Analysis of Vertebrate Structure

SECOND EDITION

MILTON HILDEBRAND

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Preface

A first characteristic of this book is breadth. Description of structure is included, as it always is, because knowledge must precede interpretation. Interpretation of structure in terms of phylogeny is included, as is usual, because organic evolution is one of the greatest stories biology has to tell, and the lineages of vertebrate animals illustrate the story with more continuity and persuasion than do the known lineages of other animals or plants. Also included, however, are interpretations of structure that relate to function, development, and some other factors.

A second characteristic of this book is its placement of emphasis. Phylogeny is stressed, yet is less dominant than in some other texts. More than usual emphasis is given to interpretation of structure on the basis of function. This is currently the emphasis of much research, and thus provides the opportunity to add recent advances to classical knowledge. It brings to attention the variety and perfection of vertebrate structure, and it lends itself to analytical treatment to which, in my experience, students respond with interest. Moderate attention is given to the evident and engaging relationship between development and adult structure. Developmental biologists now place less emphasis on the broader aspects of evolution than they did several generations ago, yet much excellent work is being done on relative growth and evolutionary morphogenesis. Interpretations of structure based on body size, age, sex, and individual variation round out the narrative.

A third characteristic of the book is its style and coverage. It is uniform, integrated, and easy to use. All illustrations are cited in text by figure number if in the same chapter and by page number if elsewhere. Figures are fully labeled

(not keyed to complex legends) and legends distinguish (by capital and lowercase letters) between the point illustrated and subordinate material. I intend that the presentation be sound and solid, yet not overly technical. The book does offer a lot of material. However, description as an end in itself is minimized—particularly in Part III. Details that do not serve interpretations are omitted. The qualifying words "usually" and "sometimes" are used frequently for the sake of accuracy, but specific exceptions to usual structure are "usually" omitted. A reasonably full vocabulary of the basic terms of morphology is provided without introducing unusual terminology or saying in Latin what can better be said in English. An effort has been made to sort concepts from illustrative material, and free use has been made of parenthetical statements to subordinate the examples and qualifications.

Fourth, the book is profusely illustrated with original artwork of high quality and uniform style. My wife and I worked together closely on the illustrations. It is principally her talent that makes the artwork distinctive; she made all the carbon pencil drawings and some of the pen and ink drawings (about 44% of the total). I selected materials (largely from my teaching collection), and made most of the pen and ink drawings (about 43% of the total). The publisher's staff artists completed the more diagrammatic illustrations (about 13% of the total) from my sketches and did all labeling. For each subject we sought an appropriate compromise between illustration that is so pictorial as to introduce extraneous detail, and illustration that is so simplistic as to reduce the living body to mechanical analogs. In preparing the second edition, 27 illustrations were deleted, 12 modified, and 47 added.

Fifth, this book presents vertebrate morphology as a living discipline. The transformations from fin to limb, from jawbone to ear ossicle, from branchial artery to carotid circulation, and many more, are classic stories that should be retold to new generations of students, yet note is also made of recent studies, unsolved problems, tentative explanations, active areas of research, and current trends in the discipline.

Finally, it is hoped that this book will be found interesting. No field of study as large and complex as this one is likely to interest every student in all its aspects. Application will be needed: The book is not intended as light entertainment. Nevertheless, it is a tragedy that the teaching of comparative anatomy has sometimes been a parade of dull facts, dusty skeletons, and much-preserved specimens. Nothing else in nature has more exquisite structure than the vertebrate body. I will be pleased if the reader occasionally forgets the forthcoming examination and reads on thinking "Wow, that's really something!"

Part I of the book is a survey of the vertebrates. Students must be able to recognize and relate the major taxa in order to follow Parts II and III. Brief descriptions that stress typical features and recognition characters serve as preparation for these parts. Extinct groups are included or not, according to their relation to what will follow.

In Part II, the customary organ system approach is used to present the general structure of the classes and subclasses of vertebrates and to review the structural

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evidence for their evolutionary relationships. Features that do not characterize major taxa or do not show progressive change between successive categories are deemphasized or omitted. The treatment is less detailed than in several other texts, yet includes, I believe, as much "meat" as can be learned in one course of study. Many students think that teachers of anatomy tend to pack into their courses more detail than will be useful. The proportionately few students who will become professional morphologists can easily find supplementary information elsewhere.

Part III presents knowledge and analysis of the major functional groups of vertebrates. Following two chapters on bone-muscle mechanics, successive chapters consider the major locomotor and feeding adaptations in order. Unrelated, often convergent, groups of animals are taken together to see how evolution has provided for their common requirements. Extreme modifications (which would be distractions in Part II) are included.

About 327 selected and partly annotated references are listed at the end of the book to give students a start on assignments and seminars and to indulge the curiosity of anyone having unanswered questions. Some 85 titles were deleted, and 133 added in updating for the second edition. The meanings of more than 150 word roots are given parenthetically where first used in the text. These are intended as aids to understanding, and hence memory, not as etymology lessons. A glossary of 565 terms is added to the second edition.

A preparatory course in general biology or zoology is assumed; most of the requisite fundamentals and terms are reviewed here, but would come as a big dose if none were already familiar. A prior foundation in embryology, physiology, or evolution is desirable to give the student the benefit of additional familiar ground, but is not assumed. Similarly, recollection of algebra and geometry, and a course in physics would make Part III easier, but more for the security provided than for formulas remembered.

Some students complain that textbooks present more than can be learned. Well, the gourmet is not able to eat all that is on the menu, but does not therefore desire few selections; others have other tastes and he will himself choose differently another time. I urge instructors not to serve up more of this book than can be assimilated in the time available. In a two-term course, most of the chapters can be presented. In a one-term course, selection is necessary. A balanced diet can be obtained by combining portions of both Parts II and III, thus illustrating more than one of the major approaches to the analysis of structure and abandoning the myth that any one approach would be "covered" merely by assigning all relevant chapters in this, or any other, text. Unassigned chapters can become the bases for special reports. Furthermore, I hope that students and instructors will permit the terms and the illustrative and parenthetical material in the book to support but not substitute for the ideas.

Of the nearly 1000 separate drawings comprising the illustrations, about 64% are completely original, about 20% are largely original, and the remainder are all redrawn with some modification. We acknowledge our debt to more than 150 authors whose illustrations have been used to a greater or lesser extent as a

World, by E. P. Walker, 18 drawings are taken at least in part from one or another of the books by A. S. Romer, and 15 drawings are patterned on illustrations in *Traité de Zoologie.*

Prepublication reviewers are never responsible for the deficiencies of a book, yet they are responsible, if competent and conscientious, for great improvement in the manuscript. I have been fortunate in having such reviewers. Carl Gans and David B. Wake each read the entire text and made hundreds of very valuable suggestions. Five chapters were reviewed by Karel F. Liem, two chapters each by R. Glenn Northcutt and Irving H. Wagman, and one chapter each by Paul F. A. Maderson, Paul S. Moller, Terry A. Vaughan, and Marvalee H. Wake. I also thank reviewers of the first edition and the following reviewers of the manuscript for the second edition: Margery C. Coombs, University of Massachusetts; James Edwards, Michigan State University; Abbot S. Gaunt, Ohio State University; William B. Muchmore, University of Rochester; Bedford M. Vestal, University of Oklahoma; and Ralph M. Wetzel, University of Connecticut. I gratefully accepted most of the suggestions of most of them.

I shall be thankful to instructors and students who send me corrections, comments, and sources of material for subsequent revisions.

Milton Hildebrand
Davis, California

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STRUCTURAL ADAPTATION:
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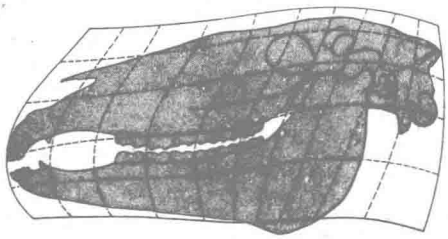

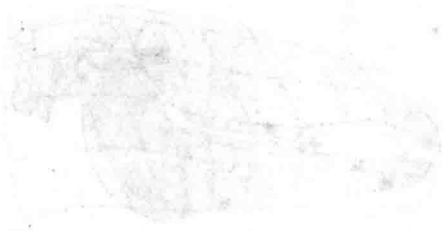

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The Nature of Vertebrate Morphology

DEFINITION, SCOPE, AND RELATION TO OTHER DISCIPLINES

Anatomy is the science of the observation and description of structure. Gross structure, microstructure, and ultrastructure are included, though this book stresses the first and presents little of the last. Morphology is the broader science of *relating* and *interpreting* observed structure.

Since structure is influenced in many ways, information is needed from many sources if interpretation is to be reasonably complete: (*1*) Much interpretation follows from knowledge of the historical origins, or phylogeny, of form. Thus, morphology relates closely to paleontology, taxonomy, and the principles of evolution, and draws upon other fields such as serum chemistry and analysis of chromosome structure that provide evidence of evolutionary affinity. (*2*) Also, much interpretation is dependent upon knowledge of functional adaptation (i.e., suitability to fill a need effectively). Morphology is therefore related to ecology, ethology, physiology, biophysics, and biochemistry. Some adult structure is interpreted through (*3*) knowledge of embryology, and some through (*4*) analysis of the relation between form and size. Other structure is (*5*) age-dependent or (*6*) sex-dependent. Finally, (*7*) individual variation of structure may have genetic, nutritional, pathologic, or other environmental origins.

Thus vertebrate morphology relates to many other sciences. It is desirable for the morphologist to supplement training in the principles of biology at all levels and grounding in vertebrate structure by gaining familiarity with the concepts and methodology of one, or preferably more, related disciplines.

This book describes the anatomy of the major structural and behavioral groups of vertebrate animals, and interprets their morphological differences primarily in terms of ancestry and function, employing related fields as needed to further this objective.

WHY STUDY VERTEBRATE MORPHOLOGY?

In order to generate the interest and application needed to derive full value from any course of study, the student must be convinced that the returns will justify the effort. Different students derive different benefits from studying vertebrate morphology, but the following advantages, in varying proportions, accrue to most students:

1. Knowledge of anatomy has direct application to many specializations within biology. The surgeon and veterinarian, experimental embryologist and neural physiologist, paleontologist and pathologist, all need to be familiar with the structure of their materials.

2. Knowledge of animal structure has made important contributions to human health and technology. The selection of experimental animals, the conduct of innumerable studies in basic and applied physiology and medicine, and the design of prosthetic devices are examples. Some engineers are studying animals for clues to improved design of bearings, ships, and aircraft.

3. Study of morphology increases the biologist's understanding of the materials at hand. Through interpretation one becomes less of a practitioner and more of a professional, less a technician and more a scholar, less a catalog of facts and more an expert. This benefit is difficult to measure, yet can be of great value to the individual.

4. Analysis of structure may increase the biologist's interest in, and even fascination with, animal form. This subtle benefit can be very rewarding.

5. Vertebrate morphology provides particularly favorable evidence for the process and product of organic evolution. It contributes to the answering of questions that have long been important to man: What forces govern the stream of life? How can one gain perspective in time and space? How can one account for the perfection of the animal body?

Study of vertebrate morphology is unlikely to bring wealth, fame, or influence, but it *is* likely to increase the biologist's competence and pleasure in his or her work.

SOME PRINCIPLES AND CONSIDERATIONS

HOMOLOGY AND ANALOGY Features of two or more organisms are **homologous** if they share common ancestry (see examples 1 to 4, Figure 1-1). Homology is established if the features can be clearly linked through time by continuity in the fossil record, and is reasonably sure if they can be shown to develop similarly in the embryo from identical primordia. Homology may be difficult to establish in specific instances, and the acceptable remoteness of the common ancestor may be disputed. Nevertheless, the concept is clear and very important.

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