FOUNDATIONS OF PARASITOLOGY

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PREFACE

This book is intended for use in introductory courses in parasitology. Although each teacher will address the subject differently, we believe that the foundation material for any approach can be found here. The format is basically traditional, with up-to-date contributions from electron microscopy, biochemistry, immunology, and other disciplines woven into the text. We believe that a sound knowledge of the biology, morphology, and ecology of parasites is essential to understanding and appreciating the more subtle aspects of the host-parasite relationship, pathogenesis, and epidemiology.

In the chapters that follow, each group of parasites is described and differentiated from all others, and any peculiarities of the group are discussed. For illustrations of parasitic types and principles, we have emphasized species of medical or veterinary importance, for we all are interested in diseases that may infect our own species or affect our pocketbooks. Many parasites that do not infect humans or domestic animals are still of considerable scientific interest, however, and we have included numerous examples of these. Many of the organisms discussed are available from commercial suppliers, which should aid in planning laboratory exercises. Because of space limitations and because courses in medical entomology are available at most universities and colleges, we have not included chapters on medically important or other parasitic arthropods. An exception is the parasitic Crustacea, which provide fantastic examples and insights into parasitism, but which often are neglected in both medical entomology and invertebrate zoology courses. We feel that coverage of parasitic Crustacea is appropriate in parasitology, and we hope that students and teachers will enjoy our introduction to these organisms.

Physiological adaptations of parasites are essential requirements for the exploitation of their modes of life. Therefore, where possible we have integrated physiological information within each section, organizing a complete foundation upon which the student can build. Some topics, such as energy metabolism and principles of immunology, are offered as separate units, which can be included or deleted at the pleasure of the instructor. Though necessarily brief, we hope that these sections will be understandable to students who have no prior training in the areas.

Any advanced undergraduate or graduate student in biology should have the following prerequisite background to use this textbook: a year of biology, including basic introductory invertebrate zoology, and chemistry through organic, preferably with a first course in biochemistry.

In our years of teaching we have found that students want to know what treatment, if any, is available for the diseases they study. Accordingly, we have included mention of chemotherapy at appropriate places in the book. However, we have tried to name the classes of drugs, or in some cases the drugs of choice, rather than suggesting clinical procedures. We want the reader to have a feeling for what might be done for those who suffer from parasitic diseases.

The world literature in parasitology is already so vast and is expanding so rapidly that it is impossible to review it all. Almost any chapter, or even many parts of chapters, could themselves be expanded to book length, but we hope that we have omitted nothing essential to the purpose of this basic text. We have tried to rely extensively on recently published information to be as timely as possible, but some material doubtless will be dated even as the manuscript goes to press. This is an inevitable consequence in a vital and active field. In our effort to reach a high level of accuracy, we have had each chapter read and corrected by authorities on the various topics. We sincerely hope that any remaining errors are minimal; they are, of course, our responsibility.

No one could hope to write a book such as this without the assistance of many people. We have drawn shamelessly on the expertise of numerous colleagues and friends, whose experiences have exceeded ours in certain specialized fields. Experts who have contributed their time and special knowledge to this book are too numerous to list in entirety, but we especially wish to thank Lawrence R. Ash, W. S. Bailey, Wilbur Bullock, Edelberto J. Cabrera, Donald W. Duszynski, Reino S. Freeman, Arthur G. Humes, Z. Kabata, Richard Komuniecki, Delane C. Kritsky, Robert E. Kuntz, John S. Mackiewicz, Ralph Muller, George S. Nelson, Brent B. Nickol, Robert L. Rausch, J. Teague Self, and Robert B. Short. B. M. Honigberg read all chapters on protozoa and made his personal library available for our use. Many persons and publications gave freely of published and unpublished illustrations. These are greatly appreciated and are credited along with the relevant pictures.

Andra Schmidt transformed our grammar and syntax, making sense out of nonsense, and typed the first two drafts of this book. Joann Sharp typed the final draft, bringing order to the chaotic cut-and-paste copy that we presented her. We offer grateful thanks to them.

Gerald D. Schmidt

Larry S. Roberts

CONTENTS

Chapter 1

INTRODUCTION TO PARASITOLOGY

Big fleas have little fleas
upon their backs to bite 'em,
Little fleas have lesser fleas
and so, ad infinitum.

SWIFT

Few people 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 parasitic way of life, generally speaking, is a highly successful one, for it evolved independently in nearly every phylum of animals, from protozoans to arthropods and chordates, as well as in many plant groups. Organisms that are not parasites are usually hosts. Humans, for example, are hosts to over 100 kinds of parasites, again not counting viruses, bacteria, and fungi. 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 protozoans or other parasites. Often the parasites themselves are the hosts of other parasites. It is no wonder then that the science of parasitology has been developed out of efforts to understand the parasites and their relationships with their hosts.

THE RELATIONSHIP OF PARASITOLOGY TO OTHER SCIENCES

Parasitology has passed through a series of stages in its history, each of which, today, is an active discipline in its own right. The first and most obvious stage is the discovery of the parasites themselves. This undoubtedly began in the shadowy eons of prehistory, but the ancient Persians, Egyptians, and Greeks recorded their observations in such a way that later generations could, and often still can, recognize the animals they were writing about. The discovery and naming of unknown parasites, their study, and their arrangement into a classification is an exciting and popular branch of parasitology today.

When people became aware that parasites were troublesome and even serious agents of disease, they began a continuing campaign to heal the infected and eliminate the parasites. The later discovery that other animals could be the **vectors,** or means of dissemination, of parasites opened the door to other approaches for control of parasitic diseases.

Development of better lenses led to basic discoveries in cytology and genetics of parasites that are applicable to all of biology. And, in the twentieth century, refined techniques in physics and chemistry have contributed much to our knowledge of host-parasite relationships. Some of these have added to our understanding of basic biological principles and mechanisms, such as the discovery of cytochrome and the electron transport system by David Keilin in 1925[3] during his investigations on parasitic worms and insects. 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. Thus, parasitologists employ the tools and concepts of many scientific disciplines in their research.

Parasitology today usually does not include virology, bacteriology, and mycology, because these sciences have developed into disciplines in their own right. Exceptions do occur, however, for it is not uncommon for parasitological research to overlap these areas. Medical entomology, too, has branched off as a separate discipline, but it still is 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

Human welfare has suffered mightily through the centuries because of parasites. Fleas and bacteria conspired to destroy one third of the population of Europe 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 in many parts of the world, parasitic diseases in association with nutritional deficiencies are the primary killers of humanity. A recent summary of the worldwide prevalence of selected parasitic diseases shows there are more than enough existing infections for every living person to have one, were they evenly distributed.[4]

Disease category	Number of human infections
All Helminths	3.5 billion
Hookworms	700 million
Schistosomiasis	200 million
Onchocerciasis	40 million
Malaria	25 million

These, of course, are only a few of the many kinds of parasites that infect humans. This points out that parasitic diseases are an important fact of life for many people. The majority of the more serious infections are in the so-called tropic zones of the earth, so most dwellers within the temperate regions are unaware of the magnitude of the problem. For instance, of the approximately 60 million total annual worldwide deaths from all causes, 30 million are children under 5 years. Half of these, 15 million, are attributed to the combination of malnutrition and intestinal infection.[2]

However, the notion held by the average person that we are free of worms in humans in the United States is largely an illusion—an illusion created by the fact that the topic is rarely discussed. It 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 1 million, though this is certainly a gross underestimation if one includes such parasites as pinworms *(Enterobius vermicularis)*. Only occasionally is the situation accurately reflected in the popular press: "If I brought in a jar of some child's roundworms, a great many people would be thoroughly nauseated. It is the sort of thing that is left unsaid, undiscussed and unreported throughout the U.S. A good note to close on! Let's not disturb folks. The thought of that jar upsets refined people. Things should be kept in their place, in the . . . well, let's skip it. Sleep well, good people—only a few million kids are affected."[6]

But 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, hookworms, and other parasites—some of which are communicable—currently live in the United States. It is estimated that there are about 100,000 cases of *Schistosoma mansoni* (see Chapter 17) in the continental United States that originated in Puerto Rico. Servicemen returning from abroad often bring parasite infections with them. In 1971 the Center for Disease Control reported 3,047 cases of malaria in the United States, about three fourths of which were acquired in Vietnam. There are still viable infections of filariasis in ex-servicemen who contracted the disease in the South Pacific 25 years ago! 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. Small wonder, then, that "exotic" diseases confront the general practitioner with more and more frequency. The family physician of one of the authors claims to have treated virtually every major parasitic disease of humans during the years of his practice in Amherst, Massachusetts.

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, as the result of inefficient use of arable land and the inefficient use of food energy. Only 3.4 billion of the 7.8 billion acres of total potentially arable land in the world is now under cultivation.[2] Much of the remaining 4.4 billion acres cannot be developed because of malaria, trypanosomiasis, schistosomiasis, and onchocerciasis. In Africa alone, there is an area of land equal to the size of the United States where people cannot live and grow livestock due to trypanosomes. How many starving people could be fed if this land were cultivated? As many as half of the world's population today is undernourished. The population will double again in 35 years. It is impossible to ignore the potentially devastating effects that worldwide famine will have on all humankind.

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 due to malaria requires approximately 5,000 calories, or an energy demand equivalent to 2 days of hard manual labor. To extrapolate, in a population with a 2,200 caloric average diet 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 7,500 tons of rice per month per million people over and above normal requirements. That is a waste of 25% to 30% of the total energy yield from grain production in many societies.[5]

Another cause of energy loss is malabsorption of digested food. This is a common occurrence in parasitic infections. It is difficult to quantify this loss, but it undoubtedly is highly significant, especially in those who are undernourished to begin with.

People create much 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 developing countries, not more than 10% or 15% of the world population is thus served. Usually an adequate water supply has first priority, with sewage disposal running a poor second. 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.

At first glance it seems incongruous that the nations that suffer the most from disease are also the nations whose populations are undergoing the most rapid growth. The world's population has doubled three times in the past 200 years, and it will double again in the next 35 years, from 3.5 billion to 7 billion. During this time Latin America will add 400 million, and Asia will double its 1.6 billion to 3.2 billion, which together equal the total current world population. The efforts at family planning are beginning to be felt in several countries, especially those where disease is at a minimum. But what can we say to a mother who wants to have seven children so that three can survive? A Johns Hopkins University study on family planning motivation confirms the importance of child survival to the sustained practice and acceptance of family planning.[2] The parasitologists' role then, together with other medical disciplines, is to help achieve a lower death rate. But it is imperative that this be matched with a concurrent lower birth rate. 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. For instance, malaria costs the government of India about $21 million a year in death, treatment, and loss of manpower. It has been estimated that malaria can be eradicated from India within 2 years at a cost of about $14 million. But it is a cheerless prospect to contemplate the effect of a sudden increase in population under current levels of birth rate and standards of nutrition in that 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 of the world. Parasitologists have a unique opportunity to break the deadly cycle by contributing to the global eradication of communicable diseases, while, at the same time, 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 massive deaths, or **epizootics,** because of the normal dispersal and territorialism of most species. But domesticated animals are usually confined to pastures or pens year after year and often in great numbers, so that the parasite eggs, larvae, and cysts become very dense in the soil, and the burden of adult parasites within each host becomes devastating.[1] For example, the protozoans 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.[5] In 1965 the U.S. Department of Agriculture estimated the annual loss in the United States as the result of coccidiosis of poultry alone at about $45 million. Many other examples can be given and some are discussed later in this book. Agriculturists, then, are forced to expend much money and energy in combating the phalanx of parasites that attack their animals. Thanks to the continuing efforts of parasitologists all over 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 on the biochemistry of the organisms continue to suggest modes of action for chemotherapeutic agents.

Less can be done to control parasites of wild animals. While 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. They are unable to stray from these areas because of human pressure. Consequently, lungworms, which probably have always been present in big horn sheep, 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 large game animals in Africa in recent years. These animals are heavily infected with species of *Trypanosoma,* a flagellate protozoan of the blood. The game animals tolerate infection quite 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, their parasites are the indirect cause of their death. It is hoped that this parasitological quandry 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 a minute nematode, *Trichinella spiralis.* This worm exists in a **sylvatic cycle** that involves rodents and carnivores and in an **urban cycle** chiefly among rats and swine. People become infected when they enter either cycle, such as by eating undercooked bear or pork. Another zoonosis is echinococcosis or hydatid disease. Here, humans accidentally become infected with larval tapeworms when they ingest eggs from dog feces. *Toxoplasma,* which is normally a parasite of felines and rodents, is now known to cause many human birth defects.

New zoonoses are being recognized

from time to time. 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 them and refer to them by name in their own work. Thousands of species of parasites of wild animals are still unknown and will occupy the energies of taxonomists for many years to come.

CAREERS IN PARASITOLOGY

It can truly be said that 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's career in parasitology. It is a satisfying career, for one knows that each bit of progress made, however small, contributes to our knowledge of life and to the eventual conquering of disease. As in all scientific endeavor, every major breakthrough depends on many small contributions made, usually independently, by individuals around the world.

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. Certainly 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 and serology, genetics, and systematics. Most parasitologists hold a Ph.D. or other doctoral degree, but significant contributions have been made by persons with a master's or bachelor's degree. Such intense training is understandable, for 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 continue to be active in research for the sheer joy of it. Parasitology does indeed have something for everyone.

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Chapter 2

BASIC PRINCIPLES AND CONCEPTS

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

TALIAFERRO

DEFINITIONS

The science of parasitology is largely a study of **symbiosis,** especially the form known as parasitism. Although some authors, especially in Europe, restrict the term "symbiosis" to relationships wherein both partners benefit, we prefer to use the term in a wider sense, as originally proposed by de Bary in 1879.[6] We consider any interaction between two organisms to be symbiotic, in keeping with the meaning of the word, "living together" as contrasted with "free-living." The relationship may be of long or short duration, and it may benefit one or both **symbionts** or neither. Usually the symbionts are of different species, but not necessarily. The study of all aspects of symbiosis is called **symbiology.**

For the sake of convenience we can subdivide symbiosis into several categories, based on the amount of interdependence of the symbionts. It should be recognized that not all relationships fit obviously into one category or another, for they often overlap each other, and further, the exact relationship cannot be determined in some cases. Not all authors agree on the definitions of these categories, and some subdivide them further. We have selected definitions that seem to us to be concise and meaningful.

Predation. Predation is obviously a short-term relationship in which one symbiont, the **predator,** benefits at the expense of the other symbiont, the **prey.** Two lives have crossed and interacted to the betterment of one and the detriment of the other. The point here is that the predator kills the prey outright and does not subsist on it while it is alive.

Phoresis. Phoresy exists when two symbionts are merely "traveling together." Neither is physiologically dependent on the other. Usually, one **phoront** is smaller than the other and is mechanically carried about by its larger companion (Fig. 2-1). Examples would be bacteria on the legs of a fly or fungous spores on the feet of a beetle.

Mutualism. In this relationship the partners are called **mutuals** because both members benefit from the association. Mutualism is usually obligatory, for in most cases the mutuals have evolved physiological dependence on one another to such a degree that one cannot survive without the other. A good example is the termite and its intestinal protozoan fauna. Termites cannot digest cellulose fibers because they do not secrete the enzyme cellulase. However, a myriad of flagellate protozoa, which dwell within the termite's gut, synthesize cellulase freely and are able to utilize as nutrient the wood eaten by the termites. The termite is nourished by the fermentation products excreted by the protozoa. That the protozoa are necessary to the termite can be shown by defaunating the insects (killing the protozoa by subjecting their hosts to elevated temperature or oxygen tension); the termites then die, even with plenty of choice wood to eat. The protozoa benefit by living in a stable, secure environment, constantly supplied with food, and by being provided with a low oxygen environment, since they are obligate anaerobes. The termite-flagellate association is but the most often cited example of insect-microbe mutualism. A wide variety of insects have bacteria or yeast-like organisms in their gut or other

Fig. 2-1. Barnacles attached to the carapace of a crab. Sponges and coelenterates are attached to both, providing several examples of phoresis. (Photograph by Warren Buss.)

organs, and these are physiologically necessary for the insects in almost all cases studied, apparently furnishing vitamins or other micronutrients. Some insects even have specialized organs (**mycetomes**) where they "keep" their microbes, and the symbionts are passed to the progeny transovarially. Other examples of symbiotic mutualism are the alga and fungus that together form a lichen, and the relationship between a cow and the flora and fauna of its rumen.

One form of mutualism that is not obligatory is usually called **cleaning symbiosis.** In this instance certain animals, called cleaners, remove ectoparasites, injured tissues, fungi, and other organisms from a cooperating host. For example, often one or several cleaners establish cleaning stations at a particular location, and fish to be cleaned visit that station repeatedly to enjoy the services of the cleaners. The fish to be cleaned may remain immobile at the cleaning station while the cleaners graze its external surface and enter its mouth and branchial cavity with impunity. There is some evidence 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.[13] Some terrestrial cleaning associations are known; two examples are the cleaning of a crocodile's mouth by the Egyptian plover and the cleaning of the rhinoceros by tick birds. Some excellent accounts of a wide variety of mutualistic and related associations are found in the volumes edited by Henry[14] and Cheng.[4]

Commensalism. When one symbiont, the **commensal,** benefits from its relationship with the **host,** but the host neither benefits nor is harmed, the condition is known as commensalism. When the commensal is on the surface of its host, it is an **ectocommensal;** when internal, it is an **endocommensal.** The term means "eating at the same table," and most, but certainly not all, examples of commensalism involve the commensal feeding on unwanted or unusable food captured by the host.

Pilot fishes *(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, with which it attaches to large fish, turtles, and even submarines! It gets free rides this way and perhaps some crumbs left over when its host makes its kill, but in no way does it harm the host or rob it of food. In fact, it has now been found that some species of remoras perform important cleaning functions for their hosts, feeding at least partially on the host's parasitic copepods.[8] Thus, remoras, the "classic" commensals, are often mutuals. Depending on the species of echeneid and its degree of specialization, the association may be more or less **facultative,** the remora being able to leave its host at will. Other species are more specialized; for example, *Remoropsis pallida,* at certain stages in its life, lives entirely in the branchial chambers of marlin.

An example of an obligatory commensal is *Entamoeba gingivalis,* an ameba that lives in the mouth of humans. Here it feeds on bacteria, food particles, and dead epithelial cells, but never harms the tissues of its host. It cannot live anywhere else, and in fact has no cyst stage to withstand life outside the buccal cavity; it is transmitted from person to person by direct contact. Other, often cited, examples of commensalism are the clownfish that live among the tentacles of sea anemones (although this association too has its mutualistic aspects—if the clownfish lures other fish into the anemone's waiting tentacles); the pearlfish that hides within the respiratory tree of sea cucumbers and the coelomic cavity of certain starfish; and some of the bacteria that live in the intestines of humans. Humans harbor several species of commensal protozoans, and for this reason parasitologists must be able to distinguish between commensal and parasitic species. It is not always easy to determine whether or not a symbiont is harming its host; tapeworms universally are referred to as parasites, yet in at least some cases they have no known ill effect and might possibly be regarded as commensals.[15]

Parasitism. When a symbiont actually does harm its host, it is then a **parasite.** It may harm its host in any of a number of ways: by mechanical injury, such as boring a hole into it; by eating or digesting and absorbing its tissues; by poisoning the host with toxic metabolic products; 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 **obligatory parasites,** that is, they must spend at least a part of their lives as parasites to survive and complete their life cycles. However, many obligatory parasites have free-living stages outside any host, including some periods of time in the external environment within a protective egg shell or cyst. **Facultative parasites** are not normally parasitic but can become so, at least for a time, when they are accidentally eaten or enter a wound or other body orifice. Two examples of facultative parasitism are "vinegar eels"—small roundworms that normally live in decaying fruit but, when eaten, can become true parasites—and the larva of a latrine fly, *Fannia scalaris,* which can live in the ear canal.

When a parasite enters or attaches to the body of a species of host different than its normal one, it is called an **accidental** or **incidental** parasite. For instance, it is common for nematodes, normally parasitic in insects, to live in the intestines of birds or for a rodent flea to bite a dog or human. Accidental parasites usually are unable to stay long on, or live long in, the wrong host. While there, though, they may add a good deal of confusion to the life of a parasite taxonomist!

Some parasites live their entire adult lives within or on their hosts and may be called **permanent** parasites, while a **temporary** or **intermittent** parasite, such as a mosquito or bedbug, only feeds on the host and then leaves. 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 individual at several discrete times).

Of course, a parasite sometimes kills its host, but it is clearly not a selective advantage, since the parasite's life also is thereby terminated. To produce little pathogenesis is often regarded as one mark of a well-adapted parasite.

Definitions of hosts

Hosts also are placed into different categories. The host in which a parasite reaches sexual maturity and reproduction is termed the **definitive host.** If there is no sexual reproduction in the life of the parasite, such as an ameba or trypanosome, we arbitrarily call the host we believe is most important the definitive host. An **intermediate host** is one in which some development of the parasite occurs but in which it does not reach maturity. Hence, in the case of the malarial organism, *Plasmodium,* the mosquito is the definitive host, and humans or other vertebrates are the intermediate hosts.

When a parasite enters the body of a host and does not undergo any development but continues to stay alive and be infective to a definitive host, the host is called a **paratenic,** or **transport,** host. Paratenic hosts are often useful, or even necessary, for completion of the life cycle of the parasite, for they may bridge an ecological gap between the intermediate and definitive hosts. An owl may be the definitive host of a thorny-headed worm, while an insect is the intermediate host. The parasite might have little chance of being eaten by the owl while in the insect, but when a shrew eats the insect and the larval worm encysts in the shrew's mesentery, it stands a better chance of a happy life in the alimentary tract of the owl. Further, the shrew might accumulate large numbers of larvae before it becomes an owl's dinner, thereby increasing the chances of both sexes of a dioecious parasite sharing a common host.

Some parasites can live and develop normally in only one or two species of host. These exhibit high **host specificity.** Others have low host specificity or something in between. For example, the pork tapeworm, *Taenia solium,* apparently can mature only in humans, so it has absolute host specificity, while the trichina worm, *Trichinella spiralis,* seems to be able to mature in any warm-blooded vertebrate. If an animal *other* than a human is normally infected with a parasite that can also infect humans, we call that animal a **reservoir host,** even if the animal is a normal host of the parasite. It is a reservoir for a zoonotic infection to people. Examples are the rat with the trichina and dogs, cats, and armadillos with the agent of Chagas' disease, *Trypanosoma cruzi.*

Finally, there are many examples of parasites hosting other parasites, a condition known as **hyperparasitism.** Examples include *Plasmodium* in a mosquito, a tapeworm larva in a flea, an ameba within an opalind protozoan, and a monogenetic trematode *(Udonella)* on a copepod parasite of fish.

In nearly all cases of parasitism the host is a different species than the parasite. Exceptions do occur, however, as in the case of the nematode parasite of rats, *Trichosomoides,* where 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, and in the echiurid worm, *Bonellia viridis,* the female of which is free-living. An even stranger relationship has evolved in some species of anglerfish where 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! *Syngamus trachea,* a common hookworm of birds, is known to pierce the body wall and feed on the fluids of other worms of the same species. This might better be called predation, but specimens are found with healed wounds and so were not killed by the attack.

A very obvious example of parasitism within the same species is the **mammalian embryo** and **fetus.** Here we have an organism obtaining its nourishment at the expense of its host, poisoning its host with its metabolic wastes, and physically damaging its host at birth, occasionally even killing it. And for some time after birth, it continues to suck secretions from its mother-host's body, further robbing her of vital calcium, protein, and fat.

The ultimate in intraspecific parasitism would be that of a tumor. Here self (tumor) parasitizes self (host), often very much to the detriment of the host, such as a malignancy, or with only minor inconvenience to the host, such as a wart. The tumor may be stimulated by a virus, but it is still the tumor itself that harms the host.

Modern authors increasingly have realized the utility of de Bary's distinction, but for many people, symbiosis still means mutualism. Nevertheless, symbiosis has evolutionary, morphological, ecological, and physiological implications, whether mutualistic, commensalistic, or parasitic, that a free-living habitus does not.

It must be stressed that definitions are always arbitrary, and when we construct pigeonholes to receive descriptions of situations in the real world, we must not be dismayed to find one or another situation that does not quite fit our assignment. Thus, we may cite symbiotic associations with greater or lesser dependence, of greater or lesser duration, or with some grading over into free-living. Certainly many symbiotic associations cannot be specified with certainty as to what the effects on the hosts are; an apparent case of commensalism may have damaging effects on the host that are subtle, have not been observed, or are only present in certain circumstances. Conversely, a case of assumed parasitism may, on closer inspection, turn out to be commensalism. But definitions are necessary to communication; therefore, we must strive for definitions that are concise, meaningful, and, above all, useful.

EVOLUTION OF PARASITISM

The question of the evolution of parasitism is, as in all speculations regarding evolution, impossible to answer definitely. However, many indirect indications that are impossible to ignore suggest several factors involved in past and continuing adaptations to a parasitic mode of life. Paramount among these is the process of preadaptation, the touchstone of evolutionary philosophy. In a preadapted organism, accumulated mutations and other chance genetic changes give it the potential to live in a different environment. Such potentials may never be realized, but if *by chance* the organism finds itself in an environment for which it is preadapted, it may successfully invade and survive in an entirely new niche.

Such preadaptation may be morphological or physiological and may also allow such organisms to pass from a generalized type of environment to a more specialized one. For example, arthropods of several types may have fed on carrion that was also found and eaten by primitive humans. Any arthropod eaten along with the carrion may well have been digested, but if the colory of pinworm nematodes in its hind gut were preadapted to survive at a higher temperature, they might have then colonized the hind gut or cecum of the human. This isolated population could no longer share the gene pool with its arthropod-dwelling relatives and would thus be free to undergo genetic drift and become different from them. Although the likelihood of such an event happening seems chancy, at best, it has been such a successful process that nearly every species of living organism has several kinds of parasites peculiar to it. The result is more species of parasites than of nonparasites.

Of course, the immense number of parasites today is the result of other processes as well. Once in the relatively stable environment of a host, selective pressure by the environment is decreased. Both beneficial and nonharmful mutations could accumulate in the gene pool, preadapting the species to invade a new host, organ, or tissue successfully should the opportunity arise. It is also conceivable that a parasite could become nonparasitic, but this probably never occurs, because the organism will have become too specialized, and evolution generally does not progress from the more specialized to the more generalized. The parasite could not compete with well-adjusted organisms already occupying external niches.

The probability that two organisms will establish a host-parasite relationship depends largely on ecological and behavioral factors. In order for a prospective parasite to succeed it must come into frequent contact with a potential host. The behavior of both must favor such contact. Ultimately, the distribution of closely related parasites reflects the opportunities available to them when they became parasitic. This can lead to similar species parasitizing phylogenetically unrelated hosts. For instance, the nematode genus *Molineus* has species in primates, insectivores, rodents, and carnivores, the ancestors of which were available to the ancestors of the worms at the time of their radiation.

Undoubtedly, parasitism arose in many different ways at many different times. Ectoparasites may well have evolved from nonparasitic omnivores or predators or from ancestors that sought out body secretions from nearby animals. A hypothetical example of the latter is seen in certain moths of the family Noctuidae in southeast Asia. Some species feed on plant secretions, while others, such as *Calpe thalictri*, can pierce ripe fruit to suck the sweet juices inside.[2] One species, *Lobocraspis goiseifusa*, gathers around the eyes of a large mammal, such as a cow, and sucks tears