MODERN THEORIES OF DEVELOPMENT

AN INTRODUCTION TO THEORETICAL BIOLOGY

By

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PREFACE

THE present work is identical in subject-matter with a book which has already been published in German under the title *Kritische Theorie der Formbildung*. It now appears, however, almost as a new book, because, in the first place, the treatment of the material has been adapted to the interests of the English biological public, secondly, the results of investigations published since the completion of the German edition have been included, and thirdly, as complete a picture as possible of the standpoint of the author is here presented in a concise form. For a fuller treatment of problems which are here dealt with briefly the reader may be referred to the German book which appeared in the well-known series of 'Abhandlungen zur theoretischen Biologie'.

It will be advisable to state the aim of the book in a few words. The book deals with *theoretical* embryology, i.e. it is not a summary of investigations on the physiology of development. Experimental embryology stands to-day at the focus of interest. This is evident from the fact that even in the last few years nearly a dozen books have appeared which summarize recent work in this branch of biology. We have the larger works of Morgan (1927), Korschelt (1927), Dürken (1928), Schleip (1929), Przibram (1929), smaller books by Brachet (1927), and Schleip (1926), and recently the excellent book by P. Weiss (1930). The reader is especially referred to the admirable little book by Mr. de Beer, *An Introduction to Experimental Embryology*, published by the Clarendon Press, which will serve as a companion volume to the present work. There is thus no lack of monographs of experimental embryology, and no occasion to add to their number. In consequence of its special standpoint the arrangement of the material in the present work departs considerably from that in books on experimental embryology. The simplest arrangement for a theoretical embryology seems to be one which describes and evaluates the principal current theories.

And although a description of experimental results is avoided by reference to the existing monographs, yet—if our book is not merely to appeal to a narrow circle of specialists—the most important of these results must be described. Consequently those results which are most essential from the theoretical standpoint must be described in order that the reader who is not familiar with this branch of biology will be in a position to follow the theoretical discussion. If he has also read the little book by Mr. de Beer above mentioned he need find no difficulty in understanding what follows.

The fact that the German book has enjoyed a very friendly reception—of which the desire for an English edition is evidence—seems to suggest that our undertaking in supplementing the usual works on experimental embryology corresponds to a real need. For this reason we have not thought it necessary to alter its general aim and standpoint, in spite of a good deal of rewriting in detail.

But beyond giving an account of the present state of theoretical embryology, the book has yet a second object, namely, to establish and describe the 'organismic' point of view which the author supports. For this reason Part II, which deals with the embryological theories, is preceded by a more general Introductory Part. The presence of this part appears to be a necessary presupposition of the second; for the clarification of the general theoretical foundations of biology must precede the building up of theories in the special branches. Epistemological and logical problems have, as far as possible, been avoided; the attempt being made to give a formulation of the views presented which is independent of particular philosophical points of view. On the other hand, theoretical embryology forms the application and the test of the views obtained in the more general part. From considerations of space, this introduction must be short, and what is here offered is an extract from a work by the author entitled *Theoretical Biology*, recently published, with the assistance of the Österreichisch-Deutsche Wissenschaftshilfe.

In view of the increasing growth of 'organismic' views, we may perhaps point out that the German book appeared in 1928, and thus before Dr. E. S. Russell's *The Interpretation of Development and Heredity*, and about simultaneously with the excellent account by W. E. Ritter and E. W. Bailey, *The Organismal Conception*. We do not doubt that in the striking parallelism which exists between Russell's book and the author's *Kritische Theorie der Formbildung*, the famous 'Law of the Series' exhibits itself; or, better, this correspondence is a sign that this way of thinking is 'in the air', and is forcing itself upon the attention of independent authors.

In connexion with this publication we have to thank the Österreichisch-Deutsche Wissenschaftshilfe which, in spite of the difficult conditions in Austria and Germany, enabled the author to devote himself to the above-mentioned book, and so at the same time promoted the present work. We have also to express our warmest thanks to Dr. J. H. Woodger, who not only undertook the English translation, but has whole-heartedly placed his understanding of the questions here discussed at our disposal, and given us many valuable suggestions, references, and criticisms. We have further to thank Professor Schaxel, the editor, and Dr. Thost, the publisher, of the 'Abhandlungen zur theoretischen Biologie' who have kindly permitted the use of the German work for the present English publication. Our thanks are due, finally, to the Clarendon Press for their readiness to publish this English edition.

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PRINCIPLES OF THEORETICAL BIOLOGY

I

BIOLOGICAL METHODOLOGY

1. The Crisis in Biology

In the natural science of the present day we are witnessing a strange and disturbing spectacle. It is as though the grand sweep of its historical development, stretching from its beginnings in early Greek times up to the turn of the twentieth century, had to-day received a check. The foundations of our thought and investigation, hitherto regarded as assured, have collapsed. In their place new ways of thought, often paradoxical and apparently contradictory to the plain man, have appeared in bewildering variety, and among these still hotly contested ideas it is not yet possible to discover those which are destined to win an enduring place in our view of the world. Some years ago this state of affairs could be regarded as the break-down of Western science. But the remarkable developments which have recently been coming to fruition in physics suggest a totally different interpretation: we can see in the present state the raw and as yet unsettled early phase of a new step in scientific thought—the fruitful chaos out of which a new cosmos, a new system of thought will develop, albeit a view which will differ in essential points from that which we owe to Galileo, Kepler, and Newton.

In this place we need not describe the powerful revolutions which have occurred in mathematics and logic through the non-Euclidian geometries and the theory of aggregates, in physics through the Relativity and Quantum theories, and in psychology through the *Gestalttheorie*. The mere mention of these transformations suffices to indicate the place in the whole

contemporary picture of the critical condition which we also find in the biology of the present day. When we speak of a crisis in biology it will be understood that we are not in any way saying anything prejudicial to its value. These general transformations in modern science signify rather the most powerful forward development which it has experienced since its foundation at the Renaissance. But it is at the same time essential that this state of affairs should be clearly reviewed, and that no attempt should be made to conceal it by entrenching ourselves behind theories which are now no longer tenable, or by shutting our eyes to the difficulties of our science.

'Modern biology is not in a position to display the results of systematic research in a system of concepts, or to represent the orderly behaviour which is common to its objects in a general theory. The place of theoretical science is taken rather by a heterogeneous multitude of facts, problems, views and interpretations. . . . Such a state of affairs cannot be improved upon by the piling up of new facts and opinions upon the old ones, but only by a fundamental re-organization after a process of careful sifting of those we already possess.'

These assertions of Schaxel (1922, pp. 1 and 298) admirably express the present position of biology and its primary task. We find in biology a bitter dispute between spheres of investigation, opinions, and principles. In their methods and fundamental concepts the various branches of biology are extraordinarily diverse and disconnected, and occasionally even in direct opposition to one another. The physico-chemical investigation of the vital process has given us, from the time of Harvey's fundamental discovery up to the most modern results of colloid-, ion-, and enzyme-chemistry, an uninterrupted chain of important discoveries—and yet there are good grounds for the belief that they still scarcely touch the essential problems of biology. The physiology of development and of behaviour work with systems of ideas which, at least at present, show only superficial relations to physics and chemistry. In genetics we have the most developed branch of biology, the only region in which we have

an insight into the real biological laws, but we are still far from possessing a satisfactory theory of phylogenetic development, the fundamental idea of which is the most comprehensive that has so far appeared in the biological sphere. Attempts to master biology philosophically and theoretically are common enough outside the science, and stand in emphatic contradiction to its mechanistic point of view.

Whilst the majority of investigators find only physical and chemical processes in the object of their study, others find problematic metaphysical entities at the bottom of the vital phenomena. Between physico-chemistry and metaphysics biology pursues a strange and crooked path. Because there is no generally adopted theory of the organism, a thousand different individual opinions, personally coloured in varying degrees, confront one another, among which a given worker will choose according to his personal taste and the requirements of his special sphere.

It is not our intention to describe in detail in this place the numerous controversies underlying the great biological theories of the last century, such as Mechanism, Vitalism, Selection Theory, Lamarckism, and Theory of Descent.[1] Under the influence of these theories, doctrines once belonging to the 'assured acquisitions' of biology were established but have since been as much shaken as the seemingly 'matter of course' ideas of space and time, of mass and causality, in physics. The above remarks will perhaps suffice to justify us in some measure in speaking of a state of crisis in biology.

But how can we speak of a crisis in this science when our knowledge of vital processes is being increased every year by a multitude of publications? It might be said that all such general conceptions are more or less fragile: let them go. We need not waste regrets over philosophical or semi-philosophical constructions. True science consists only in the knowledge of

[1] A review of these controversies is given in our *Kritische Theorie der Formbildung*, 1928.

facts, and even the bitterest opponent of science cannot deny that this grows daily or even hourly.

Many investigators will perhaps adopt this attitude towards the state of uncertainty regarding fundamental doctrines in biology to which we have alluded. The empirical investigator is apt to look down upon 'theory' with more or less disrespect, and therefore may not feel much distress at the uncertainty of the great theories.

But the empiricist is apt to forget two things. He forgets, in the first place, that a collection of facts, be it never so large, no more makes a science than a heap of bricks makes a house. In his scathing *Schöpfungsliedern* Heine makes God say: 'Allein der Plan, die Überlegung, da zeigt sich's, wer ein Meister ist.' Only if the multiplicity of facts is ordered, brought into a system, subordinated to great laws and principles, only then does the heap of data become a science. Secondly, he forgets that no empirical science is even possible save on a basis of theoretical assumptions. Schaxel remarks very appropriately that 'The empiricist moves hesitatingly between different attitudes. He wants to seem free, and yet is dependent upon ideas adopted at second hand with insufficient understanding.' (1922, p. 5.) Thus the procedure of the biology of yesterday has failed: on the one hand 'theory' has been looked down upon, and on the other, fact and theory have frequently been confused in an arbitrary and subjective manner.

A resolution of the present critical state of biology can thus only be sought in a theoretical clarification. Theoretical thinking must be recognized as a necessary ingredient of science. In biology until to-day such recognition has been rare, but in physics—which is taken as its model—it has always been a generally adopted demand. So much for criticism. Our critique will consist rather of construction, since we shall try to show a way to a new organization of biology which, we believe, will permit the present difficulties and contradictions—or at least many of them—to be overcome.

2. The Tasks of Theoretical Biology

If biology is to emerge from the crisis of its foundations and the accumulation of unrelated facts, as a critically purified exact science, the attainment of an assured theoretical biology will be necessary. But the term 'theoretical biology' has two meanings denoting two different, but not completely separable, spheres of knowledge.

Theoretical biology in the *first sense* is the logic and methodology of the science of organisms. It establishes the foundations of biological knowledge and thus forms a branch of general logic and epistemology, whilst it may also be important for biological investigation. Problems requiring logical investigation, e.g. that of teleology, of the relation between fact and theory, of the significance of experiment in biology, &c., may be of the greatest importance for the whole direction of research in biology. Critical methodological clarification may constitute an active protection against the fallacies of hurried hypotheses.

But theoretical biology in the *second sense* signifies a branch of natural science which is related to descriptive and experimental biology in just the same way in which theoretical physics is related to experimental physics. That is the task of a theory of the various single branches of the vital phenomena, of development, metabolism, behaviour, reproduction, inheritance, and so on, and, in the last resort, of a 'theory of life', in just the same sense in which there is a 'theory of heat', a 'theory of light', &c.

Since what has hitherto been called 'theoretical biology' has consisted in great part of philosophical speculation, and since theoretical biology in the 'first sense' consists of logical investigations, something must be said in clarification of the relations between theoretical biology and philosophy. As we have already mentioned, theoretical biology ('second sense') is just as much a branch of natural science as theoretical physics, i.e. it deals exclusively with the exact theoretical systematization of facts,

and has no place for speculations. This point requires emphasis because voices are often raised in biology in rejection of theoretical biology as 'merely philosophical' or 'speculative' and superfluous. Such objections are entirely justified against many 'theoretical biologies', especially those of a vitalistic character, which, however, are to a great extent 'philosophical' and speculative and do not constitute scientifically applicable theorizing. But such objections are totally unjustified against theoretical biology conceived as a legitimate branch of natural science in the manner described above.

Naturally, it is not suggested that theoretical biology in the first and second senses, logic of biology and theory of life, should be regarded as totally unrelated to one another. Such a view would rather misrepresent the nature of theoretical science. Just as it is scarcely possible, in relation to the fundamental questions concerning space and time, action, deterministic or statistical law, &c., to draw a sharp line between physical theory and theory of knowledge, so will it also be the case in biology, in which the most general concepts (first of all that of 'organism') on the one hand require logical clarification, and, on the other, form the foundation of biological explanations and theories. Such general scientific assumptions must be clarified in close connexion both with logical and epistemological considerations and with the empirical study of the relevant phenomena. It need hardly be mentioned that, like the fundamental questions of physics, those of biology, such as Vitalism and Evolution, touch upon philosophical and cosmological problems of the most important kind.

If we are to overcome the state of crisis in biology which we have discussed above, we require theoretical biology in both the 'first' and in the 'second' senses. We must first of all make clear to ourselves the methodological principles which must be applied in the different branches of the system of biological sciences. In doing this we shall be carrying out the task of theoretical biology in the 'first sense' (Chapter I, 3–4). Then

we must endeavour to reach a sound basis for a theory of life (Chapter II); and finally (in the main part of this book) we shall try to carry through the proposed programme of theoretical biology in a particularly suitable example, the phenomena of development. We shall endeavour to sift the current theories in this sphere and bring into application the theory we have traced in the general considerations.

3. The System of Biology

The attempt to arrange the various spheres of biology in a general system can be carried out in the following way.[1] We distinguish three stages in the system of biology.

1. Every science begins with an exact description and classification of its objects. Hence at the beginning of biology stands *systematics*, the aim of which is to give a catalogue, as complete and exact as possible, of all kinds of animals and plants. Related to this is the exact description of the different living forms, or *anatomy* (including microscopical anatomy). *Comparative anatomy* and *morphology* result from the comparison of the structure of different organisms. Finally, in addition to classification in a system, in addition to simple and comparative description of living forms, the description of their distribution in space and time is necessary. In this way we have *bio-geography* and *palaeontology*. These two sciences are—to use Meyer's expression—not logically pure, but logically complex, since they involve oecological and phylogenetic problems, in addition to simple description of distribution in space and time.

2 *a*. After the objects of biology have thus been described and classified there remains the demand for a description of organic *processes*. It is clear that every vital process must first be *causally* described, and, if possible, by the method of causal explanation employed in the more advanced sciences of physics and chemistry. This is the method of investigation followed in

[1] For other systems of biology see the discussions of Tschulok (1910), Meyer (1926), and Bertalanffy (1928, chap. ii).

physiology. About the conceptual methods of the physico-chemical investigation of life little need be said. It is clear that 'the methods of the physiological chemist are peculiar only in very few cases. They are almost exclusively taken from the neighbouring sciences of chemistry and physics' (Abderhalden). It is also widely believed that since biology in general coincides with the physical and chemical investigations of vital processes there is no necessity for peculiarly biological points of view, or for a special theoretical biology.

2 *b*. We believe that this view is not correct, since there are vital phenomena for the description of which other points of view are required. The first of these special biological points of view is the *organismic*.[1] We can undoubtedly describe the organism and its processes physico-chemically *in principle*, although we may still be far removed from reaching such a goal. But as *vital* processes they are not characterized in this way at all, since what is essential in the organism—as will be shown later (cf. p. 33 f.)—is that the particular physico-chemical processes are organized in it in quite a peculiar manner. We need not delay by entering into details in this place, and the reader may be referred to the discussions of Ungerer (1919, 1922, 1930), Rignano (1926, 1930–1), Sapper (1928), and Bertalanffy (1929). Whether we consider nutrition, voluntary and instinctive behaviour, development, the harmonious functioning of the organism under normal conditions, or its regulative functioning in cases of disturbances of the normal, we find that practically all vital processes are so organized that they are directed to the maintenance, production, or restoration of the wholeness of the organism. On that account the physico-chemical description of the vital processes does not exhaust them. They must also be considered from the standpoint of

[1] This word replaces the old term 'teleological'. It will be seen in what follows that 'teleology' as we conceive it has nothing to do with any psychological or vitalistic assumptions which were often confused with this point of view.

their significance for the maintenance of the organism. And we see that in fact—in spite of the postulate that science must only proceed physico-chemically—biology has at all times applied organismic ideas, and must apply them, and that whole spheres of investigation are concerned with the establishment of the significance of the organs and of organic processes for the whole.

The notion of 'organ', of visual, auditory, or sexual organ, already involves the notion that this is a 'tool' for something. As soon as we say that an animal has legs 'in order to' run, the giraffe a long neck 'because' it browses on the leaves—modes of expression which cannot be avoided in biology—we have already introduced a point of view which characterizes the significance of the organ for the maintenance of the organism—an organismic point of view. This point of view cannot be avoided so long as we cannot exclude the notion of an organ as 'serving' some definite purpose. Similarly, the concept of 'function' has an organismic sense: it only has significance within an organism, to the maintenance of which the function is exerted. We thus find *physiological anatomy* to be the first branch of biology which investigates the organs in connexion with their functions, in their so-called 'purposefulness' for the maintenance of the organism. Physiological anatomy furnishes a continual demonstration of the necessity of an organismic point of view in biology. As a second such branch we have *oecology*, which investigates the organic forms and functions as adaptations to their inorganic and organic environment. But since such concepts as disease, norm, disturbance, &c., are only significant in reference to the maintenance of an organism, *pathology* also belongs to the sphere of organismic branches of biology, but it is a logically complex discipline, since simple description and physiology have an important place in it.

For us there is no doubt that an organismic point of view of this kind is unavoidable. Organisms, as Kant knew, force this point of view upon us. It provides 'a means of describing the organism and the vital processes from an aspect which is not

touched by the causal standpoint' (Ungerer, 1919, p. 250). Indeed it might be said that the real biological problem lies just in this question of the significance of organs and vital processes for the organism. The best proof of the necessity of organicism and the insufficiency of the purely causal point of view is that mechanism also, contrary to its express declaration that only the physico-chemical causal standpoint is scientific, nevertheless cannot escape the use of 'teleological' notions (cf. pp. 35 ff.). Thus the mechanist Plate, in reply to the objection that 'the purposefulness of the organic is not a problem for research' and that 'exact investigation is only concerned with the search for causes', rightly says:

> 'The attempt to disavow the purposiveness of the organic as a problem for investigation leads to an arbitrary restriction of biology; for the latter must investigate and explain *all* relations of organisms, and hence one of its chief tasks must be to analyse and explain causally the great difference which exists between living and non-living natural objects.' (1914, p. 31.)

In modern biology there is, however, a strong movement in favour of excluding the 'teleological' point of view as unscientific. In the first place the occurrence of dysteleology is brought forward as an objection. It is pointed out that even in organic nature by no means everything is 'purposeful' or teleological. From the dystelelogical occurrences it is concluded that teleology only represents a subjective and anthropomorphic point of view and that, in consequence, the physico-chemical causal procedure is the only legitimate one in biology as well as in physics. This is the attitude of such authors as Goebel, Rabaud, B. Fischer, Needham, &c., who declare war upon the teleological point of view, whether it be Darwinistic, vitalistic, or purely methodological, and seek, or believe themselves to have already found, an ateleological standpoint.

Now, the refutation of this ateleological position has already been given in our foregoing discussions: we see that such a view would uproot whole branches of investigation, such as physio-