

Preface to the Third Edition

For this edition of *Invertebrates*, Wendy Moore and Stephen M. Shuster joined as co-authors. In addition, 22 other contributing authors graciously agreed to revise selected chapters or chapter sections. And two dozen reviewers were kind enough to critically read various chapters of the book. There is likely no way *Invertebrates*, Third Edition could have the depth and accuracy it has without the help of these wonderful professionals and specialists, and we are deeply indebted to them.

An information explosion has occurred since the Second Edition of this book, especially in the fields of molecular biology and phylogenetics. Just as the Second Edition of *Invertebrates* was going into production, the beginning framework of a new metazoan phylogeny was starting to appear in the scientific literature, although at that time it was based almost entirely on ribosomal gene trees and considerable disagreement existed. In the intervening decade, this new phylogeny was refined—although many details still remain to be worked out. Most importantly, Protostomia and Deuterostomia have been redefined, and the long-standing Articulata group (based upon a hypothesized sister-group relationship between Annelida and the Panarthropoda) has been disarticulated with annelids now being placed among the Spiralia, and arthropods among the Ecdysozoa. The phyla Echiura and Sipuncula have been subsumed into Annelida. The basal, diploblastic phyla have been shuffled about near the base of the Metazoa tree, and they might continue to shuffle about for a bit longer; as this edition goes to press. We predict that, by the Fourth Edition of *Invertebrates*, the phylogenetic positions of all (or at least most) of the metazoan phyla will be stabilized—a lofty goal long sought by zoologists.

As in the Second Edition, important new terms are printed in boldface when first defined (and these are noted in the Index). Specific gene names, like species

names, are italicized (though note that names for classes of genes, e.g., Hox and ParaHox genes, are not italicized). We have again included the protists in the book, because instructors teaching Invertebrate Zoology usually cover the “kingdom Protista” and have asked for it. Our knowledge of protistan biology and phylogeny has expanded so much since the Second Edition that the amount of new information, even briefly presented, is substantial. The ICZN (International Code for Zoological Nomenclature) eschews use of diacritical marks in formal taxonomic names, and we follow that recommendation. However, for other terms we generally retain the original spellings and diacritics. So for example, there are archoöphoran and neoöphoran flatworms (the terms describing modes of egg development), but there are also the (now largely abandoned) taxa Archoophora and Neoophora.

Much of the art for this edition has been updated. However, we continue to include diagrams that will be useful to students in the laboratory, including for animal dissections. We also continue to provide rather detailed classifications and taxonomic synopses within each phylum. We don’t expect these to read in the same way as the rest of the chapter, but rather to be used as a reference to look up taxonomic names, understand the traits that distinguish groups, or get an overall sense of the scope of the higher taxa in a phylum.

To say this book is a “labor of love” would be an understatement. Without a deep passion for invertebrates, on the part of all the contributors, it would not have been possible. Hopefully this book elevates in its readers their own passion and enthusiasm for that 96% of the animal kingdom that has so successfully flourished without backbones.

R.C.B.

Tucson, Arizona
December 2015

Preface to the Second Edition

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

During the revision of *Invertebrates* my brother Gary passed away. For a while the project was stalled. But, buoyed by the support of family, friends, and colleagues, I eventually returned to the task, which, at times, seemed overwhelming. The field of invertebrate biology is so vast, and cuts across so many disciplinary lines, that even in a book of this size it is necessary to generalize about some topics and to slight others. As university instructors, my brother and I realized early on that the teaching of invertebrate zoology should not be compartmentalized. Thus, in planning this book we were concerned about two potential dangers. First, the text might become an encyclopedic list of "facts" about one group after another, the sort of "flash-card" approach that we wanted to avoid. Second, the book might be a rambling series of stories or vignettes about randomly selected animals (or "model organisms") and their ways of life. The first book would be dull, would encourage rote memorization instead of understanding, and might give the misconception that there is little left to discover. The second book might be full of interesting "gee whiz" stuff but would seem disorganized and without continuity or purpose to the serious student. Either approach could fail to present the most important aspects of invertebrates—their phenomenal diversity, their natural history, and their evolutionary relationships. We also held to the belief that what we *know* about these animals is not as important as how we *think* about them. You should be prepared to assimilate much new material, but you should also be prepared for a great deal of uncertainty and mystery, as much remains to be discovered.

To avoid the pitfalls noted above, and to establish threads of continuity in our discussions about invertebrates, we developed our book around two fundamental themes: **unity** and **diversity**. The first theme we approach by way of functional body architecture,

or what we call the bauplan concept. The second theme we approach through the principles of phylogenetic biology. Our hope was that weaving the book tightly to these themes would provide a meaningful flow as readers move from one phylum to the next. The first five chapters provide background for these themes and thus provide an important foundation upon which the rest of the book rests. Please read these chapters carefully and refer back to them throughout your study.

The bulk of this book 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. A consistent organization is maintained throughout each chapter, although we did 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" biologically than smaller or more homogeneous ones. (Five chapters are devoted to the arthropods and their kin.) In certain chapters more than one phylum is covered. In some cases the phyla covered 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.

Certain aspects of this book have, of course, been influenced by our own biases; this is especially true of the discussions on phylogeny. We use a combination of phylogenetic trees (cladograms) and narrative discussions to talk about animal evolution. Cladograms are used when appropriate, because they provide the least ambiguous statements that can be made about animal relationships. We always knew that some of you, professors and students both, would disagree with our methods and ideas to various degrees—at least we *hoped* that you would. Never placidly accept what you see in a textbook, or anyplace else for that matter, but try to be critical in your reading.

The book's final chapter is a phylogenetic summary of the animal kingdom. It reinforces the point that

much remains to be explored and learned about the evolutionary relationships of invertebrates. Like all scientific knowledge, we are dealing here with provisional, transient "truths" that always remain open to challenge and revision. And, of course, scientists disagree. It is this disagreement and the constant challenging of hypotheses that enliven the field and push the frontiers of knowledge forward.

There are a few other things you should know about this book. A brief historical review of the classification of each major group is provided. We felt this material was not only interesting but also served 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 section in each chapter deals only with extant taxa. Descriptions of taxa in these annotated classifications are written in somewhat telegraphic style to save space; we never expected these sections to be "read"—they are for reference. 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. We tried hard to be consistent in our usage of zoological terminology, but the existence of similar terms for entirely different structures in certain groups is notoriously troublesome—these are noted in the text.

For this Second Edition of *Invertebrates*, of course, we have tried to be as current as possible with the research literature, but even as this book goes into production important new publications appear daily. It has been estimated that the volume of scientific information is doubling about every 10 years (or faster). 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." My goal has been to provide sufficient reference material to lead the interested student quickly into the heart of the relevant literature. 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 citations) references of a general nature may be listed only once, usually in the introductory chapters. You will also notice citations of a fair number of references that are quite old, some from the nineteenth century. These are included not out of whimsy, but because many of these are benchmark research papers or they stand out as some of the best available descriptions

for the subject at hand. (It is surprising how many of the illustrations in modern biology texts can be traced back to origins in nineteenth-century publications.) It is distressing to see how commonplace it has become for researchers to ignore the excellent (and important) work of past decades. For example, many phylogenetic research papers completely ignore 150 years of careful embryological research that was published, largely in the German and American literature, in the nineteenth and twentieth centuries. For some scientists, biological research seems to be little more than "sound bites" from the past decade. Sadly, today, this "sound bite research culture" is often imbued in graduate students—a shocking and dangerous trend that encourages dilettantes. To understand animals requires a thorough understanding of their overall biology, and the dedication of a career, not just dabbling.

Since the first edition of this book, there has been an explosion of research in the field of molecular biology. Much of this has been in molecular phylogenetics, but huge strides are also being made in the area of molecular developmental biology. Papers in these fields now appear at such a pace that it is difficult to write about them in a textbook, for fear the ideas will be obsolete in six months. There have been many new phylogenetic hypotheses proposed on the basis of DNA sequence analyses since the first edition of this book. Many of the molecular phylogenetic trees that were published before 2000 were quirky and troublesome, due to the simple fact that the field is still new and emerging. Because most of these trees are relatively new and still await rigorous testing with independent data, we do not discuss them all. However, we do discuss molecular-based hypotheses that have a growing body of support or have received widespread attention. But, in general we have taken a conservative approach in this regard—we are only just beginning to discover which genes are appropriate for different levels of phylogenetic analysis, and how best to analyze them.

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

R.C.B.
Tucson, Arizona
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