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EPIGENESIS OR EVOLUTION.

Zeit- und Streitfragen der Biologie. Von Prof. Dr. Oscar Hertwig. Heft 1: Präformation oder Epigenese? Grundzüge einer Entwicklungs-theorie der Organismen. (Jena: Gustav Fischer, 1894.)

THE theory of preformation, or rather let us say predetermination, as revived at the close of the nineteenth century, is much more formidable than its prototype of the eighteenth century. Not only is it stripped of all its earlier crudities, such as the doctrine of *ëmboitement*, but it is supported by a mass of evidence accumulated by the researches of the last quarter of a century. Its fundamental assumption, that of the existence of minute, qualitatively unlike, ultimate particles of living matter, is strengthened, if not supported, by the analogy of the atomic theory, and the observed phenomena of mitosis accompanying the maturation of the ovum and spermatozoon, and the subsequent acts of impregnation and segmentation have been skilfully blended with the fundamental assumption in such a way that they are made to seem to be a proof of it. This strong position is now assailed by Dr. Oscar Hertwig, who is in many respects peculiarly well fitted to the task. He is the master of a simple, lucid and logical style, he has himself been, in conjunction with his brother, a pioneer in many of the discoveries on which the doctrine of predetermination is founded, and he has recently set himself to the task of verifying the experiments of Roux and others, and of examining the evidence which they afford for or against the doctrine which he attacks. His answer is unequivocal. The phenomena of development are to be explained on epigenetic, not on evolutionary grounds, and the latter hypothesis is contradicted by a number of well-ascertained facts.

In an introductory chapter Dr. Hertwig refers to and accepts Roux's definition of development, evolution, and epigenesis, which may be repeated here, as they give precision to terms which are often loosely used or little understood. By "development" is meant the origin of perceptible heterogeneity. Epigenesis means, not merely the formal increase of perceptible heterogeneity in a substance apparently similar but possibly extremely complex, but a real increase of pre-existing heterogeneity. Evolution means, the becoming perceptible of pre-existing latent imperceptible differences. Dr. Hertwig goes on to describe the positions taken up by Weismann and Roux, and deals particularly with the former, who, as he shows, regards the germ as a veritable microcosm, in which every separate variable part which appears in the course of the whole ontogeny is represented by a living particle; on the characters of these particles the characters of the parts of the adult organism, whether composed of one cell or many, depend. The sum of these particles forms the germ-plasm. Agreeing with Weismann that a theory of heredity must be founded on and brought into harmony with the cell theory (and therefore rejecting the opposite view of Nägeli), Dr. Hertwig proceeds to attack Weismann's fundamental

assumptions. As he rightly says, the foundation and corner-stone of Weismann's theory is the assumption of differential or anisocleronomic¹ division of the cell nucleus. All-important as this assumption is, there is no foundation of fact to be found for it in all Weismann's work. Instead we find purely dialectical argument, and more than this, we find that Weismann has attributed the most opposite characters to his "idioplasm," declaring it, in one place, to be stable and unchangeable, in another to be labile and changeable. But, Hertwig points out, the facts are directly opposed to the assumption of anisocleronomic division of the germ substance. In the Protozoa the division is clearly isocleronomic, and we know of no instance among them in which the act of division, as such, is a means of producing new species. Moreover, the numerous cases (e.g. *Podophrya gemmipara*) of complicated life histories among Protozoa show that the dissimilarity which may at first obtain between the two products of cell division is no indication of permanent and essential difference. The case of the lowest multicellular organisms is adduced as showing that in these also the cell division is isocleronomic, for each cell of which the soma of many of these organisms is composed, retains the power of giving rise to the whole organism. The phenomena of regeneration and heteromorphosis afford evidence that there are in the tissues of many highly differentiated organisms cells, or groups of cells, which retain, in a high degree, the power of giving rise to new and complicated structures, and this is particularly exemplified in cases of heteromorphosis, which is to be distinguished from regeneration by the fact that, in the former case, lost organs are replaced by organs which differ in form and function from those which were lost, or organs are, as a result of special conditions, produced in abnormal positions on the body. Under this head of phenomena of heteromorphosis, Dr. Hertwig groups the extraordinary phenomena which have been brought to light by his own researches and those of Driesch and E. B. Wilson on the segmenting ova of such different animals as frogs, echinids, and amphioxus, and these observations have been extended, since the publication of Dr. Hertwig's book, by the researches of Prof. Raffaello Zoja on the developing ova of cœlenterates. Briefly stated, the results of these experiments are as follows: In the case of echinids, amphioxus, and cœlenterates, the first two, four, or even eight blastomeres may, by suitable means, be isolated without impairing their vitality. Each blastomere, instead of giving rise to an incomplete embryo, or a portion of an embryo, begins the developmental course afresh, as it were, and produces an embryo perfect in all its parts, but one-half, one-fourth, or one-eighth the size, as the case may be, of the normal embryo. In the case of the frog it was not possible to isolate the blastomeres; but Hertwig was able, by pressure, to so alter the segmentation, that the normal relations of the blastomeres, one to another, were completely changed, and yet a perfectly normal embryo resulted. Unquestionably this proves that, in the first stages of segmentation, at any rate, the division of the germ substance is not differen-

¹ The German words "erbgleich" and "erbungleich" being untranslatable into English, I have coined the equivalents isocleronomic and anisocleronomic from the Greek *κληρονόμος* an heir.—G. C. B.

tial but integral, not qualitative but quantitative, and this undermines the most important of Weismann's positions.

Very important are Dr. Hertwig's criticisms on the doctrine of determinants, so sharply and clearly defined by Weismann. This doctrine is inseparably connected with that of the anisocleronomic division of the germ-plasm, and it might appear that if the latter is disproved, it is unnecessary to enter into a detailed criticism of what depends upon it. But the criticism is not without its utility, since, Dr. Hertwig shows us, the conception of determinants is only an extreme instance of a false conception of causality common in current biological literature. Weismann has supposed that the ultimate vital particles, which he calls biophors, are grouped in the germ-plasm into "determinants," and that every smallest cell-group in the adult organism which has definite characteristics and a definite situation is represented in the germ-plasm, both of ovum and spermatozoon, by a definite determinant. These last are so arranged in the germ-plasm, and are endowed with such special forces, that they are able, in the course of ontogeny, to move at the right time into the right place—this movement being effected by the almost purposive anisocleronomic division of the germ-plasm. This very definite idea is founded on an erroneous conception of the relations between primordium (Anlage) and primordial product, which are supposed to stand in relation to one another as cause and effect. More or less unconsciously, the biologist commonly assumes that, because a given animal proceeds of necessity from a given egg, there is an identity between primordium and primordial product; so much so, that the developing organism is often spoken of as if it were a self-contained system of forces, a sort of organic perpetuum mobile. He overlooks the fact that for the fulfilment of the developmental processes many other conditions are necessary, without which the primordium could never arrive at the condition of its final product. Between the two there is clearly no identity, and it is false and mischievous to suppose, as the older evolutionists did, and the new evolutionists are again trying to make us believe, that the perceptible heterogeneity of the last stage of the developmental process is only the final expression of an invisible corresponding heterogeneity of the first stage. Throughout the whole of the ontogeny there is an exchange of material taking place, the adult has arrived not only to its bulk, but to its complexity as the result of metabolism; inorganic material is perpetually changed into organic, and serves for the growth and development of the primordia. It is true that the form changes are constant and invariable for the species, from a certain kind of germ a certain kind of animal is invariably produced; but is not this largely because, in the ordinary course of events, the ovicell is always subject to similar conditions of assimilation and excretion, and to similar conditions of gravity, light, temperature, &c.? Throughout the course of organic development things which were external are transformed into things internal, and the primordium grows and is changed at the expense of the environment. In thus recalling to our attention the fact that an organism is above all things metabolic, that its growth and changes are the result of its metabolic

activity, and that its ultimate mass is the result of assimilation, of the taking up and making an integral part of itself of matter which was previously apart and different from itself, Dr. Hertwig does a real service to biology. He forces us back to the consideration that physiology and morphology are not two separate and independent lines of study, but that they are so closely interdependent that no generalisations can be made on the evidence of one kind of observation alone; they must be supported by equally cogent arguments from the other side. The theories of the evolutionists are essentially morphological, and in this they resemble the theories of the last century, that they take no account of one of the most wonderful of all vital phenomena, that of metabolism, but strive to find an explanation of the ultimate perceptible differences in form by asserting that the differences were always there, and have only expanded so as to become perceptible. Weismann's attempt to deal with this question by assigning the power of change as the result of metabolism to the biophors, does not really offer more than a purely formal explanation of the question, for what he predicates of the biophors may very well be predicated of the whole cell. Our ideas of increase of complexity as the result of metabolism are made none the clearer by shifting the responsibility of the change, if one may express oneself so, to subordinate parts.

It is indeed apparent, on reflection, that the characters of the perfected organism are not and cannot be the characters of a single cell—or even of a cell fusion such as the oosperm—and the converse of this is true that the characters of a cell cannot be the characters of the perfected organism. For what is a perfected metazoon or metaphyte but an aggregation of cells of most numerous and unlike characters? The characteristics of the perfected organism are the result of the correlation of all its parts, of the relations of cell to cell and of groups of cells to groups of cells; and are we to attribute to a single cell which has no relations characters which are essentially the results of the relations of innumerable cells one to another? Of the importance of the correlation of the parts of the perfected organism we can have no doubt, nor can we escape from the corollary that the characteristics of the organism reside not so much in the cells themselves as in the aggregation and interdependence of the cells, and if we may demur to the suggestion of the *colonial* character of the metazoa which is contained in the sentence, we must at least admit much of the truth of Hertwig's statement (p. 85):

"That the ovum is an organism which multiplies itself by division into many organisms similar to itself, and that it is through the reciprocal action (*Wechselwirkung*) of all these many elementary organisms at each stage of the development that the organism as a whole is gradually and progressively established."

Dr. Hertwig institutes the comparison which was made long ago by Herbert Spencer, between an organism and a human society, and it is worth while mentioning his illustration as showing his conception of the relations of the cell to the organism. The organisation of a complex human society, he says, is something new, and not to be thought of as existing beforehand in the organisation of an individual man. It is nevertheless founded in

human nature, but we cannot in gross, mechanical fashion seek for the organisation of a society in the primitive nature of man. In a like manner the character of the perfected organism is founded on the nature of the cells which compose it, but it contains in itself a new element, a heterogeneity due to correlation and reciprocity, which is limited by the specific nature of the cell substance, but is not to be sought for as a specific constituent of the substance of any individual cell. Starting from this point of view, we may consider Dr. Hertwig's own doctrines which he sets forth in the second part of his work entitled "*Gedanken zu einer Entwicklungstheorie der Organismen.*" Whereas Weismann seeks the cause of the orderly development of the primordium in the primordial substance itself, Hertwig considers that the development of the primordium is dependent on conditions or causes which lie outside of the primordial substance of the ovicell, but are none the less produced in regular succession during the process of ontogeny. Such are, in the first instance, the reciprocal relations in which cells stand one to another in increasing degrees of complexity, whilst they increase in number by division; and in the second place, the action of the external environment on the organism. The argument in support of this proposition is given in so condensed a form that it is almost impossible to give any part or abstract of it without giving the whole. The following sentence is so important that it may be quoted at length, and the reader should refer to the work itself for the rest of the argument and the conclusion:—

"One of the most important and essential causes of the appearance of heterogeneity in the course of development is to be found in the specific power of the ovicell, to multiply itself by division. From this fact alone, that the nuclear substance is able, in the course of most manifold chemical processes, to assimilate, step by step, matter from the reserve material stored up in the egg, and oxygen from the surrounding atmosphere, it is able at the same time to evoke an ever-increasing heterogeneity. The increase of mass of the nuclear substance involves its progressive division into 2, 4, 8, 16 parts, and so forth. But the division is again the cause of a constantly changing spatial distribution of the substance. The 2, 4, 8, 16 and following nuclei which arise by division give way to one another in opposite directions, and attain to new positions at definite distances from one another within the limits of the egg. Whilst all the material particles of the ovum were at first arranged round the fertilised nucleus as a single centre of force, they are now grouped around as many individual centres as there are new nuclei, and they segregate themselves around these as cells. It is therefore clear that the ovum as a unicellular organism, when compared with the ovum as a multicellular organism, has altered its quality to an important extent, and that merely by the process of isoclonomic division."

This is what Hertwig calls the function of growth as a form-producing principle. The other principles which he invokes are the relations of the cells to external conditions, or the function of their position, and finally the reciprocal influence of the parts of the whole on one another and on the whole, or the function of correlation. It is not to be denied that these are principles of considerable importance, and it may be said that their importance has never quite been lost sight of, but they do not bring us any nearer to the explanation of the totally different

reaction of apparently similar substances to the same stimuli. What we want to know is why, when we place under a hen her own eggs and those of a duck, and so expose them to identical conditions, chickens and ducklings are hatched as unlike one another as may be. The answer given, "the difference can be due to nothing else than to the different nature (the different micellar structure) of the substance," is unsatisfactory, in that it is only a restatement of the fact, and is not an explanation at all. In attempting to give a more definite account of the different natures of the egg substance, Hertwig is obliged to take his stand upon much the same ground as the evolutionists. "In the hen's egg the species is present as fully as in the hen, and the hen's egg is as different from the frog's egg as the hen is from the frog." He is compelled to agree with the evolutionists in assuming the existence of a specific, and even of a very highly organised primordial substance as a basis of developmental processes, but he claims that his concept of this substance is different from and better than theirs, in that he ascribes to the primordial substance or germ-plasm characters which are congruous with the concept and character of a cell, and does not ascribe to it the innumerable characteristics which are only evoked through the union of many cells and the concomitant action of external conditions. The distinction appears to be a slight one, yet on careful consideration it assumes more important dimensions. Hertwig, if I interpret him rightly, conceives of the germ-plasm as a substance of many and definite potentialities. He does not attribute this potentiality to one part, and that to another part of the germ-plasm, but argues that as a result of multiplication by division the relations of the cells with their contained germ-plasm are continually undergoing change, both with regard to one another and to the environment. In consequence of the different conditions thus induced, this potentiality is evoked in the germ-plasm of one cell, that in the germ-plasm of another, and so on in ever-increasing grades of complexity. The differentiation of any cell is the result of its position, which determines which of its many potentialities shall be called into action. It is the reaction of the living substance to the stimulus which evokes a particular potentiality, which brings about its form changes, and it may be supposed that a profound form change following on constant action in one direction incapacitates the cell in question for the performance of any of the many other duties for which it was primitively fitted. This conception is epigenetic in that it admits the coming into being of a new heterogeneity which was not pre-existent in the ovum as such; that which was present was a capacity for certain kinds of heterogeneity. Very different is the conception of the evolutionists, who define the exact potentialities of the germ-plasm, and assign each to a given material particle or group of particles. The heterogeneity is already present; thenceforward there is no room for the increase of complexity in response to external stimuli. Dr. Hertwig rightly says that Weismann's explanation amounts to nothing more than a renunciation of an explanation. His doctrine of determinants leads us into an invisible world in which there is no foothold for research. For this reason, if for no other, we should welcome Dr. Oscar Hertwig's invitation to return to the paths

of epigenesis. A theory which has a formal answer for every question, which regards everything that we can see and lay hold of as predetermined and unalterable, which relegates the causes of phenomena to the unseen and unknowable—such a theory, if accepted as true, does not stimulate, but stifles inquiry. Fortunately it has had the opposite result. It has not been accepted, and it has developed an attack of a brilliant and overwhelming character. All the best arguments which Dr. Hertwig can bring against the theory of predetermination are derived, not from simple observation, but from experiment. A few simply conceived interferences with the normal course of the segmentation of the ovum have sufficed to strike down the doctrine of determinants. May we not hope that an extension of these methods may illuminate the regions which are still hidden from us? After all his attempts to supply an acceptable alternative to Weismann's scheme, Dr. O. Hertwig makes a partial confession of failure. To many his failure will seem complete, and it must be so since the evidence derived from experiment is as yet wholly inadequate. But his attempts indicate the paths along which research may be conducted, and he is very right when he claims, in conclusion, that it is the great merit of his conception of the developmental processes, that it opens the gates once more to research, with some brighter hope of results than the formal theory of predetermination afforded us.

G. C. BOURNE.

COAL-DUST AND COLLIERY EXPLOSIONS.

Coal-Dust an Explosive Agent, as shown by an Examination of the Camerton Explosion. By Donald M. D. Stuart. (London : Office of the *Colliery Manager*, and E. and F. N. Spon.)

IT is significant of the conservatism—not always wholly disinterested—that surrounds an old-established industry that, in spite of all that has been written and said on the action of coal-dust as an explosive agent during the last twenty years, we should still find people persistently clinging to the belief that the only possible cause of a colliery explosion *must* be fire-damp. It would be amusing, were the matter less serious, to note the extraordinary hypotheses and absurd surmises to which the believers in this time-honoured doctrine are occasionally driven in order to account for the existence of fire-damp in places where the common testimony of unbiassed people affords no proof of its presence. The hard logic of facts is, however, surely, even if slowly, undermining the mass of prejudice with which this question has been surrounded, and we may hope that before the close of the century the action of the Legislature will compel these people, whose obstinate unbelief jeopardises men's lives, to give practical heed, even more directly than at present, to the teachings of intelligent observation and inspection. The causes and conditions which lead to a colliery explosion are now so well understood that such a catastrophe ought to be no longer possible. If it does occur, we must lay the blame on the management and discipline of the mine, and it should not be difficult, under these circumstances, to fix the responsibility.

The master of a vessel who carelessly navigates his ship, is liable to have his certificate dealt with in a very summary fashion. It does not avail him to plead that his crew are picked from a class that is proverbially reckless and foolhardy, and that his "look-out," therefore, was probably in fault. The Assessors take it for granted that he has a proper knowledge of his business, and they hold him responsible for the discipline on his vessel. Public opinion demands that a mine-manager should be treated in a similar manner. How difficult it is for the law, in spite of the length of its arm, to get at a manager who has been guilty of culpable carelessness, has been shown in more than one inquiry that could be named.

As an illustration of the mental attitude to which we allude, we may refer to a recent report on the cause of the explosion at the Albion Colliery, South Wales, in June last. All the circumstances connected with that explosion seemed to indicate that it was due to the same cause as that which accounted for the explosions at the Park Slip, Apedale, and Malago Collieries, viz. the presence of coal-dust, and this conclusion was confirmed by the report of the inspectors appointed by the Home Office to inspect the colliery.

In a report prepared for the colliery proprietors by six engineers, we find that these gentlemen are unanimously of opinion that the disaster was caused by an outburst of fire-damp, and they have great satisfaction in stating that no blame in the matter can be attributed to any of the officials or employes. There is no wonder, in view of this conflict of testimony, that the men of the Rhondda district should have demanded a fresh inquiry by the Government into the cause of the disaster.

The changes of opinion among "practical" men on this question of coal-dust are very suggestive, and strikingly exemplify the course through which a new truth has to run when it is in conflict with the settled conviction of interested persons. Like the course of true love, it does not run at all smooth under these circumstances. The idea that coal-dust could be the cause of a colliery explosion was, in the outset, scouted as absurd. Then, as facts multiplied, the dust was allowed to have a share in the catastrophe: it aggravated the violence of a fire-damp explosion. Next, the proportion of the fire-damp became smaller by degrees, until it reached the vanishing-point. Now we have reached the stage that all dusts are not explosive, and the colliery manager is satisfied that his dust is not as other men's dust. Even in the case of those who were more receptive of the teaching of experiment and of trained observation, the recognition of the real facts has had to run the conventional course. First they were not true, then they were not new, and we knew of them before; for did not Faraday and Lyell tell us all about the matter in the Haswell report? In a question of this kind, colliery management ought to be in advance of public opinion. That it has not always been so in the past, the history of coal-mining shows only too plainly. It was the shock to public sentiment, caused by a succession of disastrous explosions, which occurred in the early part of this century, that indirectly brought about a revolution in the art of coal-getting. People in the colliery districts, who were witnesses of the terrible loss