MORPHOGENESIS OF THE VERTEBRATES

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PREFACE

This book is the outgrowth of a course recently inaugurated at Indiana University wherein the usually separate considerations of comparative vertebrate anatomy and vertebrate embryology have been integrated into a single unit. I make no claim for originality for such a treatment. The plan has been employed successfully at a few other colleges and universities for some time; yet it is an approach of such rarity as to make it still something of an innovation, so much so that those few of us who present courses in this fashion are still obliged to rely on conventional textbooks of embryology and/or comparative anatomy.

I have long felt that the dichotomy of approach to the origin of vertebrate form that is reflected in separate courses in anatomy and embryology is unfortunate because it has no reality with vertebrate morphogenesis itself. Comparative anatomical and embryological studies are actually two facets of an analysis of the total operation responsible for new body form. In the case of the individual, the obvious fact is that the embryo precedes the adult and that an understanding of the fabrication process, development of the embryo, contributes to an understanding of the end product, the adult. Conversely, preliminary knowledge of the end product furthers an appreciation of the embryonic process which creates it. On the broader evolutionary front, we find in the facts of comparative anatomy the record of successive changes in end product which have culminated in modern vertebrates. It was not without reason that nearly fifty years ago H. H. Wilder entitled his admirable textbook *The History of the Human Body,* for man's own form and function are the product of a long evolutionary history whose chapters are revealed in the lower vertebrates, both living and extinct. But because every adult begins as an embryo and every adult structure reflects a given embryonic history, the changing vertebrate bodies which have culminated in modern forms, including man, have been anticipated and accompanied by changing patterns of embryonic development. Whether we consider, then, the origin of the individual per se, or its derivation through a line of evolutionary descent, structure and development are indivisible.

Equally unnatural is a separation of form and function. There surely is no such thing as a nonfunctioning structure, nor do functions occur in the abstract without benefit of structure. Although our primary concern here admittedly is with the origin of form, to ignore its functional accompaniment is not only to ignore reality but also to lose sight of the very *raison d'être* of that form. For instance, the permutations of the adult excretory system have no meaning except in terms of disposal of metabolic wastes and the maintenance of delicate adjustments in blood stream content; and many of the transformations and accessories exhibited by the embryonic body relate as much or more to the embryo as a functional "going concern" as they do to the final adult product.

Consider, also, the status of modern embryology. Students of development have long since gone far beyond a preoccupation with description of changing form. Prime concern now is with causal analysis—the seeking out of the mechanisms, interdependencies, and genetic and biochemical factors that underlie the structural transformations which we observe and describe. Elusive as the final answers still are, the large body of analytical data presently available does provide important preliminary concepts and suggestive leads which, in my judgment, should be incorporated in even an introductory account of embryogenesis.

The very wealth of material available calls for judicious selection and careful blending. I have attempted throughout to keep in mind that the students who will read this book are beginners in the study of vertebrate morphogenesis. They cannot be expected to master, much less have an interest in, the minutiae and all the ramifications of descriptive, analytical, and functional anatomy and embryology. They seek to know only the broad sweep of morphogenetic events, and thus every fact introduced must stand the test of its use to this end. This does not necessarily make for superficiality. A book can be rigorous in content, as I believe this one is, without being encyclopedic. At the same time there should be challenges for those students with the interest and desire to pursue beyond the minimum. These have been provided by selected references accompanying each chapter and periodic "excursions" (set off in smaller type) into certain special issues. Also, as a matter of intellectual honesty and to cultivate critical thinking in those prone to believe that anything written is necessarily gospel, I have not hesitated to point up historically older ideas, conflicting or dubious interpretations, and unresolved problems.

It so happens that here at Indiana University the course which this book serves is organized on a one-semester basis. This circumstance derives in part from the fact that many of our enrollees are pre-medical and pre-dental students whose programs provide a niche of this size only. Yet even without this circumstance we should probably adhere to the one-semester pattern because of our conviction of the need for a speedier and more compact coverage of the groundwork of zoology. If present-day students are to become literate in modern experimental biology, as we feel they should, they must be provided "elbow-room" in an otherwise rigid structure of major and degree requirements to elect certain advanced courses. We cannot expect them, in an unchanging framework of time, to learn anything of the new unless we are willing to make some concessions in our demands for the old. Thus we feel it our obligation to prune and condense the standard fare so as to provide an opportunity for exploration on the frontiers of modern biology. Our one-semester "package" also reflects the view that all learning should not depend upon supervised study via courses. Our job is to get the fundamental things presented in as efficient a fashion as possible, then turn the responsibility for further learning over to the student himself. Much of what we regard as peripheral, and even some of the central, can and should be acquired through self-instruction. But since there may be teachers who will prefer a full year program, the coverage of the book has been designed to serve their needs as well. Used in its entirety, the book should provide ample material for a year; with the omission of certain chapters, for example, those on the musculature and integument, some selection within other chapters, and relegation of the "excursions" to an optional basis, the book is readily adaptable for a shorter course such as we give.

It is difficult to identify the source of all the material which has been dealt with. Much of it derives from information accumulated over many years of reading and study and who can say just when and where a particular item was acquired. Yet no teacher and author can gather and retain complete knowledge of everything; he must constantly tap the reservoir of the library. Some of the better standard textbooks of embryology and comparative anatomy have been consulted freely, but more for the purpose of gaining suggestions for organization and treatment than as sources of information. Textbooks are not the most healthy parents for other textbooks. I have chosen, rather, to turn directly to the many short papers, monographs, and books dealing with special topics, plus certain large general works of comprehensive scope. Some of the more provocative references in the first category are provided at the end of each chapter. It will be understood that these in no sense comprise a complete bibliography; they are intended only as suggestive leads for the student and teacher who may wish to pursue a particular topic in depth. The more notable of the general treatises, any one of which is a veritable mine of information in itself, are the following:

Bolk, L., et al., 1931–1933. *Handbuch der vergleichenden Anatomie der Wirbeltiere.* Urban and Schwarzenberg, Berlin.

Brachet, A., 1935. *Traité d'Embryologie des Vertébrés.* Edition Revue et Complétée par A. Dalcq et P. Gerard. Masson, Paris.

Bronn, H. G., 1874–1938. *Klassen und Ordnungen des Thier-Reichs.* Abt. VI. Leipzig.

Goodrich, E. S., 1930. *Studies on the Structure and Development of Vertebrates.* Macmillan, New York.

Grassé, P. P., 1952–1955. *Traité de Zoologie.* Tome XI, XVII. Masson, Paris.

Gregory, W. K., 1951. *Evolution Emerging.* Macmillan, New York.

Ihle, J. E. W., et al., 1927. *Vergleichende Anatomie der Wirbeltiere.* Berlin.

Needham, J., 1942. *Biochemistry and Morphogenesis.* Macmillan, New York.

Romer, A. S., 1945. *Vertebrate Paleontology.* University of Chicago Press, Chicago.

Willier, B. H., P. Weiss, and V. Hamburger, 1955. *Analysis of Development.* W. B. Saunders, Philadelphia.

Wilson, E. B., 1925. *The Cell in Development and Heredity.* 3rd Ed., Macmillan, New York.

Young, J. Z., 1950. *The Life of Vertebrates.* Oxford University Press, New York.

Such quality as this book may have is in no little degree the consequence of the reactions of students to the evolving course which spawned it. For a long period, when the book was only an idea in the making, successive classes served as a testing ground for possible approaches and sequences. As the idea materialized in a manuscript, many persons were to provide helpful and constructive suggestions. I am particularly grateful to my colleagues, Professors William R. Breneman, Sears Crowell, and Frank J. Zeller. In addition to a number of anonymous readers, who because of their anonymity had no fear of hurting my feelings, Professors Florence Moog of Washington University and Louis DeLanney of Wabash College were frank and helpful critics. Of course, final responsibility for the content (including errors) and organization of the book belongs to me alone. Although I myself either designed or selected for adaptation the drawings to be employed, and also prepared some, the accurate and attractive execution of most of them derives from the skill of Messrs. James Loveless and Tom Turpin, graduate students in our Department of Fine Arts.

THEODORE W. TORREY

Bloomington, Indiana
October 1961

CONTENTS

part 1 PANORAMA

1 HISTORY OF THE HUMAN BODY

The Continuity of Life

The essential substance of which all living things are composed is known as **protoplasm,** a complex colloidal system of organic and inorganic constituents long ago aptly characterized as the "physical basis of life." Not only are all organisms composed of protoplasm (and its products), but all the activities which collectively comprise life and by way of which we distinguish the living from the nonliving are associated with it. Conversely, protoplasm exists solely in the form of organisms and any consideration of it apart from living things is a meaningless abstraction. By the same token the word protoplasm does not describe a homogenous something which, like water, possesses distinctive chemical properties; on the contrary, the term is a pervasive one which describes all the permutations of form and function in living systems.

The task of the biologist has been and still is to understand this remarkable material in all its variety. The magnitude of the task is suggested both by the physical and chemical intricacy of protoplasm and by the kinds of things it does. That is, life is more than a structural complication. It is the distinctive behavior of which this physicochemical structure is capable that makes it the vehicle of life. Paramount in this behavior is the capacity for **reproduction,** without which life would disappear from the earth because of two important conditions.

First, all organisms and the various parts thereof have a limited life span. Although an organism has a measure of ability to cope with the ravages of aging and use on its parts, sooner or later the forces of decay gain the upper hand and death of the individual ensues. Thus the persistence of life upon the earth calls for replacement of the mortal individual. Second, although there is no final reason to assume that living systems of the simplest kind may not originate from nonliving matter on the earth at present, there is no positive evidence that such "spontaneous generation" of new life occurs nowadays or ever has occurred since the original inception of life countless millions of years ago, and there is much reason to believe it cannot. Hence it follows that all present-day organisms have been derived from preexisting organisms and those, in turn, from previous forms, and so on back to the beginning of life. "Where a cell exists there must have been a preexisting cell, just as the animal arises only from an animal and the plant only from a plant. The principle is thus established . . . that throughout the whole series of living forms, whether entire animal or plant organisms or their component parts, there rules an eternal law of continuous development." (Virchow, 1858)

Evolution

It has become increasingly clear in recent years, especially through genetic and biochemical studies on viruses and bacteria, that the basis of reproductive behavior lies in the ability of that entity which we call the **gene** to duplicate itself. In fact, we may envisage the origin of life itself in the assembly out of nonliving ingredients of a molecule capable of reproducing itself. But in addition to the mere(!) capacity for duplication, the primeval gene also possessed the ability to reproduce its chemical variations, thus providing for an increased variety of genes. Consequently, we may conceive of the original genes as having assumed the role of centers of chemical activity for the construction of organized systems of chemical substances that constitute the cells and tissues of organisms as we usually think of them. From these simple beginnings, thanks to the ability of genes to reproduce their variations and to imprint these variations on their host cells, there arose the present multitudinous variety of living things.

What we are saying is essentially this: (*a*) in contrast to the relatively simple structure and limited variety of the first living things, present-day plants and animals exhibit a bewildering array of kind and form; and (*b*) there has been, so far as we know, no spontaneous creation of new form; new organisms have been derived only from pre-existing organisms. Therefore it follows that, as new generations of organisms have arisen down through the ages, changes have occurred. If this were not so, present-day living things would differ in no way from the original living things. This is the essence of the principle of **evolution**—that all organisms have arisen from common ancestry through a gradual process of change and diversification.

Nowadays among biologists there are no dissenters with the principle of evolution. That this was not always so is revealed by 200 years of history in which the evolutionary mode of thought struggled to establish itself. Yet even after evolution as a basic principle became a conviction of the scientific mind, the mechanism of the evolutionary process remained at issue. Accordingly, numerous hypotheses attempting to explain evolution were advanced and debated from time to time. It is beyond our province to review these. Suffice it to say that the Darwinian view of natural selection, implemented by modern genetic theory, presently appears to provide the most satisfactory answer. The intention here is to point up the distinction between the fact of evolution, the evidence for which with respect to the vertebrates will be marshaled in the coming chapters, and theories of evolution designed to explain how the changes described may have come about.

History of the Human Body

With the principle of the continuity of life in mind, it follows that all living things, past and present and including man, are related. Any two organisms, however great the structural differences between them, are joined by intermediate links and, ideally, we should be able to plot the ancestral course of any species along this connecting chain. That this can rarely if ever be done completely derives from apparent discontinuities in the chain resulting from past extermination of many forms that are largely unknown to us today.

The closeness of relationship between two organisms is measured by the number of structural and functional features that they possess in common. Thus John Doe is most like his brothers and sisters and parents, that is, they are his nearest relatives. He has fewer points of identity with, is more distantly related to, his aunts and uncles and cousins. There is established in the same fashion John Doe's position in relation to all other men, to primates, to mammals, and to vertebrates. In other words, man is a vertebrate and is related in some degree to all other kinds of vertebrates. But since man, compared to other vertebrates, is a relatively recent arrival on the evolutionary scene, we may find in these earlier established forms indications of the evolutionary pathway that has led to man. The history, then, of these vertebrate relatives is man's own history; the evolution of the vertebrates is the "history of the human body."

The succession of forms which culminates in any given structural entity constitutes the race history, or **phylogeny,** of that entity. By common consent the concept of phylogeny is applied either to the total body form or any part thereof. In other words, we may speak of the phylogeny of man or the phylogeny of the excretory system or the phylogeny of a single organ such as the heart. The relationships and lines of descent comprising a given phylogenetic history are established through comparison of anatomical features, **comparative anatomy.** When such comparative study involves data from extinct organisms, available only as fossils, it is designated **paleontology.** But sometimes the likenesses and unlikenesses of parts of organisms are not self evident and it is necessary to turn to another line of evidence. We refer to the sequence of transformations presented during the embryonic life of the individual, for the real nature of an adult part is often revealed by the developmental events that bring it into being. This developmental history of the individual or its parts is known as **ontogeny.** Now it is obvious to everyone that the newly hatched bird or the newborn human infant is not fully formed; some measure of development follows hatching or birth. That is, the term ontogeny, "origin of the individual," refers to the totality of developmental operations. For that more restricted segment of ontogeny which precedes hatching or birth we employ the term **embryogeny,** "origin of the embryo." The study of an embryo is designated as **embryology.**

Not only is understanding of adult form furthered by revelation of the embryonic history of that form, but comparative embryological studies have demonstrated that the more closely related animals are, the more nearly alike are their ontogenetic histories. Ontogeny thus provides an important tool for the establishment of the relationships upon which the lines of evolutionary descent are based.

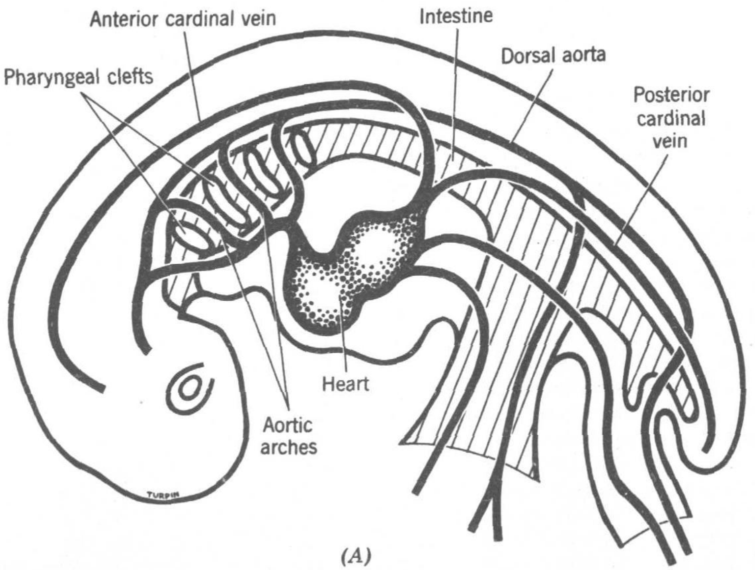
The Recapitulation Principle. The suggestion that the facts of ontogeny may throw light on the course of phylogeny brings us face to face with an issue of interpretation that has been of paramount importance in the history of biology. Because history is a continuous thing, with its beginning lost in the ages and its end not in sight, it is difficult to know where to break into the story. But a suitable start may be made at that stage in human thought when it was believed that all the varieties of form and function exhibited by living things represented the product of a divine creator. Moreover, the universe and everything in it was considered to be fixed and unchanging as it had been from the moment of creation and as it would be until time ran out. Yet during and even before the period when this view predominated, there were those who had reason to believe that organisms had not always been as they are; on the contrary, it was felt that over the ages organisms had changed and, as a consequence, new and more complex forms had arisen. This is a restatement of the fact of evolution which, with the advent of Charles Darwin, was to become established as a keystone in biological thought. The point to be made here is that, as a consequence of the rise of evolutionary doctrine, living things ceased to be looked upon as immutable entities to be cataloged in some fashion of convenience or in a way that presumably reflected a divine blueprint. The fixed unit of classification gave way to the evolving unit and, more importantly, the arrangement and grouping of units began to be done in terms of the relationships between them and the order of descent one from the other. Thus it is that a modern scheme of classification provides a summary of phylogenetic history. In its crudest outline the phylogeny of man and other mammals is found in the succession: fishes → amphibia → reptiles → mammals (man).

But let us also remember that every individual animal starts out as a fertilized egg which, by a series of transformations, is converted to final form. This series of developmental events is encompassed in the term ontogeny of which the earlier, more circumscribed events comprise embryogeny.

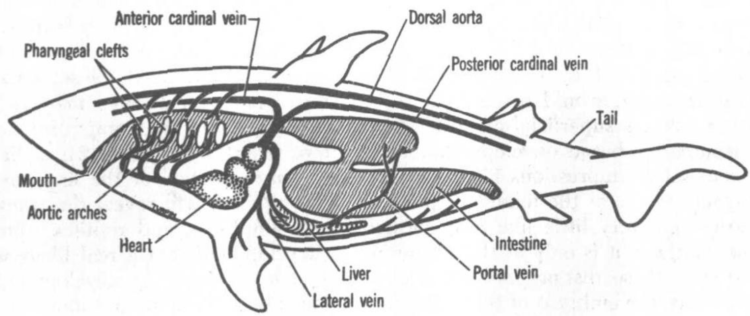
It is difficult to identify the first germ of the idea, for it appears in the writings of several biologists from 1821 onward, but in 1891 Ernst Haeckel, the German morphologist, proposed a marriage between ontogeny and phylogeny that was to affect profoundly the interpretation of developmental anatomy. Haeckel argued for what he called the **principle of recapitulation,** according to which the successive stages of individual development (ontogeny) correspond with successive adult ancestors in the line of evolutionary descent (phylogeny). The scheme may be thought of as working something like this: if, for instance, a series of ontogenetic stages *a-b-c* produces an adult fish, the addition of new steps, making the ontogeny *a-b-c-d-e*, would produce an amphibian, and so on through reptile to mammal. Accordingly, a developing mammal would first be a fish, then an amphibian, and then a reptile before it became a mammal; it would, in other words, pass through the adult stages of its ancestors. As Haeckel put it, "die Ontogenie ist eine Recapitulation der Phylogenie (ontogeny recapitulates phylogeny)." In its application, the principle was made to work in two directions: on the one hand, it provided a causal explanation for the order of ontogenetic events; on the other, the events of embryonic development were employed to help establish phylogenetic relationships.

Obviously, if the idea of recapitulation was to be embraced, as it was whole heartedly, and was to persist, as it does in some measure to this very day, it had to embody an element of truth. This derives from the fact that a developing embryo proceeds toward its goal of final form by an indirect route. Along the way it exhibits conditions which are indeed suggestive of those possessed by its ancestors. Comparing, for example, a human embryo with an adult shark (Figure 1-1), we note in the embryo such features as a tail, a series of gill-like pouches in the neck region, and a layout of blood vessels—all of which are fish-like in general appearance. Closer scrutiny, however, would reveal that the likenesses between embryo man and adult fish are superficial at best. In fact, if we expand the comparison to encompass a broad developmental series of vertebrates (Figure 1-2), a different set of impressions begins to emerge. An inspection of the first embryonic stages of the mammals pictured in Figure 1-2 will reveal that they really look very little like fully formed fishes, amphibia, and reptiles. On the contrary, it is only at the beginning of development that a real likeness between these distinct categories of vertebrates obtains. As development proceeds, the embryos of these different animals become more and more dissimilar. The more distantly related two animals are, the earlier these differences begin to manifest themselves; conversely, the developmental pathways of more closely related forms run parallel for a longer time (vide the mammalian embryos in Figure 1-2).

It was observations of this kind which led the great German embryologist Karl von Baer, many years before the rise of evolution theory, to make two major points which generalized the situation far more accurately than did Haeckel's aphorism. (1) Animals are more similar at early stages of their



(A)



(B)

Figure 1-1. Schema of the structure of a human embrvo (*A*) compared with that of an adult fish (*B*).