B. I. Balinsky, Dr.Biol.Sc.
PROFESSOR OF ZOOLOGY
UNIVERSITY OF THE WITWATERSRAND
JOHANNESBURG, SOUTH AFRICA

An Introduction to
EMBRYOLOGY

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Preface

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 some of 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.

Johannesburg B. I. BALINSKY

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PART I

The Science of Embryology

CHAPTER **1**

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 make the student familiar 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 membranes) 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 the studies of the juvenile forms of animal life to the period before the animal is hatched from the egg or born. It is customary, therefore, to study the life history of an animal as a whole, and accordingly to interpret the contents of the science of embryology as **the study of the development of animals.**

Now the word "development" has to be qualified in turn. In the sphere of biology with which we are concerned here, 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, as a rule, **diploid.** Once a cell has gone through the process of meiosis, it can no longer function as an integral part of the parent body but is sooner or later extruded to serve for the formation of a new individual. In multicellular animals there exist two types of sex cells: the female cells or **ova,** and the male cells or **spermatozoa.** As a rule the two cells of the opposite sexes must unite in the process of fertilization before development can start. When the two gametes (the ovum and the spermatozoon) unite, they fuse into a single cell, the **zygote,** which again has a diploid number of chromosomes. The zygote, or fertilized ovum, then proceeds to develop into a new adult animal.

Side by side with sexual reproduction there exists in many species of animals a different mode of producing new generations—asexual reproduction. In asexual reproduction the offspring are not derived from generative cells (gametes) but from parts of the parent's body, consisting of somatic cells. The size of the part which is set aside as the rudiment of the new individual may be large or small, but in the Metazoa it always consists of more than one cell. The development of an animal by way of asexual reproduction obviously belongs in the same category as the development from an egg and should be treated as a special form of ontogenetic development. It will be dealt with in Chapter 20. To distinguish between the two forms of ontogenetic development, the term **embryogenesis** may be used to denote the development from the egg, and the term **blastogenesis** may be used for the development of new individuals by means of asexual reproduction.

1–2 THE PHASES OF ONTOGENETIC DEVELOPMENT

From what has already been said it is clear that the processes leading to the development of a new individual really start before the fertilization of the egg, because the ripening of the egg and the formation of the spermatozoon, which constitute the phase of **gametogenesis,** create the conditions from which the subsequent embryogenesis takes its start. In both oogenesis and spermatogenesis meiosis, by discarding half of the chromosomes, singles out the set of genes which are to operate in the development of a particular individual. The cytoplasmic differentiations of the spermatozoon enable it to reach the egg by active movement and to fertilize it. On the other hand, the egg cell accumulates in its cytoplasm substances which are used up during development—either directly, by becoming transformed into the various structures of which the embryo consists, or indirectly, as sources of energy for development. The elaboration in the egg cell of cytoplasmic substances to be used by the embryo, and their placing in correct positions, are essential parts of what occurs during the first phase of development.

The second phase of development is **fertilization.** Fertilization involves a number of rather independent biological and physiological processes. First of all, the spermatozoa must be brought into proximity with the eggs if fertilization is to occur. This involves adaptations on the part of the parents, ensuring that they meet during the breeding season, discharge their sex cells simultaneously in cases of external fertilization, or copulate in cases of internal fertilization. Next, the spermatozoa must find the egg and penetrate into the egg cytoplasm. This entails a very finely adjusted mechanism of physicochemical reactions which serve to direct the spermatozoa to the egg. Next the egg is **activated** by a spermatozoon and starts developing. A further rearrangement of the organ-forming substances in the egg is among the first changes that take place in the egg after fertilization. (See section 3–5.)

The third phase of development is the period of **cleavage.** The fertilized egg is still a single cell, since the nucleus and cytoplasm of the spermatozoon fuse with the nucleus and cytoplasm of the egg. If a complex and multicellular organism is to develop from a single cell, the egg, the latter must give rise to a large number of cells. This is achieved by a number of mitotic cell divisions following each other in quick succession. During this period the size of the egg does not change, the **cleavage cells** or **blastomeres** becoming smaller and smaller with each division. No far-reaching changes can be discovered in the substance of the developing embryo during the period of cleavage, as if the preoccupation with the increase of cell numbers excludes the possibility of any other activity. The whole process of cleavage is dominated by the cytoplasmic organoids of the cells: the centrosomes and achromatic figures. The nuclei multiply but do not interfere with the processes going on in the cytoplasm. The result of cleavage is sometimes a compact heap of cells, but usually the cells are arranged in a hollow spherical body, a **blastula,** with a layer of cells, the **blastoderm,** surrounding a cavity, the **blastocoele.**

There follows the fourth phase of development, that of **gastrulation.** During this phase the single layer of cells, the blastoderm, gives rise to two or more layers of cells known as the **germinal layers.** The germinal layers are complex rudiments from which are derived the various organs of the animal's body. In the higher animals the body consists of several layers of tissues and organs, such as the skin, the subcutaneous connective tissue, the layer of muscles, the wall of the gut, and so on. All these tissues and organs may be traced back to three layers of cells—the aforementioned germinal layers. Of these the external one, the **ectoderm,** always gives rise to the skin epidermis and the nervous system. The layer next to the first, the **mesoderm,** is the source of the muscles, of the blood vascular system, of the lining of the secondary body cavity (the **coelom,** in animals in which such a cavity is present), and of the sex organs. In many animals, in particular in the vertebrates, the excretory system and most of the internal skeleton are also derived from the mesoderm. The third and innermost germinal layer, the **endoderm,** forms the alimentary canal and the digestive glands. In the Coelenterata the mesoderm is missing as a separate germinal layer, and only ectoderm and endoderm are present.

The germinal layers are produced by the disappearance of a part of the blastoderm from the surface and its enclosure by the remainder of the blastoderm. The part that remains on the surface becomes ectoderm; the part disappearing into the interior becomes endoderm and mesoderm. The disappearance of endoderm and mesoderm from the surface sometimes takes the form of a folding-in of part of the blastoderm, so that the simple spherical body becomes converted into a double walled cup, as if one side of the wall of an elastic hollow ball had been pushed in by an external force. This infolding or inpushing of endoderm and mesoderm is known as **invagination,** and the resulting embryo is known as a **gastrula**—whence the term **gastrulation.** The way in which the endoderm and mesoderm become separated from each other in the interior of the gastrula varies a great deal in different animals, and cannot be described in this general review. (See Chapter 5.) If the gastrula is formed by invagination, the cavity of the double walled cup is called the **archenteron,** and the opening leading from this cavity to the exterior is called the **blastopore.** In animals in which the gastrula is formed in a