Elements of Comparative Vertebrate Embryology

BY HAROLD W. MANNER

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Preface

THERE ARE MANY good embryology textbooks on the market today. It would be unwise to add another at this time, unless it were sufficiently different to warrant its existence. Science today is progressing rapidly. In educating our students we must keep abreast with the latest developments. In many embryology courses it has been the practice either to study only one form, such as the chick or mammal, or to study a few forms which are considered to be representative of the entire vertebrate subclass. In many comparative vertebrate embryology courses, the animals utilized are the frog, the chick, and the foetal pig. Embryology on the undergraduate level is not, and should not be, the same type of course designed for medical and dental students. It should not only be a thorough investigation into the principles underlying all vertebrate development, but, in addition, should unify the vertebrates

by noting the similarities and dissimilarities of as many vertebrate ontogenies as time allows. A knowledge of the embryology of the chick is relatively useless unless it is related to the development of other vertebrate types. Many competent investigators recently have been adding to our knowledge of the descriptive embryology of the vertebrates. Two vertebrate classes, the osteichthyes and the reptiles, whose embryology is often omitted in a basic embryology text, have been included in this book.

The first part of the text is concerned with those general principles of embryology that underlie all vertebrate development. The second half incorporates these principles into a descriptive survey of six chordate types. Since this book is entitled *Elements of Comparative Vertebrate Embryology,* no attempt has been made to include anything but basic development. The omissions are numerous, but it was felt that by presenting only the basic tenets to the student, the teacher would be free to expand upon these in the classroom. The same is true for the illustrations. All the line drawings in this book are original and are designed to show, to their best advantage, specific embryological details. For this reason the number of labels has been kept to a minimum. If the instructor feels that the diagrams are inadequately labeled, additional ones of his own choosing can be easily added.

No book can possibly be the work of one person. I am indebted to many who have worked diligently with me throughout the preparation of the manuscript. The entire manuscript was read with care by Dr. Nelson Spratt, Jr., an embryologist for whom I have the greatest respect. His numerous suggestions have been most helpful. The chapter on reptilian development could not have been written were it not for the generosity of another fine embryologist, Dr. Chester Yntema, who allowed me unlimited use of both his laboratory and his slides of reptilian embryos.

Drawings are an extremely important part of any textbook. Mr. Louis Rintrona, a former student of mine, has painstakingly worked to create illustrations to explain concepts that are sometimes difficult to put into words. Mrs. Mabel Levine, my untiring secretary, methodically typed the final manuscript and caught many errors which might otherwise have gone unnoticed. Mrs. Dorothy Sickels was extremely helpful in the proofreading and indexing of the final manuscript. Mr. Thomas Rotell and the staff of The Macmillan Company worked very closely with me through-

out the preparation of this book. Finally, I must acknowledge the stimulation and encouragement offered me by all my former students.

To all the above people I am extremely grateful, for without them this book would have remained simply an author's dream.

HAROLD W. MANNER

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PART I

Embryology is a vast field full of the intricacies associated with any sophisticated science. It cannot be comprehended if approached in its entirety. If a solid foundation of basic facts can be mastered first, it becomes much easier to comprehend the entire field. Although each embryo develops along specific lines, each with its own peculiar ramifications, certain processes of each are similar to many others. The first part of this book, therefore, is generalized. No specific embryo will be studied. Instead, embryological terms and processes will be explained. Each of these plays an important role later in this book, when the embryological development of specific vertebrates will be studied.

General Embryology

CHAPTER 1

Introduction

OBSERVING AN EMBRYO change from an apparently homogeneous sphere into an organized individual with a pulsating heart, a differentiated brain, and other equally developed organs, within the relatively short span of a few hours, cannot help but leave an indelible impression upon any serious student. The factors involved in this awe-inspiring transition are, for the most part, still little understood. It is possible, however, to describe with accuracy the sequences that occur throughout the developmental period. A better understanding of the vertebrates is obtained when the close similarities of their embryos are observed. Describing the embryology of selected vertebrates and relating these developmental sequences phylogenetically are the aims of this book. Perhaps the knowledge of what is happening within the developing embryo will stimulate some to join the rapidly grow-

ing ranks of experimental embryologists who are dedicated to the analysis of the factors involved in causing these developmental changes.

In the initial phase of the study of any science, the terminology appears overwhelming to many students. Of necessity there are many new terms which must be learned. A close examination of embryological terminology, however, reveals that a majority of the terms are meaningful combinations of various Latin and Greek roots. A knowledge of these roots facilitates the learning of the embryological terms.

It is difficult to study embryology from a textbook alone. For this reason the student should have at his disposal the embryos of as many different chordates as possible. Most biology laboratories are equipped with whole mounts and cross sections of frogs, chicks, and pigs. These should be studied in the laboratory as the various embryos are discussed. Only by comparing the actual embryo with the diagrams in this book will a full appreciation be gained of the events occurring during embryological development. No drawing can be more than an approximation. The drawings in this book are certainly generalized and can do no more than try to represent what is actually occurring in nature.

What Is Embryology?

Practically speaking, the life of an individual animal begins when a sperm and an egg are united in the process of fertilization. It might be more correct to say that an animal's life begins when the primitive germ cells that are destined to give rise to the egg and sperm begin to mature. At the other end of the life scale is death. During the intervening time a series of stages are passed through by every organism. These stages, although they differ specifically from one animal to another, can loosely be identified as the gamete formation, development, posthatching, larval, and adult periods. The entire sequence is referred to as the *ontogeny* of an animal (Fig. 1). If we consider the development of an organism in terms of its evolutionary past, we speak of the *phylogeny* of the animal. Specifically, *embryology* is that period between the fertilization of the egg and hatching, or birth. There is, however, a period before fertilization during which the *gametes,* the egg

and sperm, are formed. This is the period of *gametogenesis.* For our purposes, embryology will include the entire period of gametogenesis, fertilization, and development, up to hatching.

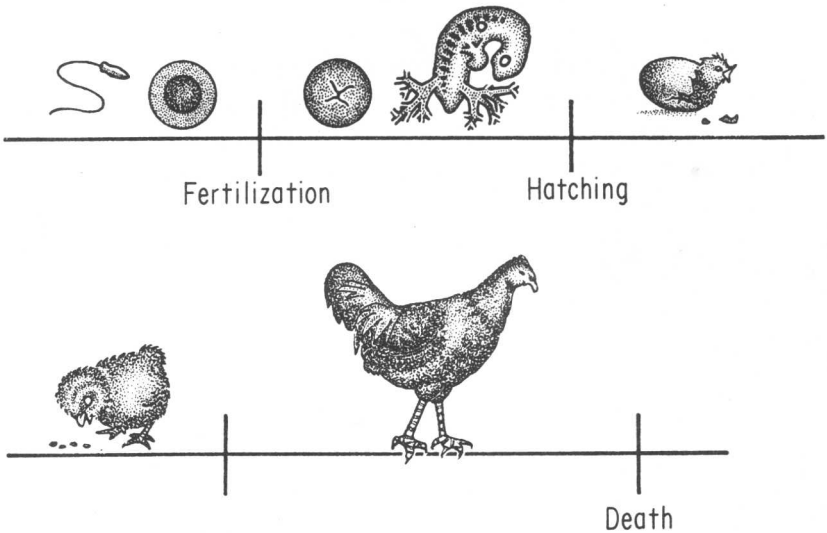

Fig. 1. **Ontogeny of the chick, depicting the gamete formation, embryological development, early posthatching, and adult stages of the life cycle.**

Types of Embryology

Now that we have defined the term "embryology," we must realize that there are different methods by which embryological development can be studied. Each is, in its own way, a very important aspect of the over-all science of embryology. One method is to observe what is occurring in a developing embryo, and where it is taking place. We can watch, for example, the development of the brain, the arms and legs, and all the other organ systems of the body. We can also indicate the time of appearance of these various organs. Embryology so studied is called *descriptive embryology.* Basically, a descriptive embryologist is interested in describing what is happening, where it is happening, and at what time it is occurring in the developmental sequence. Other embryologists, however, are more concerned with analyzing the causes underlying this development. These men are not as much interested in the chronological sequence of events in the development

of the limb as they are with such questions as: What is causing the limb to develop? Why does it grow? Where does it grow? What causes it to grow at a specific rate? This analysis of the causes of development forms the basis for *experimental embryology*.

Many different subsciences are included under the general heading of experimental embryology. Some experimental embryologists are concerned with the chemical nature of the causes underlying development. These men are *chemical embryologists*. Others believe that the developmental events occurring in the embryo are simply manifestations of the same basic physiological processes. This branch of experimental embryology is referred to as *developmental physiology* and includes the study not only of the basic embryological sequences but also of such developmental phenomena as regeneration and tumor growth in the adult animal.

Finally, certain scientists are not concerned primarily with either the descriptive or the experimental aspects of embryology. The branch of embryology that is concerned with comparing the embryological development of all vertebrates is called *comparative embryology*. The comparative embryologists, recognizing that there are certain basic similarities underlying the development of all vertebrates, believe that there might be a clue to the phylogenetic relationships among the vertebrates that might be found by studying their embryonic development on a comparative basis. We find, for example, that the embryos of the human, the salamander, and the tortoise go through a period of development in which they all possess rudimentary gill slits which are very similar to the gill slits of the teleost fish (Fig. 2). Quite a few other structures are similar in many embryos. The development of the aortic arches, the heart, the respiratory system, the kidney, and many other organs and organ systems are basically similar throughout the vertebrates. The only logical explanation for these similarities is that the embryos of higher forms carry in their developmental repertory the embryological remnants of those animals from whom they have been phylogenetically derived.

The science of genetics has shed some light on these developmental similarities. Point mutations or changes in genes are reflected in changes in the developmental patterns of animals. If these changes occur relatively early in the developmental sequence, the consequences are so drastic that usually the animal

doesn't live. Those changes that are most successful and have the greatest chance of being incorporated into the permanent genotype of the animal occur rather late in the developmental period.

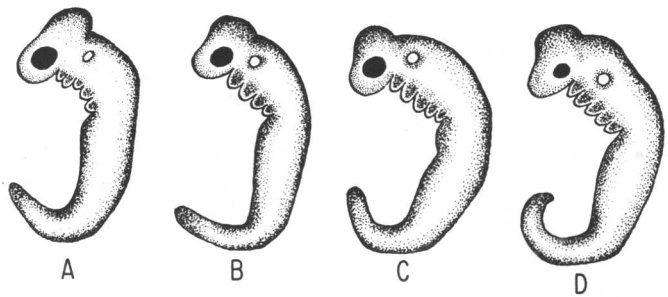

Fig. 2. **Embryos of the [*A*] teleost fish, [*B*] salamander, [*C*] tortoise, and [*D*] human. Note the striking similarities of the embryos of these representatives of four separate vertebrate classes.**

Since these occur near the end, the embryological sequences become longer and longer. This is known as *ontogenetic hypertrophy*. This has an important influence on the phylogenetic relationships among various animals. Because the changes occur rather late in the embryology, the original or early portions of the embryology remain rather similar. This means that the higher forms will reflect in their ontogenetic development the phylogenetic ancestry through which they have passed. It is this similarity of embryos which has led to the development of the biogenetic law that states simply that ontogeny recapitulates phylogeny. In simpler terms this means that the embryos of higher forms resemble at some stage in their development the embryos of lower forms.

The Animals to Be Studied

The animals discussed in this textbook have been chosen because of their phylogenetic relationships to one another. Figure 3 shows these animals on an evolutionary tree. It will be noted that the Amphioxus, a cephalochordate, is the prototype from which all higher vertebrates have evolved. The teleost fish, although not in a direct line of evolution, has been chosen because of its relatively low position on the evolutionary tree. Actually there are no embryological remnants of the primitive Osteichthyan types