THE BIOLOGY OF
ANIMAL PARASITES

PREFACE

Along the course of evolution, many organisms found suitable habitats on land, in streams, ponds, estuaries, and oceans. Still other organisms accidentally entered the bodies or became attached to the exterior of dissimilar organisms and adapted to these environments. The term *free-living* has been used to describe the first group and *symbiotic,* the second group. Many biologists have taken up the study of the free-living species; others, fewer in number, have specialized in the symbiotic or parasitic species. Thus parasitology has come into being. The study of parasites and parasitism, in the broad sense of these terms, seems to have been neglected in many ways, especially when one considers that there are many more parasites than free-living animals. As the following pages indicate, the field is multifold, ranging from the chemical to the organismal to the ecological levels. No student can be well grounded in the principles of biology without being exposed to parasitology—the study of the biology of parasites. The teaching of parasitology belongs in every institution of higher learning devoted to the pursuit of scientific truths.

Although the term *parasitism* is commonly thought by the layman, and even some biologists, to be synonymous with disease, this is not the case. It is true that many parasitic animals do cause disease; however, parasitism in the majority of cases does not lead to disease. Parasitism is a natural way of life among a large number of organisms, and its study remains as one of the most challenging aspects of biology. It is true that in the past those phases of parasitology that deal with human and animal diseases have dominated the scene. Parasitologists have served humanity well, sometimes to the point of self-effacement, and it has been only in the last two or more decades that biologists have aggressively sought to understand through experimentation the basis for the evolution of parasites and the mechanisms involved in parasitism. Our knowledge at present indicates that this aspect of biology represents one of the most fascinating and rewarding avenues of investigation. As the number of biologists interested in the fundamental aspects of parasitology increases, more and more colleges and universities are offering courses in parasitology apart from those applied courses offered in schools of human and veterinary medicine. These developments have demanded teaching aids that do not place their primary emphasis on medical and veterinary parasitology.

The need for a general introductory parasitology textbook directed at courses taught in liberal arts colleges was indicated while I was teaching at the University of Virginia and at Lafayette College. Furthermore, this need has been repeatedly expressed to me by many friends and former associates who are presently teaching courses in parasitology in colleges and universities of this nature.

Because it is felt that students being introduced to parasitology should be well grounded in the basic concepts of this discipline and divorced from the medical, veterinary, and agricultural implications, lengthy discussions concerning clinical symptoms, epidemiology, chemotherapy, and field eradication programs have been omitted. Pathogenesis and pathology, as correlated with host-parasite relationships, have been discussed only briefly. Some may feel that in so doing I have overlooked some important aspects of the field. However, I believe that if parasitology is to continue to contribute to the academic world as a branch of biology, it must be presented as a basic science in the liberal arts colleges and universities, from which future specialists arise. The place for training chemotherapy experts, medical and veterinary diagnosticians, and public health officers does not lie in the liberal arts colleges but in the professional and specialized graduate schools.

The Biology of Animal Parasites is not intended to be a definitive reference book. It is an introductory textbook and guide. However, it is my hope that students and investigators will find the sections devoted to basic taxonomy, morphology, and physiology of assistance while tackling laboratory work. Some may feel that too much detail has been included in certain sections and not enough in others. The choice of material has been deliberate to emphasize the basic biology of parasites. This text emphasizes such fundamentals as taxonomy, chemical composition, morphology, development, life cycles, physiology, and ecology. It is felt that such information serves as the foundation on which more highly specialized questions can later be asked and answered.

From past experience, I know that students enrolled in an introductory course in parasitology have generally had experience with general biology or zoology, vertebrate anatomy, introductory invertebrate zoology, and perhaps some introductory phases of physiology. Hence, this book has been oriented at this level.

I have chosen to consider the parasitic animals from the phylogenetic standpoint—that is, each group of animals is considered in a separate chapter or section. My teaching experience has indicated that this is the most effective method of introducing the material. It is the most efficient from the students' standpoint, and with a book so organized, the teacher can select the particular taxa he wishes to emphasize or assign the reading of chapters on certain groups he intends to omit from his formal lectures.

Much space has been given to the morphology, both gross and microscopic, of the various animals considered. This has been done because I have found such material to be of great assistance to the beginning student in basic laboratory work. Furthermore, this volume can serve as a quick reference for advanced students being introduced to research, since morphology is the basis for almost all phases of investigation at the organismal level.

In considering the physiology of parasites, only certain aspects are included—for example, oxygen requirements, growth requirements, metabolism, effects of parasite on host, and effects of host on parasite. The excellent monographs by von Brand (1952: *The Chemical Physiology of Endoparasitic Animals*) and Rogers (1962: *The Nature of Parasitism*) should be read by those seeking greater depth in the area of chemical parasitology. For those desiring more information on immunity to parasites, the Monograph of Sprent (1963: *Parasitism*) should be consulted.

Finally, a short list of suggested readings is included at the end of each chapter. These recommended selections have been limited to the more readily available books and journals.

I am deeply indebted to several friends and authorities who have very kindly read and criticized sections of this volume during the preparative stages. Their constructive criticisms are greatly appreciated and many changes were made as the result of their advice. Errors that may still remain are totally the responsibility of the author and do not in any way reflect on these individuals.

Appreciation is due Dr. Jesse C. Thompson, Jr., Hampden-Sydney College; Dr. William J. Hargis, Jr., Virginia Institute of Marine Science; Dr. Martin J. Ulmer, Iowa State University; Dr. Arthur W. Jones, University of Tennessee; Dr. Helen Ward, Oak Ridge Institute for Nuclear Studies; Dr. John J. McDermott, Franklin and Marshall College; Dr. Harry L. Halloway, Jr., Roanoke College; Dr. Howard G. Sengbusch, University College at Buffalo, The State University of New York at Buffalo; Dr. Frank J. Etges, University of Cincinnati; Dr. Leslie A. Stauber, Rutgers University; Dr. Dominic L. DeGiusti, Wayne State University; Dr. David Causey, University of Arkansas; Dr. Robert Short, Florida State University; Dr. William D. Lindquist, Michigan State University; Dr. Marvin Meyer, University of Maine; and Dr. Edwin J. Robinson, Macalester College.

Acknowledgments are also due the following individuals who contributed invaluable assistance in checking the generic names included in this volume and for suggesting certain inclusions: Dr. Allen McIntosh and Mrs. M. B. Chitwood, both of the Beltsville Parasitological Laboratory, U. S. Department of Agriculture; Dr. Joseph P. E. Morrison, U. S. National Museum; Dr. J. C. Becquaert, Harvard University; Dr. Robert P. Higgins, Wake Forest College; and Dr. David Erasmus, University of Wales, Great Britain. A special thanks is due Dr. George W. Chu, University of Hawaii, for placing his personal library at my disposal during my stay in Hawaii.

I am also grateful to my wife Barbara Ann and to my colleagues in the Department of Biology, Lafayette College, for their patience and encouragement during the years this book was in preparation. In addition, I wish to acknowledge the hospitality offered me by the Mountain Lake Biological Station, University of Virginia, during the summer of 1963, and the Pacific Biomedical Research Center, University of Hawaii, during the academic year 1963–64, while I was completing the manuscript, and to acknowledge the receipt of an award from the National Science Foundation administered by the University of Virginia. I also wish to acknowledge the invaluable editorial assistance provided by the staff of the W. B. Saunders Company.

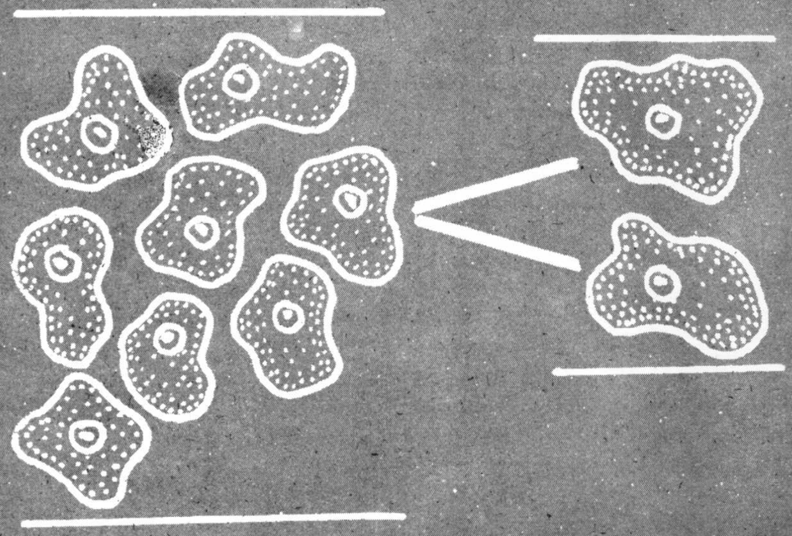
It is the hope of the author that teachers of parasitology will find this volume to be of assistance in initiating the student to the complexities of parasites and parasitism. Suggestions, constructive criticisms, and notices of errors will be greatly appreciated and will be given careful scrutiny.

The views expressed in this book are solely those of the author. They do not represent the official views of the U. S. Public Health Service.

Narragansett, Rhode Island THOMAS C. CHENG

CONTENTS

PART ONE



INTRODUCTION

1

PARASITES AND PARASITISM

Parasitology, the study of parasites and their relationship to their hosts, is one of the most fascinating and rewarding phases of biology. This discipline actually includes several approaches to the study of parasitic organisms. Through the years the field has enjoyed contributions from those who have studied parasites and parasitism from the phylogenetic standpoint, those who have investigated from the ecological aspect, from the morphological, physiological, chemotherapeutic, serological, immunological, and nutritional standpoints, and with advances in our understanding of biochemistry, even from the chemical standpoint.

TERMINOLOGY

The concept of parasitism is often misunderstood because of the complexity of the relationship between the parasite and its host. Any animal or plant that spends a portion or all of its life cycle intimately associated with a different and larger species of animal or plant, during which there is a physiological exchange, is considered a symbiont. The relationship is known as symbiosis. Although three subordinate categories of symbiotic relationships—parasitism, commensalism, and mutualism—are commonly distinguished to facilitate understanding, the lines of demarcation between these categories are often tenuous and almost impossible to define.

Strictly defined, the term *parasitism* is that condition of life normal and necessary for an organism that lives on or in its host (which is of a different and usually larger species) and that nourishes itself at the expense of the host without rapidly destroying it as a predator does its prey, but often inflicting some degree of injury affecting its welfare.

An organism that lives at the expense of its host but does not inflict any harm is known as a *commensal,* and the relationship is known as *commensalism.* A classic example of commensalism is the unique relationship between the pilot fish *Naucrates ductor* and the shark. The pilot fish accompanies the shark in a free-swimming manner, eating the fragments of food that become available as the shark tears apart its prey. Much as a piece of iron is attracted by a magnet, the pilot fish follows the shark, responding instantly to the incessant and irregular directional changes of the larger fish. A similar commensal relationship is that between the remora, *Echeneis remora,* and the shark, but the remora actually attaches itself to the shark by its dorsal fin, which is modified as a sucker.

Like the pilot fish, the remora feeds on "left-overs" and does no harm to the shark.

Another interesting commensal relationship involves a fish of the genus *Trachichthys*, which always remains among the tentacles of the large sea anemone, *Crambactis arabica*, found in the Red Sea area. When another fish comes within reach, it is immediately captured and swallowed by the sea anemone. At that instant, the *Trachichthys* follows the prey into the mouth of the "host" and takes its share of the victim. In this case, it would appear that *Trachichthys* must possess an immunity against the paralyzing poisons of the sea anemone.

Sometimes the commensal has a closer association with the host. The crab *Eumedon convictor* of the Gambier Islands, for example, lives in a large cavity formed by the fold on the back of the apical region of the sea urchin, *Echinothrix turca*. Resting in this nest, the commensal does not have to exert any energy in continuously swimming around the host, yet it is on hand to share the food of the sea urchin and enjoy its protection. A similar relationship exists between *Pocillopora* and another crab, *Hapalocarcinus marsupialis*.

The interesting associations between certain intestinal flagellates and wood-eating termites and roaches have often been cited as typical of the third type of relationship, *mutualism*. Several species of these flagellates, living in the gut of termites, are able to produce cellulases—the enzymes responsible for the digestion of cellulose, which constitutes the major bulk of the termite host's food. The host itself is unable to produce the enzymes and is dependent on the protozoa to digest its food; in return, the host provides the cellulose, which the protozoa also utilize as food. Removal of the flagellates from the host (a process known as defaunation) usually results in the death or severe starvation of the latter. This mutually beneficial relationship is cited as a classic example of mutualism.

Many rumen-dwelling ciliates of herbivores may be said to be engaged in mutualism, because several species of these protozoa produce cellulases and evidence indicates that the protozoa also utilize the cellulose ingested by their hosts. The degree of dependency of the host on these protozoa differs, however, since defaunation of lambs harboring such ciliates does not result in any appreciable change in their metabolism. In fact, the lambs continue to grow normally; thus the presence of the ciliates in their stomachs cannot be considered essential, as is the case of the flagellates found in termites and woodroaches. The ciliates of ruminants, however, do perform the service of cellulose digestion for their hosts and do derive some benefit, and so they are, by definition, engaged in mutualism.

Several types of parasitism are recognized. An organism that does not absolutely depend on the parasitic way of life, but is capable of adapting to it if placed in such a relationship, is known as a *facultative* parasite. If an organism is completely dependent on the host during a segment or all of its life cycle, the relationship becomes markedly physiological, and in such instances the parasite is known as an *obligatory parasite*. If an organism accidentally acquires an unnatural host and survives, it is known as an *incidental parasite*.

An *erratic parasite* is one that wanders into an organ in which it is not usually found; a *periodic* or *sporadic parasite* is one that visits its host intermittently to obtain some benefit; a *pathogenic parasite* is one that is the causative agent of an almost immediate disease in the host.

Parasites that live within the body of their host in such locations as the alimentary tract, liver, lungs, gallbladder, and urinary bladder are known as *endoparasites*. Those attached to the outer surface of their host, or situated subcutaneously, are known as *ectoparasites*.

The *host* is the larger of the two species in the symbiotic relationship. It may be classified as: (1) a *definitive* or *final host*, if the parasite attains sexual maturity in it; (2) an *intermediate host*, if it serves as a temporary environment but is necessary for the completion of the parasite's life cycle (for example, molluscs and arthropods commonly serve as first and second intermediate hosts in which digenetic trematodes complete a part of their development); and (3) a *transfer host*, if it is not necessary for the completion of the parasite's life cycle but is utilized as a temporary refuge until the appropriate definitive host can be reached. Arthropods and other invertebrates that serve as intermediate hosts, as well as carriers for protozoan and other smaller parasites, are referred to as *vectors;* for example, various species of mosquitoes serve as vectors for the protozoan malarial parasites, *Plasmodium* spp. From the evolutionary standpoint, some intermediate hosts may have been definitive hosts at one time. On the other hand, other intermediate hosts may have been transfer hosts.

Animals that become infected and serve as a source from which other animals can be infected are known as *reservoir hosts.*

PARASITISM IN THE ANIMAL KINGDOM

A quick survey of the Animal Kingdom shows that there are parasitic members in practically every major phylum. Among the Protozoa, many species of amoebae, flagellates, ciliates, and all of the Sporozoa are parasitic. It is of interest to note that despite their small sizes, certain protozoa, such as *Stentor* and *Spirostomum,* can serve as hosts for the flagellate *Astasia* sp. Small amoebae are known to parasitize opalinid ciliates and *Trichodina.*

The Mesozoa, which are minute, wormlike, acoelomate organisms, include forms that are common parasites in cephalopods and other marine invertebrates. *Dicyema,* for example, is a common parasite in the nephridia of squids and octopuses. *Rhopalura* is a less common mesozoan parasite encountered in various tissues and body cavities of marine turbellarians, nemerteans, brittle stars, oligochaetes, and clams.

Although parasitic coelenterates are not common, some are known (p. 622).

One of the most popular subdivisions of parasitology is *helminthology,* which deals specifically with the parasitic representatives of the Platyhelminthes, the Nematoda, and the Acanthocephala.* All platyhelminths, except the turbellarians, are parasitic, and even a few cases of parasitism have been reported among turbellarians. Numerous species of nematodes are parasitic, many as parasites of animals and others as parasites of plants. The Acanthocephala are all parasitic.

In addition to these major groups of helminths, the less commonly encountered Nematomorpha, or horsehair worms, are of interest to helminthologists, because the larvae of most species are parasitic in insects although the adults are free-living in aquatic situations.

Some species of the phylum Mollusca, in addition to serving as definitive or as intermediate hosts for protozoan and helminth parasites, may also be ectoparasitic continuously or during some phase of their life cycle (p. 677).

Among the Annelida, the leeches are common ectoparasites on various vertebrates.* It is estimated that 25 per cent of the leech species are parasites, but few of them are totally parasitic. Some are known to serve as vectors for protozoan parasites. The medicinal leech, *Hirudo medicinalis,* which is usually 2 inches long and less than an inch in diameter, will engorge itself with blood until its length increases to 9 inches and its diameter to approximately 2 inches. In China, North Africa, and Israel, horses and men may suffer, even fatally, from loss of blood caused by the ectoparasitic habits of the horse leeches, *Limnatis* or *Haemopis,* which enter the nasal passages and pharynx while the hosts are drinking from pools and streams. Some leeches are known to enter the urinary bladder, where they attach themselves and hang on for days, literally draining the host of its blood. Aquatic leeches are known to serve as vectors for certain species of blood flagellates that belong to the genus *Trypanosoma* and that infect fishes and amphibians.

Among the Polychaeta, *Ichthytomus sanguinarius* and other related species are ectoparasites attached to the fins of eels and fishes. Parasitic forms are few among the Arachiannelida and Oligochaeta, but these annelids represent an important group of intermediate hosts.

The arthropods are represented by many parasitic species. Even more species serve efficiently as definitive hosts for various protozoa and helminth parasites and as intermediate and transfer hosts for both protozoa and helminths. Among members of the class Arachnoidea, the Acarina (ticks and mites), especially the mange mites (Sarcoptidae), soft ticks (Argasidae), hard ticks (Ixodidae), and members of the Dermanyssidae, are of medical and veterinary importance. They act both as ectoparasites and as vectors. The insects are represented by a large number of ectoparasites and intermediate hosts. The mosquitoes and flies (Diptera) are well known as vectors and ectoparasites. The chewing lice (Mallophaga) and sucking lice (Anoplura) are important ectoparasitic pests. Another important group is the fleas, which are both ectoparasites and transmitters of microorganisms.

* *Helminthological Abstracts* includes the literature pertaining to the Hirudinea, reflecting the consensus of those who consider leeches to be helminths.

The importance of the Vertebrata in parasitology needs little elaboration. Vertebrates serve as intermediate, reservoir, transfer, and definitive hosts for practically all forms of parasites. Man and domestic animals harbor numerous species of parasites, many of which are of considerable medical and veterinary importance.

This brief sampling shows that parasitic forms are well represented in the Animal Kingdom, and that many nonparasitic animals are directly or indirectly involved in the "parasitological world" as definitive hosts, vectors, intermediate hosts, and as hosts of accidental infestations.

THE PHYSIOLOGY OF PARASITISM

Of great importance in parasitology is the study of the relationship between the host and the parasite. This intimate relationship invariably involves physiological adaptations, hence investigations of parasite and host physiology have become an integral aspect of the discipline. Questions such as "How do parasites affect their hosts?" and "How do hosts affect their parasites?" are basic in parasitology. It is imperative that those interested in parasitism and parasites should become familiar with the physiology of these animals. Knowledge of the enzymatic activities, the synthesis of food, protective mechanisms, secretions and excretions, composition, respiration, and metabolism of parasites in general is of great importance to our understanding of the parasitic way of life.

Although biologists have been interested in the physiology and chemical composition of parasites since the 1800's, most of our knowledge in this area has come to light during the 1900's, especially in recent years with the advent of new techniques.

Research in such indispensable areas as morphology, taxonomy, development, phylogenetic relationships, chemotherapy, and pathology is still progressing, but in recent years the trend has been to advance our understanding of the physiology of parasites. In 1952 von Brand published a volume on the chemical physiology of endoparasites, and in 1957 he reviewed some of our knowledge of parasite physiology. More recently, Rogers (1962) contributed a stimulating treatise on the physiology of parasites and parasitism. These books, along with the establishment of the journal *Experimental Parasitology,* reflect the upsurge of interest in this area of parasitology.

The reader will find a specific section at the end of each chapter devoted to certain aspects of the physiology and host-parasite relationships as these apply to each phylum.

As Cameron (1956) has pointed out, "No organism is an entity unto itself." All animals live in some form of relationship with surrounding organisms. One might state that all animals are directly or indirectly "parasitic" on plants, and in turn plants are "parasitic" in many ways on animals. This being the case, the traditional separation between free-living and parasitic organisms becomes less justifiable.

The study of the relationship between the host and parasite may be considered an ecological subject. Investigations of ecological relationships reveal that free-living and parasitic organisms do not represent two distinct groups. A gradient occurs between the two extremes. For example, among the platyhelminths, the free-living planarians are capable of synthesizing their own digestive enzymes, and the chemical constituents of their bodies are derived from materials ingested or absorbed from the physical environment. On the other hand, the ectoparasitic monogeneids, also capable of synthesizing their own digestive enzymes, depend mainly on the blood of their hosts (primarily fishes and amphibians) for nutrients. Although most of these chemical building blocks used in their bodies are derived from the blood of the host, this is not the only source, for oxygen and possibly other chemicals can be derived from the aquatic environment. The endoparasitic digenetic trematodes can synthesize their own enzymes, but all the constituents of their body tissues are synthesized from those obtained within their hosts, some even from the hosts' tissues. Finally, the tapeworms are largely dependent on their hosts for the digestion of food, for present information indicates that tapeworms cannot synthesize many of the essential digestive enzymes. Food already digested by the host is absorbed through ultramicroscopic microtriches on the body surfaces of the tapeworm and utilized within their bodies. Thus it is apparent that there is a gradation between free-living planarians and obligatory endoparasitic tapeworms. Quantitative studies of enzymatic activities, source of body chemicals, etc. could lead to quantitative analyses of the dependency of parasites on their hosts. Such information may in time become available and should prove to be exceedingly interesting.

EFFECTS OF PARASITES ON THEIR HOSTS

Since true parasites bring about some change within their hosts that may be interpreted as affecting the hosts' welfare, it is necessary to give some consideration to the types and degrees of changes caused by parasitic animals. With our advancing knowledge of host-parasite relationships, it is increasingly apparent that in many instances it is extremely difficult, if not impossible, to distinguish between a true parasite and a commensal, because the effect of the parasite in some cases may be so minute that it can hardly be considered injurious. However, some classic types of parasite-inflicted effects on hosts can be cited. In classifying the various types of effects, one should remember that in a number of cases multiple effects may be present, and it is often not possible to state that a given parasite causes only one specific type of effect. Furthermore, the types of effects often merge into each other so that sharp lines of demarcation between types cannot always be recognized.

Utilization of Host's Food

Utilization of the host's nutrient to a detrimental point by parasites is probably the first type of damage that comes to one's mind. Although in the past some biologists have doubted the importance of parasites in this regard, since the amount of food a microscopic parasite can utilize seems negligible, more recent physiological studies of nutritional requirements of parasites, especially endoparasitic forms, have indicated that depletion of host's nutrients by parasites may have serious consequences. *Dibothriocephalus latus* in man has been known to cause an anemia similar to pernicious anemia because of the affinity this tapeworm has for vitamin B_{12}. This tapeworm can absorb 10 to 50 times as much B_{12} as other tapeworms. Since B_{12} plays an important role in blood formation, its uptake by *D. latus* causes anemia.

Studies of cestode nutritional requirements show that tapeworms absorb not only simple sugars from their hosts but also nitrogen-containing amino acids, some constituent of yeast in the host's diet, and other nutrient essentials presumably from secretions of the host. It is not only possible but probable in cases of heavy infections that an appreciable amount of such materials is drained from the host, and in instances of undernourished hosts—poor sanitary conditions conducive to parasitic infections often go hand in hand with undernourishment —that this drainage has considerable effect.

Utilization of the Host's Non-nutritional Materials

In some cases parasites also feed on host substances other than nutrients. The endo- and ectoparasites that feed on the host's blood are examples. It is extremely difficult to estimate the amount of blood any organism can rob from its host. Table 1-1 lists some estimated amounts taken in by a few bloodfeeding species. From the data presented, it should be obvious that the blood lost through parasitic infestations can become an appreciable amount over periods of time. Lepage (1958) estimated that 500 human hookworms can remove 250 cc. of blood, or one twenty-fourth of the total volume of blood, each day. This estimate may be too high, for others have estimated that no more than 50 cc. of blood are removed. Nevertheless, the loss of even 50 cc. of blood per day constitutes a serious drainage of blood cells, haemoglobin, and serum.

Destruction of Host's Tissue

Not all parasites are capable of destroying the host's tissues, and even among those that do, the gradation in the degree of damage is large. Some parasites injure the host's tissues when they enter the host, while others inflict tissue damage after they have successfully entered. A combination of these two types of injury may occur. The hookworms, *Necator americanus* and *Ancylostoma duodenale,* exemplify the first instance, for the infective larvae of these nematodes do extensive damage to cells and underlying connective tissue during penetration of the host's skin. The cercariae of certain schistosomes that cause "swimmer's itch" while penetrating the host's skin, cause inflammation and damage the surrounding tissues. Although cercariae-caused dermatitis is extremely irritating, fortunately, as the result of host incompatibility, these worms do not become established in the host's blood. Penetration of the host's skin by schistosome cercariae not only involves slight tissue damage but, more important, involves an allergic reaction.

Various armed (with attachment hooks) helminths, such as the Acanthocephala, certain

Table 1-1. Blood Intake of Certain Bloodfeeding Parasites*

Species of Parasite	Host	Number of Parasites	Amount of Blood Ingested
TICKS			
Ixodes ricinus (larvae)	Sheep	1000	5 cc.
Ixodes ricinus (adult female)	Sheep	1	1 cc.†
LEECHES			
Haemadipsa zeylanica	Man and animals	–	Sufficient in heavy infections to cause anemia.
Limnatus nüotica	Man and animals	–	Sufficient in heavy infections to cause anemia.
NEMATODES			
Ancylostoma caninum	Dogs and man	1	0.5 cc. each day
Ancylostoma duodenale	Man	500	250 cc. each day
Necator americanus	Man	500	250 cc. each day
Haemonchus contortus	Sheep	4000	60 cc. each day

*Tabulated from data collected and presented by G. Lapage (1958) in *Parasitic Animals.*

†Heavily infected sheep may lose 250 cc. of blood per week.

flukes, and tapeworms, often irritate the cells lining the lumen of their host's intestine while they are holding on. In most cases the damage is minute, but repeated irritations over long periods can result in appreciable damage. Furthermore, microscopic lesions resulting from such irritation can become sites for secondary infections by bacteria. The amoebic dysentery-causing protozoan, *Entamoeba histolytica,* actively ingests the epithelial cells lining the host's large intestine, causing large ulcerations that are not only damaging in themselves but that also serve as sites for secondary bacterial infections (Plate 1-1). This same amoeba is known also to cause large ulcers in the host's liver. Partial or total destruction of the hepatopancreatic cells of molluscan intermediate hosts harboring larvae (rediae and sporocysts) of digenetic trematodes is also known (Plate 1-2). Cheng and James (1960) reported one such case, in which the liver of the fresh-water bivalve *Sphaerium striatinum* was completely destroyed through ingestion by the rediae of *Crepidostomum cornutum,* a fluke that as an adult is parasitic in the intestine of various species of bass. In some cases, the molluscan hosts were killed by the severe damage. In addition to direct ingestion, disruption of hepatopancreatic cells caused by the parasites' movements, and cytolysis caused by the parasites' excreta, both contributed to the destruction.

During migration of larvae of the large nematode *Ascaris lumbricoides* within its host, these larvae pass through the lungs of the host. As the result of the migration of a large number of worms, damage sometimes is done to the lung tissue (Plate 1-3).

Ancylostoma duodenale, one of the hookworms, is a good example of a parasite that causes both internal and external tissue damage. The external damage phase has been discussed. Once established within the host's intestine, this roundworm causes considerable damage to the gut wall. It may actually engulf small pieces of tissue, thus producing small lesions.

Histopathological studies of parasite-damaged tissues reveal that cell damage other than removal by ingestion or from mechanical disruption is of three major types: (1) Parenchymatous or albuminous degeneration occurs when the cells become swollen and packed with albuminous or fatty granules, the nuclei become

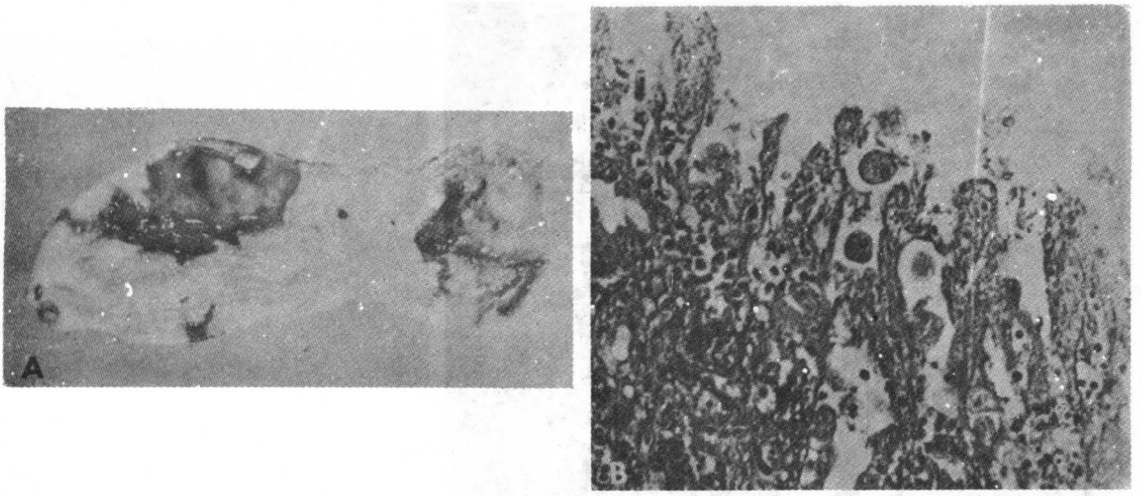


Plate 1-1 Host tissue damage caused by animal parasites. A. Section of colon of kitten experimentally infected with *Entamoeba histolytica* showing lesions of acute amoebiasis. **B.** *E. histolytica* invading gland crypts and interglandular stroma of the superficial mucosa of large intestine of kitten. (A and B after Sister Josephine, M. A., 1958. Am. Jour. Trop. Med. Hyg., *7:* 158–164.)

indistinct, and the cytoplasm appears pale. This type of damage is characteristic of liver, cardiac muscle, and kidney cells. (2) Fatty degeneration describes the condition in which the cells become filled with an abnormal amount of fat deposits that give them a yellowish appearance. Hepatic cells display this type of degeneration when in contact with parasites. (3) Necrosis occurs when any type of cell degeneration persists. The cells finally die, giving the tissue an opaque appearance. In the encystment of *Trichinella spiralis* in striated muscle, necrosis of the surrounding tissues is followed by calcification.

Abnormal Growth

In certain parasitic infections abnormal growth of host tissues, known as hyperplasia (increase in the rate of cell division), results. The presence of the trematode *Fasciola hepatica* in bile ducts is known to effect rapid division of the lining epithelial cells. The presence of the protozoan *Eimeria stiedae* is known to cause hyperplasia of the hepatic cells of the rabbit.

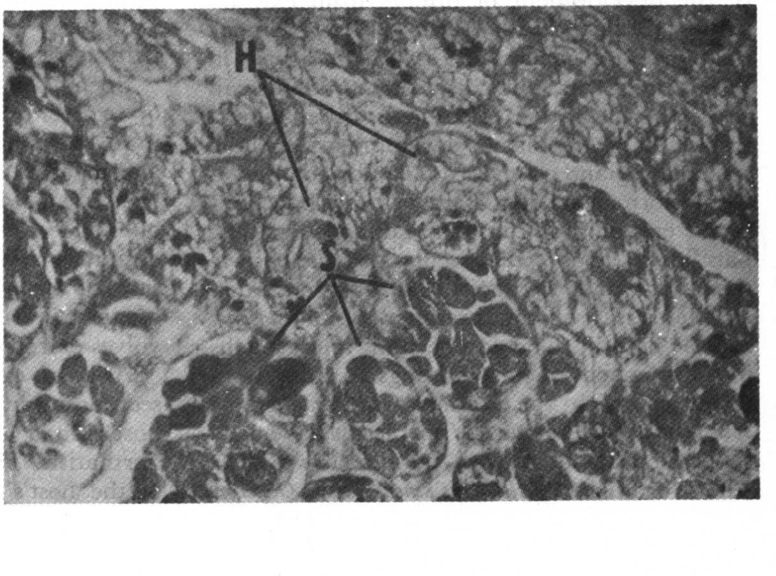


Plate 1-2 Destruction of hepatopancreas of mollusc by larval trematodes. Photomicrograph showing the mechanical invasion by trematode sporocysts of the space normally occupied by the hepatopancreatic tubules of the fresh-water snail *Nitocris dilatatus*.

(H, hepatopancreatic tubules; S, sporocysts.)

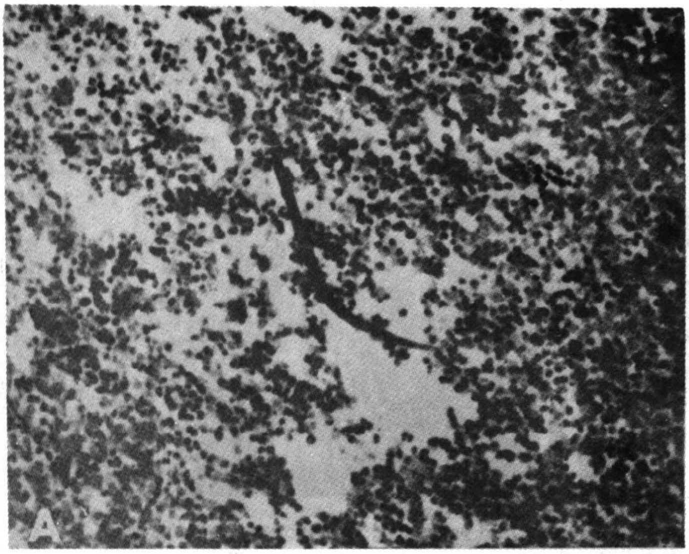
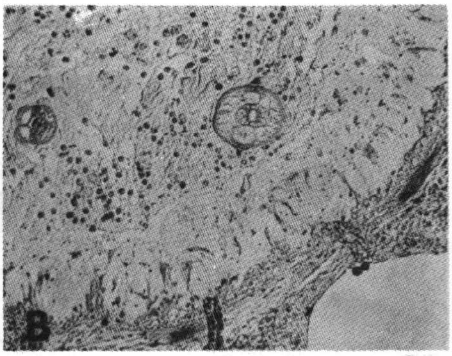



Plate 1-3 **A.** Larva of *Ascaris lumbricoides* during migration through lung of human host. Notice displacement of host cells. (Courtesy of Armed Forces Institute of Pathology, negative No. 80930.) **B.** Photomicrograph of human lung showing bronchiole entirely filled with mucopurulent material containing a larva of *A. lumbricoides* cut transversely through the esophagus and midintestine. (After Beaver and Danaraj, 1958. Photograph loaned by Dr. P. C. Beaver, Tulane University.)

The eggs of *Schistosoma haematobium* with their spinous projections are known to irritate the transitional epithelium of human urinary bladders, causing hyperplasia.

When the lung fluke *Paragonimus westermani* parasitizes man and carnivores, the normal cuboidal cells lining the bronchioles commonly undergo both hyperplasia and metaplasia (the change of one type of cell into another) and are transformed into stratified epithelium.

Hyperplasia resulting from parasitic infections may result in neoplastic reactions—that is, the development of tumors from existing tissues. Bullock and Curtis (1920) demonstrated that cysticerci of *Taenia taeniaeformis* in the livers of rats, mice, and other rodents can cause the formation of tumors. Other known instances of neoplasm development include adenoma (gland cells surrounded by connective tissue) formation from *Eimeria stiedae* infections in the epithelial lining of bile ducts of rabbits; papilloma (a core of vascularized connective tissue surrounded by epithelial cells) formation as the result of the presence of *Schistosoma mansoni* eggs in the colon of man; and growths in the stomachs of cats and dogs resulting from infections with the roundworm *Gnathostoma spinigerum.* True cancerous neoplasms have been reported associated with helminth parasites. The liver flukes *Opisthorchis sinensis* and *O. felineus* have been suspected of initiating cancer in the liver of man; the lung fluke *Paragonimus westermani* has been suspected of contributing to cancer in the lungs of tigers. Siedlecki (1902, 1907) reported that the coccidian parasite *Caryotropha mesnili,* parasitizing the spermatogonial cells of the annelid *Polymnia nebulosa,* brings about hypertrophy of the parasitized cells, involving both the nucleus and the cytoplasm (Plate 1–4). Some of the surrounding cells undergo similar changes and eventually fuse with the infected cell to form a giant multinucleated cell.

Effects of Toxins, Poisons, and Secretions

Specific poisons or toxins, egested, secreted, or excreted by parasites, have been cited in many cases as the cause of irritation and damage to hosts. This phase of parasitology is in need of a great deal of research since toxins are often cited as the causative factors when no definite proof is at hand. Isolation or localization of toxic substances is the only reliable means of verifying their existence, and this involves extremely painstaking procedures.

A good example of an irritating parasite secretion that elicits an allergic reaction in the host is that which causes schistosome cercarial dermatitis. The severe inflammatory reaction of the host's tissue strongly suggests that the

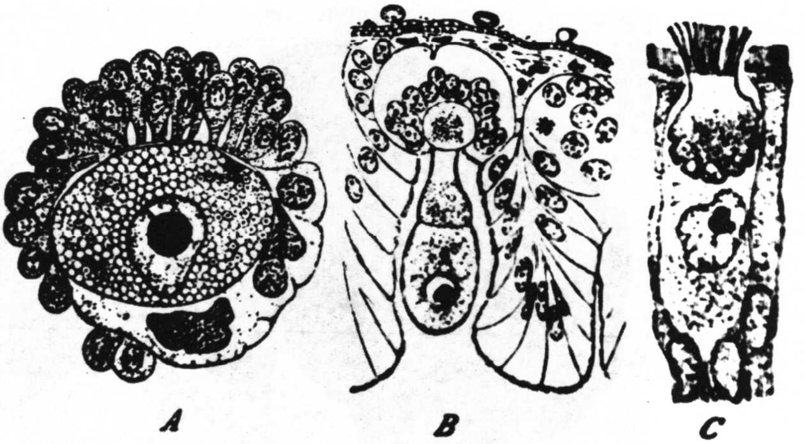


Plate 1-4 **A.** Hypertrophy of spermatogonial cell of the annelid *Polymnia nebulosa* infected with the coccidian *Caryotropha mesnili.* (After Siedlecki, 1902.) **B.** Invasion of intestinal epithelial cells of *Gryllomorpha* by the gregarine *Clepsidrina davini* causing host cells to fuse into a syncytium. (After Léger and Duboscq, 1902.) **C.** Hypertrophy of an intestinal epithelial cell of *Blaps* parasitized by the gregarine *Stylorhynchus longicollis.* Only epimerite of gregarine is visible in this picture. (After Léger and Duboscq, 1902.)

fluke secretes some substance that causes the inflammation, and indeed such a secretion is now known to exist. In the case of bloodsucking insects, such as mosquitoes, the swellings resulting from the bites represent the host's response to the irritating salivary secretions of the insect.

A known parasite toxin is the peri-intestinal or coelomic fluid of the nematode *Parascaris equorum.* The irritability of this fluid to the cornea and to the mucous membranes of the nasopharyngeal cavity is well known. Weinberg and Julian (1911, 1913) collected a quantity of this fluid under aseptic conditions and injected it into guinea pigs. Not surprisingly, they found that 0.5 cu. mm. of this highly toxic fluid kills a guinea pig. Weinberg also placed drops of this fluid in the eyes of horses and found that it generally caused a violent reaction. Some horses, however, were not affected. Further investigation revealed that the unaffected horses were heavily infected with *P. equorum,* thus suggesting that these hosts had developed an immunity against the toxin.

Mechanical Interference

Less is known about injuries to the host resulting from mechanical interferences by parasites. However, the author suspects that they are more common than is generally supposed. Probably the best known case of this type of damage is elephantiasis. In humans infected with the filarial nematode *Wuchereria bancrofti,* the adult worms become lodged in the lymphatic ducts. The continuous increase of the number of worms, coupled with the aggregation of connective tissue in the area of interference, eventually results in complete blockage of the lymph flow, and the excess fluid behind the blockage seeps through the walls of the lymph ducts into the surrounding tissues, causing edema. The frequency of extremes of this condition, known as elephantiasis (Plate 1–5, Fig. 2), is often exaggerated in medical textbooks, which carry photographs of humans with extremely edemic legs and scrotums. Such extreme instances are of many years standing.

Mechanical damage by a nematode is also demonstrated by *Ascaris lumbricoides* in the intestine and bile ducts of their hosts. This intestinal parasite, which measures up to 14 inches in length, when present in large numbers, can easily block the normal flow of bile down the bile duct and the passage of chyme into the intestine.

The sheer occupancy of a large portion of the liver and other organs of man and dogs by hydatid cysts of the tapeworm *Echinococcus granulosus* constitutes another type of mechanical interference (Plate 1–5, Fig. 1). These fluid-filled cysts can attain a diameter of several inches, and one cyst removed from a human in Australia contained 50 quarts of fluid. *Coenurus cerebralis,* the cysticercus larva of the dog tapeworm, *Multiceps multiceps,* is known to exert extreme pressure on the brain and spinal cord of sheep, which serve as intermediate hosts. Infected sheep are said to suffer from *staggers* or *gid* because of the staggering movement resulting from pressure on the brain.

It is known that erythrocytes of chickens infected with the avian malaria organism *Plasmodium gallinaceum* have a tendency to stick together, thus clogging the fine capillaries. Blood vessels dammed up by the infected blood cells often rupture. Those rupturing in the area of the brain permit blood to leak into the brain