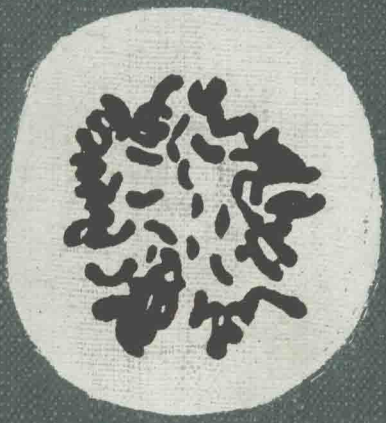
Foundations of Embryology



FOUNDATIONS OF EMBRYOLOGY

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with 962 drawings and photographs
grouped as 313 illustrations
24 of which are in color

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PREFACE

Embryology in the last half century has expanded so tremendously in scope that the offering of a single all-purpose course is no longer logical or adequate. Students planning a career in the zoological sciences need to be well grounded in both comparative and experimental embryology. These phases of the subject can be effectively taught only in relatively small classes limited to students who already have some foundation in elementary embryology. Those looking forward to a career in medicine or the related health sciences will need to study advanced mammalian embryology. As preprofessional students they should, of course, build some groundwork, but most of the phases of the subject of special interest and importance to them cannot be effectively handled until they have entered professional school and have acquired a knowledge of, or are concurrently studying, gross human anatomy, histology, and biological chemistry.

In addition to those who will ultimately take further work in the subject, there is that large group of students who properly regard some knowledge of the biological sciences as an essential part of their general education. Many of them would be eager to take a subject with the inherent interest of embryology if it were presented in broad, simple terms. They have no inclination, however, to elect courses that have the reputation of being primarily preprofessional, or those that, by student standards, are regarded as being "too technical."

The logical way of meeting all these problems is to offer a first course in embryology which will familiarize students with the nature of the basic developmental processes and acquaint them with the language and the problems of the subject. With such a foundation the qualified and interested zoology major can proceed to advanced work in comparative and experimental embryology. A premedical student, after such a course, is ready to cope with the phases of advanced mammalian embryology which are of special significance for him. Finally, the student who is taking embryology as part of his general education is not swamped by technical details he will promptly forget. Instead he is offered readily understandable material from which he can grasp some of the major events in the story of the start of his own life. This book has been written with the objective of furnishing a suitable text

for such a first course in embryology at collegiate level. The implication that it is designed to form a basis for future work of a more advanced character is suggested by its title, "Foundations of Embryology."

The fact that my elementary books on the development of the chick and the pig have proved themselves over the years with beginning classes has led me to draw heavily on them in the writing of this new book. Because each of the earlier books was written to be a complete account by itself, there was in them considerable duplication of foundational material. In the preparation of this new book such duplication could be avoided, so it has proved possible to add a considerable amount of information on the simpler phases of human embryology without making the book unduly long.

An acute awareness of the importance of illustrations in presenting any phase of embryology had led me to spend many hours in the planning and execution of each drawing prepared, either for previous books or for journal articles. I offer, therefore, no apology for illustrating this book very largely with figures from my own previous publications. On the contrary, the illustrations are presented in this new context with pride that even those drawn years previously are still sound in the light of subsequent advances, and with satisfaction that their use by many succeeding classes has demonstrated their effectiveness.

The plan of the book, in essence, is to tell the story of vertebrate development as simply and clearly as possible. For illustrating the various processes involved, use has been made of the forms in which those processes are most effectively exemplified and best understood. Thus for Part One, which covers the early stages of development culminating in the formation of the germ layers, the illustrative material has been drawn largely from the amphibians. The laying down of the basic plan of the body and the establishing of its organ systems, which forms the subject matter of Part Two, has been based on the chick. Part Three, dealing with organogenesis, has utilized mammalian material. But instead of emphasizing species differences, the basic similarity of the major developmental processes in the vertebrates as a whole has been stressed. And instead of a series of still pictures of selected stages, every effort has been made to present developmental processes as a succession of dynamic events. Throughout changing conditions the functional significance of structural arrangement has been emphasized. My aim has been to write an account in which the essentials stand out adequately interpreted, but unobscured by a multiplicity of details; to lay a foundation which can be further built upon in accordance with special needs or individual objectives.

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ACKNOWLEDGMENTS

The pleasantest thing about working on this book has been the interest and friendly helpfulness of my students and colleagues. I wish I might acknowledge all of my debts to students individually, but they are far too numerous. Their critical evaluation of approaches and sequences and their constructive suggestions as to figures in the making have been of special value because they were made from a point of view difficult for an instructor to appreciate without such aid.

Among my colleagues Dr. Russell T. Woodburne has been an unfailing source of information on the late phases of organogenesis that have their consummation in gross anatomical relationships. Whenever there was need for especially skilled photomicrographic work I have had the generous help of Dr. Theodore C. Kramer. For checking the interlocking endocrine mechanisms involved in the reproductive processes I have depended on the unusual knowledge of this field possessed by Dr. Burton L. Baker. Throughout the development of the book Dr. Alexander Barry has been a constant adviser and shrewd critic of both text and figures.

Mrs. Ruth Elliott, embryological technician in the Department of Anatomy, has given me much patient assistance in the assembling of material. Our illustrator, David Sterrett, has drawn a number of new figures most effectively, and has given me valuable advice in the revision of many others. My secretary, Mrs. Dorothy Hargis, prepared the final copy with scrupulous care. Her unusually accurate typing and critical proofreading have averted many errors that would otherwise have crept in.

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PART ONE

Early Developmental Processes Common to Vertebrate Embryos

CHAPTER 1

Embryology—Its Scope, Objectives, and Methods

Embryology. Every one of the higher animals starts life as a single cell—the fertilized ovum. This fertilized ovum, as its technical name *zygote* implies, has a dual origin. It is formed by the fusion of a germ cell from the male parent with one from the female parent. The union of two such sex cells to form a zygote constitutes the process of fertilization and initiates the life of a new individual. Embryology is the study of the growth and differentiation undergone by an organism in the course of its development from a single fertilized egg cell into a highly complex and independent living being like its parents. It is the first phase in an individual's complete life history, or *ontogeny*. Ontogeny is regarded as commencing with fertilization, and including the embryological period and the periods of infancy, childhood, adolescence, maturity, and finally old age. Some authors have advocated extending the meaning of the term embryology to include all developmental processes up to maturity. It is more usual, however, to regard embryology as the phase of development before metamorphosis in the amphibia, before hatching in birds, and before birth in mammals. It should be recognized, however, that hatching or birth is but a convenient landmark in a continuing process and that development is in reality an uninterrupted chain of correlated events.

Historical Background. How we develop before we are born has always been a matter of intriguing interest. "Where did I come from?" is one of a child's first thoughtful questions. Among primitive peoples—peoples in their cultural childhood—this same interest was urgent and intense, for offspring meant the life of the tribe. There were, however, many centuries when groping curiosity turned only toward speculation and mysticism. Aristotle's work on embryos is now of significance not because of the information he secured, surprisingly accurate as some of it was. His work is for us rather a symbol of the beginning of the turning of man's mind away from superstition and conjecture, toward observation. Unfortunately, such an approach did not take firm root. Through much of the Middle Ages

the spark that the better of the Greek and Roman scholars had been attempting to fan was smothered by bigotry and authoritarianism.

But the manner of approach was not the only reason for the lag in the growth of our knowledge of embryology. The early phases of development involve exceedingly minute structures, and curiosity and the willingness to learn by observation were not enough. Galen, it is true, had learned much about the structure of relatively advanced fetuses, but it was not until toward the close of the seventeenth century when the microscope began to be developed into an efficient instrument that the early stages of embryology could be effectively studied.

The human sperm was first seen by Hamm and Leeuwenhoek in 1677, shortly after ovarian follicles were described by de Graaf (1672). Even then the significance of the gametes in development was not understood. Two camps grew up, one contending that the sperm contained the new individual in miniature (Fig. 1-1) which was merely nourished in the ovum, the other arguing that the ovum contained a minute body which was in some way stimulated to growth by the seminal fluid. The war between the homunculists and the ovists was bitter and vituperative. Their ardor for their cause was not dampened even by the absurdity of the inevitable implication of the encasement concept—the implication that each miniature must in turn inclose the miniature of the next generation and so on for as many generations as the race was to survive.

This bootless controversy continued into the next century, finally to be laid to rest by the studies of Spallanzani (1729–1799) and Wolff (1733–1794). The work of Spallanzani is of special interest to us in that it was an initial step in bringing the experimental method to bear on embryological problems. By an ingeniously planned series of experiments, he demonstrated that both the female and the male sex products were necessary for the initiation of development.

Working contemporaneously with Spallanzani, Kaspar Friedrich Wolff, in a brilliant thesis written when he was but twenty-six years of age, set forth his conception of epigenesis. This idea of development by progressive growth and differentiation rapidly replaced the old encasement theories. Although this was an important step forward, it rested too largely on theoretical grounds to give a lasting impetus to the subject. There followed more than half a century with but little advance in our knowledge of the early stages of development, although accurate observation and recording was becoming less and less uncommon.

Von Baer's important work (1829) gave us the foundations of our knowledge of the germ layers in embryos. But the real significance of these layers, and of the sex elements from which they arose, could not be grasped until the cellular basis of animal structure became known. With the formulation of the cell theory by Schleiden and Schwann (1839), the foundations of

modern embryology and histology were simultaneously laid. The knowledge that the adult body was composed entirely of cells and cell products paved the way for a realization of the basic fact of embryology, that the body of the new individual is developed from a single cell, the cell formed by the union, in fertilization, of a germ cell contributed by the male parent with a germ cell contributed by the female parent. Thus, although curiosity had been at work since before the times of written history, and with Aristotle

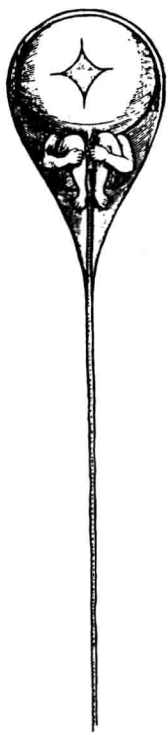

Fig. 1-1. Reproduction of Hartsoeker's drawing of a spermatozoon showing a preformed individual (homunculus) in the head. (From "Essay de Dioptrique," Paris, 1694.)

critical observation had begun to replace conjecture, it was not until the development of the microscope, the advent of the experimental method, and the discovery of the cellular structure of the body that embryology began to become a science.

Special Fields in Embryology. The various special fields we now recognize within the general subject of embryology have developed as a logical outcome of progress in the natural sciences as a whole and the availability of new apparatus and techniques. The earlier studies of the modern period were still chiefly concerned with learning the basic structural pattern of the embryonic body. But from general body configuration interest gradually shifted to more detailed studies of the structure and arrangement of the minute internal organs of the embryo. Work of this type received a great impetus and gained much in accuracy from the new techniques that were developed between 1880 and 1890, the making of serial sections (His)