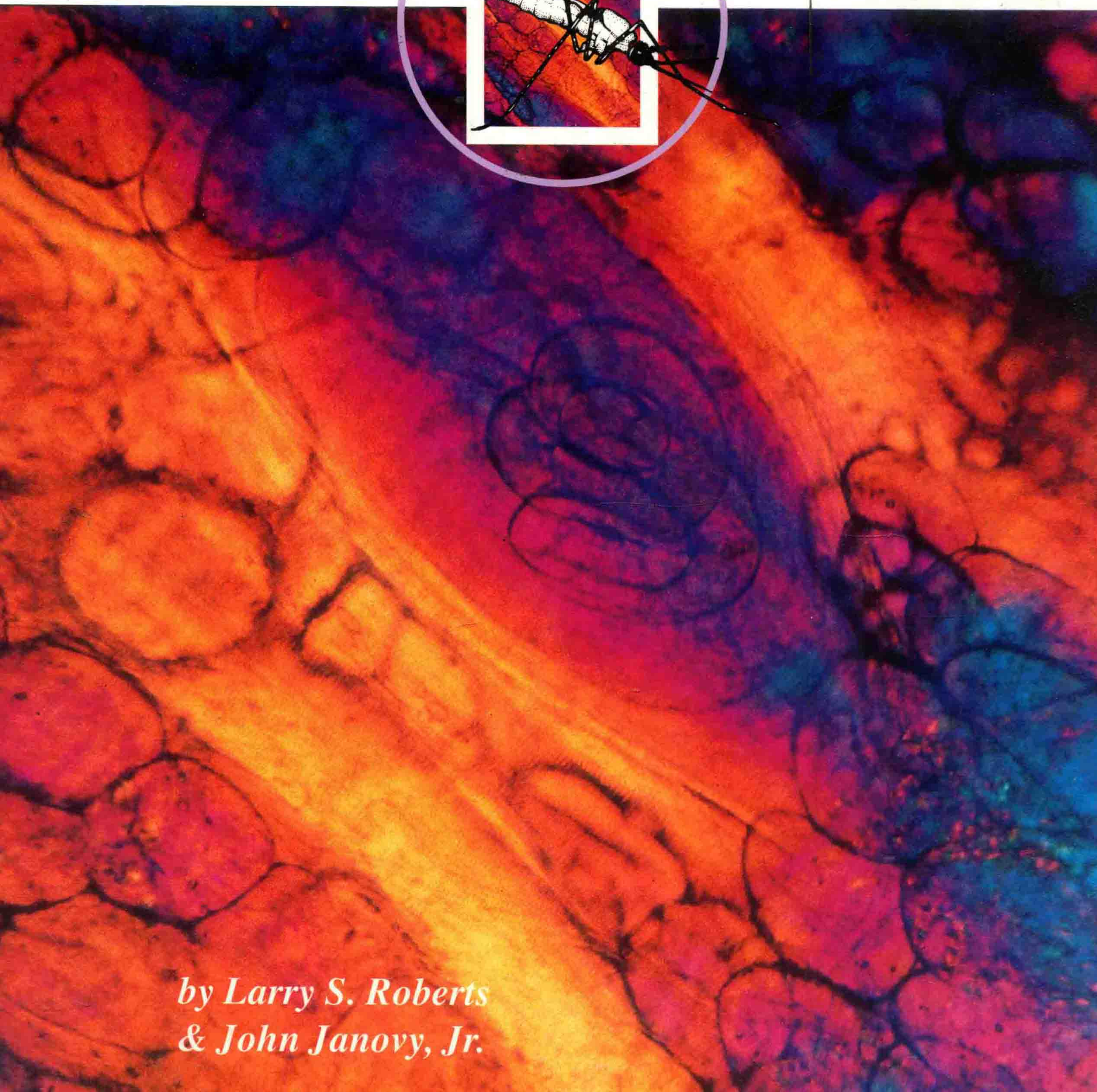
GERALD D. SCHMIDT & LARRY S. ROBERTS'

FOUNDATIONS OF PARASITOLOGY

FIFTH EDITION



by Larry S. Roberts
& John Janovy, Jr.

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Juveniles of *Anisakis* sp. on the stomach of a bocaccio (*Sebastes paucispinus*), a commercially important marine fish. The normal definitive hosts of these nematodes are marine mammals, but they cause severe pain when people eat them inadvertently with raw fish (see p. 428).

Photograph courtesy of J. Sakanari.

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PREFACE

It has been too long since the last edition, partly as a result of the tragic death of our friend and colleague, Gerald D. Schmidt. He taught us all much, and we greatly miss him.

One result of the long interval between editions is that this version is the most thoroughly revised of any yet published. A new coauthor has come on board, bringing new insights and a fresh approach. We do believe, however, that we have retained the essential qualities of the text that students and professors liked in the first four editions. The reception accorded *Foundations of Parasitology* has been most gratifying. Your comments and suggestions are always welcome. Keep them coming.

THE SCOPE OF THIS BOOK

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

The first three chapters delineate important definitions and principles in various areas, including evolution, ecology, immunology, and pathology. Chapters on specific groups follow, beginning with protistans and ending with arthropods. With the exception of the first three chapters, however, presentations in each chapter are not predicated on the students having first studied groups that come earlier in the book. Therefore, the order can vary as the teacher desires. Different instructors emphasize different materials, so there is more in the book than can be covered adequately in a single semester. As always we have strived for readability, the words being enhanced by photographs, drawings, electron micrographs, and tables.

NEW TO THIS EDITION

The book you are holding represents a milestone in the life of this text. This edition integrates a wealth of new discoveries and literature. Many areas of parasitology are theaters of intense research effort and fruitful results. Chapters covering such areas required extensive updating and rewriting. Addition of so much material compelled us to prune out an equal amount of text and illustrations so as not to increase the book length, but we hope that we have been judicious in our reshaping. Previous users of this text will notice many smaller changes, in addition to the points we mention in the paragraphs to follow, compared with the fourth edition. One of the most obvious of these is the trenchant quotation 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.

In this edition, coverage of parasite evolution (primarily phylogenetic systematics) and ecology required expansion, and basic definitions have been transferred to Chapter 1. Propelled in large measure by modern molecular methods, immunologists continue their torrent of discoveries. The 1980s 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 been almost completely recast. We hope that instructors will emphasize the concepts in these first three chapters; later chapters harken back to them frequently.

The "Form and Function" chapters on protistan 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 we could find published cladograms, we have added them to show phylogenetic relationships of some of the major groups.

Chapter 5 on the Kinetoplastida includes more recent discoveries on the molecular biology of trypanosomes and new material on the still-unfolding mystery of immune reactions in Chagas' disease and leishmaniasis. 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.

Intense scrutiny of malaria continues, reflecting its widespread importance as a human disease, and Chapter 9 has been revised accordingly. Note particularly the expanded table comparing *Plasmodium* spp., new methods of diagnosis, the role of cytokines in pathogenesis and immunity, progress toward vaccines, and drug action and resistance.

The chapter on Monogenea has been moved to a position preceding the cestode chapters, reflecting the closer relationship of monogenes and cestodes as indicated by cladistic analysis.

In Chapter 16, the sections on pathogenesis, diagnosis and treatment, and control of schistosomes have been almost completely rewritten. A table illustrating the major groups of *Schistosoma* spp. has been added. The chapter on echinostomes has been extensively rewritten as warranted by the growing use of these worms in experimental studies of host-parasite relationships.

The chapters on nematodes have been revised in many ways. Some noteworthy changes include emphasis on intracellular parasitism in *Trichinella;* recognition of five species of *Trichinella;* the nasofrontal migration of *Strongyloides;* haplodiploidy in Oxyurida; more evidence for distinctiveness of *Ascaris lumbricoides* and *A. suum;* expanded coverage of visceral larva migrans and *Anisakis* spp.; evidence that *Ancylostoma caninum* is sometimes a parasite of humans; sections on horse strongyles, *Syngamus,* and *Oesophagostomum;* coverages of immunity, immunopathology, immunotolerance, and chemotherapy of lymphatic filariasis; the revolutionary role of ivermectin in treatment of onchocerciasis; expanded coverage of *Dirofilaria immitis;* and the potential eradication of *Dracunculus medinensis.*

Among the numerous revisions of Chapter 34 on parasitic Crustacea, we have added the following: a brief description of parasitic copepods that are so highly modified they cannot even be assigned to orders; the concept of cryptogonochorism as applied to rhizocephalans; and a description of the bizarre little tantulocaridans with a diagram of their proposed life cycle. The arthropod chapters in general include many new illustrations, all of them quite instructive and many of them truly beautiful. Chapter 40, the acarines, has been expanded by additions of sections on Lyme disease, immunity, and pheromonal control of tick behavior.

INSTRUCTIVE DESIGN

Students using the fifth 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. New to this edition, and in response to student requests, we are providing 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.

We have been fortunate indeed to have William C. Ober and Claire W. Garrison draw many new illustrations for this edition, including many new life cycle diagrams. Their artistic skills and knowledge of biology have enhanced the other zoology texts coauthored by Larry Roberts. Bill and Claire bring to their work as illustrators 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:

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Larry S. Roberts
John Janovy, Jr.

I want to add a few words of welcome to the new coauthor of *Foundations of Parasitology.* Although John and I have known each other for years, this is our first opportunity to collaborate. He is an excellent writer and a biologist with broad expertise. I count myself and the readers of this book as very fortunate to have him join us. It has been a joy to work with him in preparation of this revision.

LSR

CONTENTS

Chapter 1

INTRODUCTION TO PARASITOLOGY

So, naturalist observe, a flea
Hath smaller fleas that on him prey,
And these have smaller fleas to bite 'em.
And so proceed ad infinitum.

J. Swift

Few persons realize that there are far more kinds of parasitic than nonparasitic organisms in the world. Even if we exclude the viruses and rickettsias, which are all parasitic, and the many kinds of parasitic bacteria and fungi, the parasites are still in the majority. The bodies of "free-living" plants and animals obviously represent a rich environment that has been colonized innumerable times throughout evolutionary history.

In general the parasitic way of life is highly successful because it evolved independently in nearly every phylum of animals, from protistan phyla to arthropods and chordates, as well as in many plant groups. Organisms that are not parasites are usually hosts. Humans, for example, can be infected with more than a hundred kinds of flagellates, amebas, ciliates, worms, lice, fleas, ticks, and mites. It is unusual to examine a domestic or wild animal without finding at least one species of parasite on or within it. Even animals reared under strict laboratory conditions are commonly infected with protozoa and other parasites. Often the parasites themselves are the hosts of other parasites.

The relationships between parasites and hosts are typically quite intimate, biochemically speaking, and it is a fascinating, often compelling, task to explain just why a species of parasite is restricted to one or a few host species. It is no wonder that the science of **parasitology** has developed out of efforts to understand parasites and their relationships with their hosts.

RELATIONSHIP OF PARASITOLOGY TO OTHER SCIENCES

The first and most obvious stage in the development of parasitology was the discovery of parasites themselves. **Descriptive parasitology** probably began in prehistory. **Taxonomy** as a formal science, however, started with Linnaeus's publication of the tenth edition of *Systema Naturae* in 1758. Linnaeus himself is credited with the description of the sheep liver fluke *Fasciola hepatica,* and through the next 100 years, many common parasites, as well as their developmental stages, were described. The discovery and description of new parasite species continues today, just as does the description of new species in almost every group of plants and animals. Although biologists have a massive "catalog" of the planet's flora and fauna, this list is far from complete. Indeed, based on the rate of new published descriptions, scientists estimate that humans are destroying species faster than they are discovering them, especially in the tropics. There is every reason to believe this generality applies to parasites as well as to butterflies.

Today **systematists** rely on published species descriptions, as well as on studies of DNA, proteins, ecological niches, and geographical distribution, to develop **phylogenies** (phylogeny, singular), or evolutionary histories, of parasites. **Epidemiologists** may need to understand sociological factors, climate, local traditions, and global economics, as well as pharmacology, pathology, biochemistry, and clinical medicine, to devise schemes for controlling parasitic infections.

When people became aware that parasites were troublesome and even serious agents of disease, they began an ongoing effort to heal the infected and eliminate the parasites. Curiosity about routes of infection led to studies of parasite **life cycles;** thus, it became generally understood in the last part of the nineteenth century that certain animals—for example, ticks and mosquitoes—could serve as **vectors** that transmitted parasites to humans and their domestic animals. As more and more life cycles became known, parasitologists quickly realized the importance of understanding these seemingly complex series of ecological and embryological events. It is naive to try to control an infection without knowledge of how the infectious agent, in this case the parasite, reproduces and gets from one host to another.

Parasite biology does not differ fundamentally from the biology of free-living organisms, and parasite systems have provided outstanding models in studies of basic biological phenomena. In the nineteenth century van Beneden described meiosis and Boveri demonstrated the continuity of chromosomes, both in parasitic nematodes. In the twentieth century refined techniques in physics and chemistry applied to parasites have added further to our understanding of basic biological principles and mechanisms. For example, Keilin discovered cytochrome and the electron transport system during his investigations of parasitic worms and insects.[20] Today biochemical techniques are widely used in studies of parasite metabolism, immunology, serology, and chemotherapy. The advent of the electron microscope has resulted in many new discoveries at the subcellular level. Molecular biology and recombinant DNA techniques have contributed new diagnostic techniques and new knowledge of relationships between parasites, and they offer much hope in the development of new vaccines. Certain parasitic protozoa (for example, trypanosomes) today serve as models for some of the most exciting research in molecular genetics and gene expression.[4,9,24]

Historically centered on animal parasites of humans and domestic animals, the discipline of parasitology usually does not include a host of other parasitic organisms, such as viruses, bacteria, fungi, and nematode parasites of plants. Thus, parasitology has evolved separately from virology, bacteriology, mycology, and plant nematology. Medical entomology, too, has branched off as a separate discipline, but it remains a subject of paramount importance to the parasitologist, who must understand the relationships between arthropods and the parasites they harbor and disperse.

PARASITOLOGY AND HUMAN WELFARE

Humans have suffered greatly through the centuries because of parasites. Fleas and bacteria conspired to destroy a third of the European population in the seventeenth century, and malaria, schistosomiasis, and African sleeping sickness have sent untold millions to their graves. Even today, after successful campaigns against yellow fever, malaria, and hookworm infections in many parts of the world, parasitic diseases in association with nutritional deficiencies are the primary killers of humans. Recent summaries of the worldwide prevalence of selected parasitic diseases show that there are more than enough existing infections for every living person to have one, were they evenly distributed:[11,16,26,30,31]

Disease category	Human infections	Deaths per year
All helminths	4.5 billion	
Ascaris	1000 million	20 thousand
Hookworms	900 million	50–60 thousand
Trichuris	750 million	
Filarial worms	657 million	20–50+ thousand
Schistosomes	200 million	0.5–1.0 million
Malaria	489 million	1–2 million

These, of course, are only a few of the many kinds of parasites that infect humans. In addition to causing many deaths, they complicate and contribute to other illnesses. The majority of the more serious infections occur in the so-called tropical zones of the earth, so most dwellers within temperate regions are unaware of the magnitude of the problem. Money for research on tropical infections is very scarce because pharmaceutical companies are reluctant to spend money to develop drugs for treating people who cannot pay for them, and the less-developed countries have many other urgent financial problems. In 1980, $209 for each known case of cancer was spent for cancer research in the United States, $8 per case was spent on research on cardiovascular disease, and 4½ cents per case was spent worldwide for schistosomiasis research.[30]

The notion held by the average person that humans in the United States are free of worms is largely an illusion—an illusion created by the fact that the topic is rarely discussed because of our attitudes that worms are not the sort of thing that refined people talk about, the apparent reluctance of the media to disseminate such information, and the fact that poor people are the ones most seriously affected. Some estimates place the number of children in the United States infected with worms at about 55 million, although this is a gross underestimation if one includes such parasites as pinworms (*Enterobius vermicularis*).

However, the public is becoming more conscious of some other parasites. Some protozoa, such as *Pneumocystis, Toxoplasma,* and *Cryptosporidium,* are among the most common opportunistic infections among patients with acquired immunodeficiency syndrome (AIDS). Lyme disease, which is a syndrome produced by infection with a bacterium that can lead to chronic, disabling arthritis, is transmitted by ticks and is by far the most common arthropod-borne disease in North America.[2]

Even though there are many "native-born" parasite infections in the United States, many "tropical" diseases are imported within infected humans coming from endemic areas. After all, one can travel halfway around the world in a day or two. Many thousands of immigrants who are infected with schistosomes, malaria organisms, hookworms, and other parasites—some of which are communicable—currently live in the United States. It is estimated that about 100,000 cases of *Schistosoma mansoni* (Chapter 16) in the continental United States originated in Puerto Rico. Service personnel returning from abroad often bring parasite infections with them. In 1992, 302 of 917 U.S. Peace Corps volunteers in Malawi tested positive for *Schistosoma* infection.[5] There are documented cases of viable filariasis and *Strongyloides* 40 or more years after the initial infection![3,25] A traveler may become infected during a short layover in an airport, and many pathogens find their way into the United States as stowaways on or in imported products. Travel agents and tourist bureaus are reluctant to volunteer information on how to avoid the tropical diseases that a tourist is likely to encounter since bringing up the topic might lose the customer.[12] Small wonder, then, that "exotic" diseases confront the general practitioner with more and more frequency. One family physician claims to have treated virtually every major parasitic disease of humans during the years of his practice in Amherst, Massachusetts. A survey of intestinal parasites of 776 Southeast Asian immigrants in New Mexico revealed 20 different species of parasites, some of which are not common in the United States.[29]

There are other, much less obvious, ways in which parasites affect all of us, even those in comparatively parasite-free areas. Primary among these is malnutrition: 500 million people in the world have protein-energy malnutrition, and 350 million have iron-deficiency anemia.[30] Malnutrition is exacerbated both by population increase and by environmental degradation. From 2 billion in 1930, the population of the earth doubled to 4 billion in 1976, passed 5.5 billion in 1992, and is expected to exceed 10 billion in 2025.[14] Meanwhile, environmental degradation such as erosion continues to decrease the available supply of cropland. The increasing scarcity of resources contributes to violent conflict in the world.[15] The contributions of parasites to malnutrition are important but are underestimated because of underreporting.[30] Hospitals usually list what appears to be the most obvious cause of death, but most patients have multiple infections that have contributed to their disease state.

Even where food is being produced, it is not always used efficiently. Considerable caloric energy is wasted by fevers caused by parasitic infections. Heat production of the human body increases about 7.2% for each degree rise in Fahrenheit. A single, acute day of fever caused by malaria requires approximately 5000 calories, or an energy demand equivalent to two days of hard manual labor. To extrapolate, in a population with an average diet of 2200 calories per day, if 33% had malaria, 90% had a worm burden, and 8% had active tuberculosis (conditions that are repeatedly observed), there would be an energy demand equivalent to 7500 tons of rice per month per million people in addition to normal requirements. That is a waste of 25% to 30% of the total energy yield from grain production in many societies.[27]

Humans create many of their own disease conditions because of high population density and subsequent environmental pollution. Despite great progress in extending water supplies and sewage disposal programs in less-developed countries, not more than 10% to 15% of the world population is thus served.[17] Population shifts from rural to urban areas commonly overload the water and sewage capabilities of even major cities. Usually an adequate water supply has first priority, with sewage disposal running a poor second (Fig. 1.1). When one recalls that most parasite infections are caused by ingesting food or water contaminated with human feces, it is easy to understand why 15 million children die of intestinal infections every year.

FIGURE 1.1

Nightsoil is a logical use of human feces and urine. Here it is applied to a vegetable garden, a technique practiced in much of the world. Although sometimes controlled by government regulations, it still serves as a significant means for distribution of eggs of some helminths and certain protozoan cysts.

Courtesy of Robert E. Kuntz.

Parasites are also responsible for staggering financial loss. Malaria, for example, is usually a chronic, debilitating, periodically disabling disease. In situations where it is prevalent the number of hours lost from productive labor multiplied by the number of malaria sufferers yields a figure that can be charged as loss in the manufacture of goods, in the production of crops, or in the earning of a gross national product. On the basis of estimates this figure is about $2 billion annually. Nations that import goods from countries infected with malaria, schistosomiasis, hookworm, and many other parasitic diseases pay more for these products than they would had the products been produced without the burden of disease. Plant parasites further diminish the productive capacities of all countries.

National and international efforts to increase productivity and standard of living in less-developed countries sometimes inadvertently increase parasitic disease. Schistosomiasis in Egypt increased after construction of the Aswan High Dam on the Nile River (p. 243). Smaller dams for drainage and agriculture have promoted transmission of schistosomiasis, onchocerciasis, dracunculiasis, and malaria.[28] The World Bank loaned Brazil funds to pave highways into the Amazon region to settle poor urban workers for farming, despite contrary advice from their own agricultural experts.[21] This produced an increase in malaria and spread the disease to new foci when the migrants returned to the cities after their farms failed (p. 149).[23]

An important role of parasitologists, together with that of members of other medical disciplines, is to help achieve a lower death rate. However, it is imperative that a lower death rate be matched with a concurrent lower birthrate and higher quality of life. If not, we are faced with the "parasitologist's dilemma"—that of sharply increasing a population that cannot be supported by the resources of the country. Dr. George Harrar, president of the Rockefeller Foundation, observed, "It would be a melancholy paradox if all the extraordinary social and technical advances that have been made were to bring us to the point where society's sole preoccupation would of necessity become survival rather than fulfillment." Harrar's paradox is already a fact for half the world. Parasitologists have a unique opportunity to break the deadly cycle by contributing to the global eradication of communicable diseases while making possible more efficient use of the earth's resources.

PARASITES OF DOMESTIC AND WILD ANIMALS

Both domestic and wild animals are subject to a wide variety of parasites that demand the attention of the parasitologist. Although wild animals are usually infected with several species of parasites, they seldom suffer as a result of massive deaths, or **epizootics,** because of the normal dispersal and territorialism of most species. However, domesticated animals are usually confined, often in great numbers, to pastures or pens year after year, so the parasite eggs, larvae, and cysts become extremely dense in the soil and the burden of adult parasites within each host becomes devastating. For example, the protozoa known as the coccidia thrive under crowded conditions; they may cause up to 100% mortality in poultry flocks, 28% reduction in wool in sheep, and 15% reduction in weight of lambs.[27] Agriculturists are forced to expend much money and energy in combating the phalanx of parasites that attack their animals. Infections in poultry are controlled by the costly method of prophylactic drug administration in feed. Unfortunately, the coccidia have

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become resistant to one drug after another.[6] Many other examples can be given, some of which are discussed later in this book. Thanks to the continuing efforts of parasitologists around the world, the identifications and life cycles of most parasites of domestic animals are well-known. This knowledge, in turn, exposes weaknesses in the biology of these pests and suggests possible methods of control. Similarly, studies of the biochemistry of organisms continue to suggest modes of action for chemotherapeutic agents.

Less can be done to control parasites of wild animals. Although it is true that most wild animals tolerate their parasite burdens fairly well, the animals will succumb when crowded and suffering from malnutrition, just as will domestic animals and humans. For example, the range of the big horn sheep in Colorado has been reduced to a few small areas in the high mountains. The sheep are unable to stray from these areas because of human pressure. Consequently, lungworms have so increased in numbers that in some herds no lambs survive the first year of life. These herds seem destined for quick extinction unless a means for control of the parasites can be found in the near future.

A curious and tragic circumstance has resulted in the destruction of many large wild animals in Africa. These animals are heavily infected with species of *Trypanosoma,* a flagellate protozoan of the blood. The wild animals tolerate infection well but function as **reservoirs** of infection for domestic animals, which quickly succumb to trypanosomiasis. One means of control employed is the complete destruction of the wild animal reservoirs themselves. Hence, the parasites of these animals are the indirect cause of their death. It is hoped that this parasitological quandary will be solved in time to save the magnificent wild animals.

Still another important aspect of animal parasitology is the transmission to humans of parasites normally found in wild and domestic animals. The resultant disease is called a **zoonosis.** Many zoonoses are rare and cause little harm, but some are more common and of prime importance to public health. An example is trichinosis, a serious disease caused by minute nematodes, *Trichinella* spp. (Chapter 23). These worms exist in **sylvatic** cycles that involve rodents and carnivores and in an **urban** or **domestic** cycle chiefly among rats and swine. People become infected when they enter any cycle, such as by eating undercooked bear or pork. Another zoonosis is echinococcosis, or hydatid disease, in which humans accidentally become infected with juvenile tapeworms when they ingest eggs from dog feces (Chapter 21). *Toxoplasma gondii,* which is normally a parasite of felines and rodents, is now known to cause many human birth defects (Chapter 8).

We recognize new zoonoses from time to time. Lyme disease, mentioned before, was long present in deer and white-footed mice, but frequent transmission to humans began only in the 1970s.[2] It is the obligation of the parasitologist to identify, understand, and suggest means of control of such diseases. The first step is always the proper identification and description of existing parasites so that other workers can recognize and refer to them by name in their work. Thousands of species of parasites of wild animals are still unknown and will occupy the energies of taxonomists for many years to come.

Aside from their roles as causative agents of disease, parasites provide us with an almost unlimited supply of fascinating, and challenging, problems in ecology and evolution (Chapter 2). Presence of a parasite species with a complex life cycle demonstrates unequivocally that intermediate hosts occupy an area and that an ecological relationship exists between hosts and parasites. Parasites also may be one of the factors, along with predation and abiotic events, that function to regulate host populations. And finally, virtually every species of animal is parasitized by at least one other species. Thus, much of the overall diversity found in any ecosystem can be attributed to parasitism.

CAREERS IN PARASITOLOGY

There is an area within parasitology to interest every biologist. The field is large and has so many approaches and subdivisions that anyone who is interested in biological research can find a lifetime career in parasitology.[1] It is a satisfying career because each bit of progress made, however small, contributes to our knowledge of life and to the eventual conquering of disease. As in all scientific endeavors, every major breakthrough depends on many small contributions made, usually independently, by individuals around the world. Previously little-known parasites suddenly became life-threatening infections in AIDS patients. Had their identifications and life cycles been better understood, much expense and time would have been saved in recognizing this complex disease.

The training required to prepare a parasitologist is rigorous. Modern researchers in parasitology are well-grounded in physics, chemistry, and mathematics, as well as biology from the subcellular through the organismal and populational levels. They must be firmly grounded in medical entomology, histology, and basic pathology. Depending on their interests, they may require advanced work in physical chemistry, immunology, molecular biology, genetics, and systematics. Most parasitologists hold Ph.D.s or other doctoral degrees, but contributions have been made by persons with master's or bachelor's degrees. Such intense training is understandable, since parasitologists must be familiar with the principles and practices that apply to over a million species of animals; in addition they need thorough knowledge of their fields of specialty. Once they have received their basic training, parasitologists continue to learn during the rest of their lives. Even after retirement, many remain active in research for the sheer joy of it. Parasitology indeed has something for everyone.

SOME BASIC DEFINITIONS

The science of parasitology is largely a study of **symbiosis,** or, literally, "living together." Although some authors restrict the term *symbiosis* to relationships wherein both partners benefit, we prefer to use the term in a wider sense, as originally proposed by the German scholar A. de Bary in 1879: *Any two organisms living in close association, commonly one living in or on the body of the other, are symbiotic, as contrasted with "free living."* Usually the **symbionts** are of different species, but not necessarily.

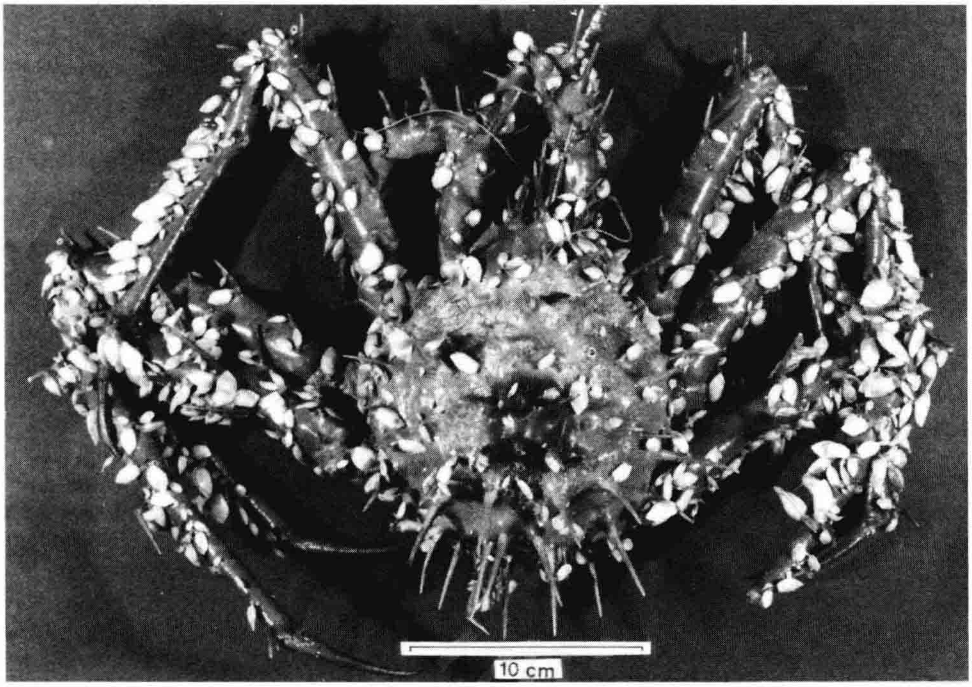

FIGURE 1.2

Gooseneck barnacles (*Poecilasma kaempferi*) growing on the legs and carapace of a crab (*Neolithodes grimaldi*). This is an example of phoresis since the two species are merely "traveling together." However, the relationship could grade into commensalism; some advantages probably accrue to the barnacles.

From R. Williams and J. Moyse, "Occurrence, distribution, and orientation of *Poecilasma kaempferi* Darwin (Cirripedia: Pedunculata) epizoic on *Neolithodes grimaldi* Milne-Edwards and Bouvier (Decapoda: Anomura) in the northeast Atlantic," in *J. Crust. Biol.* 8:177–186. Copyright © 1988.

Symbiotic relationships can be further characterized by specifying the nature of the interactions between the participants. It is always a somewhat arbitrary act, of course, for people to assign definitions to relationships between organisms. But animal species participate in a wide variety of symbiotic relationships, so parasitologists have a need to communicate about these interactions and thus, have coined a number of terms to describe them.

Interactions of Symbionts

• Phoresis

Phoresis exists when two symbionts are merely "traveling together," and there is no physiological or biochemical dependence on the part of either participant. Usually one **phoront** is smaller than the other and is mechanically carried about by its larger companion (Fig. 1.2). Examples are bacteria on the legs of a fly or fungous spores on the feet of a beetle.

• Mutualism

Mutualism describes a relationship in which both partners benefit from the association. Mutualism is usually obligatory, since in most cases physiological dependence has evolved to such a degree that one mutual cannot survive without the other. Termites and their intestinal protistan fauna are an excellent example of mutualism. Termites cannot digest cellulose because they cannot synthesize and secrete the enzyme cellulase. The myriad flagellates in a termite's intestine, however, synthesize cellulase and consequently digest the wood eaten by the host. The termite uses molecules excreted as a by-product of the flagellates' metabolism. If we kill the flagellates by exposing termites to high temperature or high oxygen concentration, then the termites die even though they continue to eat wood.

An astonishing variety of mutualistic associations can be found among animals, bacteria, fungi, algae, and plants. Blood-sucking leeches cannot digest blood, for example, but their intestinal bacteria, species that are restricted to leech guts, do the digestion for their hosts. What is apparently an evolutionary origin of a case of mutualism has been discovered in a common free-living ameba, *Amoeba proteus*. A strain of *A. proteus* became infected with a parasitic bacteria, and over a period of several years the amebas became unable to survive without the bacteria.[19] As in the termites, when the symbionts are killed by elevated temperature, the amebas (of this particular strain) die unless reinfected by microinjection.[22] Although the nature of this relationship is not known, we presume it is metabolic; that is, the partners exchange needed molecules. As is the case with many such relationships, exploration of the basis for the mutualism would make an interesting doctoral dissertation project!

Mutualistic interactions are not restricted to physiological ones. For example, **cleaning symbiosis** is a behavioral phenomenon and occurs between certain crustaceans and small fish—the cleaners—and larger marine fish. Cleaners often establish stations that the large fish visit periodically, and the cleaners remove ectoparasites, injured tissues, fungi, and other organisms. Some evidence exists that such associations may be in fact obligatory; when all cleaners are carefully removed from a particular area of reef, for example, all the other fish leave too. You can find other examples of mutualistic and related associations in the texts edited by Henry[13] and Cheng.[7]

• Commensalism

In **commensalism** one partner benefits from the association, but the host is neither helped nor harmed. The term means "eating at the same table," and many commensal relationships involve feeding on food "wasted" or otherwise not consumed by the host. Pilot fish (*Naucrates*) and remoras (Echeneidae) are often cited as examples of commensals. A remora is a slender fish whose dorsal fin is modified into an adhesive organ that it attaches to large fish, turtles, and even submarines! The remora gets free rides and scraps, but it does not harm the host or rob it of food. Some remoras, however, are mutuals, since they clean the host of parasitic copepods (Chapter 34).[8]

Commensalism may be **facultative,** in the sense that the commensal may not be required to participate in an association to survive. Stalked ciliates of the genus *Vorticella* are frequently found on small crustaceans, but they survive equally well on sticks in the same pond. Related forms, however, such as *Epistylis* spp., are evidently **obligate** commensals since they are not found except on other organisms, especially crustaceans.

Humans harbor several species of commensal protistans—for example, *Entamoeba gingivalis.* This ameba lives in the mouth where it feeds on bacteria, food particles, and dead epithelial cells but never harms healthy tissues. It has no cyst or other resistant stage in its life cycle. In the laboratory beginning parasitology students are usually asked to learn to distinguish between commensal and parasitic amebas. When you are studying prepared slide specimens, the task is not too difficult. But when faced with real live animals, sometimes the distinctions are not so clear. Adult tapeworms are universally regarded as parasites, yet in some cases they have no known ill effects on their host.[18]

• Parasitism

Parasitism is a relationship in which one of the participants, the parasite, either harms its host or in some sense lives at the expense of the host. Parasites may cause mechanical injury, such as by boring a hole into the host or digging into its skin or other tissues, by stimulating a damaging inflammatory or immune response, or simply by robbing the host of nutrition. Most parasites inflict a combination of these conditions on their hosts.

If a parasite lives on the surface of its host, it is called an **ectoparasite;** if internal, it is an **endoparasite.** Most parasites are **obligate parasites;** that is, they cannot complete their life cycle without spending at least part of the time in a parasitic relationship. However, many obligate parasites have free-living stages outside any host, including some periods of time in the external environment within a protective eggshell or cyst. **Facultative parasites** are not normally parasitic but can become so when they are accidentally eaten or enter a wound or other body orifice. Two examples are certain free-living amebas, such as *Naegleria* (p. 108), and free-living nematodes belonging to the genus *Micronema.*[10] Infection of humans with either of these is extremely serious and usually fatal.

When a parasite enters or attaches to the body of a species of host different from its normal one, it is called an **accidental,** or **incidental, parasite.** For instance, it is common for nematodes, normally parasitic in insects, to live for a short time in the intestines of birds or for a rodent flea to bite a dog or human. Accidental parasites usually do not survive in the wrong host, but in some cases they can be extremely pathogenic (see *Baylisascaris, Toxocara* in Chapter 26). Parasitism is usually the result of a long, shared evolutionary history between parasite and host species. Accidental parasitism puts both host and parasite into environmental conditions to which neither is well-adapted; it is not surprising that the result may be serious harm to either or both participants.

Some parasites live their entire adult lives within or on their hosts and may be called **permanent parasites,** whereas **temporary,** or **intermittent, parasites,** such as mosquitoes or bedbugs, only feed on the host and then leave. Temporary parasites are often referred to as **micropredators,** in recognition of the fact that they usually "prey" on several different hosts (or the same host at several discrete times).

Predation and parasitism are conceptually similar in that both the parasite and the predator live at the expense of the host or prey. The parasite, however, normally does not kill its host, is small relative to the size of the host, has only one host (or one host at each stage in its life cycle), and is symbiotic. The predator kills its prey, is large relative to the prey, has numerous prey, and is not symbiotic. **Parasitoids,** however, are insects, typically flies or wasps (orders Diptera and Hymenoptera, Chapters 38 and 39, respectively), whose immature stages feed on their hosts' bodies, usually other insects, but finally kill the hosts. Parasitoids resemble predators in this regard, but they only require a single host individual.

Hosts

Parasitologists differentiate between various types of hosts based on the role the host plays in the life cycle of the parasite. A **definitive host** is one in which the parasite reaches sexual maturity. Sexual reproduction has not been clearly shown in some parasites, such as amebas and trypanosomes, and in these cases we arbitrarily consider the definitive host the one most important to humans. An **intermediate host** is one that is required for parasite development, but one in which the parasite does not reach sexual maturity. Definitive hosts are often but not necessarily vertebrates; the malarial parasites, *Plasmodium* spp., reach sexual maturity and undergo fertilization in the mosquito, which by definition is, therefore, the definitive host, while vertebrates are the intermediate hosts (see Chapter 9).

A **paratenic** or **transport host** is one in which the parasite does not undergo any development but in which it remains alive and infective to another host. Paratenic hosts may bridge an ecological gap between the intermediate and definitive hosts. For example, owls may be parasitized by thorny headed worms (Chapter 31), which undergo development to infective stages in insects that pick up the worm eggs from owl feces. Large owls rarely if ever eat insects, but shrews eat them regularly, sometimes accumulating large numbers of juvenile worms encysted in their mesenteries. Owls catch shrews, sometimes becoming heavily infected with the worms. In this case the shrew is the transport host between the insect intermediate and the owl definitive host.

Most parasites develop only in a restricted range of host species. That is, parasites exhibit varying degrees of **host specificity,** some infecting only a single host species, others infecting a number of related species, and a few being capable of infecting many host species. The so-called pork tapeworm, *Taenia solium,* apparently can mature only in humans, so it has absolute host specificity. The nematode *Trichinella spiralis* seems to be able to mature in almost any warm-blooded vertebrate.

Any animal that harbors an infection that can be transmitted to humans is called a **reservoir host,** even if the animal is a normal host of the parasite. Examples are rats and wild carnivores with *Trichinella* spp., dogs with *Leishmania* spp., and armadillos with *Trypanosoma cruzi,* the causative agent of Chagas' disease (see Chapter 5).

Finally, many parasites host other parasites, a condition known as **hyperparasitism.** Examples are *Plasmodium* spp. in mosquitoes, a tapeworm juvenile in a flea, and the many insects whose larvae parasitize other parasitic insect larvae.

Although the vast majority of parasites are different species from their hosts, exceptions do occur. In *Trichosomoides* a nematode parasite of rats, the male lives its mature life within the uterus of the female worm, obtaining its nourishment from her tissues. This is also the case with *Gyrinicola japonicus,* a nematode parasite of frogs. An even stranger relationship has evolved in some species of anglerfish in which the male bites the skin of the female and sucks her blood and tissue fluids for nourishment. Eventually they grow together, and he shares her bloodstream! And, of course, the term *parasite* is used occasionally to condemn our fellow humans who seem to take more than they return to society.

Definitions are always arbitrary, and when we construct pigeonholes to receive descriptions of phenomena in the real world, we expect to find situations that defy easy assignment to one of our precise categories. Many symbiotic associations cannot be classified with certainty as to the effects of the symbiont on the host. An apparent case of commensalism may have damaging effects on the host that humans have not even thought about, much less observed. Conversely, a case of assumed parasitism may, on closer inspection, turn out to be commensalism. Nevertheless, definitions are necessary to communication, so we accept that sometimes they are not exactly precise because they are almost always useful. The terms defined in this chapter convey large amounts of inferred information about ecology, evolutionary history, biochemistry, and development.

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Chapter 2

BASIC PRINCIPLES AND CONCEPTS: PARASITE ECOLOGY AND EVOLUTION

The host is an island invaded by strangers with different needs, different food requirements, different locations within which to raise their progeny.

W. Taliaferro

Ecology is the study of relationships between organisms and their environments. A parasite's environment is primarily the host, of course, but transmission stages such as spores, eggs, and often juveniles must also survive abiotic conditions. A host usually represents a rich and highly regulated supply of nutrients. Most animal body fluids have a wide array of dissolved proteins, amino acids, carbohydrates, and nucleic acid precursors; virtually all animals have mechanisms for maintaining the chemical makeup and osmotic balance of their body fluids; and vertebrates such as birds and mammals control body temperature as well. We should expect parasites to exhibit traits that allow them to exploit such environments but at the same time deny them access to others. A flea cannot live in the white-footed mouse's habitat, for example, unless the mouse itself is living there too.

But hosts are relatively small patches within the vast matrix that is their own habitat; that is, they are "islands" in the true sense of Taliaferro's quote as well as in the metaphorical sense. Thus, suitable parasite environments are dispersed, in addition to being rich and regulated. For example, there is an enormous volume of water in a lake compared to the volume of fish in that same lake. This seemingly trivial observation, however, points to a major problem for monogenean flatworms (p. 281) that must live on these fish: Unless the worm's reproductive stages are able to keep finding fish to infect, the parasite is likely to become locally extinct. Indeed, many parasite control strategies are based on reducing the probability of host and parasite encounter, and conversely, many parasites possess traits that function to increase the probability of finding a host.

The basic situations just described are reflected in a number of parasite characteristics that can be interpreted within an ecological context. These characteristics include feeding adaptations, transmission mechanisms, population structures, and membership in "communities" or assemblages of parasite species within a single host. And ultimately, because the host is the parasite's environment, we should expect evolutionary changes in hosts to be accompanied by parallel, perhaps adaptive, changes in their parasites.

PARASITE ECOLOGY

The Parasite's Ecological Niche

• Trophic Relationships

Parasites always live at a higher trophic level than their hosts.[22] Thus, all parasites are at least primary consumers, and those infecting top predators such as hawks, owls, and carnivores live quite high on a typical food pyramid. Trophic relationships are direct and obvious for parasites that eat host tissue and fluids, such as hookworms (p. 405), frog lung flukes (p. 264), and ticks. But parasite use of the host can also be somewhat indirect. For example, all free-living animals spend significant amounts of energy regulating their internal milieus and producing their own offspring. Thus, parasites can be thought of as "preying" on the homeostatic mechanisms and reproductive efforts of organisms at lower trophic levels.

All parasites are heterotrophic, requiring their energy and carbon in the form of existing complex organic molecules and their nitrogen as a mixture of amino acids.[21] In this respect parasites are no different from other kinds of animals. A parasite's feeding devices, however, may differ considerably from those seen in most free-living animals. For example, tapeworms (phylum Platyhelminthes, Chapter 20) and spiny-headed worms (phylum Acanthocephala, Chapter 31) have no digestive tracts and absorb sugars and amino acids directly across their body walls. These worms feed through uptake sites on the plasma membrane. The anticoagulant of tick saliva (Chapter 40) is an integral part of the parasite's feeding mechanism, another illustration of an adaptation to a characteristic of the host—in this case, the clotting property of blood.

• Dimensions on Resources

Ecologists are able to quantify ecological niches by measuring some aspect of the habitat—such as tree height, water temperature, and seed sizes—and then observing the range of values over which a species occurs or uses. This range is called a species' **dimension on a resource.**[14,18] A parasite's niche consists of dimensions on resources provided by the living body of another species, as well as on abiotic resources encountered by transmission stages such as eggs, cysts, spores, and young. But while it is easy to describe a parasite's niche in very general terms (eye, gut, lung), it is often quite difficult to quantify that niche—that is, measure dimensions on resources—in the same way you could for many free-living animals.

Host intestinal length is one example of an easily measured resource, and much research has been done on the distribution of cestodes, nematodes, and acanthocephalans within

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