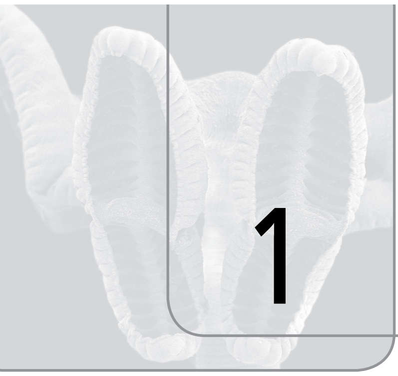

1 Introduction

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.

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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

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 distils 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.

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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 multidisciplinarity 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.

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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.

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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 Erlich 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.

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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

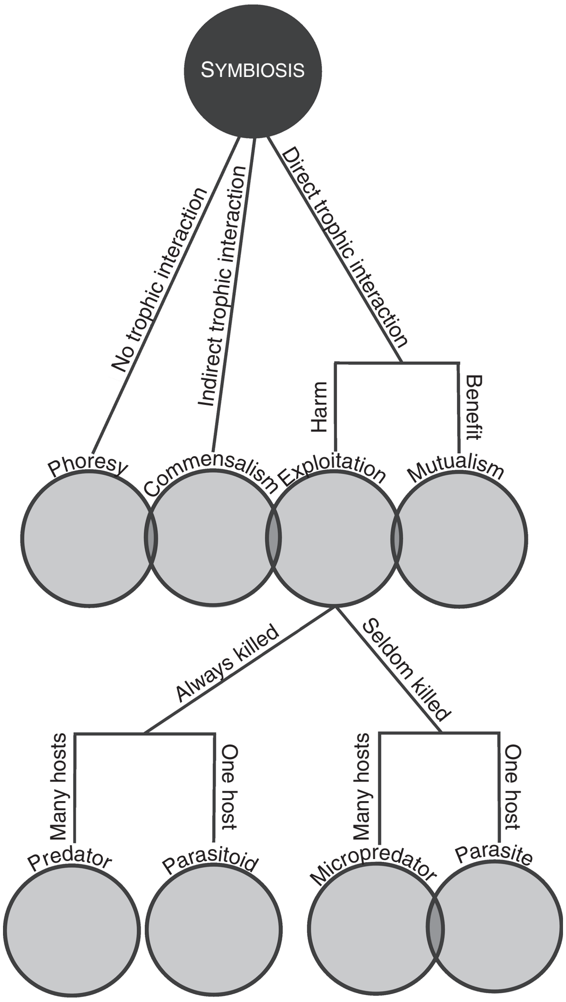

Fig. 1.1 ‘Parasitism’s place’ within the context of symbiotic relationships. This is one way of looking at parasitism and it is based, initially, on trophic relationships, followed by ‘harm,’ and finally, quantity of hosts involved. The final criterion, number of hosts attacked, is meaningful only if 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.)

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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.

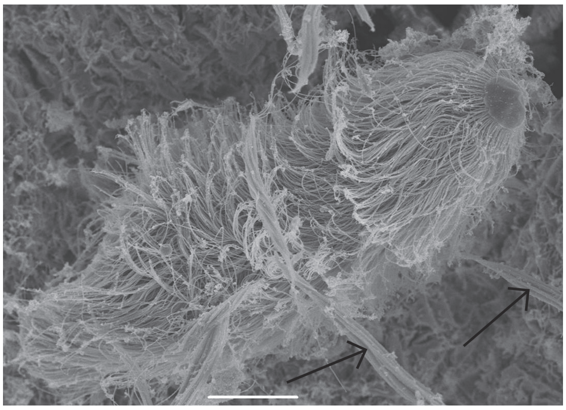

Fig. 1.2 Scanning electron micrograph of the mutualistic hypermastigote flagellate *Trichonympha campanula* from the intestine of a termite. Another, much smaller flagellate *Streblomastix* sp. (arrows) is also present. (Micrograph courtesy of Ron Hathaway.)

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

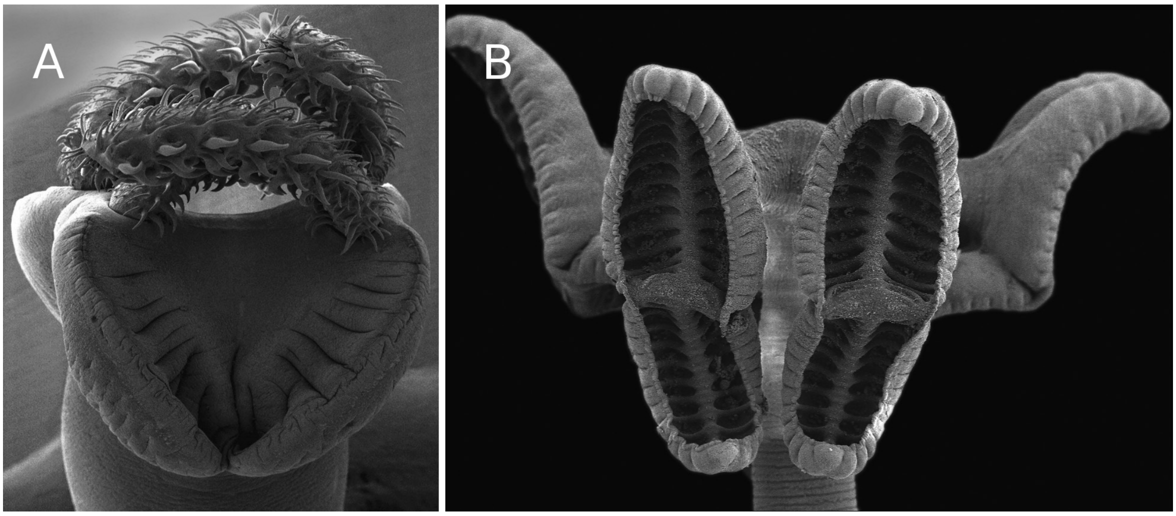

Fig. 1.3 Scanning electron micrographs illustrating the elaborate holdfasts of host-specific tapeworms of elasmobranchs. (A) Scolex of the trypanorhynch cestode *Paragrillotia similis* from the spiral intestine of the Atlantic nurse shark *Ginglymostoma cirratum*; (B) scolex of the rhinebothriidean cestode *Rhinebothrium megacanthophallus* from the spiral intestine of the freshwater whipray *Himantura polylepis*. (Micrographs courtesy of Janine Caira (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, *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. 1.4 Host and site specificity exhibited by the mesoparasitic copepod *Phrixocephalus 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.)

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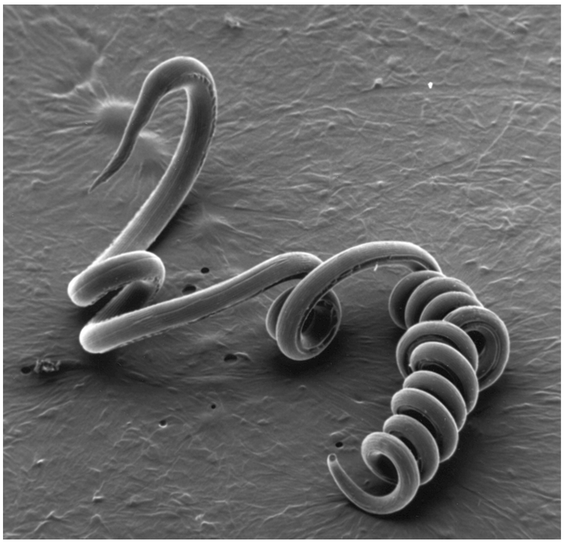

Fig. 1.5 Scanning electron micrograph of the nematode *Heligmosomoides polygyrus* from the intestine of a mouse. This macroparasite–host system is a widely used model in experimental parasitology. (Micrograph courtesy of Doug Colwell.)

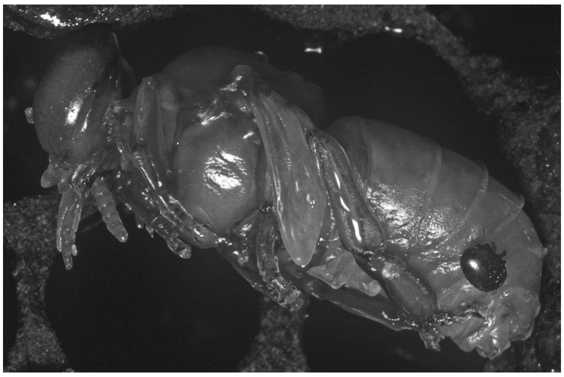

Fig. 1.6 Female of the ectoparasitic mite *Varroa destructor* attached to the abdomen of a developing honey bee. (Photograph courtesy of Scott Bauer, USDA Agricultural Research Service, Bugwood.org.)

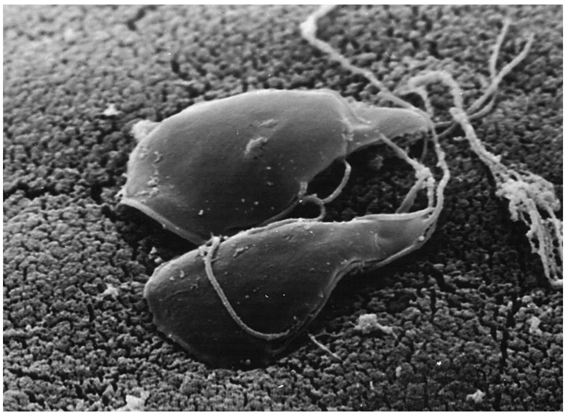

Fig. 1.7 Scanning electron micrograph of the trophozoites of the flagellated protist *Giardia muris* attached to the villi of the small intestine of an experimentally infected mouse. This microparasite reproduces asexually via binary fission. (Micrograph courtesy of Břetislav Koudela.)

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 leopeophtherii*, 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 hosts via food web interactions. Life cycles in which more than one host are required are referred to as indirect life cycles. Many parasites have remarkably complex life cycles with several hosts and both free-living and obligate parasitic larval stages.

Some protists and filarial nematodes have **vectors** as hosts. Vectors are micropredators that transmit infective stages from one host to another. A vector may be an intermediate or a definitive host, depending on whether the sexual phase of the parasite's life cycle occurs in it or not. For example, the insect vectors for species of *Plasmodium*, the causative agents of malaria, are certain species of female mosquitoes that actively inoculate infective stages of the parasite into the next host during their blood meals. Sexual reproduction occurs within the stomach of the mosquito; consequently, mosquitoes are the definitive hosts for the parasite.

A number of parasites may use hosts in which there is no development and that are not always obligatory for the completion of a parasite's life cycle. These are called **paratenic** or **transport hosts**. Such hosts are most frequently used to bridge an ecological, or trophic, gap. For example, adults of the fluke, *Halipegus occidualis*, live under the tongue of green frogs (Color plate Fig. 1.1). Snails in the genus *Helisoma* are obligate first intermediate hosts, whereas aquatic micro-crustaceans such as ostracods are obligate second intermediate hosts. But green frogs do not normally consume these small crustaceans. It turns out that various species of odonate (dragonflies and damselflies) prey upon ostracods, thus acting as paratenic hosts for this trematode. Thus, frogs are exposed to *Halipegus* larvae when they prey on nymphs and metamorphosed odonates. In this four-host life cycle, the parasite exploits two predator–prey interactions to enhance transmission (see Fig. 6.23).

A number of animals are normal hosts for parasites that may also infect humans. These are called **reservoir hosts**. These non-human hosts act as reservoirs of infection for certain parasites. Diseases of animals that are transmissible to humans are called zoonotic diseases, or **zoonoses**. Thus, giardiasis, trichinellosis, and schistosomiasis are examples of zoonoses. Similarly, rats are important reservoir hosts for the nematode, *Trichinella spiralis*, and the human blood fluke, *Schistosoma japonicum*. Ecologically, reservoir hosts are similar to paratenic hosts since they may greatly increase transmission rates, and also help prevent local extinction of the parasite. The potential for controlling zoonotic diseases in humans is greatly complicated by the presence of these reservoir hosts. Furthermore, reservoir hosts greatly complicate the zoonotic parasite's **epidemiology**. Epidemiology is the study of all the many complex, inter-related ecological factors responsible for the transmission and distribution of a human disease. A related term is **epizootiology**. Epizootiology usually refers to the factors involved in the transmission and distribution of non-human parasites, often in reference to epizootics. The epidemiology of human parasites and the epizootiology of parasites of fishery, veterinary, and wildlife importance will be stressed throughout the upcoming chapters.

1.4 Overview

All eukaryotes have the capacity to recognize invading cells or organisms as non-self. It follows that a fundamental feature of the parasitic life style lies in the host's ability to defend itself against a limitless diversity of invaders. It is the strength and duration of host defenses that defines such features of the host–parasite relationship as specificity, parasite-induced pathology and phenotype alteration, site selection, parasite-mediated natural selection, and coevolution. Given the fundamental importance of host defenses to the ecology and evolution of parasitism, we provide an introduction to the massive field of immunology in Chapter 2. Our coverage is not meant to replace an introductory course in immunology. Instead, our aim is to cover the basics of innate and adaptive immunity in both invertebrates and vertebrates, and also provide an introduction to the interdisciplinary fields of immunoparasitology and ecological immunology.

The following nine chapters cover the biodiversity of animal parasites. In each of these chapters we take a parasite-centered approach to describe functional morphology, life-cycle variation, and biodiversity. Our