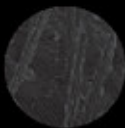
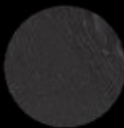




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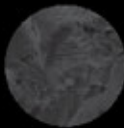
# PARASITISM



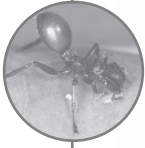
the diversity and ecology of animal parasites



TIMOTHY M. GOATER • CAMERON P. GOATER • GERALD W. ESCH







# Parasitism

The Diversity and Ecology of Animal Parasites

SECOND EDITION

Reflecting the enormous advances made in the field over the past 10 years, this text synthesizes the latest developments in the ecology and evolution of animal parasites against a backdrop of parallel advances in parasite systematics, biodiversity, and life cycles. It has been thoroughly revised to meet the needs of a new generation of parasitology students, whether their interest is in ecology, conservation biology, evolution, immunology, or health sciences.

Balancing traditional approaches in parasitology with modern studies in parasite ecology and evolution, the authors present basic ecological principles as a unifying framework to help students understand the complex phenomenon of parasitism. Richly illustrated with over 300 figures, the text is accompanied by case study boxes designed to help students appreciate the complexity and diversity of parasites and the scientists who study them. This unique approach, which is presented clearly and with a minimum of jargon and mathematical detail, encourages students to think generally and conceptually about parasites and parasitism.

**Timothy M. Goater** is Professor and former Chair in the Biology Department at Vancouver Island University, British Columbia, Canada. During the past 20 years he has taught courses in introductory biology, parasitology, ecological parasitology, invertebrate zoology, and entomology. His research interests focus on the population and community ecology of parasites.

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## **Advance praise for *Parasitism: The Diversity and Ecology of Animal Parasites, Second Edition***

“Their approach is synthetic, refreshingly original and effectively blends coverage of long-standing fundamentals of parasitology with modern advances in the field.”

Janine N. Caira, University of Connecticut, USA

“This is an extremely well written book that does an excellent job of integrating conceptual and organismal aspects of parasitology.”

Dale H. Clayton, University of Utah, USA

“There is a wealth of detail for well-selected examples, building on the rich experience of the authors as top-notch researchers and educators.”

Mark R. Forbes, Carleton University, Canada

“*Parasitism* gives the student both the systematic and zoological background to understand parasitology and the ecological and evolutionary context to understand why it is important. . . . As a team, their approach is clear and scholarly, with many important updates since the first edition.”

Kevin D. Lafferty, US Geological Survey, University of California, Santa Barbara, USA

“This new edition will be a wonderful resource for teachers of undergraduate parasitology courses. The well-illustrated and easy-to-read text is unrivalled at the moment and will be a great tool to turn on a new generation of young minds to the wonders of parasitic organisms. A true parasitological tour de force!”

Robert Poulin, University of Otago, New Zealand

“A well-organized integration of the diversity of ideas and methods that characterize this new field of parasite ecology. The style is easily readable, the details extraordinary, and the story is told from the perspective of evolutionary thought. . . . even the pros will learn from this book.”

Michael V. K. Sukhdeo, Rutgers University, USA



# Parasitism

## The Diversity and Ecology of Animal Parasites

SECOND EDITION

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Vancouver Island University, British Columbia, Canada

CAMERON P. GOATER

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GERALD W. ESCH

Wake Forest University, North Carolina, USA



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*We dedicate this book to our students,  
past, present, and future*







# CONTENTS

<i>List of boxes</i>	page ix	5.5 Phylogenetic relationships and classification	106
<i>Foreword by John C. Holmes</i>	xi		
<i>Preface and acknowledgments</i>	xiii		
<b>1 Introduction</b>	1	<b>6 Platyhelminthes: the flatworms</b>	113
1.1 Encounters with parasites	1	6.1 General considerations	113
1.2 Scope	2	6.2 Temnocephalidea	114
1.3 Terminology	5	6.3 Udonellida	115
1.4 Overview	10	6.4 Aspidobothrea	115
		6.5 Digenea	116
		6.6 Monogenea	145
<b>2 Immunological aspects of parasitism</b>	16	6.7 Gyrocotylidea	152
2.1 General considerations	16	6.8 Amphilinidea	153
2.2 Vertebrate immunity	21	6.9 Eucestoda	153
2.3 Invertebrate immunity	31	6.10 Phylogenetic relationships and classification	169
2.4 Ecological immunology	34		
		<b>7 Acanthocephala: the thorny-headed worms</b>	179
<b>3 Protista: the unicellular eukaryotes</b>	40	7.1 General considerations	179
3.1 General considerations	40	7.2 Form and function	179
3.2 Form and function	41	7.3 Nutrient uptake and metabolism	186
3.3 Biodiversity and life-cycle variation	43	7.4 Development and general life cycle	188
3.4 Phylogenetic relationships and classification	80	7.5 Biodiversity and life-cycle variation	191
		7.6 Phylogenetic relationships and classification	192
<b>4 Microsporidia: the intracellular, spore-forming fungi</b>	86		
4.1 General considerations	86	<b>8 Nematoda: the roundworms</b>	199
4.2 Form and function	86	8.1 General considerations	199
4.3 Development and general life cycle	88	8.2 Form and function	199
4.4 Biodiversity and life-cycle variation	88	8.3 Nutrient uptake and metabolism	208
4.5 Phylogenetic relationships and classification	93	8.4 Development and general life cycle	209
		8.5 Biodiversity and life-cycle variation	211
<b>5 Myxozoa: the spore-forming cnidarians</b>	96	8.6 Phylogenetic relationships and classification	237
5.1 General considerations	96		
5.2 Form and function	97	<b>9 Nematomorpha: the hairworms</b>	244
5.3 Development and general life cycle	97	9.1 General considerations	244
5.4 Biodiversity and life-cycle variation	100	9.2 Form and function	244

9.3	Development and general life cycle	246		
9.4	Biodiversity and ecology	247		
9.5	Phylogenetic relationships and classification	249		
<b>10</b>	<b>Pentastomida: the tongue worms</b>	<b>252</b>		
10.1	General considerations	252		
10.2	Form and function	252		
10.3	Nutrient uptake and metabolism	256		
10.4	Development and general life cycle	256		
10.5	Biodiversity and life-cycle variation	258		
10.6	Phylogenetic relationships and classification	260		
<b>11</b>	<b>Arthropoda: the joint-legged animals</b>	<b>263</b>		
11.1	General considerations	263		
11.2	Crustacea	264		
11.3	Chelicerata	289		
11.4	Hexapoda	308		
11.5	Phylogenetic relationships and classification	328		
<b>12</b>	<b>Parasite population ecology</b>	<b>335</b>		
12.1	General considerations	335		
12.2	Terminology and general approaches	336		
12.3	Introduction to parasite population ecology	337		
<b>13</b>	<b>Parasite community ecology</b>	<b>356</b>		
13.1	General considerations	356		
13.2	Introduction to parasite community ecology	357		
13.3	The structure of parasite infra-communities: restricted niches	361		
13.4	The structure of parasite communities: species richness	368		
<b>14</b>	<b>Parasite biogeography and phylogeography</b>		<b>379</b>	
14.1	General considerations		379	
14.2	Historical biogeography		380	
14.3	Ecological biogeography		386	
14.4	Applied aspects of parasite biogeography and phylogeography		389	
<b>15</b>	<b>Effects of parasites on their hosts: from individuals to ecosystems</b>		<b>396</b>	
15.1	General considerations		396	
15.2	Effects of parasites on host individuals		396	
15.3	Effects of parasites on host populations		411	
15.4	Effects of parasites on host communities and ecosystems		422	
<b>16</b>	<b>Evolution of host–parasite interactions</b>	<b>432</b>		
16.1	General considerations		432	
16.2	Parasite-mediated natural selection and evolution		432	
16.3	Genetic structure of parasite populations		441	
16.4	Introduction to host–parasite coevolution		446	
<b>17</b>	<b>Environmental parasitology: parasites as bioindicators of ecosystem health</b>		<b>459</b>	
17.1	General considerations		459	
17.2	Parasites as effect indicators of pollutant stress		460	
17.3	Parasites as environmental sentinels		470	
	<i>Glossary</i>		477	
	<i>Index</i>		489	
	<i>The color plates are located between pages 248 and 249.</i>			



## BOXES

1.1	A brief historical perspective of parasitology: pioneering scientists and their ground-breaking parasitological discoveries	page 4	7.4	Phylogeny of the Acanthocephala and the evolution of parasitism	195
1.2	Parasite systematics: a phylogenetics primer	11	8.1	Evolution of nematode life-cycle plasticity: developmental switching in <i>Strongyloides</i> spp.	213
2.1	Immunology: a terminology primer	18	8.2	Entomopathogenic nematodes and their microbial symbionts: tapping their chemotherapeutic potential	216
3.1	A plastid in apicomplexans: a promise for new drug therapies?	43	8.3	Transmammary transmission in hookworms	225
3.2	Protists as hosts for microbial symbionts	44	8.4	<i>Wolbachia</i> spp.: endosymbiotic bacteria in filariid nematodes	234
3.3	Giardiasis: epidemiology and pathogenesis of beaver fever	48	8.5	Classification of the Nematoda	239
3.4	Pathogenesis, epidemiology, and diagnosis of Chagas' disease	53	10.1	Pentastomids: masters of immunoevasion	254
3.5	Relapse and recrudescence in malaria	68	10.2	Fossil pentastomes from the Cambrian era suggest an alternative phylogenetic hypothesis	259
3.6	Diagnosis of human malaria	74	10.3	Classification of the Pentastomida	261
3.7	Classification of the Protista	81	11.1	Astonishing metamorphosis in pennellid copepods and rhizocephalan barnacles	280
4.1	<i>Nosema ceranae</i> : an emerging pathogen of European honey bees	89	11.2	On acorns, ticks, and mice: the epidemiology of Lyme disease	297
4.2	Classification of the Microsporida	94	11.3	A mite-y ecological and economic problem: <i>Varroa destructor</i> of honey bees	303
5.1	Pathogenesis and epizootiology of whirling disease caused by <i>Myxobolus cerebralis</i>	101	11.4	Fly maggots as agents of lethal parasitism	322
5.2	Proliferative kidney disease and solving the PKX organism mystery: an orphan parasite of bryozoans finds a taxonomic home in the Myxozoa	106	11.5	Parasite's web of death! Manipulation of spider web-building behavior by an insect parasitoid	326
5.3	Classification of the Myxozoa	108	11.6	Classification of the Arthropoda	329
6.1	'Getting in': host location, recognition, and penetration by trematode miracidia	123	13.1	Host immunity and parasite infracommunity structure: new evidence for an old hypothesis	366
6.2	'Getting out': the enigma of egg release in the human schistosomes	138	15.1	'Berry ants': parasite-induced fruit mimicry in neotropical rainforests	407
6.3	Classification of the Platyhelminthes	172			
7.1	Acanthocephalans: masters of phenotypic manipulation	180			
7.2	Sexual selection in the Acanthocephala	188			
7.3	Classification of the Acanthocephala	194			

- |      |  |     |      |   |     |
|------|--|-----|------|---|-----|
| 15.2 | The politics of parasitism: sea lice, aquaculture, and the decline of salmon populations in coastal British Columbia | 412 | 16.2 | Parasites, sex, and the Red Queen: castrating trematodes maintain sexual reproduction in New Zealand snails                                     | 449 |
| 15.3 | Avian malaria determines the distributions, biodiversity, and community structure of Hawaii's native birds           | 423 | 17.1 | <i>Ribeiroia</i> and the complexity of amphibian deformities: a multidisciplinary approach to understanding the possible link to eutrophication | 466 |
| 16.1 | Parasite-mediated natural selection on the human HbS gene  | 433 |      |   |     |



## FOREWORD

The ability of parasites to cause disease has always been an important reason to study them, and the teaching of parasitology has almost always been stimulated by conditions conducive to disease, such as war or climate change. Currently, zoonotic diseases emerging from altered ecosystems, or carried by arthropod vectors spreading their ranges due to climate changes, supply that stimulation. However, most of us who teach, or have taught, parasitology have chosen that topic because of the fascinating life cycles of many parasites and their complex interactions with their hosts. Much of that fascination stemmed from learning how parasites can affect the population dynamics of their hosts, or the behavior of the hosts, or even the evolution of their hosts. In addition, that fascination was based on how much parasites could tell us about the life of their hosts, such as their diet, travels, or evolution. Or even of the earth itself – some of the earliest evidence for continental drift was the similarity in parasites of amphibians in Africa and South America. Examples of all of these influences are provided in this book.

Many of the systems that parasitologists have used to show these fascinating features have become relatively easy to study due to new techniques, such as those in genomics and proteomics, which have provided new and more powerful ways to study systematics, evolution, and host–parasite relationships. This has attracted the attention of biologists with a wide variety of backgrounds, so that much of the very interesting work done on host–parasite systems recently has been done by those trained in other specialties, such as ecology, behavior, neurophysiology, and evolutionary biology. Very few of the students in senior-level parasitology courses will go on for further study in parasitology, but many more will go on for

further study in other biological specialties. Our courses, books, readings, and other materials used in our classes should be chosen to expose those students to the usefulness of parasites in investigations in their chosen fields.

This book is the best I have seen for that purpose. The authors have provided a wide-ranging review of the diversity of parasites, emphasizing those which provide examples of the insights provided by the use of the new techniques or examples of how parasites can provide new and exciting insights into other aspects of biology. One of the best features of this book is that it emphasizes the complexity of host–parasite systems, with full recognition that most of the outcomes are markedly dependent on the conditions in which that system is embedded. This emphasis on complexity starts with a chapter on immunity, which is the best and most succinct coverage I have ever seen of those aspects of immunity that are important in host–parasite interactions. This emphasis is most apparent in the most integrative chapters – those on the influence of parasites on their hosts, and parasite evolutionary ecology.

This is the book I would have loved to have been available when I was teaching. But, of course, it could not have been written then. Most of the more provocative insights, and especially the evidence for complexity and conditional outcomes of host–parasite encounters, have come in the past two decades since I retired. The field of parasitology has become increasingly fascinating, and its implications for other fields of biology more significant, in those two decades. Enjoy this book, as I have, and see where it leads you.

**John C. Holmes**





## PREFACE AND ACKNOWLEDGMENTS

In this second edition, we stay true to the philosophical approach that was adopted in the first. Thus, we continue to see a need for a single text with dual focus on the diversity *and* ecology/evolution of parasites. At the core, we feel that an ideal strategy for senior undergraduate and beginning graduate students to understand and appreciate breakthroughs in parasite ecology is through a solid understanding of parallel advances in parasite diversity, life-cycle variation, systematics, and functional morphology. By way of example, we suggest that an understanding of the role of *falciparum* malaria in determining the worldwide distribution of the human sickle-cell gene, and thus the role of parasites in mediating natural selection (Chapter 16), comes from an understanding of life-cycle variation, functional morphology, and biodiversity of the apicomplexans (Chapter 3). Likewise, real understanding of the evidence in support of the parasite hypothesis for the evolution and maintenance of sexual reproduction in molluscs (Chapter 16) comes from a detailed understanding of variation in life cycles and life histories of the platyhelminths (Chapter 6). This dual focus, under one cover, is the hallmark of this text.

Our aim is to provide students with a synthetic understanding of the biodiversity, ecology, and evolution of animal parasites. Thus, throughout most of the text, we unabashedly take a parasite-centered view of the phenomenon of parasitism. Yet, we also aim to provide insights on the nature of the host-parasite interaction itself. It is for this reason that following a brief introductory chapter, we provide an overview of vertebrate and invertebrate immunity, and the new discipline of ecological immunology. We turn again and again to the importance of fundamental immunological principles throughout the text.

There are now nine biodiversity chapters (Chapters 3–11). We have added chapters on the Myxozoa, Microsporida, and Nematomorpha,

reflecting developments in their systematics, and their value as models in parasite ecology and evolution. By necessity, the ‘phylogenetic relationships and classification’ sections for all of the diversity chapters have been updated, adopting the most current molecular-based taxonomic schemes. The protist chapter in particular has been completely revised from the first edition, reflecting the monumental changes in protist systematics. New text boxes that highlight key areas of development, and the scientists behind them, are integrated into each of these chapters. New life cycle diagrams and dozens of new photographs and micrographs have also been incorporated. A color plate section has been added, showcasing dramatic photographs of parasites in or on their hosts.

Armed with a solid background in parasite biodiversity, systematics, and functional biology, Chapters 12–17 cover advances in the ecology and evolution of parasites. The titles and content of these chapters have been completely revised from the first edition, reflecting in part, the interests and backgrounds of the new authors. Yet the substantial revisions also reflect the pace of development in methodologies and in overall approaches that have matured the field over the past decade. While some of these developments have confirmed earlier ideas, others have revolutionized our understanding of even the most fundamental aspects of the parasitic way of life. Thus, the incorporation of new model host-parasite interactions that are amenable to manipulation in the laboratory and field have provided key insights into how parasite populations are regulated and how they are distributed among hosts in space and time (Chapter 12). Studies at the community level (Chapter 13) have also benefited from rigorous empirical approaches involving key model systems where the composition of component species can be manipulated. In Chapter 14, we see how advances in molecular biology, genomics, and remote sensing have

transformed our understanding of parasite biogeography and phylogeography. Coverage in [Chapter 15](#) is focused on the diverse manner in which parasites can affect the biology of their hosts, whether it is at the level of the host individual, or on the structure of entire host ecosystems. Again, key advances stemming from empirical, hypothesis-testing approaches involving selected model systems have markedly advanced our understanding of the magnitude of these effects, and their underlying mechanisms. The focus in [Chapter 16](#) takes the next logical step, covering the manner in which parasites affect the evolutionary and coevolutionary trajectory of their hosts. We conclude the text by summarizing the nature of the parasite/human/habitat interface, and how the multidisciplinary field of environmental parasitology ([Chapter 17](#)) can assist in interpreting the nature of host–parasite interactions in the face of anthropogenic change.

As with all projects of this scope, this book is a collaborative effort. We extend sincere thanks to the authors of the first edition, Al Bush, Jackie Fernández, and Dick Seed for their initial vision and dedication. Several of their line drawings and photographs, incorporating the image-editing skills of Maggie Bush, have been retained here. Numerous colleagues offered valuable suggestions on specific sections/chapters, especially Carter Atkinson, Mark Blaxter, Katharina Dittmar, Eric Hoberg, Jens Høeg, Kayla King, David Marcogliese, Jim Mertins, Beth Okamura, George Poinar, John Webster, Chris Whipps, and Stephen Yanoviak. We also appreciate the insightful comments John Holmes provided for several chapters. Several of our former students, especially Martin Anglestad, Melissa Beck, Aaron Jex, Chelsea Matisz, Phillip Morrison, Vanessa Phillips, Brad van Paridon, and Chris Whipps helped to review and edit chapters. Their perspectives helped clarify and focus our efforts.

This revision contains many new drawings, as well as new photographs and micrographs. Bill Pennell spent many hours of his retirement taking several new photographs, as well as editing countless others. Doug

Bray and Brad van Paridon took several of the new scanning electron micrographs. We thank our colleagues for contributing extensive new data figures, photographs, and micrographs for the new edition. Their generous contributions are acknowledged in the figure captions. John Sullivan is especially thanked for sharing several of his photographs from his excellent parasitological resource, *A Color Atlas of Parasitology*. Several new life-cycle diagrams and line drawings are incorporated into this edition, thanks to Chelsea Matisz, Lisa Esch McCall, and Danielle Morrison. Danielle, in particular, is thanked for her patience and dedication in preparing, labeling, and editing many of the new figures and photographs.

Vancouver Island University is thanked for providing Tim Goater the sabbatical and professional development funds that enabled this revision to take shape. Special thanks also to Mike Steele, David Marcogliese, and Herman Eure for providing office space during his sabbatical, as well as Eric Demers, Larissa Nelson, Wendy Simms, and Jane Watson for their enthusiastic encouragement throughout the project. Likewise, Cam thanks Dean Chris Nicol and Chair Brent Selinger for moral support and teaching relief during the peak phases of this revision, and colleagues Doug Bray, Doug Colwell, Andy Hurlly, Joe Rasmussen, and Brian Wisenden for their constant support. Cam also extends thanks to Barb Johnson and staff at Waterton Lakes National Park for access to their cabin during key writing phases. Most sincere thanks also to Lori Goater for her monumental patience and support and to Ben and Ali for frequently reminding their dad, and their uncle, that parasite ecologists come in all ages.

Our primary editor, Katrina Halliday and her assistant, Megan Waddington at Cambridge University Press are thanked for all of their help addressing our many queries and, especially, for their patience and devotion to seeing this project to its completion.

**Timothy M. Goater**  
**Cameron P. Goater**



## About this edition

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The first edition of our book was published in 2001. Al Bush, Jackie Fernández, and Dick Seed were co-authors, along with myself. Sadly, Al died in 2010. Further, Jackie stepped aside to raise two sons and Dick retired from his faculty position at the University of North Carolina-Chapel Hill. As the only original author that was still active professionally, it became my responsibility to recruit new co-authors. Given the overall theme and target audience of the text, my choice fell upon brothers, Tim and Cam Goater. Tim was a former Ph.D. student of mine at Wake Forest University, and Cam was a former Ph.D. student with Clive Kennedy at the University of Exeter. Both brothers were mentored by Al Bush at Brandon University in Manitoba, Canada. Tim and Cam have extensive experience teaching senior undergraduate

courses in parasitology and ecology, and Cam extends his teaching perspectives to the mentoring of graduate students. Both have diverse and complementary research backgrounds that, together, span most areas of modern parasitology.

Throughout the writing of both editions, I maintained my duties as Editor of the *Journal of Parasitology*, as well as my teaching. Mrs. Vickie Hennings, my Editorial Assistant for the Journal, continued her responsibilities while I was occasionally subsumed by the book. Cindy Davis and Zella Johnson, both long-term secretaries for the Department of Biology at Wake Forest University, are thanked for their help as well. I especially express my appreciation to Ann for being such a marvelous 'listener' and for her constant support from the book's inception.

**Gerald W. Esch**





# 1

## Introduction

### 1.1 Encounters with parasites

---

On a fateful spring day in a small northern Canadian town in the 1970s, two of the authors (the two that are related) of this text came upon a sickly red fox. Following some foolhardy thinking, they handled the fox and carried it home. A few days later, health officials diagnosed the fox with rabies. To avoid the fatal consequences of the disease, the brothers required daily intramuscular injections of the prophylactic drug that was used at the time. We recall the episode with memories of pain, dismay from parents, and ruthless teasing from our friends. And so goes our introduction to the world of parasites. So too goes our introduction to the phenomenon of parasitism. Readers might envision two teenagers discussing how their predicament arose: How did that fox get infected? Why was the fox population, but not the racoon population, so heavily infected that year? How does the virus migrate from the site of a wound, to the brain, to saliva? How, and why, does it transform a normally secretive and nocturnal animal into one that is aggressive and diurnal? There are obvious parallels between these early queries and modern questions associated with host specificity, parasite site selection, the geographical mosaic of coevolution, and mechanisms of alterations in host behavior.

We hope that your introduction to parasites was (is) not as dramatic, or as dangerous, as it was for two of us! Indeed, for many, initial exposure to the concept of parasitism likely originated from media reports that describe human mortality and morbidity caused by diseases such as malaria, or other parasitic diseases that are so common in developing countries. Or, perhaps you have heard about certain parasites that are transmitted via ingestion of untreated water, or swimming in it, or from eating poorly cooked meat.

For the pet and livestock owner, parasite encounters may have occurred when a veterinarian requested a fecal sample for diagnosis of eggs/larval stages of intestinal worms. Perhaps, as a hunter or a fisherman, you have queried the identity of that animal wriggling in wild game meat or fish. In recent years, these common or at least dramatic parasites of humans, their livestock, or their pets have been made famous in the popular media (e.g., Zimmer, 2000a; 2000b), even including in situ video footage on YouTube™ and on prime-time television shows.

As undergraduate students, your first encounters with parasites and with the phenomenon of parasitism likely occurred in your introductory courses. At each of our universities, majors in many of the life sciences require an introductory course that describes the diversity and unity of the Tree of Life. In a course such as this, it would be impossible for instructors to sample that diversity without covering examples of parasites, although coverage is likely restricted to key human parasites – a protist, a fluke, a cestode, and so on. Likewise, our majors are required to take an introductory course that covers basic principles of ecology and evolution. One encouraging sign of the expanding reach of studies on the phenomenon of parasitism is its increased coverage in mainstream ecology and evolution texts (e.g., Begon *et al.*, 2006; Freeman & Herron, 2007). Nonetheless, time constraints in a single-semester introductory course likely limit coverage of examples involving parasites.

In the chapters that follow, our coverage assumes that you have encountered parasites, both anecdotally and academically. Thus, we assume that senior students in the life or medical sciences have an appreciation for basic principles of classification and phylogeny and an appreciation for variation in the life cycles and general biology of a few animal parasites.

We also assume a general understanding of basic concepts of ecology and of the fundamental and unifying nature of evolutionary processes. Although we do not emphasize the mathematical underpinnings of host–parasite interactions, we do assume that senior students have a numeracy background consistent with introductory courses in calculus, linear algebra, and/or statistics. We do not assume a strong background in immunology or pathology.

## 1.2 Scope

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Our first aim is to provide students with an appreciation for the biodiversity of animal parasites. From the perspective of understanding our planet's biodiversity, and understanding factors leading to its loss, an appreciation for the diversity of parasites is important. Parasitism is recognized as the most common strategy used by animals to obtain nutrients (Price, 1980; de Meeus *et al.*, 1998; de Meeus & Renaud, 2002), ubiquitous across the Tree of Life. Poulin & Morand (2004) consider that there have been at least 60 independent evolutionary transitions from free-living to obligately parasitic animals. Estimates of the overall biodiversity of parasites vary depending on how inclusive we define 'parasite,' but approximately 30–50% of described animal species are parasitic at some stage during their life cycle (Price, 1980; Poulin & Morand, 2004). Given that virtually all metazoan species are infected with at least one species of parasite (most species contain many more), that all viruses and many prokaryotes and fungi are parasitic, and that we underestimate the biodiversity of groups such as nematodes and mites (see Chapters 8 and 11), these rough estimates are undoubtedly low. Clearly, knowledge of parasite biodiversity equates to knowledge of key branches of the Tree of Life.

The biodiversity section of the text (Chapters 3–11) provides an overview of the main taxa of protist and metazoan parasites. Our focus is on characterization of key features that define each group, followed by coverage of how natural selection has shaped variation in their morphologies, in their life cycles and life

histories, and in their strategies for nutrient acquisition. Our intent through this section is to provide insight on 'the art of being a parasite,' a phrase coined by Claude Combes (2005) to describe the manner in which parasites of all types solve the unifying problems of entering a host ('getting in, or on'), remaining in a host ('staying in'), and reproducing ('getting out'). Our taxonomic scope is broad, with emphasis on the traditional protists and 'worms' but also on lesser-known groups such as the microsporidians, myxozoans, hairworms, and pentastomes. Much of our coverage through this section distills material that is covered in parasitology texts (e.g., Noble *et al.*, 1989; Kearn, 1998; Roberts & Janovy, 2009). However, relative to these excellent texts, we restrict our taxonomic scope to key families or orders within each group, and we emphasize those groups that provide models for enquiries on the ecology and evolution of parasitism that we cover in later chapters.

Our second aim is to develop in students an appreciation for the phenomenon of parasitism. And from our perspective, we view the core of the phenomenon to be ecological in nature. Thus, whether interest is in understanding the innumerable rates that define the outcome of host–parasite relationships (e.g., rates of exposure to infective stages, rates of within-host migration, rates of parasite-induced host mortality, rates of dispersal, and so on), or in the dynamics of the molecular exchange that occurs at the host–parasite interface, or in the global distribution of parasites, basic ecological principles can be applied to help focus our thinking about host–parasite interactions. It is this perspective that lies at the roots of 'parasite ecology' as a subdiscipline within the ecological sciences. These roots were developed and formalized some 30–40 years ago following the coincident publications of seminal works by empirical field biologists (Kennedy, 1975; Price, 1980) and quantitative ecologists (Crofton, 1971; Anderson & May, 1979). The dynamic tension between their alternative perspectives continues to richly define the direction of a field that is now seeing an unprecedented level of activity.

Over the 10 years since the first edition of our text was published, key advances have been made in virtually all areas of parasite ecology and evolution. These include the epidemiology of wildlife disease (Hudson *et al.*, 2001), parasite phylogeny and phylogenetics (Brooks & McLennan, 2002), parasites and host behavior (Moore, 2002), parasite biodiversity (Poulin & Morand, 2004), evolutionary ecology (Frank, 2002; Poulin, 2007; Thomas *et al.*, 2009; Schmid-Hempel, 2011), and parasite biogeography (Morand & Krasnov, 2010). Two texts that synthesize general advances in parasite ecology and evolution, one from an empirical standpoint (Combes, 2001) and one from a conceptual standpoint (Poulin, 2007), are especially notable. Over the past 10 years or so, the new subdisciplines of ecological immunology, landscape epidemiology, emerging diseases, and environmental parasitology have blossomed as exciting 'hot topics.' This surge in interest is partly due to the explosion in the use of modern molecular methods, enabling advances in our understanding of parasite biodiversity, phylogenetics, population genetics, and host–parasite coevolution that would have been unthinkable even 10 years ago. Yet, the pace of advance is also due to the rapid increase in the use of experimental model systems to test key hypotheses regarding the ecology of host–parasite interactions. While traditional model systems involving laboratory rats and mice as hosts continue to provide important insights, major recent advances have arisen from models involving parasites of hosts such as sticklebacks, guppies, water fleas, songbirds, and wild small mammals. Indeed, we view the multidisciplinary arising between parasitologists and ecologists, so long called for by the fathers of parasite ecology, that is perhaps most responsible for the unparalleled advances we are currently witnessing in the field (review in Poulin, 2007).

Our aim in this section of the text is to provide an overview of modern parasite ecology, evolution, and coevolution. In this edition, we update our earlier treatment by taking into account results originating from modern advances in molecular methodologies and from experimental models on a

wide range of host–parasite interactions. Our overall approach through this section is empirical, rather than conceptual. Thus, we develop our arguments based primarily upon observations from field-based and laboratory-based experiments, although we incorporate key results from field surveys of particular hosts when warranted. Although we cover the mathematical and conceptual framework of certain areas of enquiry, our perspective is empirical and rests strongly on the background that we developed in the biodiversity section of the text. Readers seeking advances in more quantitative aspects of parasite ecology and epidemiology should consult Hudson *et al.* (2001), Ebert (2005), or Schmid-Hempel (2011).

Despite the enormous strides made in methods and approaches, modern studies in parasite biodiversity and ecology continue to be influenced by traditional approaches in parasitology, in which parasites of humans and their domesticated animals have played a key role. Throughout the biodiversity section of the text, we retain some of that traditional coverage. We do so because the history of discovery in parasitology provides the roots of current enquiry, and is itself a fascinating story of human endeavour (Box 1.1). For further account of key historical developments in parasitology, readers are directed to Esch (2007). We also retain some emphasis on select human parasites because the discovery in these groups has provided unmatched opportunities for increased understanding of ecological and evolutionary phenomena. For instance, results of studies on the interaction between falciparum malaria and the gene responsible for sickle-cell anemia provide one of the best examples of parasite-mediated natural selection (Chapter 16). Yet, this example stems from years of dedicated effort that enabled detection of the single amino acid substitution that alters the structure of the hemoglobin molecule. We cover similar examples throughout the text, not necessarily in the context of human disease, but in the context of central questions regarding the ecology and evolution of host–parasite interactions.

### Box 1.1 A brief historical perspective of parasitology: pioneering scientists and their ground-breaking parasitological discoveries

Sometime around 1500 BC, an Egyptian physician assembled a large body of medical information regarding the diagnosis and treatment of diseases known to occur at the time. Written in hieroglyphics on papyrus and sealed in a tomb, it was discovered in 1872. It was translated by Georg Ebers in 1873, becoming known as the Ebers' Papyrus among Egyptologists. This volume became an invaluable source that documented the medical profession that existed in the ancient world.

Based on these writings, we now know that early Egyptian physicians were aware of at least two parasitic helminths infecting humans. One of these was a nematode, probably *Ascaris*. The recommended treatment for infection by this apparently common worm included turpentine and goose fat! The second parasite was a tapeworm, most likely *Taenia saginata*, for which a special poultice applied to the abdomen was the recommended treatment. Whereas the digenean, *Schistosoma haematobium*, was not described per se, the bloody urine produced by this parasite was a well-known symptom. Moreover, eggs of this worm have since been identified in mummies from the thirteenth century BC (Grove, 1990). It is also possible that the hookworm nematode, *Ancylostoma duodenale*, was present based on descriptions in the Ebers' Papyrus of a 'deathly pallor' in some patients, a condition that may have been caused by hookworm-induced anemia.

Concurrently, another group of ancients was acquainted with a number of helminth parasites in the Nile Valley. Thus, for example, consider Numbers 21:6–9, which refers to 'the Fiery Serpent,' now recognized as the nematode *Dracunculus medinensis*. When the Israelites misbehaved during their trek out of Egypt, they were directed by God, through Moses, to "make a serpent of brass and put it upon a pole." And, "when he beheld the serpent of brass, he lived." This treatment is still used today, that is, to remove the large female nematode from its subcutaneous site of infection, and then to slowly twist the parasite on a stick, until it is removed intact. Many feel the Hebrew law against eating the flesh of an 'unclean' animal, e.g., a pig, can be traced to the nematode *Trichinella spiralis* or the cestode *Taenia solium*. On the other hand, the Talmud (a sacred Jewish book), written in AD 390, referenced the hydatid cysts of the tapeworm *Echinococcus granulosus*, indicating that they were not fatal.

Periodic fevers due to malaria were mentioned in Chinese writings from around 2700 BC and in every civilization since. Hippocrates (460 BC–377 BC) provided the earliest detailed description of these periodic fevers. Both Hippocrates and Aristotle (383–322 BC) were aware of 'worms' and refer to cucumber and melon seeds in the 'dung' of humans. Both references are probably to the gravid proglottids of *Taenia saginata*. Galen (AD 130–200) referred to the intestinal phases of what were probably *Ascaris lumbricoides* and *Enterobius vermicularis*, saying that the former worms preferred the upper portion of the gut whereas the latter were closer to the anus. He found that tapeworms, on the other hand, were found throughout the length of the intestine. These observations, so long ago, may be the first reference to the site specificity exhibited by parasites.

### Box 1.1 (continued)

The earliest use of the microscope, by Antony von Leeuwenhoek in the seventeenth century, provided a phenomenal breakthrough for the biological sciences and parasitology. He actually observed, and described, the unicellular protist parasite *Giardia lamblia*, apparently from his own feces! Also in the seventeenth century, several scientists prepared detailed drawings of a number of parasitic helminths. One father of parasitology was Francesco Redi (1626–1697), who not only determined that mites could make one itch, but apparently was also an inveterate collector, describing some 108 species of parasites. Perhaps Redi's greatest contribution was that he showed that parasites produce eggs, dispelling the widespread myth that parasites developed through spontaneous generation. The idea of spontaneous generation persisted for many years, however, and it took Louis Pasteur's now classic experiments in nineteenth-century Paris to quash the notion.

The late nineteenth and early twentieth centuries were times of major discoveries dealing with some of the protist and helminth scourges of humans, including *Wuchereria bancrofti* as the causative agent for elephantiasis and tsetse flies as the vectors for African trypanosomiasis. Ronald Ross, while working in India in 1897, demonstrated that mosquitoes vectored *Plasmodium*, winning the Nobel Prize for physiology in 1902. At the turn of the century, Paul Ehrlich described the first chemotherapeutic agents for African trypanosomiasis and syphilis. With this discovery, he hypothesized that organic molecules with selective toxicity to parasitic organisms would be found. For this, he is considered the father of modern chemotherapy. Between 1907 and 1912, Carlos Chagas determined the identity of trypanosomes that cause Chagas' disease and worked out the parasite's life cycle in the reduviid bug vector. In the early 1880s, Algernon Thomas and Rudolph Leuckart independently completed stages in the life cycle of the liver fluke, *Fasciola hepatica*, including detailed descriptions of the swimming behaviors of the 'embryos' that hatched from eggs, their penetration into snails, and their subsequent intramolluscan development. Thomas and Leuckart and others will be remembered for their many contributions (review in Esch, 2007), and paving the way for all those who resolved so many other parasitological mysteries.

## 1.3 Terminology

We often start our courses with a request for students to define 'parasite.' This is always an interesting and engaging exercise. Often, the discussion rapidly deteriorates into a mix of vague terminology, examples, and counter-examples. Are mosquitoes and vampire bats parasites? Are leeches parasites? Is my brother a parasite? Is a fetus a parasite? To direct the

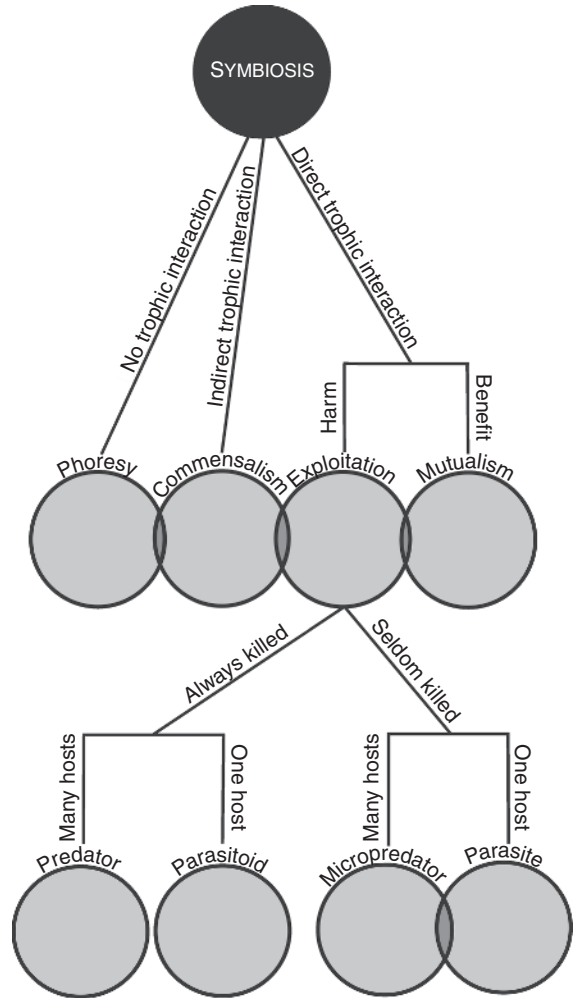
discussion, we might offer a classic dictionary definition. *Webster's Third New International Dictionary of the English Language* defines 'parasite' as follows:

An organism living in or on another living organism obtaining from it part or all of its organic nutrient, and commonly exhibiting some degree of adaptive structural modification – such an organism that causes some degree of real damage to its host.

It is here where some students may voice discomfort, especially those with an ecological background. In this characteristic definition, vague and unquantifiable terms such as 'part,' 'some,' and 'damage' are prominent. In our courses, we do not offer a solution to the fundamental vagueness that characterizes the definition of parasite. Nor do we do so in this text (for complete discussions, see Zelmer, 1998; Combes, 2001). In his influential text on coevolution, Thompson (1994) emphasizes that all definitions dealing with interspecific interactions are necessarily vague. From our perspective, we consider that a parasite has a metabolic commitment to its host, has evolved morphological and physiological adaptations to living in, or on it, and has the potential to decrease host fitness. As we have indicated previously, our focus is on the familiar parasitic protists, worms, and arthropods, although we extend our coverage to include lesser-known taxa because they provide splendid models in parasite ecology. The extent to which groups such as phytophagous insects, molecular parasites, blood-sucking leeches and flies, and brood parasites (e.g., cuckoos) apply to our coverage of animal parasitism, provides an excellent topic for discussion in our classes, but they lie outside the scope of this text.

Parasitism is one of at least four complex symbiotic relationships. Symbiosis, a term coined by de Bary in 1879, literally means 'living together of differently named organisms.' It describes the relationship in which a symbiont lives in, or on, another living host. Symbiotic interactions, or *symbioses*, include a tremendous variety of intimate partnerships in nature. In the broadest sense, there is no implication with respect to the length or outcome of the association, nor does it imply physiological dependence or benefit or harm to the symbionts involved in the partnership. Given such a broad definition of symbiosis, a functional separation can be made in relation to the feeding biology of one or both of the symbiotic partners, as well as the degree of host exploitation. Thus, categories of symbiosis relate to trophic relationships, and if and how energy is transferred between the partners. Such categories are best viewed as a continuum with overlapping boundaries (Fig. 1.1).

If there is no trophic interaction involved in the symbiotic interaction, then the relationship is called



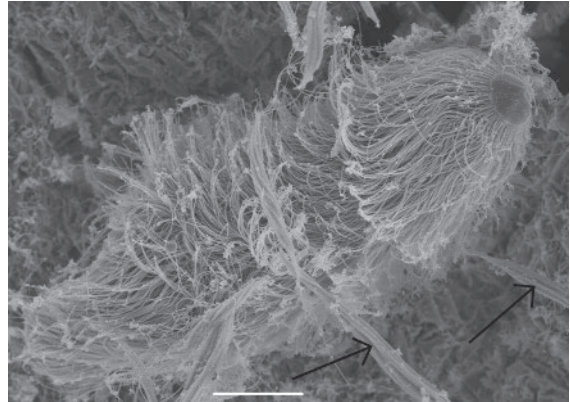
**Fig. 1.1** 'Parasitism's place' within the context of symbiotic relationships. This is one way of looking at parasitism and it is based, initially, on trophic relationships, followed by 'harm,' and finally, quantity of hosts involved. The final criterion, number of hosts attacked, is meaningful only if restricted to a single life history stage. For example, adult parasitoids may parasitize many host individuals but their larvae live in, and consume, only a single individual. Likewise, a typical helminth parasite may have both intermediate and definitive hosts, but each life-cycle stage will infect only a single host individual. These categories are arbitrary and, often, there is considerable overlap between many of the relationships. (Figure courtesy of Al Bush.)



**phoresy** (Fig. 1.1). In this case, the symbiont (=phoront) merely travels with its host; there is no metabolic commitment by either partner. Protists or fungal microbes that are mechanically carried by insects are examples of phoretic associations. Similarly, even though whale and turtle barnacles are often described as ectoparasites, there is no metabolic commitment. Functionally, they are phoronts. Phoresy grades into **commensalism**, a symbiotic interaction that implies a trophic relationship between the partners (Fig. 1.1). Commensalism means 'eating at the same table.' Here the benefit gained is unidirectional. The smaller commensal partner typically benefits via food transfer and increased dispersal opportunities, while the host is neither harmed nor benefited. When sharks feed on large prey, they scatter fragments of food that are made available to remoras. Yet, some remoras also feed on ectoparasites of their shark hosts, implying an indirect metabolic linkage. Commensalism therefore grades into **mutualism** in many cases (Fig. 1.1). Many mites are commensals, hitching a ride and sharing food with hosts as diverse as insects and molluscs to birds and mammals.

When there is a direct transfer of energy between the partners, the interaction may be either mutualistic or exploitative (Fig. 1.1). Obligate mutualists are metabolically dependent on one another. A classic example of an obligatory mutualism is the diverse microfauna of protists and prokaryotes in the intestines of wood-eating termites. A single species of flagellated protist, *Trichonympha campanula* (Fig. 1.2), may account for up to one-third of the biomass of an individual termite. These flagellates produce enzymes that digest cellulose, enabling the host to survive on a diet of wood. The mutualistic relationship between ruminant mammals and the ciliated protists and microbes in their stomach is similar. The biochemical complexity of these, and many other mutualistic associations found throughout nature, is the product of a long coevolutionary history between the partners. Such coevolved mutualisms are regarded as being creative forces in the adaptive radiations of many taxa (Thompson, 1994; Price, 1996).

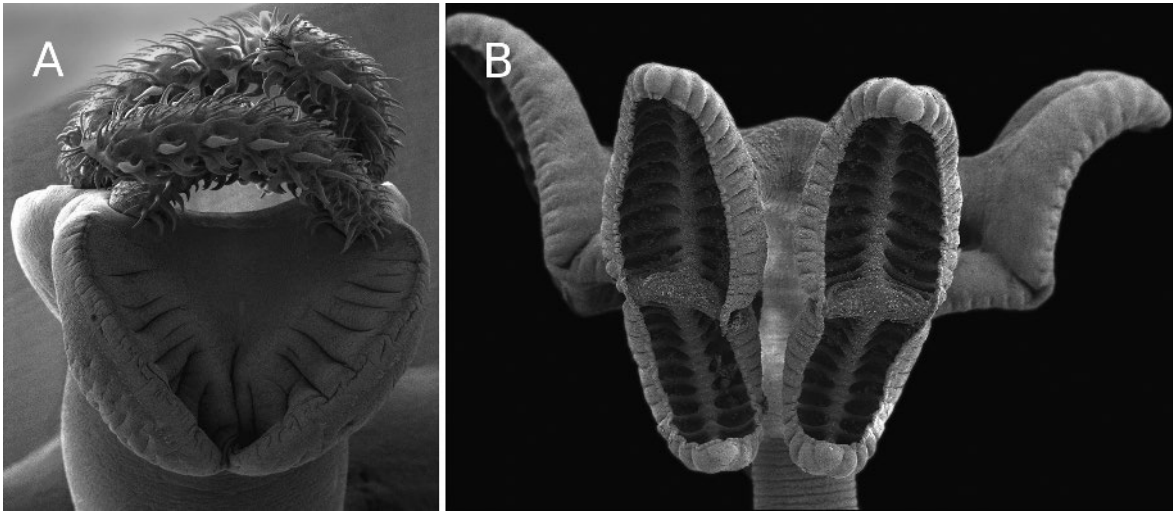
In many exploitative interactions, however, benefit is unidirectional and, moreover, some form of disadvantage, or harm, is the outcome for the other partner.



**Fig. 1.2** Scanning electron micrograph of the mutualistic hypermastigote flagellate *Trichonympha campanula* from the intestine of a termite. Another, much smaller flagellate *Streblo mastix* sp. (arrows) is also present. (Micrograph courtesy of Ron Hathaway.)

Several major categories of this kind of exploitation can be recognized, based primarily on the number of hosts attacked by the symbiont and the subsequent fate of the organism assaulted (Fig. 1.1). If more than one organism is attacked, but typically is not killed, then the aggressor is called a **micropredator**. Hematophagous organisms such as mosquitoes, and some leeches and biting flies, for example, are considered micropredators, taking frequent blood meals from several hosts. Some micropredators are often considered as ectoparasites, e.g., leeches. If more than one organism (considered as prey) is attacked and always killed, then the aggressor is considered a predator. If only one specific host is attacked and is almost always killed, then the aggressor is usually referred to as a **parasitoid**, most of which are wasps and flies.

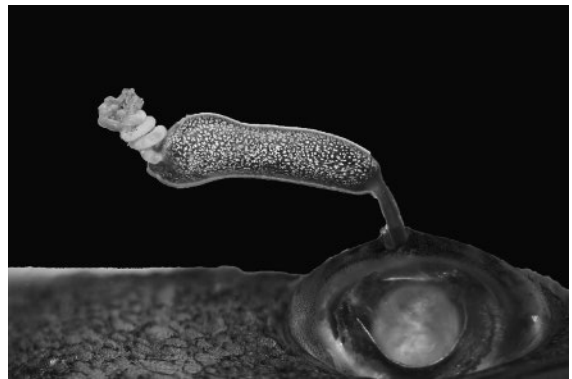
If only one host is attacked, but typically is not killed outright, the aggressor is a parasite (Fig. 1.1). **Endoparasites** include those that are confined within the host's body. They include the protists, microsporidian and myxozoans, as well as the 'worm' parasites such as flukes, tapeworms, acanthocephalans, and nematodes. A variety of holdfast adaptations often serve to anchor these endoparasites to specific sites within their specific hosts. The holdfasts of elasmobranch cestodes, for example, are often exquisitely adapted to match the



**Fig. 1.3** Scanning electron micrographs illustrating the elaborate holdfasts of host-specific tapeworms of elasmobranchs. (A) Scolex of the trypanorhynch cestode *Paragrillotia similis* from the spiral intestine of the Atlantic nurse shark *Ginglymostoma cirratum*; (B) scolex of the rhinebothriidean cestode *Rhinebothrium megacanthophallus* from the spiral intestine of the freshwater whipray *Himantura polylepis*. (Micrographs courtesy of Janine Cairra (A) and Claire Healy (B).)

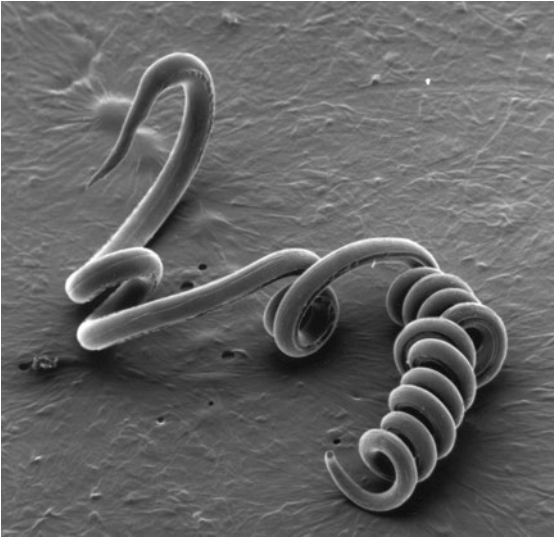
microstructure of the intestines of their specific elasmobranch hosts (Fig. 1.3). Parasites found on the surface of the host's body are called **ectoparasites**. Most parasitic arthropods and monogeneans are ectoparasitic. There are also some parasites that are classified as **mesoparasites** (Kabata, 1979). The pennellid copepods, for example, are endoparasitic in the sense that they have elaborate holdfasts that extend deeply into their host's tissues. However, their highly modified trunk regions and egg sacs extend outside the host (Fig. 1.4; Color plate Figs. 4.2, 4.3).

Anderson and May (1979) went further, highlighting key differences within groups of parasitic organisms. **Macroparasites** are large (usually visible to the eye), have generation times approximating those of their hosts, generate a low-to-moderate immune response, and the pathology they cause to their hosts is tied to the numbers of parasites present. These are typically the classical 'worms' (trematodes, cestodes, and nematodes) and the arthropods, such as copepods, fleas, lice, and mites. They can be endoparasitic or ectoparasitic. The nematode *Heligmosomoides polygyrus* (Fig. 1.5) is an example of an endoparasitic macroparasite infecting mice. The ectoparasitic mite,



**Fig. 1.4** Host and site specificity exhibited by the mesoparasitic copepod *Phrioxcephalus cincinnatus* attached to the eye of an arrowtooth flounder *Atheresthes stomias*. A metamorphosed female develops an elaborate holdfast, penetrating deeply into the eye of the specific fish host, while the egg sacs and trunk region extend out of the eye. (Photograph courtesy of Dane Stabel.)

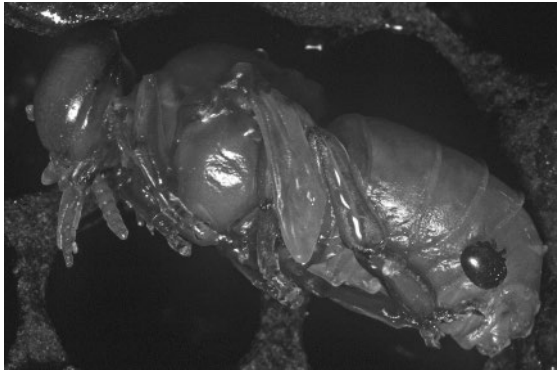
*Varroa destructor*, provides another example (Fig. 1.6). **Microparasites** are much smaller (typically microscopic), have generation times much shorter than their hosts, are capable of asexual replication within their hosts, and typically induce strong acquired immunity in recovered and re-exposed hosts. They can be



**Fig. 1.5** Scanning electron micrograph of the nematode *Heligmosomoides polygyrus* from the intestine of a mouse. This macroparasite–host system is a widely used model in experimental parasitology. (Micrograph courtesy of Doug Colwell.)



**Fig. 1.7** Scanning electron micrograph of the trophozoites of the flagellated protist *Giardia muris* attached to the villi of the small intestine of an experimentally infected mouse. This microparasite reproduces asexually via binary fission. (Micrograph courtesy of Břetislav Koudela.)



**Fig. 1.6** Female of the ectoparasitic mite *Varroa destructor* attached to the abdomen of a developing honey bee. (Photograph courtesy of Scott Bauer, USDA Agricultural Research Service, Bugwood.org.)

ectoparasitic or endoparasitic. They are typically intracellular, i.e., adapted to recognize, penetrate, and reproduce within host cells, or they may exploit extracellular tissues, or both. Eukaryotic microparasites include protists, microsporidians, and myxozoans. In the case of the protist, *Giardia* spp., (Fig. 1.7), ingestion of a single cyst originating from

untreated drinking water can lead to massive numbers of feeding stages in the intestine of a range of vertebrate hosts.

Parasites can have parasites too! The parasites living in/on other parasites are called **hyperparasites**. Parasite biodiversity will increase exponentially when we fully understand how common hyperparasitism is in nature. The sea louse, *Lepeophtheirus salmonis*, for example, is a common skin ectoparasite of salmonid species. A monogenean fluke, *Udonella caligorum*, is a hyperparasite of the egg sacs of sea lice. In addition, microsporidians such as *Desmozoon lepeophtherii*, have recently been described as intracellular hyperparasites of *L. salmonis*.

The organism in, or on, which a parasite reaches sexual maturity is the **definitive host**. Many parasites have a simple, direct life cycle, requiring only one host for transmission to occur. All monogeneans, and many nematode and arthropod parasites, have direct life cycles. Many animal parasites, however, have obligate **intermediate hosts** in which the parasites undergo developmental and morphological changes. Intermediate hosts may be the prey of the predatory definitive host in the life cycles of parasites. Thus, parasites with intermediate hosts in their complex life cycles are often transmitted trophically to definitive