PREFACE

Since the very beginning of embryology, the chick embryo has perhaps been more studied than any other, and an almost overwhelming number of books and papers have been written about it. The older literature has been summarised in the monograph of Lillie (1919). Nevertheless, the preparation of still one further book on the subject at this date does not seem to call for an apology; rather, one feels impelled to point to the recent war as an excuse to explain why it did not appear ten years ago. The last quarter of a century has seen a revolution, not only in our knowledge of the anatomy and physiology of the early stages of avian development when the fundamental ground-plan of the animal is being laid down, but also in the general framework of embryological understanding against which the particular problems of the chick are to be seen.

The modern movement in embryology, beginning perhaps with His in 1874, reached its first fruition, at least as far as vertebrates are concerned, with the work of Spemann and his school in the years around 1920. In broadest outline, the new point of view stemmed from two types of technical advance. First, from a logical if not from a chronological standpoint, the application by Vogt of the method of marking groups of cells by vital dyes revealed the extent and importance of morphogenetic movements which take the form of tissue streams, thus opening our eyes to the limitations of the older techniques of comparing a sequence of stages, each fixed as an instantaneous cross-section of the continuous process of development. Secondly, the elaboration by Spemann of more powerful operative techniques began for the first time to reveal, not merely new phenomena for which an explanation must be sought, but at least the beginning of a causal analysis of the physiological processes on which embryogenesis depends. Embryology, from this time, ceased to be a purely descriptive science, fitfully illuminated by evolutionary speculations. In future no account of our embryological knowledge can be considered well balanced unless it includes an adequate discussion of our growing understanding of the dynamic and causal aspects of the phenomena; and it is in these fields, rather

than in the more classical descriptive phases, that the growing points of the science are to be found.

Very soon after the first successes of Vogt and Spemann, attempts were made to apply their methods to the chick. Gräper, using cinematography, and Wetzel, using vital-stain marks, began in the late 1920's to discover the real events concerned in the origin of the germ layers and of the primitive streak, rescuing these phenomena—the fundamentals of avian development—from the unduly imaginative grasp of such phylogenetic speculations as the Concrescence Theory. Although the techniques are not quite so simple or satisfactory as in the amphibians, vital-staining methods, particularly in the hands of Pasteels, have immensely deepened our understanding not only of the chick but of several related forms: the teleosts, somewhat removed phylogenetically but similar in the meroblastic cleavage of the egg, and the reptiles, the nearest evolutionary relatives of the birds.

Techniques for operative experimentation on the bird embryo were also rapidly developed. Simple division of the embryo within the shell has been practised almost as long as the rather similar separation of blastomeres in the amphibians. Defect experiments, in which small areas of the blastoderm are killed by heat, electrolysis or localised X-irradiation, have also been made for many years. The blastoderm *in ovo* is under some tension, and there is a strong tendency for it to give way at the site of injury, so that the wound expands into a large hole, which may greatly distort the embryo and even render it difficult to identify the parts which develop. Nevertheless, some workers have succeeded in producing useful results in this way, although the deceptiveness of similar experiments in the amphibians has taught us the need of great caution in interpreting them. A slightly more penetrating method is that of making a graft on to the chorio-allantois (or in later developments into the coelom of an older embryo) from which it derives a blood supply which enables it to develop. The technique has been particularly used by American authors, beginning with Hoadley (1926 *et seq.*) and continuing with Willier and his pupils. It has certain technical defects, which will be discussed later (p. 3), but its main limitation is that it can only reveal the 'potentialities' of the isolated fragment. These are to be regarded rather as problems than as explanations. Causal relations can be discovered only when we can investigate the

interactions between two entities, as was done by Spemann when he described the results of the action of a graft on the surrounding host tissues. The first results of this kind in the avian embryo were obtained by Waddington (1930) who used the method of *in vitro* cultivation to keep whole embryos alive in a situation in which the necessary manipulations were possible. Since this beginning, a considerable body of data has been collected, largely paralleling the work which has been performed by the Spemann school on the amphibians.

The newer descriptive and experimental studies on the chick have been only rather cursorily summarised (Waddington, 1939, 1950; Rudnick, 1944, 1948) and have as yet found their way only in part into monographs of experimental embryology such as those of Weiss (1935), Spemann (1936), Dalcq (1938, 1941) and Lehmann (1945). This may be partly because no one of these authors has himself worked on this form. In part it may also have been a result of a lack of coherence in the literature which seems particularly to have afflicted this field, which has tended to be a stamping ground for several distinct groups of workers, each of which built up a body of doctrine of its own, and sometimes conducted vigorous polemics within itself, without apparently paying much attention to work going on in other parts of the world. Thus there was a German group, consisting mainly of Wetzel, Gräper, Kopsch and Holmdahl, joined later by Pasteels, who were concerned mainly with the kinematics of gastrulation and embryo formation. The American group under the inspiration of Willier continued for many years to make experiments involving the isolation of complex fragments containing ectoderm, mesoderm and endoderm, usually on the chorio-allantoic membrane. In England, Waddington and a few others performed operations which made it easier to bring their results into line with the phenomena which had been revealed by Spemann in the amphibians and were by then well known. The work of all these three groups had reached a certain degree of finality by the outbreak of the war; nevertheless, their results have not yet been critically reviewed in relation to each other. Since then, the European work, which suffered the greatest interruption, has hardly got back into its stride. American embryologists, however, have been carrying forward their interests into many new and exciting fields. One may mention the applications of biochemical

and biophysical techniques to problems of avian morphogenesis, with such important contributions as those of Jacobson and Brachet from Europe, and Moog, Hobson, and others in America. This has, indeed, been the main centre of interest in the last few years as far as the early stages of morphogenesis are concerned. The other main fields of recent effort have dealt with later stages of organogenesis. One may instance the work of Hamburger, Saunders and others on the limb buds, of Hamburger and his collaborators on the central nervous system, of Landauer and his group on certain genetic types, and of the Lillie and Willier schools on the development of the plumage and its pigmentation.

The central purpose of this book has been to review the literature, mainly dating from the 1930's, which deals with the primary stages of morphogenesis. Work on later stages, much of it published more recently, is reviewed rather more cursorily. It has, of course, been extremely difficult to decide where to stop. There is an immense literature on tissue culture studies of chick embryonic tissues and cells; in most cases the donor embryos had completed their basic morphogenesis and much of their histogenesis, so that the problems at issue are somewhat different, though of course related, to those of what may now be called classical experimental embryology. This material has been omitted almost completely. Again, the experimental study of sex determination and differentiation is an enormous but somewhat specialised field, which is probably better treated from a comparative point of view which does not confine itself to one Order of vertebrates; and for this reason, and because it would unduly expand the scope of the book, it has also been excluded. In fact, it may perhaps be said that the subject of pigmentation and plumage development has been taken as the borderline where experimental embryology shades off into other fields of experimental biology. A chapter is devoted to it, but the treatment is less thorough, and the coverage of the literature less complete, than that which has been given to the more central themes.

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C. H. W.

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