Invertebrate Medicine
Gregory A. Lewbart, M.S., V.M.D., Diplomate ACZM, is Professor of Aquatic Animal Medicine, North Carolina State University, College of Veterinary Medicine, Department of Clinical Sciences, Raleigh, North Carolina.

©2006 Blackwell Publishing
All rights reserved

Blackwell Publishing Professional
2121 State Avenue, Ames, Iowa 50014, USA

Orders: 1-800-862-6657
Office: 1-515-292-0140
Fax: 1-515-292-3348
Web site: www.blackwellprofessional.com

Authorization to photocopy items for internal or personal use, or the internal or personal use of specific clients, is granted by Blackwell Publishing, provided that the base fee of $.10 per copy is paid directly to the Copyright Clearance Center, 222 Rosewood Drive, Danvers, MA 01923. For those organizations that have been granted a photocopy license by CCC, a separate system of payments has been arranged. The fee codes for users of the Transactional Reporting Service are ISBN-13: 978-0-8138-1844-3; ISBN-10: 0-8138-1844-3/2006 $.10.

First edition, 2006

Library of Congress Cataloging-in-Publication Data

Lewbart, Gregory A.
Invertebrate medicine/Gregory A. Lewbart.—1st ed.
p. cm.
Includes bibliographical references and index.
ISBN-10: 0-8138-1844-3 (alk. paper)
1. Invertebrates—Diseases. 2. Veterinary medicine. I. Title.
SF997.5.I5L49 2006
639.7—dc22
2005017249

The last digit is the print number: 9 8 7 6 5 4 3 2 1
DEDICATION

To my parents, Marvin and Virginia, for their constant love and support and for introducing me to the wonders of the natural world.
CONTENTS

Contributors ix
Foreword xi
Murray E. Fowler
Preface xiii
Gregory A. Lewbart
Acknowledgments xv

Chapter 1. Introduction 3
Gregory A. Lewbart
Chapter 2. Sponges 7
Gregory A. Lewbart
Chapter 3. Coelenterates 19
Michael K. Stoskopf
Chapter 4. Turbellarians 53
Michael S. Bodri
Chapter 5. Gastropods 65
Roxanna Smolowitz
Chapter 6. Cephalopods 79
Joseph M. Scimeca
Chapter 7. Bivalves 91
Jay F. Levine, Mac Law, and Flavio Corsin
Chapter 8. Annelids 115
Gregory A. Lewbart
Color Plate Section

Chapter 9. Horseshoe Crabs 133
Stephen A. Smith
Chapter 10. Spiders 143
Romain Pizzi
Chapter 11. Scorpions 169
Fredric L. Frye

vii
CONTRIBUTORS

Robert S. Bakal, DVM, MS
US Fish and Wildlife Service
Warm Springs Regional Fish Health Center
Warm Springs, GA 31830, USA
e-mail: Robert_Bakal@FWS.gov

Ilze K. Berzins, PhD, DVM
The Florida Aquarium
Tampa, FL 33602, USA
e-mail: IBerzins@flaquarium.org

Michael S. Bodri, MS, VMD, PhD
North Georgia College and State University
School of Natural and Health Sciences
Health and Natural Sciences Building
Dahlonega, GA 30597
e-mail: MSBodri@ngcsu.edu

Robert A. Bullis, DVM, MS
Advanced BioNutrition Corporation
Columbia, MD 21045, USA
e-mail: rbullis@advancedbionutrition.com

Daniel S. Dombrowski, MS
North Carolina State University
College of Veterinary Medicine
Raleigh, NC 27606, USA

d
North Carolina Museum of Natural Sciences
Raleigh, NC 27601, USA
e-mail: dan.dombrowski@ncmail.net

Laura Foster
North Carolina State University
College of Veterinary Medicine
Raleigh, NC 27606, USA
e-mail: lfoster74@aol.com

Murray E. Fowler, DVM, Dipl ACZM, Dipl ABVT, Dipl ACVIM
University of California
School of Veterinary Medicine
Davis, CA 95616, USA
e-mail: mefowler@ucdavis.edu

Fredric L. Frye, DVM, MS, CBiol, FIBiol
La Primavera Farm
Cloverdale, CA 95425-9428, USA
e-mail: FredFrye@aol.com

Amy L. Hancock, VMD
The Philadelphia Zoo
Philadelphia, PA 19104, USA
e-mail: hancock.amy@phillyzoo.org

Craig A. Harms, DVM, PhD, Dipl ACZM
North Carolina State University
Department of Clinical Sciences
College of Veterinary Medicine
Center for Marine Sciences and Technology
Morehead City, NC 28557, USA
e-mail: craig_harms@ncsu.edu

John R. Chitty, BVetMed, CertZooMed, CBiol, MIBiol, MRCVS
Strathmore Veterinary Clinic
Andover, Hants SP10 2PH, UK
e-mail: xmo32@dial.pipex.com

John E. Cooper, DTVM, FRCPath, FIBiol, FRCVS
Wildlife Health Services (UK)
Comparative Pathology and Forensic Services
Present address:
School of Veterinary Medicine (Mount Hope)
University of the West Indies (UWI)
St Augustine, Trinidad, West Indies
e-mail: NGAGI@vetaid.net

Flavio Corsin, MS, PhD
Network of Aquaculture Centres in Asia-Pacific (NACA)
Department of Fisheries
Kasetsart University Campus
Bangkok 10900, Thailand
e-mail: flavio.corsin@enaca.org
Contributors

Mac Law, DVM, PhD, Dipl ACVP
North Carolina State University
Department of Population Health and Pathobiology
College of Veterinary Medicine
Raleigh, NC 27606, USA
e-mail: mac_law@ncsu.edu

Jay F. Levine, DVM, MPH
North Carolina State University
College of Veterinary Medicine
Department of Population Health and Pathobiology
Aquatic Animal Epidemiology and Conservation Genomics Laboratory
Raleigh, NC 27606, USA
e-mail: jay_levine@ncsu.edu

Gregory A. Lewbart, MS, VMD, Dipl ACZM
North Carolina State University
Department of Clinical Sciences
College of Veterinary Medicine
Raleigh, NC 27606, USA
e-mail: greg_lewbart@ncsu.edu

Michael J. Murray, DVM
Monterey Bay Aquarium
Monterey, CA 93940, USA
e-mail: mmurray@mbayaq.org

Edward J. Noga, MS, DVM
North Carolina State University
Department of Clinical Sciences
College of Veterinary Medicine
Raleigh, NC 27606, USA
e-mail: ed_noga@ncsu.edu

Esther C. Peters, PhD
Registry of Tumors in Lower Animals
Experimental Pathology Laboratories, Inc.
Sterling, VA 20166-4311, USA
e-mail: administrator@pathology-registry.org

Romain Pizzi, BVSc, MS, CertZooMed, FRES, MRCVS, MACVSc(Surg)
Edinburgh University
Royal (Dick) School of Veterinary Studies
Department of Veterinary Clinical Studies
Midlothian EH25 9RG, UK
e-mail: romain.pizzi@ed.ac.uk

Joseph M. Scimeca, DVM, PhD
Southern Illinois University
Research Development and Administration—SIUC
Carbondale, IL 62901, USA
e-mail: jscimeca@siv.edu

Stephen A. Smith, DVM, PhD
Department of Biomedical Sciences and Pathobiology
Virginia/Maryland Regional College of Veterinary Medicine
Virginia Polytechnic Institute and State University
Blacksburg, VA 24061-0442, USA
e-mail: Stsmith7@vt.edu

Roxanna Smolowitz, DVM
Marine Biological Laboratory
Woods Hole, MA 02543, USA
e-mail: rsmol@mbl.edu

Michael K. Stoskopf, DVM, PhD, Dipl ACZM
Department of Clinical Sciences
North Carolina State University
College of Veterinary Medicine
Raleigh, NC 27606, USA
e-mail: michael_stoskopf@ncsu.edu
It has been interesting to witness the evolution of modern veterinary care for nontraditional animal species. The year 1950 heralded the founding of the American Association of Zoo Veterinarians and attracted veterinarians interested in all types of captive wild animals. A year later, in 1951, the Wildlife Disease Association was founded. Both of these organizations had as their founding goal the sharing and dissemination of information.

With an increased interest in birds in many veterinary practices, a new group, the Association of Avian Veterinarians, was formed and with it came a plethora of literature on the subject. A number of books on reptile and amphibian medicine stimulated an intense interest in these animals, and the Association of Reptilian and Amphibian Veterinarians came into being.

If history repeats itself, the publication of this comprehensive book on the medicine of invertebrates will stimulate greater interest in the innumerable species of animals without backbones (and rightfully so, as 80% of the animal biomass of this planet consists of invertebrates, not elephants and blue whales). Insects alone account for more than three quarters of the world’s animal species.

When I began working with nontraditional animals, I would kid my colleagues that they dealt with only 2–8 species of domestic animals while I was concerned with nearly 50,000 vertebrates and millions of species of invertebrates. Early in my career, a neighbor’s little girl came to my door with a shoebox containing a crayfish that she had acquired as a pet. “Dr. Fowler, is this crayfish a boy or a girl?”—a pretty basic question that I couldn’t answer; however, I learned and answered the girl’s question.

Insectariums have become important attractions in many zoos, with some exhibits traveling from one zoo to another on contract. A zoo in Japan designed a building with the roof in the form of a butterfly. International tourists are permitted to visit a butterfly farm on the Island of Aruba on the north coast of Venezuela.

The interest in the medical care of invertebrates is not limited to the United States. A recent conference in Brazil spotlighted a veterinarian who provides intensive care, including fluid therapy, for spiders, scorpions, and praying mantises.

Interest in invertebrate medicine is not limited to captive species. A catchword in the 21st century is biodiversity. Invertebrates are important contributors to the food chain for vertebrates, including humans. Invertebrates may be involved in the transmission of epidemic diseases and may cause disease themselves.

Invertebrates are subject to many toxic substances and may become locally or regionally extinct from pollution. The Mexican red-kneed spider is currently listed in Appendix 2 of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), one of many CITES-listed invertebrate species throughout the world. Should captive breeding be contemplated to reestablish a population of endangered spiders or other invertebrates, knowledge of their diseases and medical management could be critically important.

For veterinarians to provide optimal veterinary care, they must have a basic understanding of the biology of the species they are attempting to help. Although this book is not meant to be a definitive natural history of invertebrates, it does provide basic biology.

The editor has brought together a varied group of authors who have a specialized interest in each topic, many of whom have research or clinical experience with invertebrates. The result is a comprehensive volume on the veterinary care of invertebrates that are harvested or reared for human food, are kept in captivity as pets or for exhibition, or are being used as research models. The editor and authors are fully aware that there are significant gaps in the scientific information available on some taxa. Nevertheless, this foundation work will spur others to take steps to observe, conduct research, and provide clinical care for these special animals that are the ultimate beneficiary of the dedication and efforts of the editor and authors.

Murray E. Fowler, DVM, Dipl ACZM, Dipl ABVT, Dipl ACVIM
Professor Emeritus, Zoological Medicine
School of Veterinary Medicine
University of California
Davis, California
For many decades, invertebrates have been kept as pets, displayed in aquariums and zoos, used for research, and consumed. Maintaining live invertebrates in captivity is becoming more sophisticated and popular as time passes. Arthropod zoos and insectariums, jellyfish exhibits, and captive living coral reefs are relatively commonplace today but were rare or nonexistent 20 years ago. Despite this popularity, diversity, and economic importance, though, veterinary medicine has traditionally paid little attention to this huge chunk (over 95% of the earth’s animal species) of the animal kingdom.

My own interest in invertebrates started on a family trip to Campobello Island in New Brunswick, Canada, nearly 4 decades ago. Finding a sand dollar test on the beach was an exciting moment for a young boy, as was the subsequent quest to identify it. Years later, I found myself studying invertebrate zoology at Gettysburg College; my professor was Dr. Robert D. Barnes. After exciting field trips with Dr. Barnes to the Duke University Marine Laboratory in Beaufort, North Carolina, and the Bermuda Biological Station, I was definitely hooked! These educational experiences were a pivotal point in my life and I hold a special place in my heart and mind for Dr. Barnes and his inspirational teaching.

I began thinking about working on a veterinary text for invertebrates in the early 1990s and was very happy (and just a little apprehensive) when I signed a contract to edit this text with Blackwell Publishing Professional (at the time Iowa State University Press) in 2001.

This book is the product of a concerted effort by a group of dedicated authors on the topic of invertebrate animal medicine. This is not an invertebrate zoology text and is by no means comprehensive with regard to the anatomy, physiology, natural history, and taxonomy of the myriad of invertebrate taxa. This is a veterinary text about invertebrate animals that includes pertinent biological data as well as state-of-the-science information pertaining to medicine and the clinical condition. It is my hope that this book will be a valuable guide to those charged with the medical care and well-being of both captive and wild invertebrate animals.

At the North Carolina State University College of Veterinary Medicine (NCSU-CVM), my students and colleagues continually inspire me. Several years ago, the veterinary students started the Invertebrate Medicine Club, and we now offer an intensive 1-week elective course on invertebrate medicine. The NCSU-CVM administration has been extremely encouraging of these efforts, and I am grateful and fortunate to be working in such a rich, supportive environment.

I am very excited about invertebrate animal medicine and hope you will join me in this excitement. There is much work to be done in this realm in which the opportunities are truly endless.

Gregory A. Lewbart, MS, VMD, Dipl ACZM
Professor of Aquatic Animal Medicine
Department of Clinical Sciences
North Carolina State University
College of Veterinary Medicine
A project like this could not come to fruition without the help, support, and assistance of many individuals.

For their instruction, inspiration, guidance, support, and mentoring during my student years, I thank all of my mentors and professors, but, in particular, Donald Abt, Robert Barnes, Philip Bookman, Dale Dickey, John Gratzek, Louis Leibovitz, William Medway, Trish Morse, Nathan “Doc” Riser, Ralph Sorensen, and Richard Wolke. Doc was my master’s thesis advisor and I am especially grateful for his knowledge, wisdom, and patience. I am fortunate to be associated with the North Carolina State University College of Veterinary Medicine (NCSU-CVM), a fine, progressive institution of higher learning. I am grateful to all of my NCSU-CVM friends and colleagues. Oscar Fletcher, Craig Harms, Edward Noga, Elizabeth Stone, and Michael Stoskopf have been especially supportive. Craig Harms reviewed many of the chapters, and I am indebted to him for his keen eye, advice, patience, and friendship.

I also collectively thank the veterinary students I have worked with, both at the NCSU-CVM and those from other colleges of veterinary medicine. They are the bright future of our profession, and I know some days they teach me more than I teach them. Dan Dombrowski, one of this book’s authors, deserves special mention as an inspiration to all those interested in keeping and caring for the earth’s invertebrates.

The following individuals were generous in providing case material, images, suggestions, and other assistance: Genevieve Anderson, Rich Aronson, Herman Berkhoff, Charles Bland, Shane Boylan, James Brock, Mike Buchal, Rick Cawthorn, James Clark, Angelo Colorni, David Engel, Carlton Goldthwaite, Stacey Gore, Malcolm Hill, Sarah Joyner, Kelly Krell, Wade Lehmann, Douglas Mader, Stuart May, Jim Moore, Alf Nilsen, Hendrik Nollens, David Rotstein, Clay Rouse, Melanie Rembert, Johanna Sherrill, Jerry Stevens, Cinnamon Vann, and Nicole Webster. Richard Fox and Eric Borneman were especially generous in providing images, and Esther Peters’s input on neoplasia and other aspects of the book were invaluable.

I am grateful to Alison Schroeer and Brenda Bunch, both outstanding biological illustrators, who provided high-quality images and were tolerant of my numerous requests and deadlines. I also thank the helpful personnel of the NCSU-CVM Biomedical Communications Department.

I am very grateful to the talented group of authors that constructed this diverse collection of chapters; there would be no *Invertebrate Medicine* without their hard work, dedication, and commitment to the project. As the book’s editor, I take full responsibility for any errors or omissions.

The folks at Blackwell Publishing have been exceptional through this entire process. They are true professionals and a pleasure to work with. I specifically acknowledge David Rosenbaum, the person who “signed me up”; Cheryl Garton, who helped in the early stages; Antonia Seymour, the editorial director supervising this project; Jamie Johnson, who patiently waited for appropriately formatted figures; Judi Brown, who made certain everything was in order for the presses; and, finally, Dede Pederson, my managing editor, who was always there for this book and me. Thanks Dede!

John Flukas did a tremendous job of copyediting the manuscript and deserves special mention. His meticulous proofreading and editorial skills have greatly improved the book. He’s also one of the most calm and easygoing people I’ve ever worked with.

I really don’t think I could have completed this book without the dedicated and selfless help of Shane Christian during the past 3 years. He is simply the most reliable and competent person I know, and his efforts allowed me the time to focus on this project. Thanks Shane!

Finally, I am so very grateful for the love and support I consistently receive from my wonderful wife, Diane Deresienski. Her advice is always sound. Her ideas always good. Her hugs always warm. And she’s a top-notch veterinarian who I deeply admire and respect.

Gregory A. Lewbart
Invertebrate Medicine
Chapter 1

INTRODUCTION

Gregory A. Lewbart

The book before you is the product of a concerted effort by a group of dedicated authors on the topic of invertebrate animal medicine. This is not an invertebrate zoology text and is by no means comprehensive with regard to the anatomy, physiology, natural history, and taxonomy of the myriad of invertebrate taxa. This is a veterinary text about invertebrate animals. It includes pertinent biological information as well as state of the science information pertaining to medicine and the clinical condition.

What sort of topic is invertebrate medicine? And what exactly are invertebrates? Ruppert and Barnes (1994) have said that the invertebrates are a group of unrelated taxa that share no universal “positive” traits. Undergraduate and graduate courses are dedicated to invertebrate zoology or even to specific parts of this topic, such as entomology, malacology, or protozoology. Simply put, the invertebrates are a collection of animals, comprising more than 95% of the earth’s species, unified by the lack of a vertebral column. Depending on the text or investigator, there are currently over 30 recognized phyla of invertebrates (not including the protozoans). Many of these might be considered obscure, but for no better reason than they may contain few species, microscopic representatives, or have no obvious economic value to humans. In reality, each phylum and its members are important to the diversity and survival of the planet, even if the group is only studied by a small number of investigators. Unfortunately, very little is known about the veterinary aspects of many of these taxa, and writing a comprehensive text for all invertebrate phyla would currently be a daunting and somewhat inefficient task. Consequently, I have elected to include, at least in this volume, the most economically important and “visible” metazoan taxonomic groups. Exclusively parasitic taxa (e.g., trematodes, cestodes, and acanthocephalans) are only touched upon. Table 1.1, which lists the major taxonomic groups (along with brief descriptions) that do not have their own chapter, has been included in an effort to remind readers of the diversity of the invertebrate animal kingdom. Table 1.2 provides a snapshot of animal diversity with regard to number of described species and habitat. I encourage interested readers to obtain one or more of the general invertebrate zoology texts listed under General Invertebrate Zoology References, where detailed descriptions of the various groups in Table 1.1 and throughout this book can be found.

<table>
<thead>
<tr>
<th>Table 1.1. Invertebrate phyla and major classes not reviewed in this book</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Placozoa:</strong> A monotypic phylum containing only the species <em>Trichoplax adhaerens</em>. This primitive amoebozoan metazoan is flattened, less than 3 mm in diameter, and exhibits extracellular digestion of detritus and algae.</td>
</tr>
<tr>
<td><strong>Orthonectida:</strong> A very small phylum (about 20 species) of very small (no larger than 1 mm) internal parasites of other invertebrates such as bivalves, polychaetes, tunicales, turbellarians, and nemerteans.</td>
</tr>
<tr>
<td><strong>Dicyemida:</strong> This phylum contains about 75 species of very thin renal parasites of cephalopods.</td>
</tr>
<tr>
<td><strong>Nemertea:</strong> This diverse phylum contains approximately 1150 species of <em>ribbon worms</em>, which tend to be much larger and longer than flatworms. Unlike flatworms, nemerteans have a true coelomic circulatory system. Most are marine, but there are a few freshwater and terrestrial forms. Nemerteans are predators and use a long, reversible proboscis to capture and retain prey.</td>
</tr>
<tr>
<td><strong>Mollusk groups</strong></td>
</tr>
<tr>
<td><strong>Aplacophora:</strong> This class consists of about 300 species of small, vermiciform, marine animals that live at depths of between 200 and 7000 m.</td>
</tr>
<tr>
<td><strong>Polyplacophora:</strong> Commonly known as the <em>chitons</em>, these interesting mollusks are mobile but spend most of their time tightly adhered to rocky substrates. There are approximately 800 exclusively marine species described. All have eight valves or plates (hence the name of the class) that overlap and are connected by soft tissue and surrounded by a muscular “girdle.” Most species could rest in your palm, but one, <em>Cryptochiton</em> sp., the stocky gumshoe chiton, can reach a length of about 40 cm.</td>
</tr>
<tr>
<td><strong>Scaphopoda:</strong> Known as the <em>tusk</em> or <em>tooth</em> mollusks because of their shell shape. The approximately 500 species are all marine, and most are burrowers with the head facing down within the substrate.</td>
</tr>
<tr>
<td><strong>Echiura:</strong> Commonly known as the <em>spoon worms</em>, most of the 150 species either live in U-shaped burrows or between rocks closely associated with the marine environment. Most are deposit feeders, and some are an important food source for fishes. The name comes from the large and flared prostomium that resembles a spoon or small scoop.</td>
</tr>
</tbody>
</table>

(continued)
Table 1.1. (continued)

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sipuncula</strong></td>
<td>The sipunculids, or peanut worms, are a group of about 150 marine burrowing species. Most are smaller than 10 cm, but some can reach 70 cm in length. They possess an interesting feeding structure termed the introvert that can be expelled from or retracted into the main body or trunk.</td>
</tr>
<tr>
<td><strong>Oncyphora</strong></td>
<td>This group of tropical, terrestrial animals (110 known species) are commonly referred to as velvet worms or walking worms. They are segmented and aligned with arthropods. In fact, some workers include the phyla Onychophora, Tardigrada, and Arthropoda in the superphylum Panarthropoda. Velvet worms prey on smaller arthropods by capturing them with slime ejected from paired glands near the mouth.</td>
</tr>
<tr>
<td><strong>Tardigrada</strong></td>
<td>If the water bears, as they are commonly known, grew larger (most are less than 1 mm long), they would surely be common and popular pets and display animals. There are marine, freshwater, and terrestrial representatives among the 800-plus species in this group of taxonomically mysterious animals. They have features in common with the arthropods but are different enough to warrant their own phylum. Perhaps their most interesting attribute is their ability to undergo cryptobiosis and form desiccated tun, which can withstand adverse environmental conditions. In fact, some tardigrades may live as long as 100 years with the aid of cryptobiosis.</td>
</tr>
<tr>
<td><strong>Gastrotricha</strong></td>
<td>Many of the 500 species belonging to this microscopic phylum are interstitial. Most appear like miniature bowling pins atop two small pegs. There are freshwater and marine forms.</td>
</tr>
<tr>
<td><strong>Nematomorpha</strong></td>
<td>The horsehair worms superficially resemble nematodes but are very long and free-living as adults. The larvae usually parasitize either crustaceans or insects. Approximately 325 species have been described.</td>
</tr>
<tr>
<td><strong>Priapulida</strong></td>
<td>This small phylum containing just 18 species is all marine and benthic. They are cylindrical and resemble a small cactus.</td>
</tr>
<tr>
<td><strong>Loricifera</strong></td>
<td>This interesting and microscopic marine phylum (all appear to be interstitial) was not known to science until 1983. Many of the 100 or so known species have not yet been described due to the difficulty in examining fresh, living specimens. These little creatures are so dogged in their attachment to sand grains that only freshwater will dislodge them, causing osmotic damage and distortion of their anatomy.</td>
</tr>
<tr>
<td><strong>Kinorhyncha</strong></td>
<td>The mud dragons somewhat resemble the Gastrotricha in general shape but have an oral feeding structure called the oral styles at the end of a movable introvert. Most are microscopic and are either interstitial or benthic on mud and sand. There are approximately 150 species and all are marine.</td>
</tr>
<tr>
<td><strong>Gnathostomulida</strong></td>
<td>Virtually all 80 known species are marine, interstitial, and less than 1 mm long. They are vermiform and were not known to science until 1956.</td>
</tr>
<tr>
<td><strong>Rotifera</strong></td>
<td>Most occur in freshwater, but there are marine and terrestrial (primarily in water films) species. They are defined and frequently identified by the ciliated corona or wheel organ near the head. Some rotifers are extremely important in freshwater and marine food chains (in some cases, hundreds may be found in a liter of water) and are also commonly reared to support invertebrate and finfish aquaculture. There are approximately 2000 described species.</td>
</tr>
<tr>
<td><strong>Acanthocephala</strong></td>
<td>A totally parasitic group containing 1150 species. They are commonly known as thorny-headed worms, and some are important parasites of wild and domestic vertebrates. Most use other invertebrates as intermediate hosts.</td>
</tr>
<tr>
<td><strong>Kamptozoa</strong></td>
<td>Also known as Entoprocta, the 150 species are nearly all marine. Most are stalked, and some people refer to them as nodders because of the zooid’s tendency to nod or rock at the end of the stalk. Although some zoologists still classify them as bryozoans, these animals differ in their complete lack of a coelomic cavity. Some zoologists feel the morphological similarities between the groups are convergent.</td>
</tr>
<tr>
<td><strong>Cycliophora</strong></td>
<td>This small (in size and species number) phylum was not introduced to science until 1995. The single described species, Symbion pandora, exhibits a commensal lifestyle with a lobster (Nephrops sp.). Other as yet undescribed species are commensal with other crustaceans, including the American lobster, Homarus americanus. They are suspension feeders and have a complex reproductive cycle with both asexual and sexual life stages. None of the life stages are over 0.5 mm long.</td>
</tr>
<tr>
<td><strong>Phoronida</strong></td>
<td>There are just 14 species in two genera of these sessile marine creatures. These vermiform animals live in chitinous tubes that they secrete. Although externally they are bilaterally symmetrical, internally the left side is dominant. They feed by means of a lophophore and are grouped into the superphylum Lophophorata along with the bryozoans and brachiopods.</td>
</tr>
<tr>
<td><strong>Brachiopoda</strong></td>
<td>The brachiopods, or lamp shells, are an interesting group of 350 extant marine species that grossly resemble bivalve mollusks. Thousands of species are known from the fossil record, in part due to their mineralized valves that are preserved well. They are not related to mollusks, and the hard valves that protect the soft body are oriented opposite that of the bivalve’s. They feed with the aid of a lophophore, placing them in the superphylum Lophophorata. Most are the size of small cherrystone clams and frequently turn up in shops specializing in fossils. Most species occur in colder waters.</td>
</tr>
<tr>
<td><strong>Bryozoa</strong></td>
<td>Known as the moss animals, these are common animals that can be found on many marine substrates (there are a few freshwater species), including rocks, algae, pilings, and even living animals such as sea turtles. With nearly 5000 species, this phylum is the best known of the Lophophorata and is usually studied as part of nearly all basic invertebrate zoology courses. The vast majority are colonial, although there is one solitary genus. From a distance, they may look more like plants than animals to casual observers. Some colonies are polymorphic, whereas other species are monomorphic. They are filter feeders, using the lophophore to trap and retain small food items.</td>
</tr>
<tr>
<td><strong>Arthropoda</strong></td>
<td>Known commonly as the sea spiders, this class of arthropods contains about 1000 known species. They are all marine and widely distributed, with most occurring in benthic habitats. Very few species are larger than 1 cm, and although they resemble a true spider, they are not close relatives.</td>
</tr>
</tbody>
</table>

Taxonomy and descriptions are from Ruppert et al. (2004).
Table 1.2. Habitats and approximate metazoan species numbers

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Benthic Marine</th>
<th>Pelagic Marine</th>
<th>Benthic Freshwater</th>
<th>Pelagic Freshwater</th>
<th>Terrestrial</th>
<th>Ectosymbiotic</th>
<th>Endosymbiotic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Porifera</td>
<td>###</td>
<td>—</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>#</td>
<td>—</td>
</tr>
<tr>
<td>Placozoa</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Orthonectida</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Dicyemida</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Cnidaria</td>
<td>###</td>
<td>#</td>
<td>#</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Ctenophora</td>
<td>#</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Platyhelminthes</td>
<td>###</td>
<td>#</td>
<td>###</td>
<td>—</td>
<td>#</td>
<td>#</td>
<td>#</td>
</tr>
<tr>
<td>Nemertea</td>
<td>#</td>
<td>#</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Mollusca</td>
<td>#</td>
<td>#</td>
<td>###</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Annelida</td>
<td>#</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Echiura</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Sipuncula</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Onychophora</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Tardigrada</td>
<td>#</td>
<td>—</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Arthropoda</td>
<td>###</td>
<td>###</td>
<td>###</td>
<td>###</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Gastrotricha</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Nematoda</td>
<td>#</td>
<td>#</td>
<td>#</td>
<td>###</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Nematomorpha</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Priapulida</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Loricifera</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Kinorhyncha</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Gnathostomulida</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Rotatoria</td>
<td>#</td>
<td>#</td>
<td>#</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Acanthocephala</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Kamptozoa</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Cyclophora</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Phoronida</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Brachiopoda</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Bryozoa</td>
<td>###</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Chaetognatha</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Hemichordata</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Echinodermata</td>
<td>###</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Chordata (Cephalochordata and Urochordata)</td>
<td>###</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Chordata (Vertebrata)</td>
<td>###</td>
<td>#</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

#, 1–100; ##, 100–1000; ###, 1000–10,000; ####, 10,000–100,000; and #####, over 100,000.
Modified from Pearse et al. (1987), p. 7; with taxonomic and number updates from Ruppert et al. (2004).

References


General Invertebrate Zoology References


General References for Invertebrate Medicine, Husbandry, Culture, and Pathology

The phylum Porifera is a diverse group of primitive animals commonly referred to as the sponges. Until the middle of the 18th century, sponges were actually classified as plants (Ruppert and Barnes, 1994). Sponges occur in the fossil record back to the Precambrian (over 600 million years ago) and were the most important contributors to reefs during the Paleozoic and Mesozoic Eras (Hooper and Van Soest, 2002). All members lack defined organs; differentiated cells within connective tissue perform necessary biological functions. A unique system of water canals facilitates transport of food, waste products, and gametes. Nearly all are sessile and most species are marine. Of the approximately 8,000 species belonging to over 680 genera, only about 3% occur in freshwater (Ruppert and Barnes, 1994; Hooper and Van Soest, 2002). Sponges are normally found on firm substrates in shallow water, although some occur on soft bottoms.

**Anatomy and Physiology**

There is a wide size variability among sponges, and very few are regularly or consistently shaped. Many are brilliantly colored, especially the marine forms.

**Porifera** means “pore bearing.” In the basic body plan, numerous external pores, known as ostia, open into a large central cavity called the atrium or spongocoel. The atrium terminates in a single large opening termed the osculum. Water enters the sponge through the ostia, percolates into the atrium, and then exits via the osculum (Figure 2.1).

The body wall, known as the pinacoderm, is composed of epithelial cells called pinacocytes. Some pinacocytes can produce an adhesive that fixes the sponge to the substrate. Circular porocytes form the ostia and extend from the surface of the sponge to the atrium. A connective tissue-like matrix lies beneath the pinacoderm. This layer, which frequently contains skeletal elements and amoeboid cells, is termed the mesohyl. The skeletal elements may be spongina, silicium, calcareous, or some combination of these. Spongina is a protein that is comparable to collagen. Skeletal elements are the primary means of determining sponge taxonomy. In some cases, skeletal elements may extend through the pinacoderm to the sponge's surface (Figure 2.2).

There are a number of amoeboid cells in the mesohyl. These cells carry out the basic body functions. Archeocytes are large, phagocytic, and totipotent. Collenocytes secrete collagen, scleroocytes secrete skeletal spicules, and spongocytes produce spongina. Choanocytes move water through the sponge to obtain food. All sponges lack a gut.

There are three basic sponge body plans: asconoid, syconoid, and leuconoid.
and leuconoid (Figure 2.3). Most sponges, and certainly the larger, more typical sponges, follow the leuconoid plan. The simple and primitive asconoid plan, with its radial symmetry and single atrium, has a limited surface area and hence a small maximum size. Evolving sponges solved this problem by increasing surface area by folding of body surfaces: the more folds, the more choanocytes, and the more choanocytes, the more water flow. In the intermediate syconoid body plan, the choanocytes do not line the spongocoel but are located along open channels called radial canals. The leuconoid sponge is the most evolved and has the most body folding and surface area. In this type of sponge, the choanocytes are in flagellated chambers and the spongocoel is frequently reduced to numerous canals connected to the osculum. Leuconoid sponges can grow large because mass increase leads to an increase in the number of flagellated chambers. Many forms possess more than one osculum. De Vos et al. (1991) have provided a detailed atlas of gross and microscopic sponge morphology.

Water flow sustains the life of a sponge, delivering food and removing waste products. Sponges are remarkably efficient an-
imals with regard to water flow. *Leuconia*, a small leuconoid sponge (approx. 10 × 1 cm) has 2,250,000 flagellated chambers and may pump 22.5 L/day (Ruppert and Barnes, 1994). These water currents are produced by asynchronous beating of the choanocyte flagella. In some cases (environment and species dependent), there is a passive component to water flow.

Sponges are filter feeders and subsist primarily on microscopic organisms, organic matter, and minute plankton (Reiswig, 1971). The food elements are phagocytosed by all types of sponge cells. Larger particles (5–50 µm) are consumed by pinacocytes and archeocytes while tiny pieces (<1 µm) are absorbed by choanocytes. Most digestion occurs in the archeocytes and choanocytes; archeocytes then transport nutrients to different cells. Some marine sponges use photosynthesis via symbiotic organisms—normally, blue-green algae (*cyanobacteria*). Some sponge species harbor *zooxanthellae* (nonmotile dinoflagellates). The zooxanthellae frequently impart a color to the sponge (Figure 2.4, Color Plate 2.4).

Sponges accomplish gas exchange by simple diffusion and secrete ammonia as their primary nitrogenous waste product. Ammonia is removed by water coursing through the sponge.

Sponges lack a nervous system; message substances travel from cell to cell via diffusion.

Sponges reproduce in a variety of ways: regeneration, asexual reproduction, and sexual reproduction. Most sponges are sequential hermaphrodites. Choanocytes produce sperm, and either archeocytes or choanocytes produce eggs. Environmental changes may trigger the production of gametes. Sperm are expelled through the ostia and enter other sponges via the inhalant channels. Gametes fuse, and a parenchymella larva develops. Larvae leave via the ostia and may swim freely for a period before settling and attachment. In some species, given time and the proper environment, pieces from a mature sponge will grow into a new large sponge. Some freshwater sponges (and a few marine forms) display an interesting strategy of surviving a harsh winter. Clusters of nutrient-rich archeocytes are surrounded by amoebocytes that secrete a firm coating around the cluster. These cellular survival pods, known as *gemmules*, can survive freezing and desiccation, developing into an adult sponge during the spring and summer months. The temperate marine sponge *Microciona prolifera* undergoes marked morphological changes (Figure 2.5, Color Plate 2.5), including apoptosis (programmed cell death), during the winter (Kuhns et al., 1997). The surviving archeocytes become encased in a protective tissue matrix, likely waiting for warmer temperatures, when differentiation can occur (Kuhns et al., 1997).

Sponges secrete metabolites that are toxic to fish and other potential predators. Not all predators are deterred, and some sea turtles eat a diet primarily composed of sponges and excrete the undigestable spicules in their feces. Although not thoroughly understood, the sponge immune system is simple compared with higher invertebrate and vertebrate phyla and relies on cell-

![Figure 2.4.](image) Four different sponges from the Turks and Caicos Islands. Symbiotic zooxanthellae can impart striking colors upon the sponge.
Figure 2.5. Gross and histological comparison of summer and winter *Microciona prolifera*: summer sponge (A) and winter sponge (B). The winter sponge displays less color and integrity. Microscopic view of summer sponge (C) shows more cellularity than that of the winter sponge (D). A TUNEL (terminal deoxyribonucleotidyl transferase-mediated dUTP nick end label) assay shows fragmenting nuclear DNA as brownish red (E), whereas G is the counterstained control (no TUNEL). Yellow numbers are as follows: 1 and 7, phagocytosed apoptotic cells; 2 and 5, small apoptotic cells; and 3, 4, and 6, macrophage-type (apparently healthy) and small apoptotic cells. In the winter sponge TUNEL assay (F), a small number of healthy stem cells (blue nuclei) are mixed with clumps of apoptotic debris. From Kuhns et al. (1997), Figure 1 (pp. 239–240). Reprinted by permission of the Marine Biological Laboratory, Woods Hole, MA.
mediated immunity (Van de Vyver and Buscema, 1990). Phagocytosis, primarily by archeocytes, appears to be the primary mode of defense against invading pathogens (Cheng et al., 1968a, 1968b; Rützler, 1988). These foreign body-laden phagocytic cells migrate to the excurrent canals and are expelled (Figure 2.6). In a study examining a variety of heterografts in the sponge *Terpios zeteki*, it was noted that human erythrocytes were completely phagocytosed by slightly smaller archeocytes, indicating the sponge cell’s hypertrophic capability (Cheng et al., 1968b).

Some sponges harbor antimicrobially active bacteria and can produce antibacterial and antifouling compounds (Nigrelli et al., 1959; Jakowska and Nigrilli, 1960; Burkholder and Ruetzler, 1969; Bakus et al., 1990; Thakur-Narsinh et al., 2003). Thakur-Narsinh et al. (2003) used the marine sponge *Suberites domuncula* and found antimicrobial *Proteobacteria* and a perforin-like protein with antibacterial activity associated with this species. Ectyonin, an extract of *Microciona prolifera* (the red beard sponge), showed in vitro antimicrobial activity against Gram-negative, Gram-positive, and acid-fast bacteria, as well as *Candida albicans* (Nigrelli et al., 1959). Preliminary tests in this study indicated that ectyonin (parenterally injected) is not toxic to killifish (*Fundulus heteroclitus*) and mice. Sorbicil-latone A, a bioactive alkaloid produced by *Penicillium chrysogenum* (a fungus that lives on the Mediterranean sponge *Ircinia fasciculata*), is cytotoxic to murine leukemic lymphoblasts and warrants further study (Bringmann et al., 2003).

Faulkner (1999, 2000) and Müller (2003) provide detailed accounts of natural products produced by sponges and their symbionts. This is an active research area involving the disciplines of molecular biology, organic chemistry, and biotechnology. For obvious reasons, successful maintenance and cultivation of sponges can contribute to ongoing research efforts in these areas. Brümmer and Nickel (2003) review the topic of captive sponge propagation, and Table 2.1 contains a list of pertinent data.

Sponges frequently serve as home for many other animals, including echinoderms, worms, and crustaceans.

### Environmental Disorders

As aquatic, sessile animals, sponges rely on a constant flow of life-sustaining water. Adverse water-quality parameters can have an immediate and detrimental effect on sponges because they cannot escape or avoid environmental challenges. Although there are some freshwater sponges, most are marine, and tolerance for sudden changes in salinity varies between species (De Laubenfels, 1947).

*Iotrochota birotulata*, a marine sponge, was found to tolerate salinities between 23 and 38 ppt but die in water below 20 ppt and higher than 40 ppt (De Laubenfels, 1932). One study (De Laubenfels, 1947) found that the sponge *Hymeniacidon* sp. could maintain a core temperature higher than the surrounding air and water (33°C for the sponge and 29°C for the environment). No explanation was given for this temperature differential.

A number of references address the topic of sponges as models for assessing impact of pollutants on aquatic animals (Zahn et al., 1983; Francis and Harrison, 1988; Hansen et al., 1995). Laboratory experiments (Hill et al., 2002) on developing freshwater sponges (*Heteromyenia* sp. and *Eunapius fragilis*) showed that ethylbenzene, nonylphenol, and bisphenol (all endocrine disrupters) produced developmental anomalies and retarded growth rate in these animals (Figures 2.7 and 2.8). The mechanisms for these effects are not well understood, but collagen synthesis disruption has been proposed for the freshwater sponge *Ephydatia fluviatilis* when exposed to azetidine 2-carboxylic acid (Mizoguchi and Watanabe, 1990).

It was determined that both copper and zinc are toxic to the freshwater sponge *Ephydatia fluviatilis* at concentrations of $1 \times 10^{-7}$ in water with a total hardness of 60 mg/L (Francis and Harrison, 1988). The two metals exhibited different toxic ef-
### Table 2.1. Mediterranean Sea sponges in captivity that were collected from a variety of localities

<table>
<thead>
<tr>
<th>Species</th>
<th>Interim Storage</th>
<th>Recovery After Transport</th>
<th>Long-term Maintenance</th>
<th>Growth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthella acuta</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Months/year</td>
<td>Not observed</td>
</tr>
<tr>
<td>Agelas oroides</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Months/year</td>
<td>Not observed</td>
</tr>
<tr>
<td>Aplysina aerophoba</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Months/year</td>
<td>Good</td>
</tr>
<tr>
<td>Aplysina cavernicola</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Months</td>
<td>Not observed</td>
</tr>
<tr>
<td>Axinella polyoides</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Months</td>
<td>Not observed</td>
</tr>
<tr>
<td>Axinella verrucosa</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Months</td>
<td>Not observed</td>
</tr>
<tr>
<td>Cacospongia sp.</td>
<td>Possible</td>
<td>Impossible</td>
<td>Impossible</td>
<td>Not determined</td>
</tr>
<tr>
<td>Chondrilla nucula</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Years</td>
<td>Good</td>
</tr>
<tr>
<td>Chondrosia sp.</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Years</td>
<td>Excellent</td>
</tr>
<tr>
<td>Clathrina clathrus</td>
<td>Excellent</td>
<td>Good</td>
<td>Months/year</td>
<td>Not observed</td>
</tr>
<tr>
<td>Clathrina coriacea</td>
<td>Good</td>
<td>Good</td>
<td>Weeks</td>
<td>Not observed</td>
</tr>
<tr>
<td>Ciona vermifera</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Months</td>
<td>Not observed but possible</td>
</tr>
<tr>
<td>Clithoidea hancocki</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Months</td>
<td>Not observed but possible</td>
</tr>
<tr>
<td>Crambe crambe</td>
<td>Good</td>
<td>Good</td>
<td>Weeks/months</td>
<td>Not observed</td>
</tr>
<tr>
<td>Dysidea avara</td>
<td>Excellent</td>
<td>Good</td>
<td>Months/year</td>
<td>Good/possible</td>
</tr>
<tr>
<td>Haliclona sp.</td>
<td>Not determined</td>
<td>Good</td>
<td>Weeks</td>
<td>Not observed</td>
</tr>
<tr>
<td>Hexadella racovitzai</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Months</td>
<td>Not observed</td>
</tr>
<tr>
<td>Ircinia sp.</td>
<td>Impossible</td>
<td>Impossible</td>
<td>Impossible</td>
<td>Not determined</td>
</tr>
<tr>
<td>Petrosia ficiformis</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Months/year</td>
<td>Not observed</td>
</tr>
<tr>
<td>Spirastrella sp.</td>
<td>Good</td>
<td>Good</td>
<td>Weeks/months</td>
<td>Not observed</td>
</tr>
<tr>
<td>Suberites domuncula</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Years</td>
<td>Good</td>
</tr>
<tr>
<td>Sycon raphanus</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Months/year</td>
<td>Good</td>
</tr>
<tr>
<td>Tethya aurantium</td>
<td>Excellent</td>
<td>Excellent</td>
<td>Weeks/months</td>
<td>Not observed but possible</td>
</tr>
</tbody>
</table>

Modified from Brümmer and Nickel (2003).

**Figure 2.7.** Normal development of the freshwater sponge *Heteromyenia* sp. **A:** The solid gemmule is at lower left with developing spicules and multiple ostia clearly visible within the parenchyma. **B:** Another example with a more centrally located gemmule and a visible canal system. From Hill et al. (2002), Figures 1 and 3 (pp. 297–298). Reprinted by permission of Elsevier.