Fifth Edition

INTRODUCTION TO

Vertebrate Embryology

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Preface

The preparation of a fifth edition of this book is long overdue, but the events of the past ten years have interrupted the normal course of events in many situations. Dr. Shumway was in service with the Army during World War II and since then has gone into another field of work. Thus the task of carrying out a revision of this book for a new edition fell largely to my lot.

In a general sort of way every effort has been made to retain those features of the original book which have been so successful. The book is again organized on a comparative basis, and the general account of the developmental process is supplemented by detailed material relating to the amphioxus, the frog, the chick, and man. Sufficient material is provided on each of them so that considerable stress may be laid on one or more at the wish of the instructor. The subject matter is also treated again both from the morphological and physiological viewpoints—a procedure which undoubtedly makes the subject much more interesting to the student. Basic material from the field of experimental embryology is incorporated in the body of the text, for this material has assumed such fundamental importance that it can no longer be omitted from consideration even in the most elementary treatment of the subject. The subject matter of this chapter, however, has been largely restricted to a discussion of the processes underlying the early stages of development. Other material from experimental studies is incorporated at various points in the body of the book without special emphasis. It is recognized, moreover, that the subject matter of experimental embryology is now so extensive that it constitutes a separate field of study in itself.

An attempt has been made to bring the different topics up to date, and modification of the account of early development in the chick has been particularly necessary. Above all, however, an effort has been made to preserve the objective of presenting a broad factual outline of the information that is necessary for the acquisition of a sound, basic knowledge of the subject, on which the interested student will be able to build.

The illustrations have been extensively revised to insure uniformity of quality and to preserve the realistic character of this material. Much of this work has been done by Mr. Charles McLaughlin, artist of the Zoology Department of the University of Illinois, but many of the beautiful original figures by Mrs. Katharine Hill Paul have been retained.

It is a pleasure at this time, also, to extend my thanks to many of my colleagues in the Zoology Department at the University of Illinois, in particular to Dr. S. Meryl Rose and Dr. Francis Kruidenier, who have read various sections of the text, as well as to Dr. W. M. Luce and Dr. J. B. Kitzmiller for criticism of the portions relating to genetics.

F. B. Adamstone

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The Study of Embryology

Embryology may be defined as that division of biological science which deals with the development of the individual organism. It is concerned primarily with the orderly series of changes in form and function by which the initial germ of the new individual is transformed into a sexually mature adult. In addition, modern experimental embryology seeks to determine the causes of these changes and the nature of the processes underlying them. Among vertebrate animals, at least, the germ with which development begins is normally an egg cell that has been fertilized by a sperm. These cells are the germ cells produced by the parental organisms when they reach sexual maturity, the male developing sperm cells, and the female, eggs or ova. Sometimes the word ontogeny is also employed to designate the period of embryonic development, but, more often, the term is used to define the entire life history of an individual from its origin to its death.

Early Embryologists

Speculation regarding the process of development particularly as it relates to man himself undoubtedly goes back far beyond the written record. It is desirable, therefore, at the outset, to review the history of this science in order to become acquainted with the contributions of some of the earlier workers and also to learn something of the evolution of scientific thought in this field.

Aristotle (384–322 B.C.). The earliest treatise on embryology which has been preserved is Aristotle's work entitled *De Generatione Animalium,* which describes the reproduction and development of many kinds of animals. Another treatise, *De Historia Animalium,* gives the first account of the development of the hen's egg. These works show great powers of observation, skill in comparison, and imagination in interpretation. From our standpoint, however, Aristotle's most significant contribution was his conclusion, based on his observations on the hen's egg, that development always proceeds from simple, formless beginnings to the complex organization of the adult. He pointed out that, in the early embryo, he could see certain structures such as the heart, blood vessels, etc., but no trace of other organs such as the lungs appeared until later. He concluded, therefore, that all structures are not present from the beginning, but that they develop in succession until the adult condition is attained. This explanation of the process of development is the basic concept of the theory of "epigenesis."

William Harvey (1578–1657). This is another famous name in embryology. His book, *Exercitationes de Generatione Animalium,* is based largely on the development of the chick, which he described in great detail, although he too was limited by the fact that the microscope had not yet come into general use. One of his contributions was a careful study of the development of the deer, which he compared with the chick. From purely theoretical considerations he came to the conclusion that mammals also formed eggs. The dictum "Ex ovo omnia"—all animals arise from eggs—is found on the frontispiece of the first editions of his book.

Marcello Malpighi (1628–1694). By this time the microscope invented by the Jensen brothers (1592) had come into fairly wide use, and with it Malpighi restudied the development of the hen's egg. He published an account of this work in the *Proceedings* of the Royal Society of London in an article entitled "De Ovo Incubato." This was illustrated with excellent figures of the developing chick beginning with the unincubated egg and showing the gradual increase in complexity of such structures as the heart, blood vessels, and brain. Then, in spite of these precise and accurate observations, he stated his conclusion that the various parts of the embryo were already contained in the egg, fully formed, just as a miniature plant is present in the seed and becomes visible as it increases in size. This concept of the process of development is known as the "preformation theory" as opposed to Aristotle's theory of epigenesis.

After Malpighi's time, the microscope came into much wider use and many remarkable discoveries were made with the newly invented instrument. Anthony van Leeuwenhoek (1632–1723) made many microscopes of his own and did much to improve the instrument. He made numerous studies of natural objects, and, among other things, discovered spermatozoa in human seminal fluid. It was not until many years later, however, that the real significance of these structures in the process of fertilization was thoroughly understood.

The enthusiasm resulting from such discoveries led to many wholly imaginative accounts of miniature adults in eggs and sperm. Thus, Hartsoeker (1694) illustrated a miniature human being in the sperm.

These speculations led ultimately to the theory of emboîtement first sponsored by Bonnett. This idea in its final form held that each germ cell of the female parent contained a miniature individual. Moreover, each of these, in turn, must also contain a miniature offspring; and so on, for all future generations of the race. It is highly improbable that Bonnett himself would have subscribed to the elaborate theory which was finally evolved.

Caspar Friedrich Wolff (1733–1794). Although the preformation theory was widely accepted, some investigators found reason to doubt its validity. Among these, Wolff made a very careful study of the development of the intestine of the chick and demonstrated that the tubular gut arose from the folding and remolding of a flat layer of tissue in the embryo at an early stage of incubation. This was a direct refutation of the preformationist idea, which held that the intestine was present as a tubular structure from the start. Thus, Wolff in his *Theoria Generationis* not only attacked the theory of preformation on purely logical grounds but also presented strong scientific evidence to support his views. In spite of this, it was not until sometime later that the theory of epigenesis was reestablished as the accepted explanation of the developmental process.

Toward the end of the 19th century the larger divisions of the field of embryology were mapped out, and the foundations were laid for the great progress of the 20th century. A brief review of these developments is given below.

Comparative Embryology

Karl Ernst von Baer (1792–1876) is often spoken of as the father of modern embryology. He discovered the egg of the dog (1827) and other mammals, thus substantiating the ideas of William Harvey. He made exhaustive studies on the embryo of the chick and various other animals and further elaborated the "germ-layer" concept of Wolff so that it was raised to the status of a general law. It is often called the theory of the "specificity of the germ layers," implying that the various structures of the body arise from the same germ layers in different species of animals. Von Baer also published a book on animal development (1828–1837), in which he compared in detail the development of different animals. From these he drew four important conclusions, known as von Baer's laws:

"1. The more general characteristics of any large group of animals appear in the embryo earlier than the more special characteristics.

"2. After the more general characteristics, those that are less general arise, and so on until the most special characteristics appear.

"3. The embryo of any particular kind of animal grows more unlike the forms of other species instead of passing through them.

"4. The embryo of a higher species may resemble the embryo of a lower species but never resembles the adult form of that species."

From the time of von Baer to the present, the history of embryology has been marked by increasing specialization. Thus the field of comparative embryology falls readily into two subdivisions, viz., vertebrate and invertebrate. Nevertheless, the two are very intimately connected and the study of comparative invertebrate embryology has thrown much light on vertebrate embryology because many marine invertebrates lend themselves readily to experimental procedures

Cellular Embryology

Soon after the first volume of von Baer's treatise appeared, Schleiden and Schwann (1838, 1839) announced the cell theory, stating that all living things are composed of, and arise from, living units known as cells. This resulted in an intensive study of the part played by individual cells in the development of the new organism commencing, in the latter part of the 19th century, with the germ cells, their origin and fertilization. In 1878, Charles Otis Whitman (1842–1910) traced for the first time a detailed history of cells formed by the dividing egg in the leech *(Clepsine)*, thereby initiating the study of cell lineage. Beginning about 1925 this phase of embryology has been greatly broadened by the adoption of modern experimental techniques, which make it possible to mark the tissues of the developing embryo so that they may be recognized in their final position in the embryo. Cellular embryology is, therefore, a subject which unites embryology with cytology, for it has come to be realized that the structure and activities of the cells of the embryo are of fundamental importance in the process of development.

Genetics and Embryology

In 1866, Gregor Mendel (1822–1884) first carried on successful experiments in breeding plants to discover the laws by which individual characteristics are inherited by one generation from another. His contributions were long unrecognized, but, in 1900, they were rediscovered independently both in Europe and in the United States. In addition, certain other discoveries had been made regarding the behavior of the chromosomes in the developing germ cells, which led Sutton to suggest that the behavior of the chromosomes afforded a mechanical explanation of Mendel's laws, and to formulate the chromosomal theory of inheritance. This theory was further elaborated by

Johannsen (1911), who developed the theory of the gene, a name proposed for the ultimate unit of heredity. This theory in the hands of T. H. Morgan and others has assumed a great importance to embryologists, for, to quote Brachet, "Embryology is fundamentally the study of heredity in action." Hence, the aim of embryologists from the standpoint of genetics is to determine how the gene produces its effect in the developing organism. Much fundamental work has been done in this field beginning with the work of Ephrussi and other investigators.

Phylogeny and Embryology

In 1859 Charles Darwin published his book, *Origin of Species*. This led not only to a great deal of controversy but also to a great deal of scientific work, as a result of which embryology profited greatly. In 1866, Ernst Haeckel (1834–1919) published a theory which he believed supported Darwin's theory of evolution. He called it the "fundamental biogenetic law." It is more often known as the recapitulation theory. This theory states that ontogeny is a brief and incomplete recapitulation of phylogeny; that is to say, an animal passes through stages in its development comparable to those through which its ancestors passed in their evolution. So far as the vertebrates are concerned, this would mean that a mammalian embryo must pass through stages which are definitely fish-like and later through stages which are essentially reptilian. The fact is that, although there are individual characteristics which may be reminiscent of fish-like or reptilian ancestors, there is never a time in the development of a mammal when it could be mistaken for a fish or a reptile. There are evidences that the vertebrates do retain in embryonic development certain features which also appeared in the development of their ancestors. For example, clefts appear in the pharynx of the embryos of birds and mammals, opening to the exterior just as they do in the embryos of fish. In the adult fish these clefts contain the gills, but this is not true of adult reptiles, birds, or mammals. It has been found very difficult, if not impossible, to draw up a genealogical tree of the vertebrates based solely on embryological data. Hence the recapitulation theory is not accepted and applied so unreservedly as formerly.

Experimental Embryology

Among Haeckel's contemporary opponents was Wilhelm His (1831–1904), who directed attention to the physiology of the embryo. Denying the theory of recapitulation, he called attention to the mechanical processes by which the various structures of the embryo arise from particular regions of the germ. Later, Wilhelm Roux (1850–1924) put the study of experimental embryology on a firm basis when he published a program for the new science, which he called the "mechanics of development." This has led to an intensive attack upon the problems of development from the physicochemical side, which is carried on actively at the present time. Weismann (1834–1913), a leader in theoretical embryology, suggested a theory of chromosomal inheritance which came very close to the mark. Jacques Loeb (1859–1924) discovered a method of inducing development in unfertilized eggs (artificial parthenogenesis), which has led to extensive research on the nature of fertilization.

More recently the basic studies of Vogt (1929) and others on the segregation of the potential organ-forming regions of the early embryo and the demonstration by Spemann of the role of the organizer in development have led to important discoveries relating to the mechanics of development. As more refined techniques have been developed and applied, more detailed analysis of the process of development has become possible and much progress has been made in relation to the differentiation of specific organ fields, the phenomena of induction, competence, etc. Even the part played by the gene has begun to come under investigation.

Another branch of the science of embryology which has become a field of major importance is chemical embryology. The basic work in this field has been summarized in the monumental works of Joseph Needham and Brachet. Much progress has also been made in regard to the metabolic aspects of development, including such phases as the role of food substances, enzyme activity, hormonal control, and various other conditions affecting development.

Some of the chief developments of the first half of the 20th century are outlined briefly in the table appended to this chapter, but the field of experimental embryology is so vast that in a book of this scope no attempt can be made to mention the names and contributions of other men still alive who are actively engaged in this work. To do so the roll of distinguished embryologists here and abroad would have to be called!

The Value of Embryology

To the student who specializes in zoology, embryology has a particular importance because it deals with the origin and development of the adult body. There is a fascination in tracing out the history of the different anatomical structures as they take form, grow, and gradually assume the appearance familiar to us in the mature animal. In the history of the different organs are found clues to their relationship and functions. Everyone knows, for example, that the adrenal gland secretes a hormone, epinephrin, which, circulating in the blood, rouses the sympathetic nervous system to greater activity. But in embryology the student learns that the part of the adrenal gland which secretes epinephrin is derived from those same ganglia which give rise to the sympathetic nerves.

He also finds clues to ancestral relationships. Even though the recapitulation theory has been abandoned as an explanation of development, embryologists recognize that there are structures in the body which correspond to similar parts used for the same or different purposes in the bodies of some distant ancestor. The "retention theory" has been proposed by de Beer as an explanation. Thus the vestigial tail of the human embryo arises in the same place and manner as the tails of other vertebrates, and it may be that some remote prehuman ancestor sported and made use of a tail. The embryo retains this tail not as a recapitulation of ancestral history but because it inherits the genes which initiate the development of a tail. So the student of comparative anatomy often turns to embryology hoping to find homologies in the mode of origin and manner of development of the adult organs in which he is interested.

The modern student of embryology is concerned mainly with the dynamics of development. He examines the protoplasmic organization of the egg and the sperm, their genetic constitution, and the nature of the process by which the sperm initiates development in the egg. He traces the history of the different cells into which the egg divides and tries to learn the way in which differentiation takes place. He is interested in the mechanics of the processes by which these cells arrange themselves into the different germ layers, and how the different organs arise.

To these problems he brings the methods of descriptive embryology: the delicate technique of preparing embryological material, the skilled use of the microscope and its accessories, the interpretation and reconstruction of his prepared material. He also uses the methods of experimental embryology: the alteration of the normal conditions of development, new genetic complexes, altered environmental conditions at different stages of development, the development of individual cells or parts of the embryo in isolation or transplanted into new positions or different hosts.

Embryology is not an easy subject. It requires a high type of visual imagination. The student must bear in mind that he is dealing with living objects, three-dimensional and continually changing in volume, shape, and constitution. Much of his attention must be given to the cells of the embryo, as they multiply migrate, take on different appearances, and carry on different functions. But he must always remember that the embryo has a life of its own to lead and that all the different cells and cell groups in the embryonic body must work in harmony if the development of the embryo is normal. He must not lose sight of the embryo-as-a-whole.

The student preparing for medicine has a professional interest in embryology. Teachers of human anatomy have long since agreed that a knowledge of embryological relationships is the best possible preparation for the study of human anatomy. A good working acquaintance with the outlines of human embryology is prerequisite to the study of obstetrics. The practitioner of medicine must be prepared to answer all sorts of questions about human development.

Any approach to the subject of vertebrate embryology whether morphological or experimental must be preceded by the acquisition of a sound knowledge of the basic pattern of development. Two different methods of approach are available. By the first method the different types of development are taken up one after another, e.g., amphioxus, frog, chick, man. The second method consists of discussing the different topics of embryology in turn (e.g., development of the digestive system) and comparing the conditions found in each of the types. In this book, the second, or comparative method is employed. It is helpful also to examine briefly the life histories of each of the types to be used in later discussion. This will serve to introduce the main stages of embryology and also to point out the different conditions under which development takes place.

Important Events in the History of Embryology

Embryology in the Classic Period

4th century B.C.	Aristotle	

Embryology in the Renaissance Period
(Before the general use of the microscope)

1651	Harvey	Epigenesis

(After the general use of the microscope)

1672	Malpighi	Preformation
1768	Wolff	Epigenesis

Embryology in the Nineteenth Century

1828	von Baer	Comparative embryology
1839	Schleiden and Schwann	Announced cell theory
1859	Darwin	Announced theory of natural selection
1866	Haeckel	Biogenetic law
1866	Mendel	Announced laws of inheritance

(Microscopic technique being developed)

1874	His	Experimental embryology
1878	Whitman	Cell lineage
1883	Roux	Mechanics of development
1891	Weismann	Theory of the germplasm
1899	Loeb	Artificial parthenogenesis

Embryology in the Twentieth Century

1900	Sutton	Chromosomal theory of inheritance
1900	Driesch	Theory of pluripotency
1905	Conklin	Determinate vs. indeterminate cleavage
1911	Johannsen	Theory of the gene
1929	Vogt	Theory of presumptive organ regions
1929	Holtfreter	Chemical aspects of induction
1933	Child	Axial-gradient theory
1934	Spemann, Mangold	Organizer concept
1932 et seq.	Needham, Brachet	Chemical embryology
1937 et seq.	Dalcq, Pasteels, Weiss	Field concept of development
1938 et seq.	Waddington, Ephrussi	Genic control of development

Specialized Phases of Embryology

1924 et seq.	Weiss	Regeneration
1924 et seq.	Detwiler	Neuroembryology

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Reproductive Habits and Vertebrate Life Histories

When the vertebrate organism becomes a sexually mature adult, it has reached the time when reproduction normally takes place. In many species characteristic changes in behavior pattern accompanying reproductive activity develop, and in some animals the whole plan of existence may be profoundly modified. Typical examples of such changes in behavior patterns are the long journey of the Pacific salmon from the ocean to the spawning grounds far inland at the headwaters of such rivers as the Columbia and Fraser; and the long migratory flights of many species of birds, such as the journey of the Canada goose to the Arctic tundra.

These responses are often direct reactions to changes in environmental conditions. They may have a seasonal aspect and may be associated with various physiological and morphological responses in the organism. Many species of fish, such as the suckers and sturgeon, spawn early in the springtime; others, such as the whitefish, spawn in the fall. In birds the mating season usually occurs in spring or early summer. Among mammals many species have recurring periods of reproductive activity throughout the year, e.g., rat, rabbit, monkey, and man; others, such as the deer, have a single breeding season in autumn.

Underlying the seasonal aspect of reproductive activity are other, more basic, factors, some of which vary with the season of the year. It has sometimes been found possible to change certain environmental conditions experimentally and thus bring about modification in the reproductive cycle. Light intensity is a very important factor in this respect in many animals—particularly in birds. Rowan and Bissonnette have shown that it is possible to accelerate the seasonal development of the gonads of birds by the use of artificial light, thus, in a sense, prolonging the length of daylight. In this way, Rowan caused juncoes to mate in the middle of winter. Temperature is another factor of importance, and certain species of fish will not spawn until the temperature of the water is at or very near some particular level.