HERBERT SPENCER

AND

ANIMAL EVOLUTION

THE HERBERT SPENCER LECTURE

DELIVERED AT THE MUSEUM ON
THE 2ND DECEMBER 1909
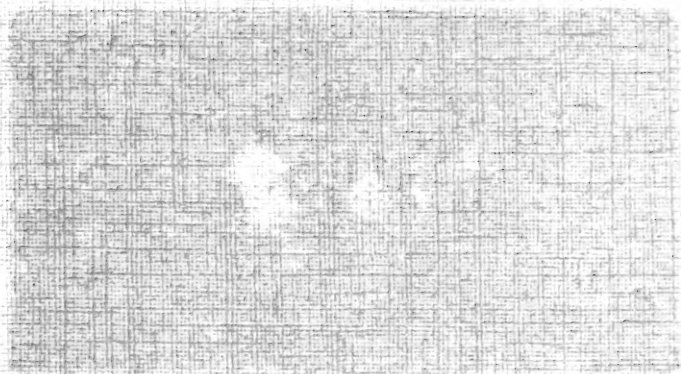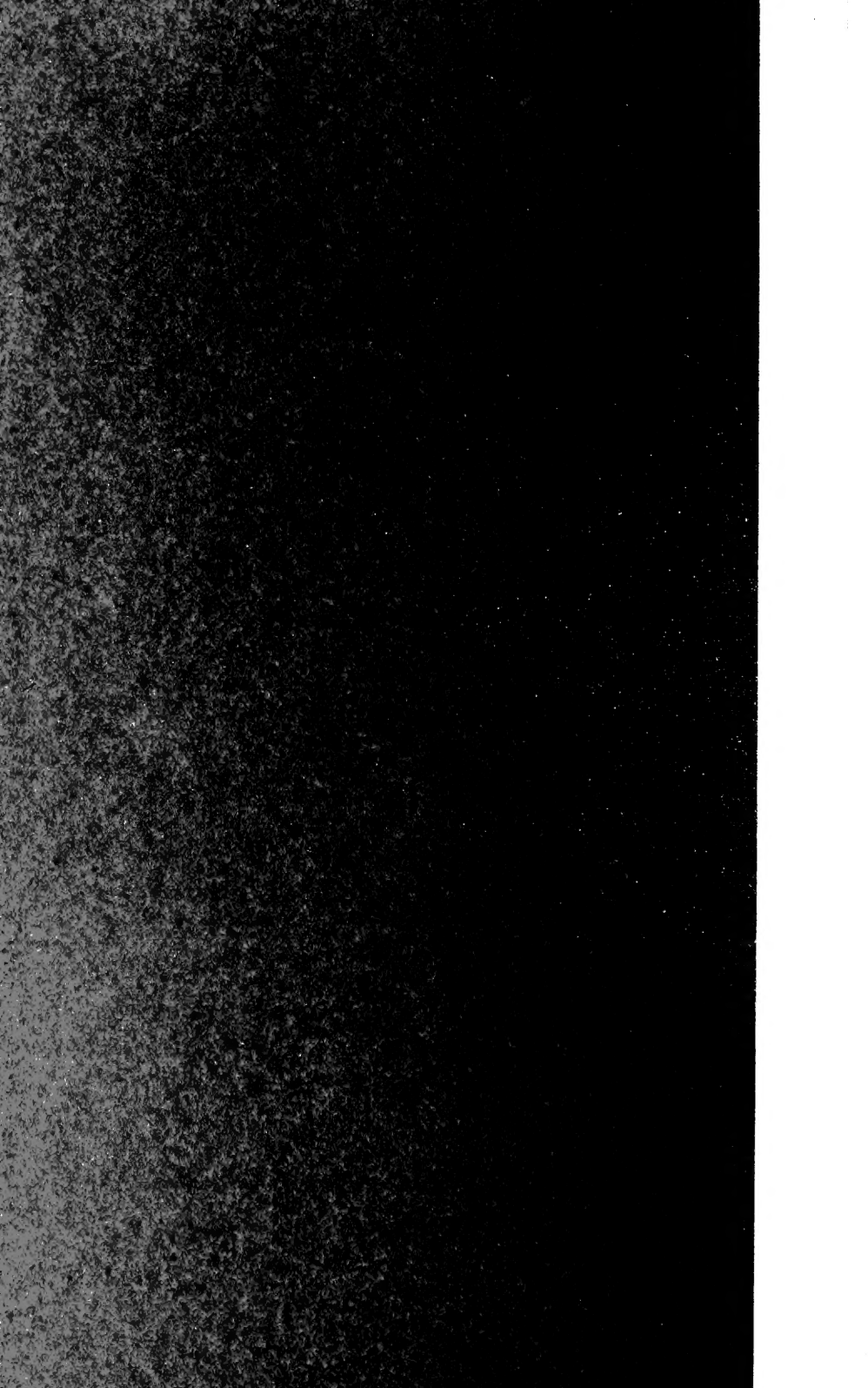
BY

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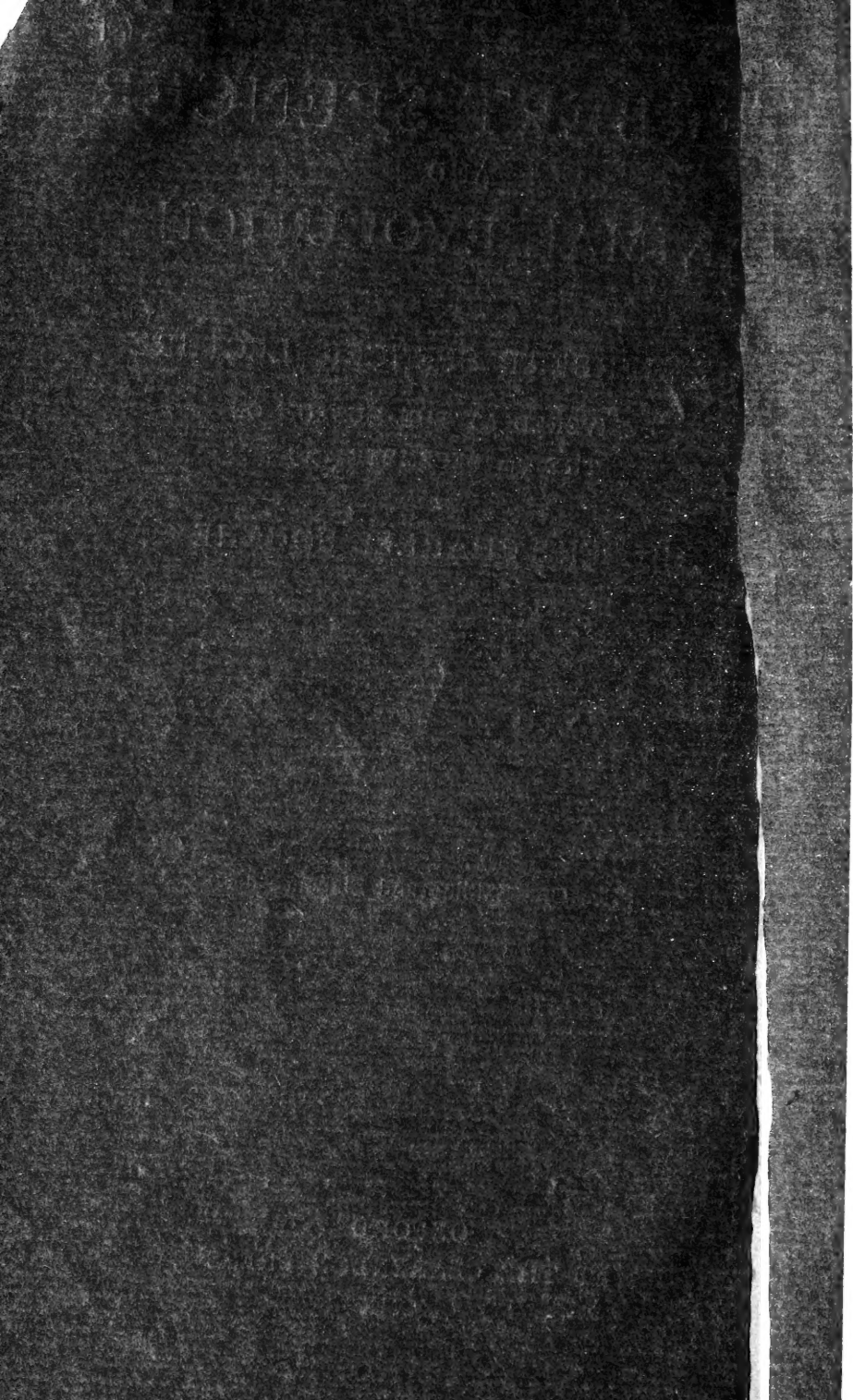
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THE subject I have chosen for the title of my lecture is a very large one, Herbert Spencer and Animal Evolution. It is impossible for me to attempt to deal with the whole or even with any considerable part of it in the course of a single lecture. But before I treat of that very limited aspect of it to which I propose to confine myself, I may, perhaps, indulge in a few generalities by way of an introduction.

During the last two years we have heard a great deal about Evolution, because of the various celebrations held in different places of the centenary of Darwin's birth, and because in July 1908 we arrived at the fiftieth anniversary of the famous meeting of the Linnean Society of London, at which the papers of Charles Darwin and Alfred Russell Wallace were read, suggesting Natural Selection as the efficient cause of the transformation of animal and vegetal species. And November 24 was the fiftieth anniversary of the publication of Darwin's *Origin of Species.* It is a popular error, but one which I need not be at the trouble to refute here, before an Oxford audience, that Darwin was the author of the theory of Evolution. We know that the idea of evolution dates back to the early Greek philosophers; that a scheme of organic evolution founded upon Greek philosophy was sketched by Lucretius; that evolutionary doctrines were freely promulgated in the eighteenth century by Leibnitz, Malebranche, Benoit de Maillet, and other philosophers, by Haller the physiologist, by Bonnet, Buffon, Wolff, and other zoologists; at the close of the century by Erasmus Darwin, and in the earliest years of the nineteenth century by Oken, Treviranus, Lamarck, only to mention a few names.

It is well known that the school of ' Natural Philo-
sophers ', of whom Oken and Treviranus were the leaders,
were Platonists and disciples of Kant, and that their
avowed aim was to explain natural phenomena on
philosophic principles. Working with such biological
evidence as the knowledge of their day afforded, they
hazarded some wonderfully shrewd guesses, and exercised
a considerable influence on the thought of their time,
an influence not altogether baneful, as some writers would
lead us to suppose. But they laboured under this great
disadvantage, that the objective evidence at their dis-
posal was altogether insufficient to sustain the bold and
sweeping generalizations that they founded on it, and
arguing deductively from these generalizations they were
soon involved in absurdities and contradictions which
were easily exposed and turned into ridicule by the more
practical and sober-minded scientific workers of the day.

Cuvier, whose reputation as an exact and wide student
of comparative anatomy and palaeontology has lost none
of its lustre to this day, was a bitter opponent of the
natural philosophers, and a strong advocate of the doctrine
of the fixity of species, and he had the support of such
eminent zoologists as Johannes Müller, von Baer, Milne
Edwards, and others. It is curious to note how much
evidence these noted investigators collected in favour of
the doctrine of organic evolution, and yet how obstinately
they set their faces against its acceptance.

But, although they appeared to have routed evolution
and to have fairly driven it, as a guiding principle, from
the scientific field ; there remained a not inconsiderable
body of scientific thinkers who could not rest content
with the dogmatic assertions of the Cuvierian and
Linnaean schools.

We have had evidence enough, during the present year,
of the early period at which Charles Darwin's thoughts
were turned towards an evolutionary interpretation of
organic phenomena. We have not heard so much of the

part played by Herbert Spencer, who, as a public exponent of organic evolution, was in the field some years before Darwin wrote, and had anticipated some of his leading ideas. Spencer did not arrive at the idea of Natural Selection ; that was first conceived by Darwin, jointly made public by Darwin and Wallace, and freely accepted by Spencer as conforming to and strengthening his scheme of organic evolution.

I have been speaking of Herbert Spencer as a biologist ; to most persons he appears as a philosopher, who got his biological knowledge at second hand and wove the discoveries and opinions of other biologists into the fabric of his philosophical system. He has been accused of borrowing his zoology from Huxley, his botany from Hooker. It cannot be denied that there is a grain of truth in this accusation. The author of the *Synthetic Philosophy* could not have completed his task—he could scarcely have begun it—if he had attempted to undertake the laborious and time-consuming labours of an original investigator of natural phenomena, or even if he had attempted to verify by personal experience any considerable part of the evidence collected and handled in the two volumes of his *Principles of Biology.* But he spared no pains to make his knowledge exact. If he was not an original investigator, he was a conscientious student, and attended the lectures and the practical courses of the most eminent biological teachers of his time. His knowledge of biological literature was great—and it is a very abundant literature—his grasp of facts was unusual and his insight unequalled. His power of co-ordinating the evidence derived from the most different branches of biological studies was equal to that of Darwin himself, and his treatment of it led him to nearly identical conclusions. In some matters he anticipated Darwin's ideas. In particular, his theory of ' physiological units ' was an anticipation of Darwin's theory of pangenesis, and the parent of all the various theories of vital units,

promulgated during the last fifty years, as explanations of vital phenomena ; particularly of the phenomena of specific transformation, of inheritance and variation.

The theory of organic Evolution was of vital importance to Herbert Spencer's whole philosophical system. His interest in biology was at least equal to his interest in sociological questions. He contributed new and important ideas to biology, and to the end of his days was engaged in active controversy with Weismann, whose theory of the germ-plasm undermined some of his most important positions. It is assumed, perhaps a little too readily, that Weismann came off victorious in the contest, and I shall devote the rest of this lecture to a re-examination of the questions at issue between these two great antagonists, in the light of some recent zoological experiments.

I have not the time, and I do not think it is necessary, to give references and quotations; but it is, I think, a fair summary of Herbert Spencer's philosophical treatment of biological phenomena, to say that, for him, evolution is, in all its forms, a becoming of the heterogeneous and complex out of the homogeneous and simple. Thus, in his *First Principles*, he begins with a consideration of chemical and physical laws, and after treating of the interaction of these laws in the production of inorganic phenomena, he proceeds to apply the same principles to the solution of the problems offered by organic phenomena. I may give one quotation to illustrate his point of view.

' The formation of molecules more and more heterogeneous during terrestrial evolution has been accompanied by increasing heterogeneity in the aggregate of compounds of each kind, as well as an increasing number of kinds ; and this increasing heterogeneity is exemplified in an extreme degree in the compounds, non-nitrogenous and nitrogenous, out of which organisms are built. So that classes, orders, genera, and species of chemical

substances, gradually increasing as the Earth has assumed its present form, increased in a transcendent degree during that stage which preceded the origin of life.'

Thus evolution was in progress long before life appeared on the globe, and the origin of life is due to the continuance of the process of the formation and recombination of more and more heterogeneous molecules. To explain the transition from non-living to living matter he assumed the coming into existence of 'physiological units '.

'There seems no alternative,' he wrote, 'but to suppose that the chemical units combine into units immensely more complex than themselves, complex as they are : and that in each organism the physiological units produced by this further compounding of highly compound molecules, have a more or less distinctive character. We must conclude that in each case some difference of composition in the units, or of arrangement in their components, leading to some difference in their mutual play of forces, produces a difference in the form which the aggregate of them assumes.'

We must take note of the fact that the physiological units are assumed to differ among themselves from the beginning, and that the interactions, resulting from these differences of chemical composition, induce further differences, which are expressed in the structure of the different parts of an organism formed by an aggregate of such units. Starting from this conception, it is a comparatively easy task to picture a gradual increase of complexity in the organic world, due on the one hand to the combinations of different kinds of units into aggregates, and the changes induced at once in the units and in their aggregates by the action and reaction of the units on one another. Due on the other hand to the action of incident forces, gravity, heat, light, electricity, chemical stimuli, mechanical stimuli, both on the units and on their aggregates, inducing change,

and these changes superinducing further changes, and so on in ever-increasing degrees of complexity.

Practically every author who has set out to explain biological evolution in terms of the ultimate constituents of organized matter, has found himself compelled to assume the existence of some such units as those postulated by Spencer, and there is a very general agreement as to the manner in which the evolution of the animal and vegetal world has proceeded from such a basis. The divergence of opinion begins when the attempt is made to interpret individual or, as we call it, ontogenetic evolution in terms of general or phyletic evolution, and when the units are used to explain the phenomena of inheritance and variation.

It is now a fact familiar to every educated person that every individual organism (exception being made, for the moment, of individuals propagated by buds or cuttings) has its origin in a germ-cell—a minute mass of the life-stuff we call protoplasm—which in its earliest phase shows no further visible structure than that it is composed of cytoplasm and nucleus.

It is further well known that, normally, the co-operation of two such cells, one called male, the other called female, is required to start those processes which lead to the building up of the adult organism. But, as we know of many cases in which a single germ-cell is capable of proceeding on its course of development without the co-operation of another, without being fertilized, as we express it ; and as a consideration of the complication introduced by the act of fertilization is unnecessary for my argument, I will leave all question of male and female germ-cells out of consideration, and treat the subject as though only one cell were necessary, as is indeed often the case. The germ-cell divides into two, the nucleus heralding and sharing in the division. The two divide to form four, the four divide into eight, the eight into sixteen, and so on, until an aggregate is formed, often

of cells that are apparently alike, but it is obvious that they are really unlike, for when a certain number— a hundred and twelve it may be—are present, they form groups, and these groups undergo changes of position resulting in the formation of layers, the cells composing each layer being generally distinguishable by their form. In each layer fresh groups arise, their cells again exhibiting differences of form ; and these groups undergo further re-arrangement, and so the process goes on until finally, as a result of the regrouping and differentiation of the cells, all derived from the original germ-cell, we get the specific organs arranged in the specific order characteristic of the adult organism.

Visibly, then, every individual animal and every plant goes through its own course of evolution.   Its life-history is a becoming of the complex and heterogeneous out of the simple and homogeneous.   Thus there is a parallelism between the evolution of any given individual .organism, and the evolution of the whole assemblage of organisms that exist or ever have existed ; more particularly a parallelism between the evolution of any given organism and the evolution of the race or kind to which it belongs.

But there is a great difference.

If, in imagination, we trace the genealogy of any animal back through the ages, we see that, in the beginning, it must have had its origin in *real* simplicity and homogeneity. All that is now complex and heterogeneous in any organism must have been added, bit by bit, part by part, as the result of countless interactions and reactions always in operation through the long course of time.

We cannot conceive, and we do not suppose, that the specific complexity of any given animal was present, in any sense, in the primordial ancestor from which it is descended. It is only a mystification to say, as some have said, that it was *potentially* present, since proto-

plasm, once it came into being, contained in itself all the properties necessary for the development of all the specific forms of life that now exist or have existed in the intervening ages. A statue is not contained potentially in a block of marble. It requires much play of incident forces before the statue is produced out of the block, and the most we can say is that the marble is, no doubt, a necessary condition of the statue. So primordial protoplasm was a necessary antecedent condition of the existing world of organization, but a vast play of incident forces has been required to develop that organization.

Phyletically, therefore, the heterogeneity that we see and recognize in animals in general has been acquired. There has been always, on the whole, an addition of something that was not there before. Sometimes, no doubt, a subtraction, sometimes neither addition nor subtraction, but a pause, for evolution has proceeded in many directions, and in some cases has stood still, but on the whole, a very great addition.

But in ontogeny—the evolution of the individual— the case is very different. Though the germ-cells of different animals appear to us very nearly or exactly alike, their behaviour shows us that they are not in the least degree alike. Their qualities are specific and tend to a specific result. That the hen's egg invariably gives rise to a fowl and a duck's egg to a duck, was a matter of wonder to the early philosophers, and it is a matter for wonder still, though the phenomenon is so familiar, that those who do not think about these things are apt to deride us for all the trouble we give ourselves about them. But it is the hall-mark of stupidity to take things for granted because they are familiar, and to fail to find matter for wonder and reflection in the common objects of life.

To Herbert Spencer the development of the heterogeneous adult out of the homogeneous germ-cell presented no great difficulty.

The germ-cell, thrown off by the parent form, is necessarily composed of the physiological units proper to that parent form, and consequently possessed of certain specific characters. These characters are nowhere clearly defined, but it is made clear that they are not to be considered as corresponding in any degree to the specific structural characters of the parent or of the adult form that is to be. The physiological units are conceived of as having a certain *polarity*, characteristic of the species to which they belong, and by reason of this polarity the units react in a certain way to the incidence of external forces, and in the course of cell-division and multiplication are redistributed in such a way as to cause them to react in a characteristic manner on one another, and thus to undergo modifications, determined in part by their own polarity, in part by the relations in which they stand to other units, and in part to the influence of external forces. These induced modifications in turn induce new modifications, both in the constituent physiological units and in the aggregate of which they form a part, and the result is an increasing complexity ; but a complexity of a specific kind, partly because the reactions of the constituent physiological units are determined by their original polarity, partly because in the normal course of development of an individual animal, the environment, that is to say the incident forces, are the same or nearly the same, as in the development of other individuals of the same species.

On this supposition the evolution of the individual is as truly a progression from the homogeneous to the heterogeneous, as is the evolution of the race, and the parallelism between the two is nearly complete. Moreover, the phenomena of inheritance and variation are accounted for. For if the polarities of the units are alike, and the incident forces are alike, then the reactions will be alike, and the adult individual will be composed of the same kind of physiological units as were contained in

the germ-cell from which it was developed. This adult will in turn throw off germ-cells containing physiological units of its own kind, and the round will be completed in the same manner and result in the production of new individuals like to the first.

But, on the other hand, as the physiological units are not *exactly* alike among themselves, and as the incident forces to which the developing germ is subject cannot ever be *exactly* alike, the reactions between the two will always produce some differences in the adults, and these differences will be due to the changed composition of the physiological units composing them. Hence in every new generation the units will not only be slightly different from those of the parents, but will also be slightly different in the individuals composing the generation, and therefore in the germ-cells which they in their turn throw off. These germ-cells will therefore give rise once more to slightly different individuals, and so forth.

It is easy to see that the theory is still more useful in explaining the origin of variations when the mingling of slightly dissimilar physiological units in sexual reproduction is taken into account. But this need not distract our attention now.

The most important thing on which to fix our attention is that Spencer's theory states that acquired characters are transmitted by inheritance. By 'acquired characters', in this connexion, we mean the changes of constitution produced in the physiological units by their reaction to incident forces.

Darwin, who devoted many years to the study of Variation, agreed to a large extent with Herbert Spencer's view that variations are produced by the action of external forces.

'Changed conditions act in two ways, directly on the whole organization or on certain parts alone, and indirectly through the reproductive system. In all cases there are two factors, the nature of the organism, which

is much the most important of the two, and the nature of the conditions. The direct action of changed conditions leads to definite or indefinite results. In the latter case the organization seems to become plastic and we have much fluctuating variability. In the former case the nature of the organism is such that it yields readily, when subjected to certain conditions, and all or nearly all the individuals become modified in the same way.' [1]

Darwin had no doubt that variations, produced in this way, are inheritable, but he did not attach great importance to the direct action of external conditions as a means of producing modifications of structure, except in so far as they cause variations to arise and thus afford the material for the action of Natural Selection. I have quoted this passage because it contains reference to the distinction between ' the nature of the organism, *which is much the most important of the two*, and the nature of the conditions '.

Darwin, in a word, attached much more importance to the character of the organism throughout its whole history from the germ to the adult condition : Spencer attached much more importance to the direct modifying action of external conditions. As Weismann has pointed out, while Spencer gave an *epigenetic*, Darwin gave an *evolutionary* account of development, and invented the theory of pangenesis to account for the great complication of germinal structure necessary for the explanation of an evolutionary process in ontogeny.

The term ' evolutionary ' as applied to ontogeny bears almost exactly the opposite meaning to that which it bears when applied to phylogeny. In the latter case it means a progress from the simple and undifferentiated to the complex and differentiated : in the former case it means the gradual unfolding and manifestation of a pre-existing complexity.

Darwin saw clearly that such a complexity must exist

[1] *Origin of Species*, 6th ed., 1880, p. 106.

in the germ ; for if it did not, the facts of heredity could not be accounted for, and in his theory of pangenesis supposed that every cell in the body gave off minute gemmules, which, passing into the circulation, were stored in the germ-cells.

Sir Francis Galton experimentally disproved the theory of gemmules, and propounded a theory of ' stirps ' to account for the phenomena of heredity. Into the details of this theory it is not now necessary to enter. It attracted little attention in this country and passed unnoticed on the Continent and in America ; but it was, in fact, an anticipation of the principles underlying Weismann's more celebrated theory of the germ-plasm.

It is not my intention to attempt to give you an account of Weismann's theory, and it would be impossible to do so in the time at my disposal. It was explained by its author in the Romanes Lecture in 1894, and has since undergone some alteration, to harmonize it with the rapidly accumulating evidence on the numerous aspects of development and heredity—this evidence being the result of researches largely stimulated by the theory itself. The main features, however, remain unaltered, and I need only mention such of them as are directly relevant to Herbert Spencer's arguments.

In the first place, Weismann, by a careful criticism of a large number of supposed cases, rejected one of the main supports of Spencer's system. He showed that not only is there no evidence that characters acquired during the lifetime of an organism are transmitted to its descendants, but the evidence points strongly to the fact that such acquired characters are not and cannot be transmitted by inheritance.

If this is accepted as an established fact (as it is by most naturalists in this country, but not in America) it follows that the secular increase of complexity of organization demanded by the theory of Evolution cannot have been produced directly by the action of incident forces as

Spencer and also, to some extent, Darwin believed ; but must have had some other origin, and this could only be sought for in the constitution of living matter itself. To show that such an origin is possible, Weismann postulated the existence of ultimate vital units, or biophors,—not very different from Spencer's physiological units,—which exhibit all the attributes of life are capable of multiplication, are of innumerable different kinds, and owe their differences to the fact that they are themselves modifiable by the action of incident forces. A simple unicellular animal or plant, composed as it is of such biophors, would vary in structure owing to the modifications induced in its component biophors, and when it propagates itself by division, its characters would necessarily be handed on to the offspring resulting from division. But in a multicellular animal propagating itself by sexual reproduction, the whole organism is not divided, but only a minute portion is separated, and this portion has the power of giving rise to the whole. This minute portion is a germ-cell, and the biophors of which it is composed must be sufficiently numerous, and of a sufficient different number of kinds, to give rise to all the different tissues and organs of the adult. The germ-cell therefore differs from the tissue cells of the adult, for the latter, as a rule, can only give rise to cells of their own kind, and not to the whole organism, and therefore must contain only special kinds of biophors, and not all the different kinds of biophors necessary for building up the entire organism.

As Darwin's theory of the circulation of gemmules is rejected, for this reason among others, that it involves the acceptance of the inheritance of acquired characters, the observed facts of development can only be explained on the supposition that the body is composed of two kinds of material. The one kind, the germ-plasm, is made up of all the kinds of biophors necessary to produce all the different qualities of the organism ; the other

kind, the somatoplasm, consists of cells in which the different kinds of biophors have been sorted out or *segregated* in exact correspondence, as regards kind and situation, with the various tissues and structures of which the cells are components.

The germ-plasm, on this conception, is the permanent material, in which all the specific characters of the race are collected, and is handed on from generation to generation. The body or soma is, in every generation, the fleeting expression of the qualities contained in the germ-plasm. These qualities are expressed, or made manifest, in the development of every individual from the germ, by the continued segregation of the biophors in the course of cell-division, some kinds passing into one cell, some kinds into another, and this process is repeated at every stage of division until, at last, all the different kinds of biophors are separated into cells or cell-groups, and then give rise to the specific characters which they represent. Their mission is then fulfilled, and, being incapable of further development, they perish in time; but not before the individual has provided for the perpetuation of the race by giving off fresh germ-cells, which are derived from a store of the original germ-plasm reserved, so to speak, during the ontogeny in a special group of cells. These are the outlines of Weismann's theory. I need not pursue it into its intricacies and show how, from a consideration of the fact that every part of an animal is independently variable, and that these variations are heritable, he had to assume that the germ must contain as many biophors as there are different kinds of cell-groups giving rise to independently variable structures, and that these biophors must be grouped into units of a higher order called determinants, and the determinants into yet higher groups called ids, each id containing all the determinants necessary for the formation of an individual and having a definite organization or architecture. Further, that every germ-cell must

contain many different kinds of ids, representing the contributions of many different ancestors. All this would take me far from my main subject, and would require many hours to set forth in sufficient detail.

It is sufficient if I have said enough to show how widely this theory differs from that of Herbert Spencer, and what very different consequences must be deduced from it.

According to Spencer, the material of the germ, out of which the individual is developed, has indeed its own properties which impose a limit upon and determine the general direction of the development ; but within these limits the material is highly plastic, and it assumes its ultimate form and qualities in response to external and internal forces acting on it throughout the whole course of ontogeny. The material, being of a certain kind, can only react in a certain way to external and internal forces, and so gives rise to a specific form ; but as the forces must always be slightly different, the reactions must always be slightly different, and thus variations arise which are perpetuated in the germ-cells separated off for the maintenance of the race and the building up of the next generation.

According to Weismann and his followers, the material of the germ is already endowed with all the properties of the adult ; the development of the individual is pre-determined by the qualities of the germ ; the germ-plasm is only slightly plastic, and such changes as are impressed on the soma by the action of incident forces perish with the soma, and are not incorporated into the germ-plasm that is to give rise to future generations.

In the words of Wilhelm Roux, the development of the individual may be likened to a mosaic-work ; the substances out of which the picture is to be formed are there beforehand : the picture is formed by sorting out these substances and combining them in a definite order.

If now we inquire into the evidence in favour of one

theory or the other, we find that it is preponderantly in favour of Weismann's.

In the last two decades a large and active school of Experimental Morphology and Embryology has come into existence, whose object it is to inquire into the very problems that we are considering. Started by Oscar Hertwig, Roux, Hans Driesch, Boveri, and many others on the Continent, this method of investigation has been taken up with great enthusiasm in America by E. B. Wilson, Morgan, Jacques Loeb, and many others, but it has as yet made very little progress in this country. In Oxford, however, it has distinguished representatives in the persons of Dr. Vernon and Dr. J. W. Jenkinson, and I hope that in the near future this University will be the English centre of this form of zoological research, which is the complement of that branch of inquiry into the hereditary transmission of structure and characters which has been so firmly established at Cambridge. The first step to be taken by this school of developmental mechanics was a renewed and much more detailed inquiry into the way and course of the development of the germ-cell into the embryo.

The earlier embryologists were contented with saying that the ovum divided into two, the two into four, the four into eight, and so forth. That the cells formed by repeated divisions arranged themselves into a hollow sphere or blastula : that one half of this sphere became tucked into the other half to form a two-layered gastrula, and thus two primary cell layers were formed—an outer and an inner—from which by further differentiation all the organs of the adult were eventually established.

The more modern embryologists go much further than this and trace the exact fate of every cell formed during the division of the ovum. The time and place of origin of every cell is noted, and its subsequent history is followed, until it is satisfactorily proved what part of

the body and what organs and tissues the descendants of that cell give rise to.

It has thus become possible to construct a large number of cell-lineages, each of which can be expressed in the form of a genealogical tree.

The tracing out of cell-lineages is a matter of pure observation, and the whole result of the work has been to show, what might have been predicted from our knowledge of the building up of embryo from the egg and the adult from the embryo by a repeated process of cell-division, that in a normal course of development, particular cells having particular positions in the embryo invariably give rise to the same organs in the larva or in the adult. This observed fact could be interpreted just as well on Herbert Spencer's principles as on Weismann's, for it could be urged that the fate of any particular cell occupying a particular position in the embryo depended, not on any qualities inherent in itself, that is to say on the particular kind of material of which it is composed, but upon the forces to which it is subject, because of its relation to other cells and to the external environment.

But reasoning on the results of simple observation can only lead to hypothetical explanations. Experiment alone can decide the questions at issue. The earliest experiments seemed to support Herbert Spencer's views. Driesch, and after him other investigators, found that, in a number of animals, the first two, or four, or even eight or sixteen, cells formed by the earlier divisions of the germ-cell, might be separated from one another, and that each would, after separation, segment as if it was an entire ovum and give rise to a normal larva, having all the specific characters of a normally developed larva, but of reduced size. O. Hertwig, Driesch, and others showed that the mutual positions of the blastomeres might be altered by pressure and other methods, and yet the altered embryo when released and kept

under ordinary conditions, would develop into a normal larva or adult.

Arguing from these observations, Driesch constructed an epigenetic theory of development not very different from Herbert Spencer's, and laid down the law that the destiny of every cell in the embryo is a function of its position.

But before this Roux had shown that if one of the first two blastomeres of a frog's egg is destroyed, the result is, not the formation of a whole embryo of half size, but a half embryo, and further observation and experiment has shown that in whole classes of the animal kingdom the materials necessary for the formation of the different organs of the larva and adult that is to be are already present and localized in the germ-cell, and are dealt out, according to their kind, at every division from the first onwards.

Here I must digress for a moment to explain that Weismann, agreeing in this matter with Strasburger and O. Hertwig, held it as proved that the biophors and the aggregates of biophors forming determinants, are located in the chromosomes of the nucleus of the germ-cell. This view, supported by a number of considerations, seemed to be amply proved by an experiment of Boveri, who fertilized the anucleate fragments of the eggs of one species of sea-urchin with the sperm of another species, and reared larvae which exhibited the *paternal* characters only. But these results have since been called into question and have quite recently been contradicted by the experiments of Kupelwieser and Loeb, who fertilized the ovum of a sea-urchin with the spermatozoon of a mollusc, and obtained the characteristic larva of the sea-urchin without any trace of paternal characters. And numerous other experiments—too many for me to recount now—have shown that, whatever may be the exact rôle of the nucleus, the cytoplasm of the germ-cell certainly contains organ-forming materials, and that if

these are removed corresponding deficiencies will occur in the larvae reared from the eggs operated upon.

Weismann himself has modified his former opinion, and in his most recent book on the Evolution Theory suggests that particles emitted by the nucleus co-operate with elements already present in the cell-body to give rise to specific tissues. That this must be in some sense true, we are bound to believe from a consideration of many phenomena of cell-division and inheritance, but I will not pursue this subject any further now. I have only introduced it to show that experiment has established beyond all doubt that specific organ-forming substances are present in the cytoplasm of the cell, and the experiment I am going to describe in detail shows that, in a number of cases at least, these substances are dealt out in the course of the division of the germ-cell, just as aces, kings, queens, knaves, &c., held in the hand of the dealer, are dealt out to the different players in a game of cards.

Fig. 1 in the diagram shows a picture of the egg-cell of *Dentalium*, the elephant-tooth-shell. This animal is a mollusc, the representative of the class Scaphopoda, and possessed of many remarkable anatomical features. For the present all that need concern us is, that in the ontogeny of this animal there is a larval form (as indeed is the case in most mollusca), whose shape is shown in Fig. 10. It is shaped something like a humming-top ; having three parallel equatorial rings of ciliated cells, dividing an upper from a lower hemisphere. At the summit of the upper hemisphere is an apical organ, consisting of a group of a few cells bearing a tuft of very long cilia. The greater part of the head region and the ' brain ' of the adult are formed from this apical organ. The lower hemisphere is at first conical, with a posterior tuft of cilia. Nearly the whole of the body of the adult is formed out of the lower hemisphere and the ciliated rings are provisional organs which become

relatively less and less important and eventually disappear.

In the egg of this animal a broad middle band of red pigment separates a colourless upper polar area from a colourless lower polar area. The lower polar area consists of a dense granular and apparently homogeneous protoplasm in which there are no yolk corpuscles—in this it differs from the rest of the egg.

When the egg is fertilized and about to divide it protrudes from its lower pole a lobe, into which nearly all the white matter of the lower polar area passes (Fig. 2). Division then takes place in such a way that the 'polar lobe' is attached to only one of the two cells formed by the division (Fig. 3). When division is accomplished this 'first polar lobe' is drawn up again into the blastomere to which it is attached. The white polar area is confined to the larger of the two cells. We call the smaller cell AB, the larger cell with the white lower polar area CD. Before the next division takes place the lower polar area is again extruded in the form of a 'second polar lobe' (Fig. 4). Each blastomere is divided into two, and the second polar lobe remains attached to one of the cell products into which CD has divided. We call this product D, and the embryo now consists of four cells, A, B, C, D. The second polar lobe is once more withdrawn into D, but before the third division takes place the white matter is once more extruded as the 'third polar lobe' (Fig. 7). In the third division each of the blastomeres, A, B, C, D, divides unequally, giving rise to four smaller cells above which we call $1a$, $1b$, $1c$, $1d$, and four larger cells below which we call $1A$, $1B$, $1C$, $1D$. The third polar lobe remains attached to $1D$, and when division is complete is withdrawn into it. Prior to the fourth division the white material of the third polar lobe moves through the blastomere $1D$ and is mostly aggregated near its upper surface. The fourth division resembles the third, inasmuch as four small cells (micro-
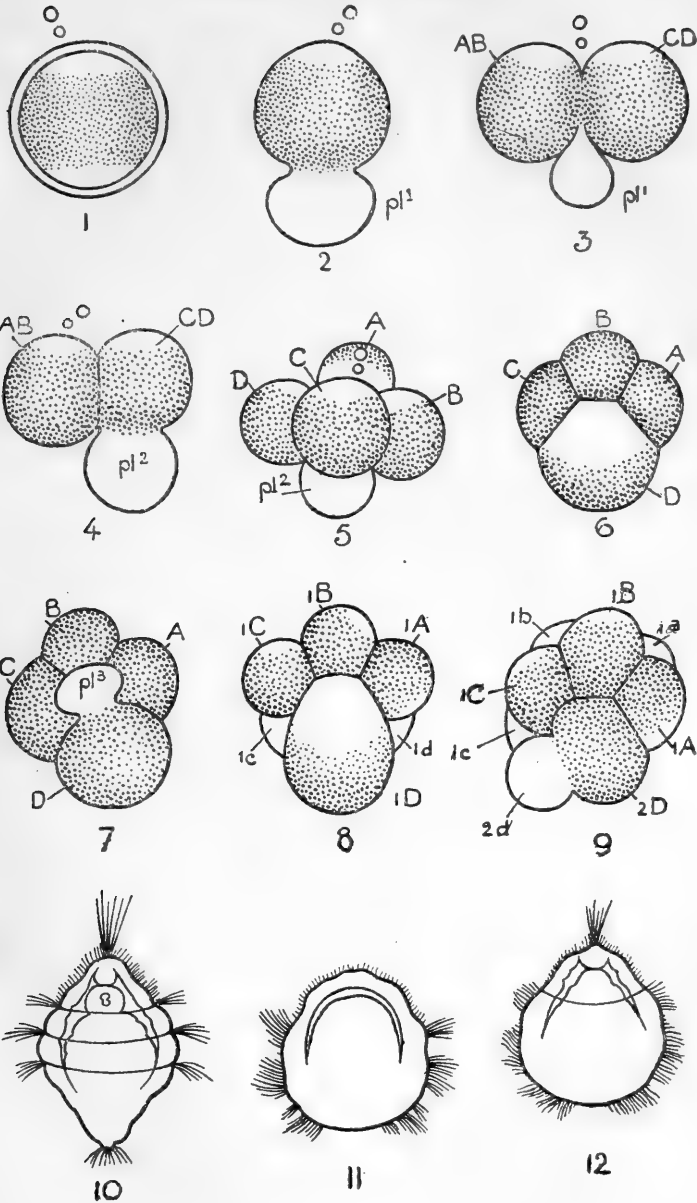
Figures 1-9., early segmentation stages and figures 10-12, normal and abnormal larvae, of *Dentalium*. (After E.B. Wilson)

meres) are formed by the unequal division of the large
cells $1A$, $1B$, $1C$, $1D$. This new ' quartet ' of micromeres
we call $2a$, $2b$, $2c$, and $2d$, and it is noticeable that a great
part of the white material which formed the third polar
lobe passes into $2d$ (Fig. 9). It is known that the products
of this particular cell $2d$ form an important part of the
ventral surface of the posterior hemisphere of the larva
and of the trunk of the adult. Further than this we need
not go in the description of the normal course of develop-
ment.

Now if the first polar lobe be removed, segmentation
continues, and ends in the production of a larva such
as is shown in Fig. 11. The upper hemisphere and the
three ciliated rings of the prototroch are there, but there
is no apical organ, and the lower hemisphere is aborted.
Such larvae are incapable of further development and
soon perish.

It is clear that the material necessary for the formation
of the apical organ and the lower hemisphere (that is,
the material for the head and trunk of the adult), was
contained in the first polar lobe.

If, in another experiment, the second polar lobe is
removed, the result is a larva such as is shown in Fig. 12.
The apical organ is present, but the lower hemisphere
is aborted. Clearly, when the first polar lobe was with-
drawn into CD, some part of its material, necessary for
the formation of the apical organ, must have passed out
of the lower hemisphere of that cell, and have been
excluded from the second polar lobe—but the trunk-
forming material remains in the second polar lobe.
Further experiments prove that this is certainly the case,
and prove further that the material for the apical lobe is
first transferred to D, and then at the third division to $1d$.

For if the blastomeres are isolated, CD produces
a larva of normal aspect, but of reduced size ; AB produces
a larva similar to that of an ovum from which the first
polar lobe was removed.

Isolated *A, B, C* blastomeres produce defective larvae without apical organ or lower hemisphere. Isolated *D* larvae are normal, except that the lower hemisphere and apical organ are disproportionately large.

The micromeres 1*a*, 1*b*, 1*c*, 1*d* may be isolated, and they continue to segment. 1*a*, 1*b*, 1*c* form curious little larvae with a prototroch and an upper hemisphere ; but no lower hemisphere, no gut, and no apical organ. 1*d* produces a similar larva as regards absence of trunk and gut, but it has a well-developed apical organ. It is possible to cut eggs of *Dentalium* into two, to fertilize the pieces, and to develop larvae from these fertilized fragments. The results are absolutely confirmatory of those I have just described. The lower hemisphere segments as a whole, and produces a dwarfed larva, but with all its parts complete. On the other hand, the upper hemisphere of the egg segments as a whole, but no polar lobe is formed, and the resulting larva has neither apical organ or post trochal lower hemisphere.

Similar and even more thorough and convincing experiments have been made on the developing eggs of the Limpet. But the details are too complicated for me to do more than refer to them. They prove, in an unequivocal manner, that the various cells formed during the cell-lineage, have each a definite and limited destiny, and this they will fulfil, even if removed from the aggregate of which they form a part. For example, early in the segmentation certain cells are formed which are destined to give rise to the prototroch. One cell arises in each of the four quadrants formed by the four large cells of the four-cell stage of development, and the cell of each quadrant behaves in the same way. It divides into two, and the two divide again into four which combine with the four similar cells derived from each of the other three quadrants to form a ring of sixteen ciliated cells constituting the prototroch. This is the normal course of development. Let us call any one of the primary proto-

troch cells p. It divides into p^1 and p^2, and each of these divides again into p^{11}, p^{12} and p^{21}, p^{22}. If in any embryo p is isolated on its first appearance, it divides twice, and gives rise to four cells each bearing a tuft of cilia. If p^1 and p^2 are isolated, each divides once, giving rise to two cells with a tuft of cilia. If any of the cells p^{11}, p^{12}, p^{21}, p^{22}, is isolated it develops a tuft of cilia, but will not divide. The number of divisions is predetermined, and that number is fulfilled whether the cell remains a part of the aggregate or whether it is removed from it.

The incident forces and the mutual actions and reactions must be very different in the two cases, but the specific number of divisions are gone through and the specific form is attained all the same.

Clearly, in such cases the destiny of a cell is predetermined, and is not a function of its position in the cell aggregate. One cannot say with Driesch 'jeder Theil kann jedes'.

It is, of course, impossible for me to give you a hundredth part of the available evidence; but this much, I think, emerges clearly from what I have told you.

All ova or eggs contain specific substances necessary for the formation of particular regions of the future animal. In the course of segmentation these substances are segregated from one another in a progressive manner, so that in the end particular kinds of substance are isolated in particular cells, derived from division of the original germ-cell. Cell-division therefore, in ontogeny, is the expression of the sorting out and separation of the materials contained in the germ.

This process of segregation sets in earlier in some species than in others. In some cases, as in *Dentalium*, it begins with the very first division of the germ-cell. In other cases the segregation is deferred until a number of cells are present (as is shown by the fact that sometimes any one of the first sixteen blastomeres is capable of

giving rise to entire larvae). But in all cases segregation sets in sooner or later.

If I had the time, and had a great number of diagrams to illustrate my argument, I could prove to you that in any one class of animals such as the Chaetopod worms or the Mollusca, the cell-lineages of different species, though very similar, are never exactly the same. The differences—which may be considerable—are mostly due to the different periods at which special cells, containing particular constituents of the future animal, are formed in the course of segmentation. And I could further show, what I can only now inform you of, that in each class, and in the sub-divisions of each class, there are clear indications that there is a definite relation between the elaboration or simplification of the ontogeny and the period at which the segregation of the specific substances is accomplished in the course of segmentation.

The life-history of an animal may be direct or indirect.

When it is direct, the course of development is straight-forward; the animal is hatched out or born with the characters proper to its species. When it is indirect, the animal is born with characters very different from those which it will ultimately assume. It is born as a *larva*, and a typical larva is an independent organism, having means of locomotion, a mouth, and a digestive tract. It feeds itself, lays up a store of nutriment, and only after a longer or shorter period of independent existence does it undergo further developmental changes which lead to the assumption of the adult characters. The caterpillar (larva) and the butterfly (adult or imago) is a familiar example of an indirect course of development.

An indirect course of development is, in a relative sense, prolonged, because there are two free stages and two developmental stages leading up to them to be provided for. If you could suppress the caterpillar stage, the condition of the perfect insect would be arrived at sooner. The development would be abbreviated.

Now in the Chaetopod worms there is a larval stage
analogous to that of the caterpillar. We know it as the
trochosphere larva. It swims about in the sea by means
of its ring of cilia; it has rudimentary sense organs; it has
a mouth and a complete digestive tract, and it feeds
itself. Eventually it gives rise to the adult worm by a
process of development which I need not detail now.

But you can see at once that the larva has a specific
form and the adult has a specific form, and that the two
are very different indeed. Both have to be provided for
in the germ-cell which is to give rise to both forms in
succession.

When we examine the cell lineage of such a worm
as *Polygordius*, it is perfectly clear that the first
materials segregated during segmentation are those
destined to form the larval organs. While this part of
the ontogenetic process is pushed on, the materials for
forming the adult organs are held in reserve, and are
contained in only a few cells, which do not proceed to
further division until the larva is perfected, has fed for
some time, and has laid up a provision of nutriment
sufficient for the performance of the next phase of develop-
ment leading to the adult condition.

But in a large number of marine worms a trochosphere
larva is produced which does not feed itself. In such
cases the egg is provided with a quantity of food material
in the shape of yolk granules. During segmentation this
yolk is segregated in the large cells of the so-called vegeta-
tive hemisphere, from which the digestive tract is ulti-
mately formed. A trochosphere-like larva is arrived at,
but it has no functional digestive tract; only an inner
mass of large yolk-laden cells, which provide the nutri-
ment necessary for the growth processes. In all such
cases adult organs begin to make their appearance early
in the ontogeny, and the larval stage is clearly in course
of suppression. In consequence, we find that the materials
necessary for the formation of adult organs are segregated

earlier in the segmentation phases than is the case in species in which the larva is fully developed and feeds itself. The more the larval stage is obscured, the earlier are the adult constituents segregated during the segmentation of the egg, and the more completely does the development manifest itself as a 'mosaic-work'. In freshwater worms and earthworms there is no larval stage, and here we find that the constituents for the formation of the adult body are segregated at an early period, while those for the formation of larval organs are perhaps indicated, for these worms are descended from marine worms, but as there are no larval organs to be formed the constituents necessary for their formation are never segregated. They have dropped out of the life-history, and cannot any longer be present in the germ, for if they were there they would make their presence manifest in the course of the development.

There is evidence that this process of abbreviation of the development, involving the suppression of the larval stage and the precocious segregation of the factors appropriate to the formation of adult organs, has not occurred once only, but has happened again and again within the limits of the class. Every time that it has happened there must have been some change in the constitution of the germ-plasm ; some loss of tendencies to produce larval organs, some hurrying up and strengthening of tendencies to produce adult organs.

Ultimately this hurrying up process, which we call precocious segregation, must affect the germ-cell itself. For in cases where the first two, four, eight, or even sixteen blastomeres are what we call totipotent, in other words, when each contains all the factors necessary to produce the specific structure of the entire organism, there cannot be any pre-localization of the factors in the germ-cell : they must be equally distributed through it. On the other hand, the cases of *Dentalium* and the Limpet—several others could be quoted—show that this

pre-localization may and does exist. From what I have said, I think it is clear that this pre-localization is a secondary and derived condition, not a primary one.

For if it were primary, it would be specially well marked in the eggs of animals which, on other evidence, we regard as primitive, but this is not the case. On the contrary, it is specially well marked in animals which we have every reason to suppose are much modified, either in their larval stages, or in their adult stages, or in both.

If then it is a secondary condition, and if this condition has been acquired several times over, within the limits of a single class, the germ-plasm has been modified and, as far as we can judge, is still undergoing modification in a large number of cases. It is always having the characters, many of them adaptive characters, of the adult thrown back into itself, and conversely, as its constitution is altered, it must reproduce these characters in every somatic generation to which it gives rise.

We are confronted with the old question, as old as the time of Aristotle, whether the egg gives rise to the fowl or the fowl to the egg.

Weismann would answer the question in this way. The germ-plasm is variable, because the biophors composing it are affected by slightly different conditions of nutrition, temperature, &c., and vary. Their variations induce further variations in the determinants, which control the structure of each separately variable part of the organism at all stages of its existence. Therefore the organism varies, and every beneficial variation, at every period of life, will be selected. Natural Selection ensures that only those forms shall survive whose germ-cells contain favourable variations. What is apparent to us is the preservation of favourable modifications in adult (or larval) individuals. What really is preserved is the kind of germ-plasm that has produced those favourable modifications, and as this is handed on from selected

individual to selected individual, any amount of modification is possible, including abbreviation of the ontogeny, the suppression of the larval stages, the precocious segregation of the primary constituents ; everything, in short, that is of advantage. I must confess that I am not quite content with this explanation, and there are others who are not content. But I have not the time to criticize it now. To do so requires a full consideration of the supplementary theories of Histonal Selection, Germinal Selection, and Amphimixis, theories not to be lightly treated of or explained in a phrase.

Nor can I offer any explanation of my own of the unquestionable fact that the modification of the germ and the modification of adult structure have proceeded *pari passu*, in the course of phyletic evolution. After struggling for some time with the difficulty, I have come to the conclusion that we must wait for fresh light from the experimental schools of zoology.

For the present, it is enough that we have ample evidence of the pre-existence of ' primary constituents ' or ' factors ' in the germ.

What the precise nature of these factors may be we are hardly in a position to say at present. But a great deal of light has been thrown on the *behaviour* of these factors by the researches of the Mendelian School of Students of Heredity, at Cambridge. It has been proved that they are resident in the germ-cells, and that they are units, in the sense that they are amenable to the laws of number, and their actions can be represented by simple arithmetical calculations. It has been clearly proved, also, that in respect of any given structure or character in an adult organism, the result manifested is not, in many cases at least, due to the action of a single factor, but to the co-operation of two or more factors. For it has been shown that, for instance, the colour of a sweet-pea is not determined by a single colour-bearing factor, but by the co-operation of two factors. For if

two varieties of sweet-pea both having white flowers
are crossed, the resulting generation is all purple.
The two white peas are apparently similar, differing
only in the shape of their pollen grains. Each kind
will breed true for generations, but when crossed
they produce the coloured sweet-pea. This coloured
form, when self-fertilized, produces several varieties
of purples, reds, and whites. I have not the time to
explain this phenomenon fully, but may state that
analysis showed that the facts are susceptible of
the following explanation : One of the original white
flowers contained a factor, which we may call C, which
by itself is incapable of producing colour. The other
contained a factor, which we may call D, which by itself
is incapable of producing colour. But when the two
factors are combined, as they are in crossing the two
varieties, colour is produced. The subsequent experiments
show that it is *red* colour, but the hybrid generation is
purple. It was shown that this was because one of the
original parent whites contained yet another factor B,
which in the presence of both C and R produces purple, but
does not produce any colour if it meets only C or only R.

I am informed that it has since been shown that in
the case of these sap colours in plants, one at least of
the factors has been discovered to be a chemical sub-
stance diffused in the sap, but the results have not yet
been published.

These discoveries seem to introduce a complication
into our conception of factors in the germ-cells, but it
seems probable that they will be found quite consistent
with the results of experimental work on developing
ova, such as I have described. For it has been shown
that certain necessary constituents for the production
of adult characters are contained in the cytoplasm of the
egg. From a large number of considerations we are
obliged to conclude that other constituents are con-
tained in the nucleus, and it seems probable that for

many characters it is necessary that the substances contained in the nucleus should act on those contained in the cytoplasm to produce the character in question in the adult, and that it may come about that one or other of these substances is absent and so the character in question is not produced, but will be if the two substances are brought together in fertilization.

But all this is as yet unproved, and it will require years of research to elucidate the many problems presented by the constitution of the germ-cell, and the manner in which organ-producing factors are combined or split up in the course of reproduction.

This much, however, is clear, that Herbert Spencer's conception of the constitution of germ-cells no longer holds good.

The germ is proved to be not a simple relatively homogeneous substance, which acquires increasing heterogeneity in the course of development, but an exceedingly complex heterogeneous substance, containing what, for want of more definite knowledge, we must call *factors*, and these factors are derived by inheritance from germs containing like factors. By intercrossing the factors may be combined, separated, added to, or subtracted, and thus variations of definite kinds may be produced; but the characters to be produced are not determined by the interaction of the constituent parts during the development of the individual, but by the bringing together or separation of the factors during the processes of maturation of the germ-cells and their subsequent union in fertilization.

We conclude that for every species of animals or plants —and by a species we mean a number of individuals capable of interbreeding freely—there is a certain stock of factors which, separately or in combination, are capable of giving rise to all the specific characters, and also to all the varietal characters, manifested by the species. The factors necessary for the production of

the *specific* characters must be present in the germ-plasm of all the individuals composing the species—for if it were not, the specific type would not be produced. But of the factors determining the varietal characters, some may be present in the germ-cells carried by any one individual and some absent. In a mixed race, where the individuals interbreed freely, the combination or separation of the various varietal characters will obey the laws of chance. By studying the segregation of the factors in the course of two or three generations of selective breeding, a pure race, true to certain characters may be established, and the advantageous characters of two or three different races may be combined. Improvement may be effected in this way, but in no case can it be secured by the selection of such modifications as have been produced in the individual by the direct action of external agencies, whatever these agencies may be. When once particular factors are brought together by the union of germ-cell with germ-cell in fertilization, the characters of the adult, including habit as well as form and colour, are irrevocably fixed, as are also the qualities which the adult in question can transmit to its descendants. This being the case, one of the most important links in the chain of argument used in the synthetic philosophy is broken, and the sociological conclusions founded upon the biological principles set forth in that system are vitiated.

But, although I do not think that we can any longer accept Herbert Spencer's conclusions, we should hold fast to his conviction that mankind is governed by the same laws as govern the animal kingdom, and that no true system of sociology can be offered which does not take full account of those laws.

It is not the business of a zoologist to offer solutions of social questions. But he is within his right if he tenders to those whose business it is to study these questions such evidence as is relevant.

Molluscs and marine worms and sweet-peas may seem to be remote from human institutions, and it may be objected that conclusions derived from biological studies of this kind cannot be applicable to ourselves. But this objection does not hold good. The phenomena of heredity and variation in mankind, as well as the physiology of man, have been studied in greater detail than in any animal, and we have ample evidence that man is as inexorably subject to the same fundamental laws of existence as are animals. And since many of the most important of human institutions are closely bound up with these fundamental laws, when we attempt by legislation or influence or education to vary our institutions in the hope of improving our present condition and transmitting the improvement to our successors, it is imperative that we should act in accordance with and not contrary to those laws.

You will probably be inclined to the opinion that the conclusions to which zoology has arrived are not sufficiently secure to warrant an attempt to apply them to affairs of state. Be it so. But it is a fact commonly overlooked that ideas derived from biological science *are* being applied to the affairs of the state, and that some who would hurry on the march of progress wish, consciously or unconsciously, to apply them still further. But these ideas are founded on the conclusions reached fifty years ago, and science has moved far forward since then. It is to be feared that much that still passes for ' progress ' is really regress, for it is founded on mistaken conceptions of the operations of Nature.

Vague as some of our conceptions still are of the operation of the forces underlying vital phenomena, I think that we are clear on one point, which I have already emphasized, that man, in common with his fellow creatures, has a past history which he cannot divest himself of. And not only man as a species, but man as an individual, for he is born with certain charac-

teristics, and he can only hand on those characteristics to his children. Hygiene, education, social institutions, may improve the lot of the individual, but they cannot produce any permanent effect on the race. And many of our apparently most promising reforms may actually do injury to the race, if they result in the multiplication of the unfit at the expense of the fit—fitness and unfitness being innate and not acquired characters.

But I will not pursue this subject further. If you ask me to point out the way, I am excused from the necessity of doing so, for it was pointed out by Sir Francis Galton in the Herbert Spencer lecture in 1907. It is sufficient if I have made it evident that zoological studies have a human interest and a human application. They are difficult studies, and they do not obviously lead to material prosperity, so they attract but little interest in this country, and I think it is a reproach to us. Perhaps we zoologists are responsible for it, for we are wont to conceal our results in language that is not understanded of the people. I have tried this afternoon to tell some of the most important conclusions of my science in plain language, and hope that I may have attracted your interest.

I will conclude by saying that, though I have been at trouble to show that some of the most important parts of his *Principles of Biology* were founded on erroneous data, I recognize with gratitude that the far-reaching importance of biological study was not only appreciated but strenuously advocated to the last by Herbert Spencer.

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