BALINSKY

FIFTH EDITION

An Introduction to EMBRYOLOGY

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PREFACE TO THE FIFTH EDITION

This fifth edition of *An Introduction to Embryology* was prepared in close collaboration with Dr. B. Fabian. Any improvements in this edition as compared with the previous one are largely due to this cooperation. Dr. Fabian's assistance was especially useful in all sections dealing with biochemical and molecular aspects of development, but also in numerous other fields. With his help, the current embryological literature has been checked up to the beginning of 1980.

Embryolgy or, as it is often referred to, developmental biology, is emerging as one of the most important and central fields of biology in general; the research contributions to this field are vast, so that in spite of many additions and improvements, this book remains only an introduction to the subject. Some of the old concepts have had to be revised in the light of new research, and withal we have attempted to provide greater precision on some crucial topics.

In the preface to the third edition of this book I wrote: ". . . the general outlines of a comprehensive theory of development are gradually emerging, though as yet not clearly enough to put them down on paper; a number of links are still missing." Although there are still obvious gaps in our understanding of the development of the animal egg, enough progress has been made to tempt me to synthesize the guiding ideas behind the presentation of the factual material in this book, in a new addition, Part Nine: "Theory of Development—a Recapitulation."

A number of persons, both in Johannesburg and overseas, have rendered valuable assistance to me in my task of preparing this edition. I must first of all express my gratitude to the anonymous colleague who prepared a detailed review of the previous edition at the request of the publishers. The review was very useful indeed. I would also like to thank the following persons for useful criticisms, advice, and encouragement: Dr. K. Barker, Canisius College; Dr. J. Bonner, California Institute of Technology; Dr. R. Briggs, Indiana University; Dr. H. Eyal-Giladi, University of Jerusalem; Dr. J. B. Gurdon, Cambridge University; Dr. Laurinda A. Jaffe, University of California; Dr. Lionel F. Jaffe, Purdue University; Dr. J. L. Koevenig, Florida Technical University; Dr. D. S. McDevitt, University of Pennsylvania; Dr. R. Miller, Temple University; and Dr. J. P. Trinkaus, Yale University.

For sending me the original prints of many photographs being used to illustrate this edition, my special thanks are due to : Dr. Y. C. Hsu, Johns Hopkins University; Dr. R. G. Kessel, University of Iowa; Dr. A. P. Mahowald, Indiana University; and Dr. K. W. Tosney, Yale University.

In the Department of Zoology of the University of the Witwatersrand, apart from Dr. Fabian, I am particularly indebted to Dr. G. V. Goldin for valuable advice and information, and to Miss Joan Kessel and Mrs. Arielle Mills for the use of photographs from their unpublished research projects.

I would like also to record my thanks to Miss Wally Maier for photographic work in connection with the preparation of this edition.

Johannesburg B. I. BALINSKY

PREFACE TO THE SECOND EDITION

In the short time since the publication of the first edition of this book, embryology has made significant progress requiring a revision of many parts of the text in respect to both factual statements and interpretations. This progress is the result mainly of investigations of a biochemical nature and the wide application of electron microscopy to embryological problems. The organization of the eggs and sperm in particular has emerged in a new light because of electron microscopic investigations of the last few years. On the biochemical side, the discovery of the way in which protein synthesis is controlled by nucleic acids has made such a profound change in biological concepts that development of the egg cannot be dealt with at present without consideration of the DNA-RNA codes and the mechanism of protein synthesis.

In preparing the second edition of *An Introduction to Embryology* I have made an attempt to reflect these advanced trends and to incorporate them into the text as well as to fill the gaps which have been pointed out by reviewers and critics.

The chapter on the organization of the egg has been greatly expanded, and much more attention has been given to the spermatozoon. The mechanism of gene action in development has been presented in the light of decoding of information encoded in the nuclear DNA. New data on the mechanism of embryonic induction and on cell growth and differentiation have been included. The list of references has been increased by over 200 titles, drawn mainly from the literature that has appeared during the last three years. The current research literature has been systematically studied and utilized.

To meet the wishes of users of the book who found that the text of the first edition contained insufficient information on the morphological aspects of development, I have considerably expanded the descriptive parts of the book and have given more emphasis to mammalian development. The illustrations have been augmented by the addition of 153 new figures, some of them composite. Some of the new figures have been grouped together to illustrate a few of the developmental stages of the frog and the chick, in the section on "Stages of Development." It is hoped that this section will help the student to grasp the development of the embryo as a whole, and that it will present a background against which the development of the various organ systems can be studied in greater detail.

Some of the views and statements contained in the first edition have been challenged by critics and reviewers, and in many cases I have accepted the criticisms and made corresponding changes in the text. Occasionally these changes concern terminology. In a few cases, however, I do not agree with the proposed corrections, and here perhaps is the right place to state my reasons, in order to avoid misunderstandings.

The controversial terms which I prefer to retain without change are "blastoderm" and "blastodisc." The term "blastoderm" is used here to denote the layer of cells surrounding the blastocoele of a blastula, in whatever form the blastula is encountered—whether as a hollow sphere formed after complete cleavage, as a disc after discoidal cleavage or as a layer of cells surrounding the yolk in centrolecithal eggs. This layer of cells should have a specific name, and the term blastoderm is a very appropriate one, as it matches the terms "blastula" and

"blastocoele." Also etymologically it is constructed similarly to the terms ectoderm, mesoderm and endoderm, and thus helps the student to see the continuity of structural units in the embryo. The term "blastoderm" in the sense just defined has been used before by both older and contemporary embryologists. It was used in this sense by Haeckel (*The Evolution of Man,* Vol. 1, 1874, English translation by McCabe; Watts and Co., 1923, p. 62), by Korschelt and Heider (*Text-book of the Embryology of Invertebrates,* Part 1, 1893, English translation 1895; Swan Sonnenschein and Co., p. 4), and in our times by Nelsen (*Comparative Embryology of Vertebrates,* 1953) and by Witschi (*Development of Vertebrates,* 1956). Also in the same sense the term blastoderm is used in Figure 5–1 of Patten's *Foundations of Embryology* (1958), although not in the text of that book.

If the term blastoderm is to be applied to the cellular lining of any type of blastula, and not only to blastulae of animals having discoidal cleavage as some would like to have it, then the cap of cells on the animal pole of a discoblastula should obviously be called a "blastodisc." In the past the term "blastodisc" has been used either to denote the concentration of cytoplasm on the animal pole of the uncleaved hen's egg or to denote the mass of cells into which this cytoplasm becomes subdivided during cleavage, or for both. In recent literature, usage of the term blastodisc has been extended to include the chick embryo in the primitive streak stage or even in later stages. Thus while some looseness in the application of the term seems to be in practice, I should like to confine the term to those stages in which the developing embryo does have the shape of a disc, that is, mainly to the stages of meroblastic discoidal cleavage.

In the task of preparing the second edition I have been greatly assisted by numerous teachers and research workers who have given me the benefit of their opinions. To all those I should like to express my sincere gratitude, but most especially to the following colleagues whose advice and constructive criticisms have been most helpful: Professor Joseph T. Bagnara of the University of Arizona, Professor James T. Duncan of the San Francisco State College, Professor Royal F. Ruth of the University of Alberta, Professor Nelson T. Spratt of the University of Minnesota, Professor Malcom S. Steinberg of the Johns Hopkins University and Professor Roland Walker of the Rensselaer Polytechnic Institute.

I should like also to record my special thanks to a number of embryologists who have kindly supplied me with original drawings and photographs, which have been invaluable in improving the illustrations. The names of these colleagues appear in the legends of the corresponding figures.

In conclusion I should like again to thank my assistants in the Zoology Department of the University of Witwatersrand, Mr. M. J. de Kock for helping me with the preparation of new figures appearing in the second edition, and Mrs. E. J. Pienaar, who has been most helpful in searching for literature when it was not at hand and in typing the new sections of the text.

B. I. BALINSKY

PREFACE TO THE FIRST EDITION

The teaching of embryology has long been an established feature at universities throughout the world, both for students in biology and students in medical sciences. Although overshadowed during a large part of the twentieth century by the rapid development of genetics and cytology, embryology has also made rapid advances, especially as an experimental science—as experimental or physiological embryology. It is realized now that embryology is a branch of biology which has a most immediate bearing on the problem of life. Life cannot be fully accounted for without an understanding of its dynamic nature, which expresses itself in the incessant production of new organisms in the process of ontogenetic development.

In the midst of the rapid changes of outlook that the experimental method has brought with it, it has been difficult to coordinate the older data of purely descriptive embryology with the new discoveries. This has hampered the teaching of embryology and is to this day reflected in the subdivision of most textbooks of embryology into two groups. Books of the first type deal with the classic "descriptive" embryology and are written mainly for the use of medical students. Short chapters on experimental embryology are appended to them, but these chapters are extremely brief and not organically connected with the description of the morphology of the developing embryos. The second type of book deals with experimental embryology or "physiological" embryology. These books are written for advanced students and the basic facts of development are more or less taken for granted, so that a student cannot profitably proceed to the study of such a book without previously making himself familiar with "descriptive" embryology from one of the books of the first type.

In the course of many years' teaching of embryology to university students I have endeavored to present embryology as a single science in which the descriptive morphological approach and the experimental physiological approach are integrated and both contribute to the understanding of the ontogenetic development of organisms. This integrated approach to development is now incorporated in the present book. Data of a more purely physiological and biochemical nature are adduced inasmuch as it is practicable to treat them in a book that does not presuppose an advanced knowledge of biochemistry in the student.

The subject of embryology is interpreted in my book in a broad sense, as the science dealing with ontogenetic development of animals, and includes therefore such topics as postembryonic development, regeneration, metamorphosis and asexual reproduction, which are seldom handled in students' textbooks at any length. Lastly, I believe that embryology cannot be presented adequately without establishing some connection with genetics, inasmuch as processes of development are under the control of genes. The connection between inheritance and development is therefore also indicated in the text.

With such a wide scope, my book can only be " an introduction to embryology." The whole field could not be covered in the same detail as is customarily given in textbooks dealing with only one aspect of the science of embryology. The student having studied this book, however, will be prepared to understand and appreciate special information in any section of the science which would be of interest to him in his further studies.

The first draft of this book was written in 1952, and duplicated copies of the manuscript were used by my students during subsequent years. This gave me an opportunity to convince myself of the usefulness of the book and also to eliminate some defects in the original text. For the present printed edition the book has been completely revised and brought up to date. An extensive study of special literature up to the end of 1958 has been carried out for this purpose (as can be seen from the list of references). Later publications could not be included in the text.

In illustrating the book I have drawn on my own experience in embryological work wherever practicable, but of course most of the illustrations have been reproduced from other sources.

In preparing the book for print I have been assisted by a number of persons to whom I should like to express my gratitude on this occasion. In the first place I wish to thank all the authors and publishers who have kindly agreed to the reproduction of figures used to illustrate this book, as well as colleagues in many countries who by sending me reprints of their publications have facilitated the arduous task of keeping track of current embryological literature.

Of my immediate collaborators and friends I am most profoundly indebted to Dr. Margaret Kalk of the University of the Witwatersrand for reading the whole text of the book and for many valuable suggestions and helpful criticism. I am indebted to Dr. H. B. S. Cooke of the same University for his expert advice on the preparation of illustrations for the book. I am very grateful for the invaluable assistance of Mrs. E. J. Pienaar, who has typed the manuscript, has assisted me in preparing the index, and has been of great help on diverse occasions during the work on the manuscript and on the proofs. I should like to thank Miss R. J. Devis, Mrs. E. du Plessis and Mr. M. J. de Kock for their help in preparing the illustrations for the book.

Last but not least I should like to express my gratitude to the staff of the W. B. Saunders Company, whose friendly encouragement has done much to bring this book to its present form.

B. I. BALINSKY

Johannesburg

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Chapter One

THE SCOPE OF EMBRYOLOGY AND ITS DEVELOPMENT AS A SCIENCE

1–1 ONTOGENETIC DEVELOPMENT AS THE SUBJECT MATTER OF EMBRYOLOGY

The aim of this book is to familiarize the student with the basic facts and problems of the science of **embryology.** The name "embryology" is somewhat misleading. Literally it means the study of **embryos.** The term "embryo" denotes the juvenile stage of an animal while it is contained in the egg (within the egg envelopes) or in the maternal body. A young animal, once it has hatched from the egg or has been born, ceases to be an embryo and would escape from the sphere pertaining to the science of embryology, if we were to keep strictly to the exact meaning of the word. Although birth or hatching from the egg is a very important occasion in the life of the animal, it must be admitted that the processes going on in the animal's body may not be profoundly different before and after the hatching from an egg, especially in some lower animals. It would be artificial to limit studies of the juvenile forms of animal life to the period before the animal is hatched from the egg or is born. It is customary, therefore, to study the life history of an animal as a whole and accordingly to interpret the scope of the science of embryology as **the study of the development of animals.**

The word "development" must be qualified in turn. In the sphere of biology with which we are concerned, the term "development" is used with two different meanings. It is used to denote the processes that are involved in the transformation of the fertilized egg, or some other rudiment derived from a parent organism, into a new adult individual. The term development may, however, also be applied legitimately to the gradual historical transformation of the forms of life, starting with simple forms which might have been the first to appear and leading to the contemporary diversity of organic life on our planet. Development of the first type may be distinguished as individual development or **ontogenetic development.** Development of the second type is the historical development of species or **phylogenetic development.** Phylogenetic development is often referred to as evolutionary development or simply **evolution.** Accordingly, we will define embryology as **the study of the ontogenetic development of organisms.** In this book we will be dealing only with the ontogenetic development of multicellular animals, the **Metazoa.**

In multicellular animals, the typical and most widespread form of ontogenetic development is the type occurring in sexual reproduction. In sexual reproduction new individuals are produced by special **generative cells** or **gametes.** These cells differ essentially from other cells of the animal, in that they go through the process of maturation or **meiosis,** as a result of which they lose half of their chromosomes and become **haploid,** whereas all other cells of the parent individual, the **somatic cells,** are,