

Preface

*It is not now, nor will it ever be given to one man
to observe all the things recounted in the following pages.*

Waldo L. Schmitt

Crustaceans, 1965

When we started this project some years ago it was our intention to produce a book of about 400 pages. Obviously, we were unable to do that. The field of invertebrate zoology is so vast, and cuts across so many disciplinary lines, that even in a book of this size we have found it necessary to generalize about some topics and to slight others. As university instructors, we realized early on that the teaching of invertebrate zoology should not be compartmentalized. Thus in preparing a single-volume work on invertebrates we were concerned about two potential dangers. First, the book might become an encyclopedic list of "facts" about one group after another, the sort of "flash-card" approach that we hope you will avoid in your study. Second, the book might be a rambling series of stories or vignettes about the animals and their ways of life. The first book would be dull, would encourage rote memorization instead of understanding, and might reinforce the misconception that there is little left to discover. The second book would be full of interesting "gee whiz" stuff but might seem disorganized and without much continuity or purpose to the serious student. Although our book has some elements of both problems—many new terms and a great deal of factual information, as well as interesting bits of invertebrate natural history—we have organized it in the belief that what we *know* about these animals is not as important as what and how we *think* about them. The primary purpose of this book is to provide enough information and ideas to enable you to understand the broad and dynamic concepts underlying the study of life and some of the ways by which biologists have come to develop these concepts. You should be prepared to assimilate much new material. Be prepared, also, for a great deal of uncertainty; much remains to be discovered.

To establish threads of continuity throughout this mass of information, we have developed our book around three fundamental themes: (1) functional body architecture, or what we call the *Bauplan* concept; (2) developmental patterns and life history strategies, mainly as they relate to adult lifestyles; and (3) evolution and phylogenetic relationships. We feel these themes are basic not only to understanding invertebrates but also to understanding life in general and how it has evolved. The first four chapters explore these themes and provide a foundation on which the rest of the book depends. Please read these chapters carefully and refer back to them throughout your study.

In the remaining chapters, we try to use these three themes as a common vehicle to tie the animal phyla together in a logical and interesting way. Furthermore, we present information in a comparative fashion wherever possible, both within and among major taxa. We also include a considerable amount of

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information on the general ecology of various groups, but this is generally incorporated into our *Bauplan* discussions.

Zoology texts have traditionally used one or the other of two approaches. One is the strictly taxonomic or "survey" approach, wherein phyla are broken down into their various subordinate taxa and each is discussed separately. This approach usually bears the double burden of redundancy and conceptual fragmentation. The second is the "systems" approach, wherein anatomical or physiological systems are surveyed. This approach can largely ignore the importance of taxonomic diversity, phylogeny, and the relationships of the whole animal to its environment. We have tried to fuse the two approaches by presenting *both* a taxonomic survey *and* a systems survey. We integrate the taxonomic and systems information largely by emphasizing the themes noted above.

The bulk of this book (Chapters 5–23) is devoted to a phylum-by-phylum discussion of invertebrates. Fairly detailed classifications or taxonomic synopses for each phylum are included in separate sections of each chapter to serve as references. We have endeavored to maintain a similar and consistent organization throughout each chapter, although we yield to the important and sometimes different lessons to be learned by investigating the special attributes of each group of animals. In addition, because of their size and diversity, some taxa receive more attention than others—although this does not mean that such groups are more "important" zoologically than smaller or more homogeneous ones. In certain chapters we cover more than one phylum. In some cases the phyla covered together are thought to be closely related to one another; in other cases the phyla merely represent a particular grade of complexity and their inclusion in a single chapter facilitates our comparative approach. Five chapters are devoted to the arthropods and their kin; for all other phyla, we discuss the entire group as a whole. The goals of our approach are to reduce redundancy, illustrate our themes, and underscore both the diversity and unifying attributes of each phylum.

Certain aspects of this book have, of course, been influenced by our own biases; this is especially true of the discussions on phylogeny. We have used a combination of cladistic analyses (cladograms), narrative discussions, and traditional (orthodox) evolutionary trees to discuss existing classifications and derive phylogenetic hypotheses. We have used cladograms whenever feasible because we believe they provide the least ambiguous statements or hypotheses of relationships that can be made about animal groups (see Chapter 2 for a discussion of cladistics). We would have liked to include more cladograms, but the field of cladistics is so new that few invertebrate cladograms have been published; and many of those must be regarded as very preliminary phylogenetic hypotheses in need of further testing and refinement. We know that some of you, professors and students both, will disagree with our methods and ideas to various degrees—at least we *hope* that you will. We implore you never to placidly accept them without question.

Most of the cladograms in this book are new and were derived by cladistic procedures based on the maximum parsimony method (i.e., the use of logical

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parsimony, or Occam's razor). Simple ones were constructed by hand, but more complex ones were generated by a computer phylogenetics program called PAUP (Phylogenetic Analysis Using Parsimony). PAUP was written and is distributed by David L. Swofford (Illinois Natural History Survey). PAUP analyzes data sets of characteristics to find the most parsimonious tree(s) possible; in other words, it strives to find the tree(s) requiring the fewest character transformations (the shortest tree) and the smallest number of homoplasies (the fewest hypothesized evolutionary convergences, parallelisms, and reversals). Thus, the maximum parsimony method is equivalent to minimizing the total number of evolutionary "steps" needed to explain the evolution of each taxon and character in the tree. Other phylogenetic parsimony programs exist, but our experience has shown that most will arrive at the same (shortest) trees given prudent application. Descriptions of numerical methods of cladistic analysis can be found in the literature (see references in Chapter 2, especially studies by Farris, Felsenstein, Kluge, and Wiley), and documentation for PAUP was, at the time of this writing, available on request from David Swofford.

We believe that it is absolutely essential for an introductory course on invertebrates to be framed within the context of evolutionary biology. To do so, one cannot rely on reductionism but must view organisms as complex systems operating and evolving together and in concert with the environment. We work in an age of specialization, and there is extensive fragmentation within every scientific discipline. This fragmentation has led to a tendency in zoology texts to deemphasize the fundamentally important fields of comparative anatomy and developmental biology. To the extent possible, we have tried to avoid this trend in our book by taking a "whole animal" approach. Most of the major animal body plans that we recognize today originated in a burst of evolutionary radiation during the Precambrian and Cambrian periods. Most of the evolutionary history of life has been a protracted period of adaptive specialization and exploitation of these fundamental body plans, or *Baupläne*. For this reason we emphasize both the phylogenetic origins of animals and the specializations that have evolved within each of the major lineages.

The book's final chapter is a phylogenetic summary, an overview of the major evolutionary ideas presented in the book. In it we reinforce the point that much remains to be explored and learned about invertebrates. Like all scientific knowledge, we are dealing here with provisional, wispy, transient "truths" that always remain open to challenge and revision. This is especially true with regard to the evolutionary relationships among animal phyla—something biologists really know very little about. And, of course, scientists disagree. It is this disagreement and the constant challenging of hypotheses that push the frontiers of knowledge forward.

There are a few other things you should know about this book. We provide a brief historical review of the taxonomy and classification of each major group. We feel this material not only is interesting but also serves to imbue students with a sense of the dynamic nature of taxonomy and the development of our understanding of each group. Unless otherwise indicated, the Classification

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section in each chapter deals only with extant taxa. Descriptions of taxa in these annotated classifications are written in telegraphic style to save space.

Important new words, when first defined, are set in **boldface type**. These boldfaced terms are also indicated by boldfaced page references in the index; thus the index can also be used as a "glossary." Although we have tried to be consistent in our usage of zoological terminology, the existence of similar terms for entirely different structures in certain groups is notoriously troublesome. We try to point these out where appropriate in the text. We also opt for contemporary spellings and usages where several options are available.

We have tried to be as current as possible with citations listed in the reference section for each chapter, but even as this book goes into production important new publications cross our desks. It has been estimated that the volume of scientific information is doubling about every 10 years. A half-million nonclinical biology papers are published annually. As Professor George Bartholomew noted, "If one equates ignorance with the ratio between what one knows and what is available to be known . . . each biological investigator becomes more ignorant with every passing day." Our goal has been to provide sufficient reference material to lead the interested student quickly into the heart of the literature for all the invertebrate phyla. Most of the references cited in the text will be found at the end of the corresponding chapter. However, to conserve space and eliminate redundancy, in a number of cases (especially in figure legends) references of a general nature may be listed only once, usually in the introductory chapters. In most figure legends, the original sources of the illustrations are cited; but when such sources predate 1940 we cite only our direct source for the illustration. We also include a fair number of references that are quite old, some from the nineteenth century. We have done so not out of whimsy, but because many of these are benchmark research papers or stand out as some of the best available descriptions for the subject in question. It is surprising how many of the illustrations in modern invertebrate texts derive ultimately from nineteenth-century publications.

These things being said, we hope you are now ready to forge ahead in your study of invertebrates. The task may at first seem daunting, and rightly so. We hope that our book will make this seemingly overwhelming task a bit more manageable. If we succeed in enhancing your education, and your enjoyment and appreciation of invertebrates, then our efforts will have been worthwhile.

R.C.B.

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