materially if his roving genius had not shifted so continuously. Swammerdam, a Dutch investigator, saw the blood corpuscles of the frog in 1653, but his work was not published until 1738, long after his death. His description lacked the clarity of Hooke's work.

In 1661, Malpighi wrote Borelli letters describing the air sacs in the lungs with their capillaries, and in 1670 his Anatomy of Plants was published containing a description of cells more accurate and significant than Hooke's. He found, according to Huxley, that the walls of the cells could be separated and he regarded them as independent entities, although they were units which coalesced to make up the plant as a whole. He called them "utriculi " or "sacculi", mentioning them repeatedly in his descriptions of the different parts of plants and illustrating them in pictures. Malpighi was the first real histologist, both of plants and animals, corpuscles of the kidney and spleen being named after him to-day, but it is evident he regarded cells as of small importance.

Van Leeuwenhoek gave the first accurate and extensive description of the blood corpuscles in 1674, using them frequently in his work as a standard of size for minute observations. He also described the speim, resolved some of the tissues into cellular units, and recognised the cross-striated fibrillæ of muscle. In 1759, Wolff gave proof that he saw the cells of both plants and animals, pointing to the correspondence between them. Huxley refers to Wolff's Theoria Generationis as follows:

"Wolff's doctrine concerning histological development is shortly this. Every organ is composed at first of a little mass of clear, viscous, nutritive fluid, which possesses no organization of any kind, but is at most composed of globules. In this semi-fluid mass, cavities are now developed, these, if they remain rounded or polygonal, become the subsequent cells—if they

elongate the vessels; and the process is identically the same, whether it is examined in the vegetating point of a plant, or in the young budding organs of an animal. Both cells and vessels may subsequently be thickened by deposits from the nutritive fluid. In each case they are mere cavities, and not independent entities; organization is not effective by them, but they are the visible results of the action of the organizing power inherent in the living mass, or what Wolff calls the 'vis essentials'."

A mass of data continued to accumulate from various men. Among these may be mentioned Treviranus, Heusinger, Prevost, Milne-Edwards, Hodgkin, Baumgartner, Arnold and Valentin. They undoubtedly saw cells and probably the nuclei of cells but the significance escaped them.

But to Rene-Joachim-Henri Dutrochet, who obtained his medical degree in 1806, at the age of twenty-nine, goes the credit for a statement of such clarity concerning the cell that he cannot be passed over in any history of the theory. Retiring from practice, broken in health, following his service as an army surgeon with Joseph Bonaparte, in Spain, he devoted himself to science, most of his papers being sent to the Paris Academy of Sciences. Although his greatest contributions were in the field of plant physiology, he made important contributions to embryology and histology.

His microscopic studies for the years 1822 and 1823 were assembled into a monograph and published in 1824 under the title:

"Recherches anatomique et physiologique sur la structure intime des animaux et des vegetaux, et sur leur motilite."

From Rich's translation we learn the following:

"I must repeat here that which I have stated above regarding the organic texture of plants: we have seen that plants are composed entirely of cells, or of organs which are obviously derived from cells; we have seen that these cells are merely contiguous and adherent to each other by cohesion, but that they do not form a tissue exactly continuous. The organic being has appeared to us, therefore, to be composed of an infinite number of microscopic parts, which are related only in proximity. Now the observations on animals which we have just described obviously confirm this view.

"In the organs of vertebrates, the globular corpuscles are so small that it is impossible to know whether they are solid or vesicular bodies; but in molluscs that is very easy to determine. When one examines microscopically the tissue of the liver, the testis or the salivary glands of Helix or Limax, one sees that these secretory organs are composed, like those of vertebrates, of little globular bodies assembled in a confused manner: but here these little bodies are not

so excessively small. They are indeed quite large (for microscopic objects) and one can see in the clearest manner that they are vesicular bodies or true cells, the walls of which contain other very minute corpuscles."

Dutrochet says further:

"One can therefore draw the general conclusion that the globular corpuscles which make up all the organic tissues of animals are really globular cells of an extreme smallness, which are united only by cohesion. Thus all the tissues, all the organs of animals are really only cellular tissue diversely modified. This uniformity of ultimate structure proves that organs really differ from one another only in the nature of the substances which are contained in the vesicular cells of which they are composed. All of the organic tissues of plants are made of cells and observation has now demonstrated to us that the same is true of animals."

Dutrochet has established the anatomical identity of the cell and went on to its physiology in another passage:

"It is within the cell that the secretion of the fluid peculiar to each organ is effected. These fluids are probably transmitted by transudation into the excretory canals. Thus the cell is the secreting organ par excellence. It secretes, inside itself, substances which are, in some cases, destined to be transported to the outside of the body by way of the excretory ducts, and in others, destined to remain within the cell which has produced them, thus playing specific roles in the vital economy.

"In each organ the cells must have different characteristics, since such different substances are secreted within them. In this connection one cannot help admiring the prodigious diversity of the products of living beings—a diversity which is even greater in the plant kingdom than in the animal kingdom.

What a variety in the physical and chemical qualities of the living body are organic solids? The membrane and the shell of the bird's egg are not formed by a real growth as true organic solids are: they are formed rather by the coagulation or hardening of certain secreted fluids. Microscopic examination reveals no organic texture in such solids formed by the hardening of secreted fluids. On the other hand, whenever one finds an organic texture in the body, one can say without hesitation that that part was once alive, and that it has consequently been formed by true growth. Now an organic texture can be clearly recognised in all parts of feathers. The spongy substance is made up of a mass of globular utricles. It is true cellular or utricular tissue resembling the cellular tissue which is seen in certain parts of plants; it is, in a way, an animal cork."

While the phenomenon of osmosis had been observed in isolated instances, it was neither understood nor applied in any way. Dutrochet made the discovery independently and applied it in fathoming the mechanism of cellular activity. Not content with his numerous observations, clearly

set down, he was eager to apply them to physiology as noted in this statement:

"The physiological connections which I have established between plants and animals make it clear that there is but a single physiology; a general science dealing with the functions of living beings—functions which vary in their mode of execution but which are fundamentally identical in all organized beings. I hope that some day, out of these first attempts, there will be born a new science—general physiology."

Certainly, as Goss says, the experiments of Detrochet made the recognition of the cell as a structural, functional, and developmental unit a necessity. Only the nucleus is left out.

It is not known whether Schwann heard Dutrochet's papers at the Paris Academy, but both men presented material through the Academy. And Schleiden, in his *Phytogenesis*, refers to Dutrochet in a foot-note.

Schleiden's claim to glory is generally considered to rest on his recognition of the fact that increase in the size and number of cells is responsible for growth. Said he,

"Growth results both from the increase in the volume of cells, and from the addition of new little cells,"

and after citing his evidence he says,

"It is evident, therefore, that during growth, new rudimentary cells are formed which, by increasing in size, finally become cells such as those which have preceded them in order of appearance and development."

Schleiden's paper on Phytogenesis, published in the same volume as Schwann's work, by the Sydenham Society, is given with such circumlocution that it is scarcely recognizable in the clearly stated abstract of it found in Schwann's work.

In the opinion of Goss, the following statement of Schleiden should divorce him completely from all connection with the cell-theory:

"The plant unfolds itself by the expansion and development of the cells already formed. It is this phenomenon especially, one altogether peculiar to plants, which, because it depends upon the fact of their being composed of cells, can never occur in any, not even the most remote form in crystals or animals."

It is difficult to comprehend how Schwann obtained the inspiration he attributes to Schleiden, unless it was a desire to disprove the categorical statement that animals could not by the remotest possibility be made up of cells. Indeed, Schwann says,

"The principal object of our investigations was to prove the accordance of the elementary parts of animals with the cells of plants,"

As if the proof of likeness between plants and animals were insufficient, Schwann finished his treatise with refutation of Schleiden's statement concerning crystals using these words:

"The material of which the cells are composed is capable of producing chemical changes in the substance with which it is in contact, just as the well-known preparation of platinum converts alcohol into acetic acid. This power is possessed by every part of the cell. Now, if the cytoblastema be so changed by a cell already formed, that a substance is produced which cannot be attached to the cell, it immediately crystallizes as the central nucleolus of a new cell. And then this converts the cytoblastema in the same manner. A portion of that which is converted may remain in the cytoblastema of new cells; another portion, the cell-substance, crystallises around the central corpuscle.

"The cell-substance is either soluble in the cytoblastema, and crystallizes from it, as soon as the latter becomes saturated with it, or else it is insoluble, and crystallizes at the time of its formation, according to the laws of crystallization of bodies capable of inhibition mentioned above, forming in this manner one or more layers around the central corpuscle, and so on."

In all Schwann's work his exposition is clear. His power to make generalizations is demonstrated in this statement of his cell-theory:

"The elementary parts of all tissues are formed of cells in an analogous, though very diversified manner, so that it may be asserted, that there is one universal principle of development for the elementary parts of organisms, however, different, and that this principle is the formation of cells. This is the chief result of observations.

"The same process of development and transformation of cells within a structureless substance is repeated in the formation of all the organs of an organism, as well as in the formation of new organisms; and the fundamental phenomenon attending the exertion of productive power in organic nature is accordingly as follows: a structureless substance is present in the first instance, which lies either around or in the interior of cells already existing, and cells are formed in it in accordance with certain laws, which cells become developed in various ways into the elmentary parts of organisms.

"The development of the proposition, that there exists one general principle for the formation of all organic productions, and that this principle is the formation of cells, as well as the conclusions which may be drawn from this proposition, may be comprised under the term cell-theory, using it in its more extended signification, whilst in a more limited sense, by theory of the cells we understand whatever may be inferred from this proposition with respect to the powers from which these phenomena result."

During the year 1838, Schwann, in the course of conversation with Schleiden was

informed of the latter's theories of cellformation in plants. It struck Schwann that there were many points of resemblance hetween animal and vegetable cells. Two circumstances contributed to the rapid and brilliant result of Schwann's subsequent observations. He made the greatest use of the nucleus in demonstrating the animal cell while emphasizing that it was the most characteristic and least variable of its constituents. Schwann, following the work of the botanists, devoted special attention to the development of animal tissues, discovering that the embryo, at its earliest stage, consisted of a number of quite similar cells. He then traced the metamorphoses or transformations which the cells underwent, until they developed into fully formed tissues of the adult animal.

He showed that while a portion of the cells retain their original spherical shape, others become cylindrical in form, and yet others develop into long threads, or starshaped bodies, which send out numerous radiating processes from various parts of their surface. He observed that bones, cartilage, teeth, and various tissues become surrounded by firm cell walls of varying thicknesses, and finally, he explained the

appearance of a number of the most typical tissues by showing that groups of cells become fused together, analogous to the development of the cell structure in plants. Schwann also studied metabolism and gave it its Greek derivation.

His materialistic view of living matter made him a scientific missionary of the first rank; his errors in observation and his conclusions in regard to the nucleus make his work seem incomplete as compared with modern cytology, but it must be remembered that he knew nothing of mitotic division and the whole science of genetics with its cytological implications was in the distant future.

Schwann led off in the great attack in which the Protoplasmic Theory was later worked out by Mohl, Cohn, Kolliker, Bischoff, Max Schultze and the physiologist, Brucke.

Hertwig-Campbell, The Cell.

Trend in Modern Genetics, Laughlin.

Historical Background of Schwann's Cell Theory, C. M. Goss.

Raw Materials of Evolution, Theodosius Dobzhansky, The Cell Doctrine, J. Tyson.

The Cell Theory, Thos., H. Huxley.

The Size and Number of the Chloroplasts and the Chlorophyll Content in Eupolyploid Forms Experimentally Produced.

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TN my previous publications1, 2, 3, 4, 5 I have shown that eupolyploidy in plants conditions a series of hereditable changes. Some are "directed," others are not. Directed, hereditable variations in plants which show an increase with the euploid increase of the chromosomes are: (1) the amount of the nucleolar substances (number of nucleolei, size, or both), (2) the size of the nuclei, (3) the amount of cytoplasm, (4) the volume of the cells, (5) the breadth of the leaves, (6) the thickness of the leaves, (7) the size of the ovules, (8) the size of the seeds or

of the grains, (9) the dark green colour of the leaves, (10) the size of the anthers, (11) the breadth of stigmas and styles and (12) the length of all kinds of trichomes. With the euploid increase of the chromosomes the vegetation period (the period between sowing and flowering) is usually prolonged. Characters like the size of the plants and the size of the flowers are also influenced by the euploid chromosome alterations, but there is no correlation between euploid chromosome alteration and the expression of these characters. In some cases the size of the plant increases with the euploid increase of the chromosomes, in other cases it decreases. The length of the flowers (corolla, calyx) vary in a similar way. The whole habitus of the tetraploids is coarser than that of the diploids,

¹ Kostoff, D., Chronica Botanica, 1938, 4.

² ___, Journal of Genetics, 1938 (in the press).

³ __, Curr. Sci., 1938 1938, 7, 108.

⁴ _, and Kendall, J. Gartenbauwissenschaften, 1934,

Bd. 9, 22-44. 5 __, and Orlov, A. Ann. Bot., N.S., 1938, 2, N. 8.