

PREFACE

The reception accorded to the first edition of this book has been very gratifying. Students and teachers countrywide have communicated their pleasure and satisfaction with the book, which is no small reward for the time and effort that went into its preparation. Many of these communicants also submitted constructive criticisms and suggestions for the betterment of the book, and my own use has revealed the need for certain modifications and adjustments. The entire text therefore has been critically scrutinized, which resulted in much rewriting ranging from individual sentences to entire sections. Some topics have been updated, others have been expanded, and still others that were originally bypassed have now been included. The illustrations have also been reexamined, and a sizable number of them have been modified or replaced. If all of the recommendations that have been received have not been followed, it is because they have often been contradictory. "One man's meat is another man's poison." Final responsibility for the content of the book therefore is mine alone.

The rationale and organization of the first edition, however, have been carried forward to this edition.

I remain convinced 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 in 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 that creates it. On the broader evolutionary front, we find in the facts of comparative anatomy and paleontology the record of successive changes in end product which have culminated in modern vertebrates. It was not without reason that a half century 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 that have culminated in modern forms, including man, have been anticipated and accompanied by changing patterns of embryonic development. Whether we consider 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 occasional "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 that this book serves is organized on a one-semester basis. This circumstance derives in part from the fact that many of our enrollees are premedical 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 "elbowroom" 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 to be 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 on 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 because 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 that 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 on 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. Daleq et P. Gerard. Masson, Paris.
- Bronn, H. G., 1874-1938. *Klassen und Ordnungen des Thier-Reichs*. Vol. VI. Leipzig.
- DeHaan, R. L., and H. Ursprung, 1965. *Organogenesis*. Holt, Rinehart and Winston, New York.
- Goodrich, E. S., 1930. *Studies on the Structure and Development of Vertebrates*. Macmillan, New York.
- Grassé, P. P., 1950-1958. *Traité de Zoologie*. Vols. XI, XII, XIII, XV, XVII. Masson, Paris.

- Gregory, W. K., 1951. *Evolution Emerging*. Macmillan, New York.
- Ihle, J. E. W., et al., 1927. *Vergleichende Anatomie der Wirbeltiere*. J. Springer, 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., 1962. *The Life of Vertebrates*, 2nd ed. Oxford University Press, New York.

I remain grateful to those persons who did so much to make the first edition a successful venture, and I add my thanks to the many students and teachers whose suggestions have guided this revision. The name of John Peterson, staff artist in our Audio-Visual Center, should be added to the roster of those whose skill is manifest in the illustrations.

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