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THE GENE AND THE ONTOGENETIC PROCESS¹

THE problem of the relations of genetics and physiology of development is essentially a modern problem much discussed of late, and recently expounded in very concrete form in Goldschmidt's "Physiologische Theorie der Vererbung." It was not visualized by Darwin and by Weismann, because, for each of them, the theory of development included the theory of heredity. However, their theories of determinants, both of development and of heredity, died on the field of battle in the "nineties" and the early years of this century. Mendelism arose, and the theory of heredity became by degrees the modern doctrine of the genes with its denial of *representative* particles and unit characters; but the determinant theory of development died childless, with no successor except a field of investigation which no single theory can compass.

Since Weismann, physiology of development and genetics have pursued separate and independent courses. Have these courses increased the divergence which became pronounced in the nineties of the last century when the untenability of a determinant theory of development was demonstrated experimentally to the point of silencing all former adherents? Or, on the other hand, has the immense progress made in both disciplines in the present century been of such a nature as to lead to an expectation of their ultimate reunion? There can be no doubt, I think, that the majority of geneticists, and many physiologists certainly, hope for and expect a reunion. The spectacle of the biological sciences divided permanently into two camps is evidently for them too serious a one to be regarded with satisfaction. The essays of Spemann, of Morgan, of Jennings and of Goldschmidt are symptomatic. The voice of Bateson on the other side, now unhappily silenced, is relatively lonely. I do not perhaps need to protest my love for both fields of work, nor my admiration of the investigations that have so widened our biological horizon in recent years. I would ask only to consider with you their mutual relations, whether to one another or with a *tertium quid* in the organism.

What are the reasons why geneticists and physiologists alike agree that there is present promise of a

¹ Evening lecture delivered at the Marine Biological Laboratory, Woods Hole, Mass., July 22, 1927.

reunion of genetics and physiology of development? The promise arose with the gradual abandonment of the essentially determinant point of view in genetics expressed in the theory of unit characters, and its replacement by the factorial hypothesis or gene theory, the most important general advance of genetic theory of our time. This advance at once broke down—or at least appeared to break down—an impassable barrier: so long as the theory of genetics continued to be determinant in character, there could be no common meeting ground with physiology of development which had definitely passed that standpoint. The promise of reunion also rests, I think, on confusion of the physiological conception of heredity as repetition of life histories, and the essentially statistical examination of the reappearance of differentiating characters in successive generations which constitutes genetics. These are really very different things. There is also the justified feeling that such a pragmatically valuable conception as that of the genes must have profound physiological applications, but that again is a very different question—or perhaps only a small part of the question.

These mutually supporting ideas are undoubtedly very convincing; otherwise we should not have so outstanding a geneticist as Morgan maintaining that the application of genetics is one of the two most promising methods of attack on the problems of the physiology of development (1926), nor so outstanding a student of the physiology of development as Spemann pledging the aid of his science to genetics, nor should we find Goldschmidt devoting all his strength to the elaboration of a theory comprising development as well as genetics in its scope, and based throughout on the conception of the gene.

Let us then inquire into the prerequisites of an alliance between genetics and the physiology of development. Since genetics has become quite a unitary science, and physiology of development is at most a field of work, we can best proceed by an examination of the necessary concepts of the latter followed by an inquiry into reciprocal relations for each concept.

I. CONCEPTS IN THE PHYSIOLOGY OF DEVELOPMENT

The necessary concepts that I propose to consider are those of the germ, of individuation, and of differentiation in its two aspects of embryonic segregation of potencies and of realization of potencies.

1. The concept of the germ is that of an organic entity of a relatively simple and undifferentiated character capable of producing a more or less specific organism of a relatively complex and differentiated

order. The concept of the germ has thus of necessity somewhat of a teleological cast, which is seen in the implications of theories of development and heredity.

The germ exhibits the duality of nucleus and cytoplasm; the geneticist has taken the former for his field, the embryologist the latter, neither arbitrarily, but both of necessity, even while both admit that neither in genetics or in embryology does either operate alone. The germ is the basis of all happenings in embryology and in genetics. A change in genetic germinal composition means changes in development all along the line. No physiological event can be the same in two germs of different genetic composition; the divergence of characters that so emerges is then correctly referred to the initial germinal difference. Let it be admitted once for all that genes are concerned in the genesis of all characters of the organism.

2. The germ is physiologically integrated as an individual at all stages. It may be first merely a cellular individual, then a definitely polarized individual with one or more axial gradients; as development proceeds, specific correlations, including those of definitely nervous and chemical natures, make their appearance. In short, the physiological principles upon which integration depends undergo differentiation, in the sense of progress from relatively simple and few to relatively complex and many, during development. While individuality may thus *appear* to grow, it is in reality complete at all stages, only the means to its realization changing and multiplying with growing complexity.

3. Successive stages of development are marked by increasing complexity of organization, and each stage has its own characteristic features. The term "differentiation" is commonly used to cover this whole series of events. We can, however, distinguish two logically very different series of phenomena overlapping in time to a great extent. The first, which is especially characteristic of early stages, is a process of origin of definitely determined loci (primordia), each with a specific potency. This process I propose to call in what follows *embryonic segregation*, on account of the resemblance of its sharply alternative character to Mendelian segregation, to which however it has no other observable resemblances. It is a process of origin of limited potencies. The second, which is especially characteristic of later stages of the life history, involves the realization of the potencies isolated in the final terms of the segregation process, thus involving histogenesis and definitive functional development.

Embryonic segregation may be characterized by the following features:

1. Its action proceeds from the more general to the more special in a definite sequence which is both dichotomous and discontinuous.

2. This results in a progressive genetic restriction, of a more or less fixed kind, in the primordia thus established.

3. These processes exhibit definite order, (a) in time, (b) in space, *i.e.*, localization in the whole, and (c) of determinate qualities coordinated both in space and in time.

4. There is a final term in each of the branches, which is followed by histogenesis and definitive functional differentiation, though certain terms (or branches) remain open throughout life. We may thus distinguish closed and open terms throughout the life history with reference to embryonic segregation.

Comments are in order upon the above characterizations, for they concern I believe the most vital features of embryological development.

The dichotomous and discontinuous character of the process is well illustrated by cell-lineage, and especially by Wilson's and Conklin's masterly analyses of this determinate form of cleavage. Cell-lineage shows us daughter cells with such different prospective potencies as ectoderm and entoderm, or anterior and posterior quadrants of the embryo; and the experimental analysis shows us that these prospective potencies are also genetic restrictions. The origin of these potencies in a single cell-division is dichotomous, and the discontinuity appears in their sharply differentiated genetic restrictions. This principle runs through all varieties of embryonic development, even if under different forms, as a great variety of experiments shows (*cf.* Spemann and Hoadley).

The space relationship in development, or the localization problem, exhibits itself with reference to the entire organism of which each primordium is a part; all primordia arise in definite areas, and their realization may involve a secondary more precise localization. For instance, the potency of the lens of the eye in amphibians lies in the embryonic epidermis at a definite stage of development, but the definitive localization within this area is not fixed until adjustment is established with the optic vesicle. The possibility of normal development depends among other things upon flexible, but finally precise, adjustments of localization of specific parts everywhere in the embryo. The situation implies correlations and inductions dependent upon extraorganic and intraorganic factors, and such relations have been demonstrated over and over again in experimental embryology. Child's gradient factors and principle of dominance are striking examples of analysis of factors of localization in the early embryo. The prob-

lems of localization, considered as such, would appear to be susceptible to physiological analysis.

Before examining the time process in development we must first consider the principle of embryonic induction of which we are hearing so much, and ask what it may be expected to explain and what it may not be expected to explain in the physiology of development. Environmental relations are very evident in many cases of embryonic localization, and it is natural to look for them in all cases. The origin of the lens of the eye as an induction in the embryonic epidermis exerted by the optic vesicle is a well established example. The experiments show that at this stage the epidermis of the head region, at least, possesses two potencies, however they may have arisen, and only two, *viz.*, to form lens cells, or epidermal cells which have lost the power of lens formation; which shall be realized in the case of any cell or group of cells depends on induction, in this case by the optic vesicle. Note that this potency exists only for a relatively brief period of time; once accomplished, it can not be repeated. In Driesch's terms the lens is positively restricted, the epidermis negatively restricted. Or take as another example the beautiful experiments of Spemann and his students. They show, for instance, that the ectoderm of the *gastrula* of Triton has two potencies and only two so long as it remains *in situ*, *viz.*, to form neural epithelium or general epidermis, each thereafter positively and negatively restricted. The experiments that show, that in this case the decision rests with the archenteron, is one of the biological triumphs of our time.

Examples might be multiplied, but all would serve to show that induction produces only the phenotype² for which ontogenetic segregation has prepared the way; that the specificity of the response lies in the stage and locus, not in the inducing agent; and that the possibilities for any induction are only two in number.

This simple situation is often confused by two prevalent ideas—the one that potencies may be more

²W. Johannsen, who introduced the word "phenotype," applies it not only to statistically determined modes in a population, but also uses it to designate in their entirety the personal qualities of any individual as given. (*Elemente der exakten Erblichkeitslehre*, dritte Aufl. 1926, pp. 162–163.) It can hardly be regarded as an extension of Johannsen's definition to apply it to any stage of the organism as the purely descriptive condition of all its parts. The usefulness of this term in embryology is to abstract from a given stage all implication of future potency. "Phenotypical realization," therefore, explains itself as including the immediate circumstances that condition a given embryonic phenotype.

than two at one time and place; the other that the inducing agent may have determining value, *i.e.*, may be a so-called formative stimulus.

The first confusion arises from taking remote potencies into simultaneous consideration with immediate ones. Thus the embryonic ectoderm of a mammal may be said to have the potencies of nervous system, lens, hairs, glands and epidermis. But these potencies do not exist simultaneously; when the ectoderm has the potency of forming nervous system, it does not have the potency of forming lens or any primordium of later origin. After the nervous system is segregated the ectoderm has lost the potency of repeating the process, and has acquired two new potencies and so on to the end of the chapter. Only two potencies at a time, and these realizable by induction. The same principle holds throughout the life history.

Secondly, there is no such thing as a formative stimulus in embryonic development. Embryonic induction is no different in principle from induction of muscular contraction, or of nervous conduction or of glandular secretion. The nature of the response is conditioned by the immediate potencies of the responding system, and the nature of the stimulus is secondary. We are much more familiar with the inductions of differentiated tissues, and are unaccustomed relatively to the idea that the ectoderm of the gastrula for instance is giving its specific form of reaction when it forms a medullary plate; or the lens epidermis when it forms lens. Both because the idea is relatively unfamiliar, and also because the inducing agencies have been but little studied up to the present, we are apt to conclude that a new principle is involved, and that environment plays a different rôle in embryonic development from what it does in adult life. But such a conclusion introduces endless confusion, and has not, in an experimental way, clarified any situation.

It is the non-repetitive character of the responses of embryonic segregation that really sets them apart from functional responses, such as the contraction of a muscle cell, for instance, which are repetitive. But this in itself does not assign a different rôle to environment in the two categories, as some have assumed.

There are theoretical viewpoints concerning development that neglect the processes of induction, and visualize only the more or less hypothetical processes of chemo-differentiation that run parallel with the ontogenetic current. Thus, visible substances in the unsegmented egg have been termed formative stuffs, on the assumption that they are the agencies of subsequent differentiations. When it was shown that visible substances of such kinds are not essentials of the specific local differentiations in which they nor-

mally occur, by the occurrence of properly localized differentiation, in spite of their displacement by centrifugal force, the theory reverted to invisible substances retaining their typical localization. Criticism must then revert to the *type* of explanation, against which it must be said that if there are as many kinds of purely hypothetical formative stuffs, as there are formations (*cf.* Goldschmidt), and so long as their physiological action is postulated only by their name, the view becomes indistinguishable from the determinant theory of Weismann. The theory does not become physiological by naming such hypothetical substances hormones (Goldschmidt), for these then become endowed with the same mysterious properties. Again such an ultra-simplified conception as the "autocatalytic theory of development," also primarily "chemical"—if any one does indeed hold such a theory, as is rumored—does no more than visualize a single aspect of growth processes in the organism to the exclusion of the really essential aspects of development.

It is a mere truism that the energy of development is furnished by metabolism. I do not, however, regard the rôle of metabolism in development as essentially different in any stage from what it is in the adult. We know, in fact, relatively little concerning embryonic metabolism save its variations in rate in the time sequence of ontogeny measured by growth, or other criteria. We know also (or at least infer), by various rough indications, that metabolism varies qualitatively according to stage and locus. These differences, however, can not be regarded in general as determining factors of the course of development. They are primarily chemical indicators of differentiations already accomplished. But, once accomplished, they become part of the intraorganic environment and function as such in development, whether as hormones or in numerous other ways.

So much concerning ontogenetic segregation. The other aspect of differentiation realization of potencies—(histogenesis and functional differentiation)—follows the final stages or terms of segregation in the various branches of the ontogenetic tree when potencies are limited to a single one. Such terms of the ontogenetic process may, therefore, be called *closed terms*. They may usually achieve their realization, to a considerable extent at least, in isolation from the remainder of the organism. Hence they are said to develop by self-differentiation. Such final terms are scattered all along the life history from a very early stage indeed. This situation, which is at least a very common one, differs from that in earlier stages of embryonic segregation, in which there are always two possibilities open to induction.

It is vastly important, however, that in the more

labile types of animals, at least, such as those of our own phylum, certain cells retain a double potency throughout life. These are the freedom-giving *open terms* of the ontogenetic process. A very beautiful example of this is found in the feather germs of sexually dimorphic birds, which according to alternative hormone conditions may blossom out as male or female feathers throughout life. The nervous system is also such an open system *par excellence*.

Let us return to the time aspect of development which concerns the sequential order of embryonic segregation. It is measured not by time units, but by events. At each stage of the ontogenetic process specific forms of reaction, whether of the whole or of its segregated parts, occur. The order is quite invariable, at least within any given system, and, so far, this order has not been experimentally inverted in any of its parts.

On the physiological side there is no adequate theory of the sequential order of ontogenetic segregation. At the most we can speak only vaguely, and merely by analogy, of chain-reactions in a complex system; or if we take biological categories, and phrase the problem in terms of senescence for instance, whether we adopt a nucleo-cytoplasmic relation theory, or a theory of accumulation of inactive products (or whatever else may be possible) there is nothing to correspond in specific character, or in manifoldness, even in general principle, to the definitely ordered sequence of developmental events.

Granted that we may resolve development into a series of inductions that come to be better and better known, more and more fully analyzed, and a series of internally determined events or processes with only one typical outcome, is it not still entirely unknown why these inductions and events should be so typically various and discontinuous at different times in the life history? Granted that we may learn indefinitely more about specific constructive metabolism, and about growth processes of the entire organism or of its parts, do not the same considerations apply to these processes so far as they are various at different stages? All current theories in the physiology of development presuppose in fact a basic process of embryonic segregation in due sequence in time.

This scanty survey of a few triumphs of physiology of development, with its large lump of pessimism at the end, illustrates the impossibility of a single theory of development. Ontogeny is a moving equilibrium, which involves all fundamental physiological process at each stage, and it can no more be envisaged under a single formula than can the conception of life itself. Genetics on the other hand is subsumed under a single formula.

II. RELATION OF GENETICS TO THE PHYSIOLOGY OF DEVELOPMENT

Now in which of these general situations of embryonic development does the theory of genetics play a rôle? or offer substantial assistance? As a matter of fact does any experimental embryologist use the conceptions of genetics in his work? If not, is it because the principles of genetics serve some entirely different situation? Let us proceed systematically.

Does genetics help in the conception of the germ? I think we may say that it certainly does, if the germ indeed contains "hundreds of thousands" of "different kinds of packets of chemicals" "massed in a haphazard way but arranged in a definite manner." Certainly no embryologist would have discovered that by his own unaided efforts. Admitting for the sake of the argument the essential validity of this addition to our actual cytological knowledge, does it aid in the experimental attack (as working hypothesis or otherwise) on the problems of the physiology of development? To answer this question we must examine each of the other concepts of the physiology of development.

Does it aid in the concept of individuation? I shall answer this question briefly because I think we shall all agree that it does not; that on the contrary it tends to confuse it. What principle is adequate to hold such a swarm within the bounds of individual being, or to direct their work! Individuation is clearly an environmental relationship, mediated through the cytoplasm, not through the nucleus.

With reference to the processes of embryonic segregation, genetics is to a certain extent the victim of its own rigor. It is apparently not only sound, but apparently almost universally accepted genetic doctrine to-day that each cell receives the entire complex of genes. It would, therefore, appear to be self-contradictory to attempt to explain embryonic segregation by behavior of the genes which are *ex hyp.* the same in every cell.

Goldschmidt has, however, attempted to do this. He has in fact postulated two mechanisms, which seem to be independent of one another in a logical sense, and which he has not clearly interrelated. The first is a theory of quantitative regulation of the genes, according to which each gene of the thousands concerned enters into activity at a rate, and therefore at a time, proportional to a precisely regulated initial quantity. This of course presupposes an underlying mechanism adequate to almost ultraphysically precise regulation in the germ, for which no model can be suggested; at the most it shifts the difficulty one step farther back. The second is the lock-and-key theory of substratum (cytoplasm) and gene, *viz.*, that each gene

reacts only with a specific substratum, from which it follows as corollary that specific substrata are always present at the appropriate time and place. This seems to me to postulate the process which it is invoked to explain, *viz.*, ontogenetic segregation and the time relationships of specific events. It is also inconsistent with his postulates of sex-genes which control, and therefore must react with, the greatest diversity of chemical processes in all parts of the organism; and of other genes similarly controlling diverse characteristics. Both conceptions postulate specific genes for all differentiating characters of each stage, and latency for all genes except those postulated for the specific event. In its essence the theory is deterministic, and not consonant either with sound physiology or sound genetics.

Apart from these conceptions I do not know of any sustained attempt to apply the modern theory of the gene to the problem of embryonic segregation. As the matter stands, this is one of the most serious limitations of the theory of the gene considered as a theory of the organism. We should of course be careful to avoid the implication that in its future development the theory of the gene may not be able to advance into this unconquered territory. But I do not see any expectation that this will be possible, even in principle, so long as the theory of the integrity of the entire gene system in all cells is maintained. If this is a necessary part of the gene theory, the phenomena of embryonic segregation must, I think, lie beyond the range of genetics.

Geneticists have, however, brilliantly demonstrated that genes are concerned in phenotypical realization at different stages of the life history, and it is therefore a reasonable postulate that this is true of all phenotypic realization. We come here, therefore, to the specific problems in which genetics and physiology of development really meet. There can be no reasonable doubt that any definable character whether of a morphological, physiological, or psychological (behavioristic) nature may be treated by methods of genetics (*i.e.*, considered statistically with reference to modes of recurrence in successive generations), as well as by methods of physiology. Thus in addition to the numerous morphological characters, for which they are already demonstrated, genes may also be posited of all physiological and behavioristic characters that can be shown to mendelize. Similarly there are genes for characters of the ovum and of the larva; and, by inference, there can be a complete genetics with corresponding genes for each stage of development.

The genetic problem thus differs from the embryological problem, inasmuch as any definable character at any time in the life history may be treated as

final, according to the methods of genetics, and its genes presumably could be located on the chromosome map.

What then in the process of phenotypical realization would be the physiological status of the gene? Apart from analogical points of view in which for instance the action of genes is compared to that of enzymes, the approach to this problem may be made by two roads, (1) through experimental modifications of the environment of known genotypes and comparison of resulting phenotypes with control cultures; and (2) through comparison of the action of varieties of gene combinations on known characters of the organism.

Morgan, for instance, cites a mutant of *Drosophila*, studied by Mrs. Richards, differing from the normal by but a single gene, which when raised in an ice-chest has one or two, or even all, of its legs doubled, but if reared at room temperature none; "at room temperature no flies result with more than six good legs." In 1911 Baur cited several analogous cases in his text-book of heredity, and pointed out that in heredity in general what is inherited is not the character as such, but only a definite form of reaction to environment.

If this is a true generalization, the underlying postulate is again the ontogenetic substratum, which this form of analysis of the action of genes does not attempt to elucidate. What is won for physiology of development by such examples is a heightened sense of the dependence of physiological reaction upon the genetic foundations of the reacting system, but not additional insight into the developmental problem.³

The method of comparing the action of varieties of gene combinations upon known characters of the organism under constant or varied conditions of the environments is the oldest method of analyzing the mode of action of genes in development, and it appears to me to be the most promising method at the present time. The study of the phenomena of multiple allelomorphism, the observed results of gene deficiency resulting from loss of a piece or all of a chromosome, and the results following from triploidy or greater additions, whether of one chromosome or the entire chromosome complex, especially as presented by the Columbia University School of Geneticists, appear to me to throw much light on the problems of the physiology of development of the final

³ Another form of environmental problem in genetics is found in attempts to modify the genes in the germ-cells directly, the indicator being the phenotypes resulting from such treated germ-cells compared with controls. This is, however, a problem in pure genetics and need not interest us farther.

terms of the underlying ontogenetic segregations. There is no time to rehearse these splendid additions to our biological knowledge, and I shall not attempt to appraise the theory of genic balance which appears so clearly to emerge.

More than this should, however, be said: one can not imagine at the present time any other experimental technique that would even remotely approach in delicacy of treatment to the superlative refinement of modifications of the gene system that the genetic method renders possible. It is an indispensable method for phenotypical analysis whether in a genetic or a physiological sense.

Its scope is, however, limited in two ways: in the first place at whatever stage of development a character may be selected for examination, and whatever the nature of the character, it must always, so far as genetic method is concerned, be treated as a finality. It has no past, except the genes postulated as a result of their appearance in previous generations—and no future. The genetic method reveals, *alpha*, the gene, and *omega*, the final term. The second limitation of genetics, considered as an approach to phenotypic realization is, of course, the failure of any direct physiological analysis of the postulated genes. This need not be a permanent limitation, but it seems to me that *at the present time* it is a definite limitation.

I suppose that geneticists would agree that there is a clear possibility that the future development of the subject may result in a considerable reduction of the number of genes necessary to be postulated. Morgan's conclusions that a single gene may be concerned in a multiplicity of characters, both in time and in space, and that a multiplicity of genes may be concerned in each character are indeed steps towards simplification. But, granted the extreme simplification, genetics could at the most explain the special quality of characters associated with particular genes or combinations of genes at given stages and loci of development, but never why the same genes are associated with different characters at different stages and in different loci.

The present postulate of genetics is that the genes are always the same in a given individual, in whatever place, at whatever time, within the life history of the individual, except for the occurrence of mutations or abnormal disjunctions, to which the same principles then apply. The essential problem of development is precisely that differentiation in relation to space and time within the life-history of the individual which genetics appears implicitly to ignore.

The progress of genetics and of physiology of development can only result in a sharper definition of the two fields, and any expectation of their reunion (in a Weismannian sense) is in my opinion

doomed to disappointment. Those who desire to make genetics the basis of physiology of development will have to explain how an unchanging complex can direct the course of an ordered developmental stream.

There remains to be mentioned the oft-noted phenotypic identity of environmental varieties of given characters and of genic modifications of the same characters. One need only call to mind the bar-eye series in *Drosophila* or Johannsen's pure lines of beans. Many similar cases exist in the phenomena of sex-differentiation, which appear to be conditioned by genes in insects, and hormones in birds, but which nevertheless exhibit comparable diversities and similar functions in the life history.⁴ How are we to understand this except on the assumption that both act on a given ontogenetic process?

Physiology of development and genetics both teach us the same lesson, *viz.*, that at the foundation of every phenotypic event there is an unanalyzed ontogenetic process, which expresses itself in time by qualitatively different types of reaction whether to the environment, or to the gene, or to both combined. This is the unrecognized presupposition of all studies in either field. I must emphasize that there is nothing in the current principles of genetics or of physiology that gives us the least clue to the nature of embryonic segregation in its time sequence, which constitutes the ontogenetic process in its strictest meaning.

In this conclusion I find myself in agreement with Bateson, who, in his last publication, says:

"Cytology is providing some knowledge, however scanty, of the material composition of the cell, but of the nature of the control by which a series of orderly differentiations is governed we have no suggestion" (p. 234), and again

"Throughout all this work, with ever-increasing certainty, the conviction has grown that the problem of heredity and variation is intimately connected with that of somatic differentiation, and that in an analysis of the interrelations of these two manifestations of cellular diversity lies the best prospect of

⁴ The gene may of course be regarded as having secondary modes of action, to the extent that it is a factor in the realization of the intraorganic environment in all of its aspects. If, for instance, we make the assumption that in birds the genic constitution determines the nature of the sex-hormones produced by the individual, then the known action of the sex-hormones on head-furnishings, plumage, spurs, reproductive tract, growth and behavior may be regarded in a certain sense as secondary modes of action of the genes. But no example would serve better to show that both primary and secondary effects are functions of the life history as to their incidence.

success. Pending that analysis, the chromosome theory, though providing much that is certainly true and of immense value, has fallen short of the essential discovery" (p. 235).

However profound our present ignorance of the method of ontogenetic segregation may be we are nevertheless bound to conceptions of strict determinism concerning the phenomena involved. The phenomena of genetics and of embryonic induction exhibit strict experimental determinism, which would be impossible if the ontogenetic processes on which both depend were not deterministic also. Nothing that has been said in this essay should be interpreted in any contrary sense. The processes of embryonic segregation are open to observation and experiment equally with the processes of genetics and of embryonic induction. My contention is merely that we have no present working hypothesis effective in this most fundamental aspect of the life history.

The dilemma at which we have arrived appears to be irresolvable at present. It is the apparent duality of the life history as exhibited in the associated phenomena of genetics and ontogeny: on the one hand the genes which remain the same throughout the life history, on the other hand the ontogenetic process which never stands still from germ to old age. It is no confession of weakness that we should admit our inability to form a picture of life-processes that have taken longer to evolve than the mobile crust of the earth itself. Instead of distorting our workable conceptions to include that which they can in no wise compass, may it not be profitable, for a while, to admit that more lies without than within our confines of mechanism and statistics? If physics and chemistry will not be complete until they have explained the action of their units in living matter, that is after all their affair. Certain it is that physics and chemistry have no place among their categories for the ontogenetic process and *a fortiori* for the phylogenetic. Why not surrender ourselves, in consideration of these problems, to the current of more naïve biological categories?

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NEWSPAPER REPORTS ON THE MEETINGS

It is commonly remarked that the general public, throughout the reading world, is increasingly interested in the progress of science. Practical achievements, such as inventions and directly useful discoveries, have long interested people not specially trained or engaged in scientific work, for such achievements affect the daily routine of ordinary life, but the last decade has witnessed a remarkable development of public interest in the more easily discussed aspects of scientific research and scientific progress. Intelligent people now wish to read about advances in knowledge that do not apply directly to their daily activities, and this desire appears to be rapidly spreading and becoming more intense. The technological or applied aspects of scientific progress remain, of course, the subjects of most popular discussion, and superficially descriptive science, including mere observational facts without discussion of relationships, naturally constitutes a large part of what is prepared for popular scientific reading.

All three of these different aspects of scientific knowledge—observational facts, applications that economize time or simply make life more pleasant or more gainful in the financial way, and theoretical or philosophical advances in interpretation or appreciation of relationships between objects of knowledge—are receiving much more popular attention than ever before. In this and many other countries writers for newspapers and magazines and for radio talks, and also those who have charge of museums, are increasingly occupied with the popular presentation of science material. Many writers are primarily so engaged; this sort of work is becoming an important branch of the teaching profession in a broad sense. The demand increases more rapidly than the supply, which may be taken to indicate that the reading public really desires all kinds of science material presented in simple fashion.

For many years the American Association for the Advancement of Science has tried to facilitate the popular reporting of its meetings, but it is only recently that its efforts have been met half-way by the