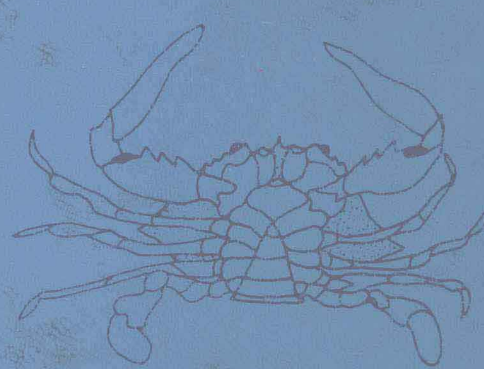
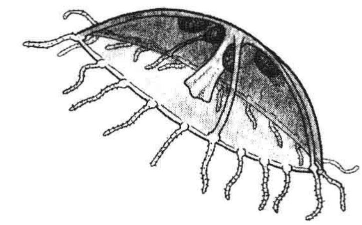
Barnes

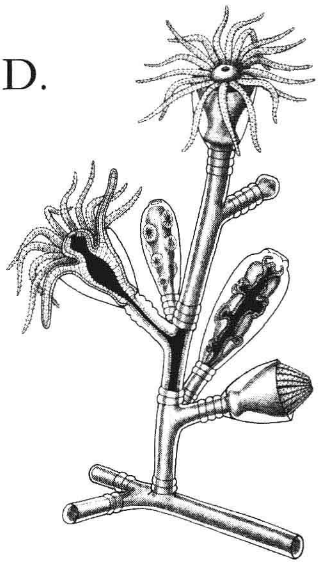
INVERTEBRATE ZOOLOGY

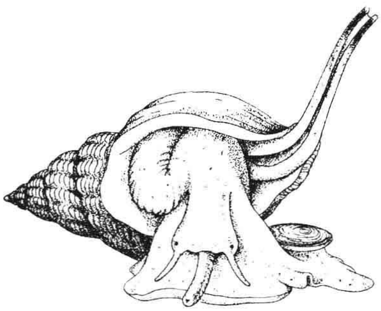




Robert D. Barnes, Ph.D.

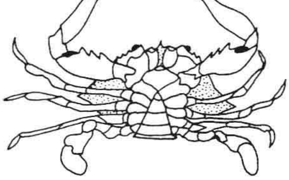
Professor of Biology
Gettysburg College

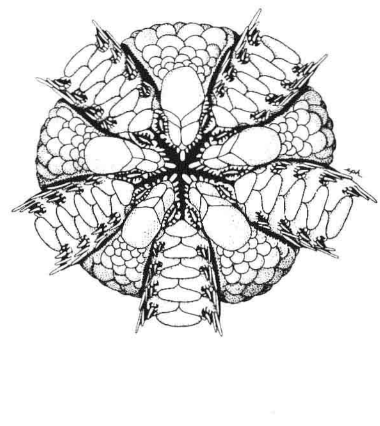




INVERTEBRATE ZOOLOGY

THIRD EDITION





W. B. SAUNDERS COMPANY

Philadelphia, London, Toronto

W. B. Saunders Company: West Washington Square
Philadelphia, PA 19105

12 Dyott Street
London, WC1A 1DB

833 Oxford Street
Toronto, Ontario M8Z 5T9, Canada

Library of Congress Cataloging in Publication Data

Barnes, Robert D.

Invertebrate zoology.

Includes bibliographies.

1. Invertebrates. I. Title.

QL362.B27 1974 592 73-89172

ISBN 0-7216-1562-7

Invertebrate Zoology ISBN 0-7216-1562-7

Print No: 9 8 7 6 5 4 3

Original photographs by Betty M. Barnes

New art work by Susan Heller

PREFACE TO THE THIRD EDITION

The emphasis of this revision was placed on the major free-living invertebrate groups that constitute the core of most courses in Invertebrate Zoology. Although updating and correction of errors were important concerns, much attention was devoted to improving the coverage and presentation. A considerable part of some chapters, especially those on flatworms, mollusks, and lophophorates, was rewritten.

I am increasingly convinced that evolution and adaptive biology are the most useful themes for facilitating an understanding and retention of the tremendous diversity presented by invertebrates. Considerable new material of this sort has been added and such topics as locomotion, feeding, and gas exchange, which most strikingly reflect different modes of existence, have been given more attention than some others. The conventional sequence of topics has sometimes been altered where I felt that other arrangements would enhance an overall understanding. Thus, for example, "gas exchange and water circulation" is an early topic in the section on gastropods, and the discussion of the evolution of feeding precedes that on adaptive diversity of bivalves.

Although a particular evolutionary hypothesis has frequently been followed in order to develop a context or framework for understanding, opposing viewpoints have always been indicated, and I have increasingly taken a neutral stand in many controversies on phylogeny.

The literature on invertebrates—books, reviews, and research papers—continues to grow at an almost overwhelming rate. The transfer of important material from that accumulation into a textbook such as this one is increasingly difficult, not only because of the dispersed volume involved, but also because of the need to keep the length of the text within reasonable limits. For this edition, considerable anatomical and embryological descriptive details were eliminated to make room for new material. The increase of approximately 100 pages over the previous edition results largely from new illustrations.

Courses in invertebrate zoology vary greatly in the emphasis of their coverage. This text, like most others, is designed to accommodate that variation. Therefore, more material is presented than a student should be expected to learn or remember. I continue to urge that this text be used to augment the instructor's course rather than be treated as a course in itself.

The illustrations received an extensive overhauling and have been greatly enriched and improved. Some older figures have been deleted, and some have been redone. Many new figures have been added. Largely responsible for this new appearance of the book are Susan Heller and my wife, Betty M. Barnes. Susan Heller, who is not only a fine artist but a knowledgeable invertebrate zoologist, provided the new drawings, including the composite figures of invertebrate inhabitants of *Sargassum* and the surfaces of coralline stones. My wife provided many fine original photographs of a great variety of material.

This text has undergone considerable evolution since the first edition appeared in 1963. Although the many changes certainly reflect the expansion of literature over the past ten years, they also reflect the author's own continual study and more sophisticated knowledge of invertebrates. The new edition further reflects the interest and generosity of many readers and friends who have provided a wealth of helpful comments, suggestions, and information. To all I am much indebted.

I am especially grateful to those persons who read sections of the manuscript for this edition. They gave valuable advice and information and corrected errors. They are not responsible for errors that may still remain. The chapter on protozoans was reviewed by R. Barclay McGhee, University of Georgia; sponges by Klaus Ruetzler, Smithsonian Institution; cnidarians by Charles E. Cutress, University of Puerto Rico; turbellarians by Reinhard Rieger, University of North Carolina; gastrotrichs by William D. Hummon, Ohio University; nematodes by W. Duane Hope, Smithsonian Institution; polychaetes by Marian H. Pettibone, Smithsonian Institution; leeches by Roy T. Sawyer, College of Charleston; mollusks by Ruth D. Turner, Armelie Scheltema, Robert B. Bullock, Elaine Hoagland, and Carol Jones, all at Harvard University; arachnids by Herbert W. Levi, Harvard University; arthropod compound eyes by Jerome J. Wolken, Carnegie-Mellon University; insects by Pedro Barbosa, University of Massachussetts; non-decapod crustaceans by Thomas E. Bowman, Smithsonian Institution; and decapod crustaceans by Dorothy E. Bliss, American Museum of Natural History. The larger parasitic invertebrate groups were reviewed by Sherman S. Hendrix, Gettysburg College.

I would also like to thank Carol Ann Gray, June Fox, Philip Price, Esther Clapsaddle, Katherine Barnes, and Christine Tougas for helping with many tasks involved in the preparation of the manuscript.

As always, the help and encouragement provided by those associated with the W. B. Saunders Co. did much to reduce the burden of the task. To my editors, Richard Lampert and Jay Freedman, I am especially grateful.

ROBERT D. BARNES

CONTENTS

Chapter 20

THE LESSER DEUTEROSTOMES

Chapter 21

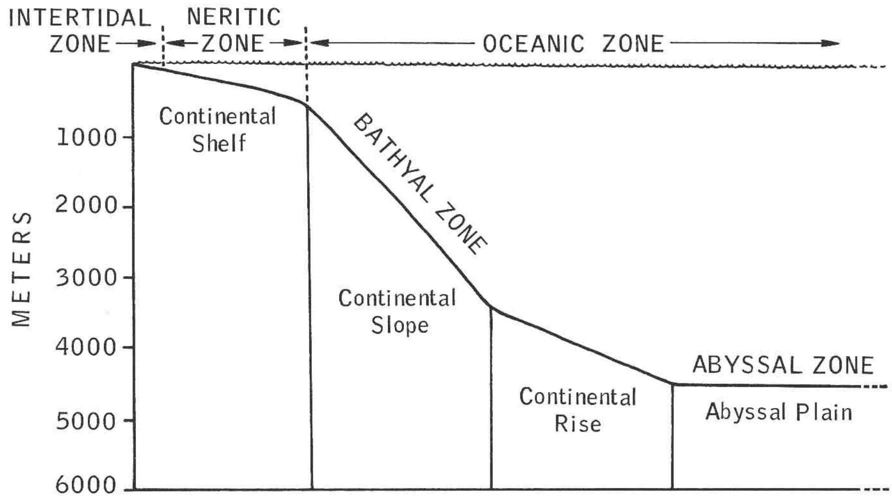


Figure 1–1. A diagrammatic cross section through an ocean basin, showing the principal horizontal and vertical zones.

tends as much as 800 miles into the Arctic Ocean.

Waters over the continental shelves comprise the *neritic zone*, and those beyond the shelf comprise the *oceanic zone* (Fig. 1–1). The edge of the sea, which rises and falls with the tide, is the *intertidal (littoral) zone.* The region above is the *supratidal (supralittoral)* and that below is the *subtidal (sublittoral).* The continental slopes form the *bathyal zone,* the abyssal plains form the *abyssal zone,* and the trenches form the *hadal zone.*

Vertical distribution of marine organisms is largely controlled by the depths of light penetration. Light sufficient for photosynthesis to exceed respiration penetrates to only a short distance below the surface or to depths as great as 200 m., depending upon the turbidity of the water. Below this upper *euphotic zone* is a transition zone, where some photosynthesis can occur but the production rate is less than the loss through respiration. From the transition zone down to the ocean floor, total darkness prevails. This region constitutes the *aphotic zone.* The animals that are permanent inhabitants of the aphotic and transition zones are carnivorous, suspension, or detritus feeders and depend ultimately on the photosynthetic activity of the microsopic algae in the upper, lighted regions. The aphotic zone animals are sometimes red, purple, or black.

The suspended or swimming animals of ocean waters constitute the *pelagic fauna,* and those that live on the bottom compose the *benthic fauna.* Bottom dwellers may live on the surface (*epifauna*) or beneath the surface (*infauna*) of the ocean floor, and usually strikingly reflect the character of the substratum, that is, whether it is a hard bottom of coral or rock, or a soft bottom of sand or mud. Many animals are adapted for living in the spaces between sand grains and compose what is commonly referred to as the *interstitial fauna* or *meiofauna.* This group includes representatives of virtually every major phylum of animals, and a number of previously unknown groups of animals have been discovered here in recent years. Pelagic and benthic animals are found in all of the horizontal zones. For example, one can refer to neritic pelagic animals or to the infauna of the abyssal zone.

The neritic, or coastal, waters support a greater population of marine life than do those of the open ocean (oceanic zone). The abundance results from the supply of nitrates, phosphates, and other nutrients dumped into coastal waters by rivers and streams or brought to the surface by upwellings and turbulence. These substances are required by photosynthetic organisms, the producers which form the base of the food chain for animal life. Oceanic waters that have a low productivity, such as the Gulf Stream and the Sargasso Sea, are clear and blue. The low concentration of plankton allows light to penetrate to a considerable depth, and the blue wavelengths are reflected from the water molecules. Sea water that is rich in plankton is green. Plankton and organic detritus reflect yellow wavelengths, which, combined with the blue wavelengths reflected by the water molecules, produce a green color.

In tropical waters of many areas the population levels are lower than in temperate and cold oceans. However, tropical and subtropical seas commonly contain a greater number of species than do temperate waters. One of the world's richest marine faunas in numbers of species occurs in the Indonesian region. The islands of this region—Borneo, Sumatra, the Celebes, and others—represent all that remains of the great, sunken land mass that once connected Australia with southern Asia. The surrounding seas, from the Gulf of Siam to the Arafura Sea between New Guinea and Australia, are very shallow and form the center of the rich Indo-Pacific fauna.

At the other extreme the oceans' abyssal plains, which are perpetually dark and icy cold, support a comparatively small fauna, both in number of species and in number of individuals.

Freshwater and Estuarine Environments. The lakes of the world also exhibit a horizontal and vertical zonation but their smaller size, shallower depth, and freshwater content make them ecologically different in many ways from oceans. The margin of a lake, where light can reach the bottom, is called the *littoral zone*. Within the littoral zone the upper lighted layer of water, equivalent to the euphotic zone of the sea, is in lakes termed the *limnetic zone*. Within and below the limnetic zone, the waters and bottom of the lake belong to the *profundal zone*.

Temperature is a primary factor controlling the environment of lakes. In contrast to salt water, which becomes increasingly dense at decreasing temperatures, fresh water reaches its greatest density at 4° C.; and thus when lakes in temperate parts of the world are warmed during spring and summer, the warm water stays at the surface while the heavier, colder water remains at the bottom. Little circulation occurs between the upper and lower levels, so that not only is the bottom zone dark, but it is also relatively stagnant from lack of oxygen and supports only a limited fauna. With the advent of cold weather, water of the upper stratum becomes heavier and sinks, resulting in a general turnover between the surface and the bottom. Conditions are stabilized again in the winter but with a reversed temperature stratification, for now the lighter, colder water in the form of ice floats at the surface, and the warmer (4° C.), heavier water is at the bottom. In the spring, following the melting of the winter ice, there is another turnover as in the fall.

Tropical lakes either have a single winter turnover or exhibit a highly stable condition, with little vertical circulation.

The junction of freshwater rivers and streams with the sea is not abrupt. Rather, the two environments grade into one another, creating the estuarine environment, characterized by brackish water, i.e., salinities considerably below the 35 per cent typical of the open sea. The estuarine environment embraces river mouths and surrounding deltas, coastal marshes, small embayments, and the finger-like extensions of the sea that probe the coast or margins of sounds. It is usually affected by tides, from which the word estuary (*aestus*, tide) is derived. The majority of marine animals are osmoconformers and stenohaline and cannot survive greatly reduced salinities. The lower and fluctuating salinities of estuaries thus restrict the estuarine fauna to those euryhaline marine invaders and few freshwater species that can tolerate these conditions. The fauna also contains some animals which have become especially adapted for estuarine conditions and are found nowhere else.

In the tropics a characteristic community of estuarine environments, as well as of more saline areas where waters are quiet, is mangrove. Mangroves are species of small trees that can tolerate saline conditions. They occupy the intertidal zone and commonly possess prop roots or special aerial roots (pneumatophores) which project above the water's surface. The most highly developed mangrove communities are found in the Indo-Pacific, where numerous species form a number of zones extending seaward. Such mangroves may occupy vast coastal areas and are virtually impenetrable. Red mangrove, *Rhizophora mangle*, which possesses long prop roots extending straight downward from the limbs, is the common mangrove of tropical America (Fig. 1–2). Mangroves trap sediment and contribute to land building. They create a habitat that is occupied by many animals and other plants.

Plankton. Both oceans and fresh-water lakes contain a large assemblage of microscopic organisms that are free-swimming or suspended in the water. These organisms comprise the plankton and include both plants (phytoplankton) and animals (zooplankton). Although many planktonic organisms are capable of locomotion, they are too small to move independently of currents.

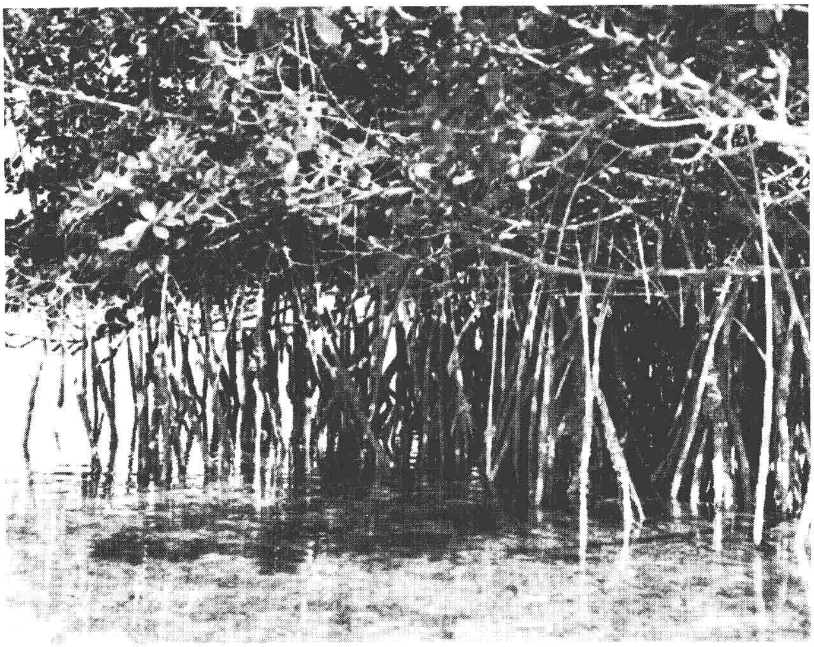


Figure 1–2. A mangrove at low tide. This is red mangrove, *Rhizophora mangle*. Note the bolsters of algae surrounding the prop roots. (By Betty M. Barnes.)

Phytoplankton is composed of enormous numbers of diatoms and other microscopic algae.

Marine zooplankton includes representatives from virtually every group of animals, either as adults or as developmental stages. Some species (holoplankton) spend their entire lives in the plankton; the larvae of others (meroplankton) enter and leave the plankton at different points in the course of their development. About 70 per cent of the bottom-dwelling marine invertebrates have a planktonic larval life. The animal constituents of fresh-water plankton are more limited in number. Plankton, especially marine plankton, is of primary importance in the aquatic food chain. The photosynthetic phytoplankton—chiefly diatoms, dinoflagellates, and minute flagellates—form the primary trophic level and serve as food for larger animals. As would be expected, plankton attains its greatest density in the upper, lighted zone; and in productive waters planktonic organisms may occur in such enormous numbers that the water appears turbid.

Phylogeny. In the subsequent chapters, the evolutionary histories of the various phyla are explored. Their evolution is frequently used as a basis for understanding the adaptive diversity within the phylum or class. The final chapter in the book examines the different theories and schemes which have been proposed to explain the phylogenetic, or evolutionary, relationships *between* phyla. In discussing phylogenetic relationships, it is convenient to use such terms as *primitive, advanced, lower, higher,* and *specialized.* Unfortunately, these terms are not always understood by students and tend to create the erroneous impression that evolution has proceeded from one group to another toward some ideal state or goal of perfection. Such terms as *primitive* and *advanced* are relative and are significant primarily in discussing evolution within a particular group of animals. For example, *primitive species* are those that possess many, or the greatest number of, characteristics believed to have been possessed by the ancestral stock from which the living members of the group arose. *Advanced species* are those that have changed considerably compared with the primitive condition, usually as a result of different environmental situations or the assumption of a different mode of existence. *Specialized* usually refers to characteristics of species that are especially adapted to a particular ecological niche. The terms *specialized* and *advanced,* however, should not be thought of as meaning *more perfect* or *better,* because the environmental conditions for which a particular, specialized species is adapted may not prevail in primitive forms. Moreover, while certain species possess some primitive characteristics, these same species frequently are specialized in other respects.

The terms *primitive* and *advanced* can be particularly misleading when comparing different phyla, because usually only one, or a few, characteristics are being referred to. For example, since multicellular animals evolved from single-celled forms, the protozoans are, in respect to this characteristic, primitive as compared to multicellular phyla. However, in other ways protozoans are not necessarily primitive as compared to metazoans, for they have undergone at the unicellular level a great evolutionary development, leading to an intracellular specialization unequaled by the cells of metazoan animals.

The terms *higher* and *lower* usually refer to the levels at which species or groups have stemmed from certain main lines of evolution. Thus, sponges and coelenterates are often referred to as *lower* phyla, since they are believed to have originated near the base of the Animal Kingdom phylogenetic tree. This does not imply that sponges and coelenterates are primitive in all respects; for they, like all other groups of animals, have followed certain independent lines of specialization. Furthermore, this does not necessarily imply that higher groups have evolved *directly* through sponges and coelenterates.

No treatment of invertebrates is complete, nor can there be a proper understanding of invertebrate phylogeny, without some consideration of fossil forms and extinct groups. As much invertebrate paleontology has been included as space permits. From time to time, reference will be made to different geological eras and periods. For the student who has only a slight background in geology, the geological time table of Figure 1–3 may be of some value for later reference.

Bibliographies. The bibliography at the end of each chapter is not intended to be a selection of titles recommended for further reading. The literature on invertebrates is enormous, as one would expect, considering the vast area of biology it covers. Most of this literature consists of research papers scattered through a great number of biological journals published throughout the world over the last 80 years. Obviously, any list of such papers that might be given here would have to be so limited in number and so arbitrary a selection that its value would be highly questionable. The bibliographies in this text therefore are of a different nature. They consist of two categories. One category comprises the literature cited in the text; the other category, which is of considerably more importance to the student, consists of important reference works on the group of in-

ERAS	PERIODS		MOUNTAIN-MAKING EPISODES	LIFE	YEARS AGO
CENOZOIC	QUATERNARY	RECENT	ALPINE-CASCADIAN	AGE OF MAN	
		PLEISTOCENE			15,000
	TERTIARY	PLIOCENE		AGE OF MAMMALS AND ANGIOSPERMS	1,500,000
		MIOCENE			30,000,000
		OLIGOCENE			
		EOCENE	HIMALAYAN		
MESOZOIC	CRETACEOUS		LARAMIDE	AGE OF REPTILES AND GYMNOSPERMS	
	JURASSIC		SIERRA NEVADA		
	TRIASSIC				180,000,000
PALEOZOIC	"CARBONIFEROUS"	PERMIAN	APPALACHIAN HERCYNIAN		225,000,000
		PENNSYLVANIAN		AGE OF FISHES AND PTERIDOPHYTES	
		MISSISSIPPIAN			
	DEVONIAN				
	SILURIAN		CALEDONIAN-ACADIAN		370,000,000
	ORDOVICIAN			AGE OF INVERTEBRATES AND THALLOPHYTES	
	CAMBRIAN				
PROTEROZOIC	"PRE-CAMBRIAN"		GRAND CANYON YOUNGER LAURENTIANS		500,000,000
ARCHEOZOIC			OLDER LAURENTIANS		2,500,000,000?

Figure 1–3. Subdivisions of geologic time. (From Darrah, W. C., 1960: Principles of Paleobotany. 2nd Ed. Ronald Press, New York.)

vertebrates with which the chapter deals. Those reference citations in which the coverage is not clearly indicated by the title have been provided a brief annotation. Many of these works contain the extensive bibliographies that the student should consult for additional information on particular topics.

A listing of journals containing papers on invertebrate zoology would serve little purpose because of the large number involved, and because so few are devoted to invertebrates alone. A few hours spent in a good biology library with a bibliography from one of the reference works described above would be of much greater value in initiating a student into the nature of journals of biology.

Bibliography

MULTIVOLUME WORKS COVERING INVERTEBRATE GROUPS

Bronn, H. G. (Ed.), 1866– : Klassen und Ordnungen des Tierreichs. C. F. Winter, Leipzig and Heidelberg. (Many volumes; series still incomplete.)

Grassé, P. (Ed.), 1948– : Traite de Zoologie. Masson et Cie, Paris. (Covers entire Animal Kingdom; still incomplete.)

Hyman, L. H., 1940– : The Invertebrates. Six volumes. McGraw-Hill Co., N.Y. (Volumes on annelids and arthropods not yet completed.)

Kaestner, A., 1967–1970. Invertebrate Zoology. Three volumes. Interscience Publishers, N. Y. (Completed, although lophophorates and echinoderms are not included.)

Moore, R. C. (Ed.), 1952– : Treatise on Invertebrate Paleontology. Geological Society of America and University of Kansas Press. (A detailed treatment of fossil invertebrates. Many volumes, but series is still incomplete.)

ONE-VOLUME GENERAL WORKS ON INVERTEBRATES

Barrington, E. J. W., 1967: Invertebrate Structure and Function. Houghton Mifflin Co., Boston. 549 pp. (A textbook organized from the standpoint of morphology and physiology.)

Gardiner, M., 1972: The Biology of Invertebrates. McGraw-Hill Co., N. Y. 945 pp. (A textbook organized from the standpoint of morphology and physiology.)

Hickman, C. P., 1973: Biology of the Invertebrates. 2nd Edition. C. V. Mosby Co., Saint Louis. 757 pp.

Marshall, A. J., and Williams, W. D., 1972: Textbook of Zoology: Invertebrates. American Elsevier Publishing Co., N. Y. 874 pp.

Meglitsch, P. A., 1972: Invertebrate Zoology. 2nd Edition. Oxford University Press, N. Y. 834 pp.

WORKS ON MORPHOLOGY, PHYSIOLOGY, OR ECOLOGY OF INVERTEBRATES

Beklemishev, W. N., 1969: Principles of Comparative Anatomy of Invertebrates. Two volumes. University of Chicago Press, Chicago.

Bücherl, W., and Buckley, E. E. (Eds.), 1971: Venomous Animals and Their Venoms. Vol. 3. Venomous Invertebrates. Academic Press, N. Y. 560 pp.

Bullock, T. H., and Horridge, G. A., 1965: Structure and Function of the Nervous System of Invertebrates. Two volumes. W. H. Freeman, San Francisco.

Eltringham, S. K., 1971: Life in Mud and Sand. Crane, Russak, and Co., N.Y. 218 pp. (An ecology of marine mud and sand habitats.)

Florkin, M., and Scheer, B. J. (Eds.), 1967–1972: Chemical Zoology. Seven volumes to date. Academic Press, N. Y. (A compilation of articles covering various aspects of biochemistry and physiology of animal groups.)

Giese, A. C., and Pearse, J. S., 1973: Reproduction of Marine Invertebrates. Vol. 1. Acoelomate Metazoans. Academic Press, N. Y.

Halstead, B. W., 1965: Poisonous and Venomous Marine Animals of the World. Vol. I. Invertebrates. U. S. Government Printing Office, Washington, D.C. 994 pp.

Kume, M., and Dan, K., 1968: Invertebrate Embryology. Clearinghouse for Federal Scientific and Technical Information, Springfield, Va.

Laverack, M. S., 1968: On the receptors of marine invertebrates. Oceanogr. Mar. Biol., Ann. Rev., *6*: 249–324.

MacGinitie, G. E., and MacGinitie, N., 1968: Natural History of Marine Animals. 2nd Edition. McGraw-Hill Co., N. Y. 523 pp.

Mileikovsky, S. A., 1971: Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. Mar. Biol., *10*:193–213.

Newell, R. C., 1970: Biology of Intertidal Animals. American Elsevier Publishing Co., N. Y. 555 pp.

Nicol, J. A. C., 1960: Biology of Marine Animals. Interscience Publishers, N. Y. 707 pp.

Prosser, C. L. (Ed.), 1973: Comparative Animal Physiology. 3rd Edition. W. B. Saunders Co., Philadelphia. 966 pp.

Russell, F. E., 1965: Marine toxins and venomous and poisonous animals. Adv. Mar. Biol., *3*:256–384.

Schaller, F., 1968: Soil Animals. Univ. Michigan Press. 114 pp.

Stephenson, T. A., and Stephenson, A., 1972: Life Between Tidemarks on Rocky Shores. W. H. Freeman, San Francisco. 425 pp. (Ecology of the intertidal zone of rocky shores. Systematic coverage of specific regions of the world.)

Swedmark, B., 1964: The interstitial fauna of marine sand. Biol. Rev., *39*:1–42.

Tombes, A. S., 1970: An Introduction to Invertebrate Endocrinology. Academic Press, N. Y. 217 pp.

Trueman, E. R., and Ansell, A. D., 1969: The mechanisms of burrowing in soft substrata by marine animals. Oceanogr. Mar. Biol., Ann. Rev., *7*:315–366.

Vernberg, W. B., and Vernberg, F. J., 1972: Environmental Physiology of Marine Animals. Springer-Verlag, N. Y. 346 pp.

Wells, M. J., 1965: Learning by marine invertebrates. Adv. Mar. Biol., *3*:1–62.