

B. I. BALINSKY, Dr. Biol. Sci.

***An introduction to***  
**EMBRYOLOGY**

**FOURTH EDITION**

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**FOURTH EDITION**

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# PREFACE TO THE FOURTH EDITION

This new edition of *An Introduction to Embryology* has given me an opportunity to restructure the text and to add new and more up-to-date material. In doing this, I have included not only work published since the third edition, but also some earlier work which has gained significance in the light of new discoveries and new ideas. Some passages of the previous text that appeared to be of less interest have been removed in an endeavor to prevent the book from becoming excessively bulky. Hopefully, in this way, the governing ideas will stand out more clearly and thus will make the book better suited for the student-reader. The section dealing with the structure of DNA and the mechanism of protein synthesis has been deleted, since the material appears to be common knowledge among biologists at this stage and is included in all elementary textbooks of biology and zoology.

In working on the text, I have had the benefit of receiving helpful criticisms and advice from many persons, to whom I would like to express my gratitude. I am particularly indebted to the following individuals: Professor J. T. Bagnara, University of Arizona; Professor Anna R. Brummett, Oberlin College; Dr. B. C. Fabian, University of the Witwatersrand; and Professor C. C. Lambert, California State University, Fullerton. I sincerely appreciate the help of my colleagues, who have been kindly sending me reprints of their publications and thus have greatly facilitated the onerous task of following the current literature. I hope my correspondents realize that only a very small portion of the results of the current work can be included in a textbook.

Mr. J. Thompson is gratefully acknowledged for helping me with the photographic work for the present edition.

It has been a great pleasure over the years to work with the staff of the W. B. Saunders Company, whose cooperation and encouragement I greatly value.

Johannesburg

B. I. BALINSKY

## PREFACE TO THE THIRD EDITION

In preparing this third edition of *An Introduction to Embryology* for publication I was guided by the intention to correct those defects and shortcomings of the second edition which I have noticed myself or to which my attention was drawn by reviewers and critics, and also to incorporate into the text the new developments that have taken place in the fields of general biology and embryology since the printing of the second edition. The most significant advances made; so far as the field covered by *An Introduction to Embryology* is concerned, are the deciphering of the genetic code and an increased understanding of the interaction of the genes and cytoplasm in development. As a result, the general outlines of a comprehensive theory of ontogenetic development are gradually emerging, though as yet not clearly enough to be put down on paper; a number of links are still missing.

One of the criticisms made against this book is that obsolete or otherwise unacceptable theories and views are included in the text. Even if the inadequacy of such theories and views is explained in subsequent pages, the student, it is claimed, is confused or has to study that which is not of value to him. I feel that this criticism is not well founded. Science develops by overcoming previous mistakes; what has been the truth yesterday may be falsehood today; but equally, a similar transformation may occur tomorrow in what today is considered as established truth. Describing some of the blind alleys into which science has stumbled in the past and criticizing the weakness of some views and theories should teach the student not to regard the information given in a textbook as absolute and immutable truth, and it should develop in the student a critical approach and an enquiring spirit that are the essence of the scientific attitude.

Embryological terminology has recently been a subject under consideration by the Subcommittee on Embryological Nomenclature of the International Anatomical Nomenclature Committee. At this time, when my work on the third edition has been completed, the proposed list of terms has not yet been finalized, as it is to be submitted for approval to the next Anatomical Congress. In the meantime I have found it desirable to implement those recommended terms which are most likely to be adopted.

In the course of reviewing the text, some parts have been rearranged so as to bring them into a more logical and streamlined form. This refers in particular to the sections on oogenesis and differentiation. The section on placentation has been expanded. Several new illustrations have been added, directly supplied, in part, by the authors, to whom I would like to express my gratitude. The recognition is given in the legends of the respective figures.

I would like to use this opportunity to thank the many biologists and embryologists who have reviewed or criticized the second edition of *An Introduction to Embryology* and by so doing have helped me to improve the book. I would like to name in particular: Professor J. Bagnara, University of Arizona; Professor R. Barnes, Gettysburg College; Professor Anna R. Brummett, Oberlin College; Dr. V. V. Brunst, Roswell Park Memorial Institute, Buffalo; Professor R. F. Ruth, University of Alberta; Professor M. S. Steinberg, Princeton University; and Professor B. Strauss, University of Chicago.

In my own Department of Zoology at the University of the Witwatersrand, I have had valuable discussions concerning changes and improvements in *An Introduction to Embryology* with Dr. Vivian Gabie, and Dr. B. Fabian, senior lecturers in the department.

As in the previous editions Mr. M. J. de Kock assisted me with the preparation of new figures, and Mrs. E. J. Pienaar has been very helpful in typing the corrections

and additions for the new edition and in checking the references. To all these persons I would like to express my sincere gratitude.

B. I. BALINSKY

Johannesburg

## 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 Malcolm 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 the 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 added 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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## Part One

# THE SCIENCE OF EMBRYOLOGY

