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THE ELEMENTS OF EXPERIMENTAL EMBRYOLOGY





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To

ROSS HARRISON and HANS SPEMANN





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PREFACE

A few words are needed to explain the scope of this book. The study of the developmental processes of animals is an enormous field, of which only a small fraction can be dealt with in a volume of this size. The observational and comparative study of embryology falls outside the boundaries of this series; in any case, it has already been treated in numerous authoritative works. Even on the experimental and physiological side, however, there remains the difficulty of selection from the vast mass of somewhat heterogeneous material which many lines of research have provided for consideration and synthesis.

In the first place, development is not merely an affair of early stages; it continues, though usually at a diminishing rate, throughout life. The processes of amphibian metamorphosis or of human puberty; the form-changes accompanying growth; senescence and natural death itself—these are all aspects of development; and so, of course, is regeneration.

We feel that it is impossible to treat the whole life-cycle in a single volume, and have accordingly set an arbitrary limit to our material. We have deliberately restricted ourselves to the early period of development, from the undifferentiated condition up to the stage at which the main organs are laid down and their tissues histologically differentiated—in other words, to Wilhelm Roux's "prefunctional period". Growth, absolute and relative; the effects of function on structure and on size; the morphogenetic effects of hormones—the details of these and of other related topics we have deliberately omitted, and we have contented ourselves with the addition of a final chapter in which the main peculiarities of the functional period are contrasted with those of the pre-functional period of primary differentiation. Any satisfactory treatment of the latter portion of the developmental cycle would require a separate volume.

In the second place, within the period of early development, we have exercised a further selection. In a new field of biology such as



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this, there are always two levels of approach. One of these is broadly biological, while the other is physiological in the stricter sense. The prime aim of the worker approaching the problem on the physiological level will always be to analyse the processes involved in terms of physics and chemistry. The worker on the biological level will aim at discovering general rules and laws which he is content to leave to his physiological colleague for future analysis in more fundamental terms, but which, meanwhile, will give coherence and a first degree of scientific explanation to his facts. Both methods are necessary for progress; and while most biologists hope and expect that one day their laws will, thanks to the labours of their physiological colleagues, be made comprehensible in the most fundamental physico-chemical terms, they can reflect that it is they who must first reveal the existence of these laws before the pure physiologist can hope to begin his analysis. The biologist can also remember that these laws have their own validity on their own level, whether they be physico-chemically analysed or not.

We may take a salient example from the contents of this book. Spemann's discovery of "organisers" in the process of gastrulation of Amphibia, and the extension of the concept to other stages of development and to other groups of organisms, have made it possible to understand on the biological level many processes of development which were previously obscure. At the moment we can only throw out crude guesses as to the underlying physiology of organisers and their effects, but the discovery opens a new field of research to physiologists, which they themselves would not have been likely to hit upon for many years. And even if and when the physiological analysis has been made, the empirical biological laws concerning organisers will not lose their validity or their interest; they will merely have been extended and deepened.

At the present moment, research into developmental problems is being actively prosecuted on both the biological and the physiological levels. Following up the early work of Roux, Hertwig, Driesch, Herbst, Jenkinson, Delage, Brachet, Morgan, and Wilson, a flourishing school of *Entwicklungsmechanik* has grown up in Germany, and another, no less successful, in the United States. Meanwhile, on the physiological side, the advance has also been



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striking, and we may perhaps cite as particular examples such works as Fauré-Fremiet's Cinétique du Développement; Gray's Experimental Cytology; Dalcq's Bases Physiologiques de la Fécondation; and Needham's classic book on Chemical Embryology.

So far, however, little progress has been made in equating the results of the two lines of approach, and it seems clear that a considerable time must elapse before it will be possible to do so satisfactorily. At the moment the two fields are almost as unrelated as were, through most of the nineteenth century, the cytological and the experimental-genetic approaches to the problem of heredity, which are now inseparable.

That being so, we have not attempted to include the results of the purely physiological study of development in this survey. This means that we have deliberately excluded such topics as the physiology of fertilisation, the mechanics of cleavage, and the biochemistry of the egg and embryo, save where they have a specific bearing on the biological problems involved.

In other words, what we have attempted to do is to give some account of the results of the experimental attack on the problem of the biology of differentiation—the production of an organised whole with differentiated parts out of an entirely or relatively undifferentiated portion of living material. Almost the only short books on this subject since Jenkinson's Experimental Embryology and his (posthumous) Lectures are Brachet's L'Œuf et les Facteurs de l'Ontogénèse, Dürken's Grundriss der Entwicklungsmechanik, Weiss' Entwicklungsphysiologie der Tiere, and de Beer's Introduction to Experimental Embryology; and each of these treats the subject along rather different lines. Among larger works, Wilson's The Cell, Morgan's Experimental Embryology, Dürken's Lehrbuch der Experimentalzoologie, and Schleip's Determination der Primitiventwicklung are the most important which have appeared since the pioneer works on the subject. A perusal of them will suffice to show the extreme diversity of their lines of approach. What we have felt is that at present there exists in the subject a vast body of facts and a relative paucity of general principles. We have accordingly aimed at marshalling the facts under the banner of general principles wherever possible, even when the principle seemed to be only provisional.



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