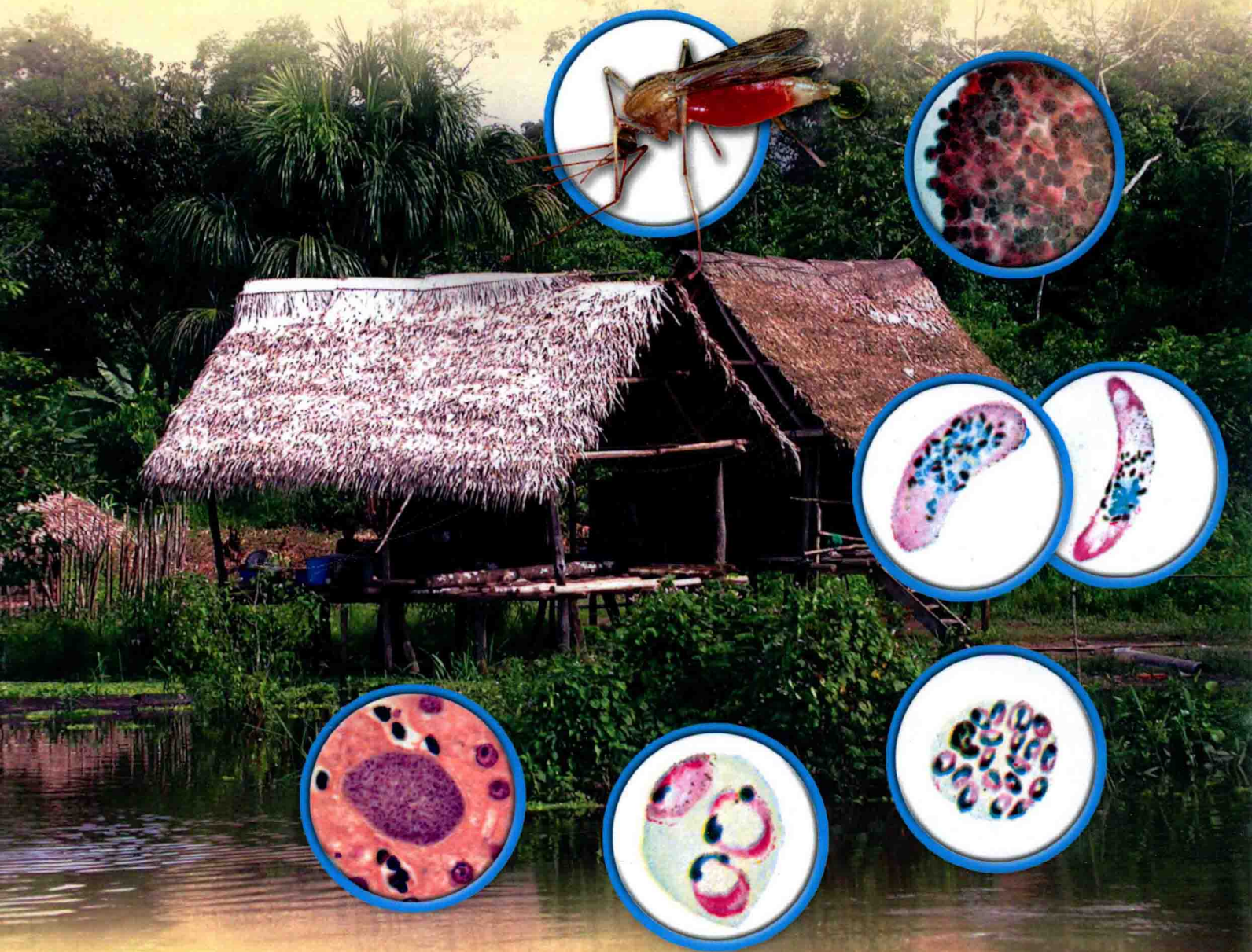


Larry S. Roberts • John Janovy, Jr. • Steve Nadler



Gerald D. Schmidt & Larry S. Roberts'

FOUNDATIONS OF

# Parasitology

Ninth Edition

NINTH EDITION

GERALD D. SCHMIDT & LARRY S. ROBERTS'

# FOUNDATIONS OF PARASITOLOGY

LARRY S. ROBERTS

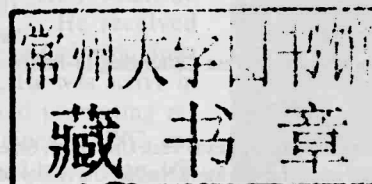
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GERALD D. SCHMIDT & LARRY S. ROBERTS' FOUNDATIONS OF PARASITOLOGY  
NINTH EDITION

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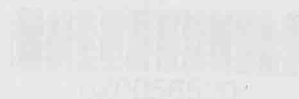
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GERALD D. SCHMIDT & LARRY S. ROBERTS'

# FOUNDATIONS OF PARASITOLOGY

LARRY S. ROBERTS

TEXAS TECH UNIVERSITY

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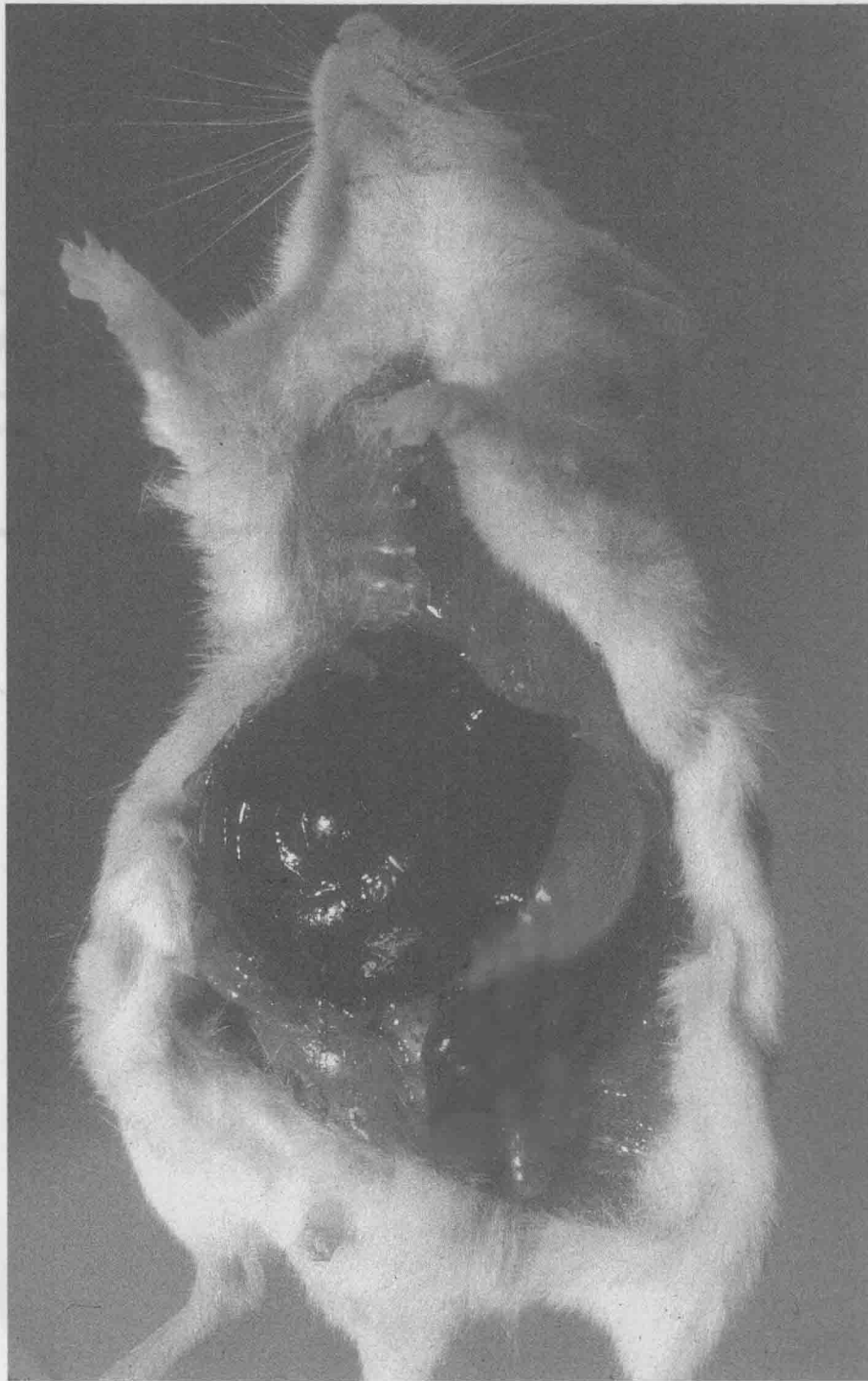
STEVE M. SHAW

UNIVERSITY OF CALIFORNIA

Intelligent to liver and spleen (hepatosplenomegaly) is a laboratory mouse infected with the rodent malarial parasite *Plasmodium berghei*. The liver and spleen enlarge and darken from the accumulation of parasite between malarial attacks in uninfected mice. The liver and spleen of these infected mice (221) hepatosplenomegaly can also occur in humans infected with their malarial parasite. The human *P. falciparum* system, like other non-human models of parasitic diseases, has been important in improving understanding of the complex interactions between hosts and parasites.



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Enlargement of liver and spleen (hepatosplenomegaly) in a laboratory mouse infected with the rodent malaria parasite, *Plasmodium berghei*. The liver and spleen enlarge and darken from the accumulation of parasite hemozoin pigment granules in reticuloendothelial cells of these organs (p. 153). Hepatosplenomegaly can also occur in humans infected with their malaria parasites. The mouse-*P. berghei* system, like other non-human models of parasitic diseases, has been important in improving understanding of the complex interactions between hosts and parasites.

# about the authors

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## LARRY S. ROBERTS

Larry S. Roberts, professor emeritus of biology at Texas Tech University, was professor of zoology at University of Massachusetts, Amherst, and was adjunct professor of biology at Florida International University and the University of Miami, where he had extensive experience teaching parasitology, invertebrate zoology, marine biology, and developmental biology. He received his Sc.D. in parasitology at the Johns Hopkins University and has coauthored *Foundations of Parasitology* from the first edition through this, the ninth edition. He is also coauthor of *Integrated Principles of Zoology*, *Biology of Animals*, and *Animal Diversity*, and is author of *The Underwater World of Sport Diving*.



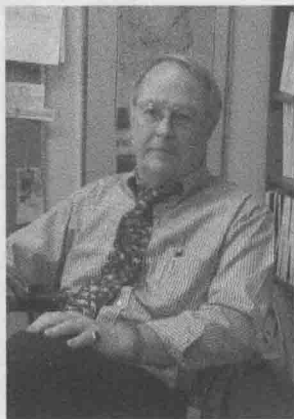
Dr. Roberts has published many research articles and reviews. He has served as president of the American Society of Parasitologists, the Southwestern Society of Parasitologists, the Southeastern Society of Parasitologists, and the Helminthological Society of Washington. He received the Henry Baldwin Ward Medal from the American Society of Parasitologists. His hobbies include scuba diving, underwater photography, and tropical horticulture.

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---

## JOHN JANOVY, JR.

John Janovy, Jr. (PhD University of Oklahoma, 1965) is Professor Emeritus at the University of Nebraska where he was the Paula and D. B. Varner Distinguished Professor of Biological Sciences for much of his career. His research interest is parasitology, with particular focus on parasite ecology and life cycles. He has been director of the Cedar Point Biological Station, interim director of the University of Nebraska State Museum, an assistant dean of Arts and Sciences, and secretary-treasurer of the American Society of Parasitologists. He is currently (2012) President-Elect



of the American Society of Parasitologists. His scholarly and creative accomplishments consist of approximately 100 scientific papers and book chapters; 14 books, including *Keith County Journal*, *On Becoming a Biologist*, *Teaching in Eden*, *Outwitting College Professors*, and *Foundations of Parasitology* (with Larry Roberts and Steve Nadler); the screenplay for the televised version of *Keith County Journal* (Nebraska Public Television); and numerous popular articles. His teaching experiences include almost continuous service in the large-enrollment freshman biology course; Field Parasitology (BIOS 487/887) at the Cedar Point Biological Station; Invertebrate Zoology (BIOS 381); Parasitology (BIOS 385); a decade in BIOS 103/204 (Organismic Biology/Biodiversity); and numerous honors seminars. He has supervised 18 MS students, 14 PhD students, and approximately 50 undergraduate researchers, including 10 Howard Hughes scholars. His honors include the University of Nebraska Distinguished Teaching Award (1970), University Honors Program Master Lecturer (1986), American Health magazine book award (1987, for *Fields of Friendly Strife*), University of Nebraska Outstanding Research and Creativity Award (1998), The Nature Conservancy Hero recognition (2000), and the American Society of Parasitologists Clark P. Read Mentorship Award (2003).

---

## GERALD D. SCHMIDT

Gerald D. Schmidt was professor of biology at the University of Northern Colorado (UNC) when he passed away. He received his PhD from Colorado State University. He was active in research and promoting research activities at UNC, and he published more than 160 research articles in scientific journals, as well as six books. He received awards from UNC for outstanding teaching and for distinguished scholarship. He was a board member of the World Federation of Parasitologists; a Fellow of the Royal Society of Tropical Medicine and Hygiene, London; and a Fellow of the Royal Society of South Australia.

Dr. Schmidt served the American Society of Parasitologists as secretary-treasurer for seven years. He was co-author of *Foundations of Parasitology* through the first four editions. His hobbies were hunting and fishing, especially fishing, and he wrote a book on fishing. Dr. Schmidt died on 16 October 1990; many more details of his life can be found in the *Journal of Parasitology*, 78:757-773.



## STEVE NADLER

Steve Nadler (PhD in Medical Parasitology, Louisiana State University Medical Center, New Orleans) is Professor of Nematology in the Department of Entomology and Nematology at the University of California, Davis. His research interests concentrate on the systematics and evolutionary biology of nematodes, including both free-living and parasitic species. He served as chair of the Department of Nematology at UC Davis for



six years. Dr. Nadler was an associate editor of the *Journal of Parasitology*, and president of the American Society of Parasitologists (2007–08). His scholarly accomplishments include approximately 90 scientific papers, and his research has been supported by grants from the U.S. National Science Foundation and the National Institutes of Health. He currently serves on the editorial boards of the journals *Parasitology*, *Systematic Parasitology*, *Zookeys*, and *Animal Cells and Systems*. His research laboratory is supported by efforts of undergraduate and graduate students, along with visiting scientists and postdoctoral scholars. At UC Davis his undergraduate and graduate teaching includes courses in parasitology, nematology, and molecular phylogenetics.



# *preface*



We enthusiastically present the ninth edition of this book with numerous updates on topics of vigorous contemporary research. We continue to preserve essential qualities of the text that students and professors liked in the first eight editions. The reception accorded *Foundations of Parasitology* has been most gratifying. Your comments and suggestions are always welcome. Keep them coming.

---

## SCOPE OF THIS BOOK

This textbook is designed specifically for upper division courses in general parasitology. It emphasizes principles, illustrating them with material on the biology, physiology, genetics, morphology, phylogeny and ecology of the major parasites of humans and domestic animals. We have found that they are of most interest to the majority of students. Other parasites are included as well, when they are of unusual biological interest.

The first three chapters delineate important definitions and principles in evolution, ecology, immunology, and pathology of parasites and parasitic infections. Chapters on specific groups follow, beginning with protozoa and ending with arthropods. Presentation of each group is not predicated on students having first studied groups presented in prior chapters; therefore, the order can vary as an instructor desires. As always, we have strived for readability, enhancing words with photographs, drawings, electron micrographs, and tables.

---

## NEW TO THIS EDITION

This edition integrates a wealth of new discoveries and literature. Many areas of parasitology are theaters of intense research effort and fruitful results. As always, addition of material compelled us to prune out an equal amount of text and illustrations so as not to increase book length, but we hope that we have been judicious in our reshaping. We have continued to include trenchant quotations at the beginning of each chapter. Well, maybe some of them are not so trenchant. Nevertheless, we hope these observations of pioneering researchers, as well as references to literature and even pop culture, will broaden your view of parasitology. Their curiosity piqued, some readers have asked us for sources of quotations, so we have included these where possible.

The numerous changes in chapter 1 included updating the table on global prevalence of various human parasites. We have retained our section with the light-hearted title of "Parasitology for Fun and Profit" to emphasize how students can earn an income while studying the fascinating world of parasites. We are including some web links because many students enjoy taking advantage of those resources. Concepts in Chapters 2 and 3 are briefly covered, but understanding them is *essential* to understanding the rest of the book.

Chapter 2 has been further reorganized to include fascinating material on the role played by parasites in food webs and ecosystems. Our increased emphasis on molecular systematics and phylogenetics has been retained, and we provide some examples here and in chapters to follow. Propelled in large measure by modern molecular methods, immunologists continue their torrent of discoveries. The 1980s through 2000s saw enormous increases in our understanding of the role and mechanisms of cytokine function and witnessed our realization of the importance of immunopathology in parasitic diseases. Thus, chapter 3 has again undergone major surgery. It has been rewritten, reorganized, and expanded, including a section introducing antimicrobial peptides (defensins) and Toll-like receptors and tables listing the many ways that protozoan and helminth parasites evade host defenses. We added a figure in the 8th edition illustrating a JAK-STAT cell signaling pathway. In this edition we expanded the discussion of  $T_{reg}$  and dendritic cells, and added a section on the microbial deprivation hypothesis relating parasitism to immune system development.

"Form and Function" chapters on protozoan parasites, trematodes, cestodes, nematodes, and arthropods have again been updated and rewritten significantly to provide a stronger base of knowledge with which to investigate each group further. When available, we include phylogenies to show evolutionary relationships of some of the major groups.

We again modified the classification section of chapter 4, making it consistent with all the major taxonomic literature published since the seventh and eighth editions. We continue use of the words "protozoa" and "protozoans" as common names with no taxonomic status and that refer to a number of phyla. Chapter 5 on Kinetoplasta includes the latest information on antigenic variation in trypanosomes. *Leishmania*-host cell relationships, and the important new anti-leishmanial drug miltefosine. In chapter 6 we continue usage of *Giardia duodenalis* to be consistent with the latest nomenclatural decisions about this important parasite. Several examples in this chapter cite the importance of molecular techniques to diagnosis and contributions to the overall biology of the organisms. Other protistan chapters address the exploding body of knowledge about opportunistic parasitic infections in immunocompromised persons and the amazing diversity of coccidians as revealed by the active systematic research on these parasites.

Chapter 7 on amebas was reworked considerably in the 8th edition, and several new figures were added, including an *Acanthamoeba*-infected eye. Both chapters 8 and 9 have information on the important membranous organelle known as an apicomplast. Intense scrutiny of malaria continues, reflecting its widespread importance as a human disease, and chapter 9 has been revised accordingly. *Plasmodium knowlesi* has been included as one of the species that often causes human malaria. We retained the expanded table comparing *Plasmodium* spp. and updated methods of diagnosis, role of cytokines in pathogenesis and immunity, progress toward vaccines, and drug action and resistance. A figure illustrates fluctuations in body temperature (fever phases) in



*falciparum* compared with *vivax* malaria and relationship of the temperature fluctuations to phases of schizogony.

In chapter 12, we recognize two phyla of mesozoans, Dicyemida and Orthonectida, in accord with recent literature, and the classification has been revised. In chapter 13 of the seventh edition, we introduced significant revision of flatworm systematics, which has been retained in this edition. We point out, in chapter 16, the potential for widespread increase in prevalence of *Schistosoma japonicum* resulting from the huge Three Gorges Dam on the Yangtze River in China. Other sections of this chapter have been rewritten, including pathology, control, and other *Schistosoma* spp.

In chapter 20 on cestode form and function we retain the revisions made for the seventh edition, and on the basis of its extremely unusual scolex, we recognize order Cathetocephalidea and include a figure of its scolex. We have followed the sensible suggestions of Kuchta et al. (2008) in suppressing the name Pseudophyllidea and recognizing two new orders of cestodes, Bothriocephalidea and Diphyllbothriidea. We have retained the numerous revisions in chapter 21 and rearranged several sections.

The most profound change in chapter 22 introducing nematodes (compared with the seventh and earlier editions) is the adoption of the phylogeny and nomenclature of De Ley and Blaxter (2002, in D. L. Lee (Ed.), *The biology of nematodes*, Taylor and Francis). This nomenclature has been updated to reflect molecular phylogenetic hypotheses published since the 7th edition. Revised and expanded phylogenies for nematodes have required some reorganization of the taxonomic groups covered in subsequent chapters. To ease the transition required by De Ley and Blaxter's classification, within certain chapters we retain common usage of nematode groups (e.g., families) used in earlier editions of this book.

We incorporated numerous other changes and updates in the nematode chapters. Throughout these chapters we have incorporated examples of how new approaches and tools, including gleaning information from nematode models such as *Caenorhabditis elegans*, are helping to advance understanding of parasites. Updated information on infection prevalence was added, when available. The eighth species of *Trichinella*, *T. zimbabwensis*, is covered and added to Table 23.1. We added the probable environmental cue that determines whether *Strongyloides* females will initiate homogonic or heterogonic cycle. In Chapter 24 we emphasized the diversity of nematodes in the suborder Tylenchina, which includes free-living species and important plant and animal parasites. In chapter 25 we remarked on the difficulties in distinguishing hookworm eggs from those of *Oesophagostomum bifurcum* and *Ternidens deminutus* in areas of Africa where they parasitize humans, and we recognize *Angiostrongylus vasorum* as an emerging infection of canids. In accord with updated molecular phylogenetic results, Camallanoidea was transferred to chapter 30 with Dracunculomorpha.

Chapter 31 of the seventh edition was an entirely new chapter on those amazing worms, Nematomorpha. This chapter brings together all findings of the most recent research on this group, especially the life cycle work. *Foundations of Parasitology* is the only text to date including invertebrate and zoology texts that has this information. Chapter 32 on Acanthocephala has an expanded discussion of recent molecular work linking this phylum to Rotifera.

Form and function of arthropods has now become chapter 33. We have added a discussion of Arthropoda phylogeny, including its position as a member of superphylum Ecdysozoa. Readers of the classification coverage in this chapter will find that we have included Pentastomida within Arthropoda as a subclass of crustacean class Maxillopoda. Chapter 34 adopts the currently most authoritative classification of Crustacea. In this chapter we include a photo of a shark embryo parasitized by trebiid copepods; these amazing organisms enter the uterus of pregnant sharks, attacking the uterine wall as well as the surface of the embryos, thus becoming endosymbiotic ectoparasites!

Chapter 35 covers Pentastomida and includes an explanation of its demotion from phylum status to a subclass of Crustacea. Much information was been added in the eighth edition to the remaining chapters on insects, such as use of endectocides for control of lice, potential for bed bugs to transmit hepatitis, and a dramatic picture of a strepsipteran emerging from a fire ant. The section on plague has been extensively reworked.

Chapter 41 on ticks and mites had new material on tick behavior in the eighth edition, especially their attraction to human breath, on dogs as carriers of various tick-borne infections, and on chorioptic mange as a veterinary problem.

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## INSTRUCTIVE DESIGN

Students using the ninth edition of *Foundations of Parasitology* are guided to a clear understanding of the topic through our careful use of study aids. Essential terms, many of which are defined in a complete glossary, are boldfaced in the text to provide emphasis and ease in reviewing. In response to student requests, we again provide pronunciation guides for glossary entries. Numbered references at the end of each chapter make supporting data and further study easily accessible. Clear labeling makes all illustrations approachable and self-explanatory to the student. Student learning outcomes are provided for each chapter, which can be used by instructors for assessment.

We have again been fortunate indeed to have William C. Ober and Claire W. Garrison draw new illustrations for this and the last several editions. Their artistic skills and knowledge of biology have enhanced other zoology texts coauthored by Larry Roberts. Bill and Claire bring to their work a unique perspective resulting from their earlier careers as physician and nurse, respectively.

---

## ACKNOWLEDGMENTS

We are indebted to the numerous students and colleagues who have commented on previous editions. We especially wish to thank the following individuals who reviewed certain chapters or the entire text. The comments were enormously helpful.

Osman Bannaga, *Miles College*  
 Dale Clayton, *University of Utah*  
 William Dees, *McNeese State University*



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