Textbook of Parasitology

Third Edition

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Parasitology

Edition

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PREFACE

The third edition of the *Textbook of Parasitology* is intended primarily as a reference text on the parasites of man. It presents the morphology and biological characteristics of the protozoan, helminthic, and arthropod parasites and the diagnosis, treatment, and prevention of the diseases that they produce. It is designed for graduate students in biology, medical students, physicians, medical personnel in the armed services, public health officials, and laboratory workers. In general the same method of presentation used in the earlier editions is followed, but special emphasis is placed on the biological characteristics and life cycles of parasites that are of fundamental significance in the control of parasitic diseases.

The present edition includes the advances in parasitology in the past ten years. New material has been added in the protozoan diseases of amebiasis, trypanosomiasis, leishmaniasis, malaria, and toxoplasmosis and in the helminthic diseases of schistosomiasis, clonorchiasis, paragonimiasis, echinococcosis, diphyllobothriasis, filariasis, enterobiasis, and hookworm infection. Recently described parasites such as *Pneumocystis carinii* and parasitic infections such as visceral larva migrans have been included. Special chapters on molluscan hosts of trematodes, diagnosis of parasitic infections, and treatment of parasitic diseases have been appended.

The practical needs of workers in the field have dictated the arrangement and selection of the subject matter. Special attention has been given to the identification of the parasites, their biological characteristics, life cycles, pathological activities, modes of transmission, and methods of prevention. The problem of selection and condensation of material has been met by featuring the common cosmopolitan parasites, by relegating the uncommon or minor parasites to small type and space, and by grouping closely allied parasites so that their biological and pathological activities may be readily compared. A uniform order of presentation has been followed so that comparable facts for each parasite may be found under the same headings, and the more important parasites have been arranged in tables, graphic representations, and keys that facilitate study and provide ready access to information. For the convenience of students the pathology and symptomatology of the parasitic diseases, wherever possible, have been correlated in tables.

As in previous editions the illustrations, largely diagrammatic or semidiagrammatic drawings to scale, are designed to give independent of the text a representation of the morphology and life cycle of each parasite. New illustrations for the leishmanian and malarial parasites have been added. The diagrams of the life cycles and a few drawings are original, and a number of previously unpublished photographs have been used. The other illustrations have been taken or adapted from various sources. Except where specific credit is given, group drawings

or those labeled schematic representations have been adapted or compiled from so many sources that it is impractical to give citations.

Numerous references to recent biological and medical literature have been provided to meet the needs of students who desire further knowledge in particular fields. These references not only indicate the sources of the information but also make available to interested readers the original presentations, discussions, and divergent opinions of the various investigators, particularly on controversial subjects. Because of the limitations of space the annotated references are from comparatively recent sources, chiefly since 1950, or refer to such older publications as mark important or historical developments. These references, corresponding to numbers in the text, are listed alphabetically at the end of each chapter. For references previous to 1950, some of which are included in the text with merely the name of the author and date, the reader is referred to the second edition of the *Textbook of Clinical Parasitology* or to the *Index Medicus*.

Treatment is briefly outlined under each parasite and is considered in more detail in Chapters 57 and 58. In these chapters a number of proved chemotherapeutic agents and some new drugs are listed, and their use in the various parasitic diseases is described. In Chapters 52 to 56 on diagnosis new procedures have been included to bring the diagnostic methods up to date.

Chapters 52 to 56 on diagnosis and diagnostic methods were written by Alice T. Marston, Ph.D., and Chapters 57 and 58 on the treatment of parasitic diseases were written by Matthew A. Derow, M.D., Ph.D. The preparation of these chapters included both new data and the revision of old material. The author is further indebted to these co-workers for their helpful correction of the manuscript and galley proof on the protozoan parasites. He is especially grateful to Dr. Alice T. Marston for her careful correction of the galley proof for the entire book.

Acknowledgement is due Ellinor Frost Belding, Ph.D., for her helpful editorial assistance and typewriting of the manuscript on the helminthic and arthropod parasites and for her painstaking correction of the galley proof, and to Beulah Merrill, B.A., for preparing the Index of Authors, library research, and typing certain sections of the manuscript. The author is indebted to Miss Florence Turner, librarian of Boston University School of Medicine, and Miss Betty Withrow, librarian of Bowman Gray School of Medicine, for bibliographic assistance. He appreciates the courtesy of Dr. George C. Shattuck in permitting the use of six plates from his *Diseases of the Tropics* and of Drs. Hunter, Frye, and Swartzwelder for two plates from their *Manual of Tropical Diseases*. The author is grateful to the many workers in the field of parasitology, whose original publications have provided the material for this book, and to the publisher for guidance throughout publication.

David L. Belding

CONTENTS

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INTRODUCTION TO PARASITOLOGY

Parasitology is the science which deals with organisms that take up their abode, temporarily or permanently, on or within other living organisms for the purpose of procuring food. In a broad sense parasitology includes plants such as bacteria and fungi; animals such as protozoa, helminths, and arthropods; and borderline forms such as spirochetes and viruses. In the more restricted sense employed in this textbook the term applies only to animal parasites.

The science of parasitology in relation to disease has been developed by zoologists and medical men. While zoologists have studied the morphology, physiology, and life history of the parasite, physicians have concerned themselves with the reaction of the host to the parasite (symptomatology, pathology, and immunity) and with the treatment of the infected host. The combined efforts of medicine and zoology are continually intensifying the importance of parasitology, particularly in the broad field of disease prevention. The medical aspect is concerned primarily with the parasites of man, but a knowledge of the parasites of other animals sheds light upon human parasitology. When information concerning the human forms is incomplete, studies of closely related species in animals foretell with considerable accuracy the probable development of similar species in man. Likewise, the knowledge derived from the study of the structure, life cycle, and activities of similar free-living forms may provide valuable information concerning the less known parasitic species.

History. The large parasitic worms were among the first agents associated with disease.[2] The earliest writings refer to these parasites and to the burden of parasitic diseases in man and animals. Knowledge of these common parasites must extend back into prehistoric times, since it is inconceivable that the large worms and ectoparasitic arthropods of man and animals could have escaped the attention of primitive peoples. The history of parasitology may be arbitrarily divided into five loosely defined periods, under which some of the landmarks and trends are presented here.

Early civilization. The physicians of ancient Egypt were familiar with several parasitic worms and insects and with the diseases characterized by hematuria and anemia. The famous Ebers papyrus (1550 B.C.) contains some of the earliest records of the presence of parasites in man. It describes four worms, evidently *Ascaris lumbricoides*, *Tænia saginata*, *Dracunculus medinensis*, and possibly *Schistosoma hæmatobium*, and furnishes information regarding ectoparasitic fleas, flies, and lice. The highly developed laws of the Mosaic Code concerning animal flesh indicate

that the Israelites had some knowledge of the relationship of helminths to human ailments. The division into clean and unclean animals and the restrictions against eating the flesh of hogs, camels, and hares were undoubtedly based on the presence of bladder worms (cysticerci) and upon the skin diseases of hogs. Possibly the plague of the fiery serpents refers to the Guinea worm. Lice, fleas, flies, and maggots are mentioned in the Bible.

Assyrian and Babylonian writers mentioned hematuria, recognized round and flatworms, connected flies with disease, and recorded scabies and pediculosis. Persian writers recognized ascarids, pinworms, tapeworms, and the Guinea worm; mentioned fleas, bedbugs, flies, lice, and the scabies mite; and noticed the presence of leeches in the nasopharynx. Early Chinese and Indian literature refers to vermifuges, and to ascarids, pinworms, tapeworms, and eyeworms from horses and camels. As early as 500 B.C. leeches were used for medicinal purposes, and lice, fleas, bedbugs, and the scabies mite were known.

The Greek physicians were familiar with the round and flatworms. Aristotle described tapeworms, ascarids, and pinworms, and noted bladder worms in the tongue of hogs. Hippocrates described the diagnosis and removal of the hydatid cyst and referred to pinworms in horses. Theophrastus was the first to prescribe extract of male fern for the treatment of tapeworm infection. Agatharchides, the geographer, gave the first complete description of the Guinea worm in 140 B.C. Later, the Roman writers were familiar with the same worms observed by the Greeks. Galen recognized the hydatid cyst and cysticerci and observed the pinworms of horses. Vegetius mentioned the parascarids and tapeworms of horses. Pliny reported the removal of leeches from the trachea, eyes, and ears of elephants. Herodotus introduced santonin for the treatment of intestinal worms. Both Greek and Roman writers mentioned lice, bedbugs, fleas, ticks, mites, mosquitoes, flies, and maggots. The Greek and Roman physicians and writers were also familiar with the diseases now associated with parasites. Lucretius was the first to call attention to anemia in mine workers, Plutarch observed urinary myiasis, and Galen and Hippocrates identified malaria by the type of fever and enlarged spleen.

700-1600 A.D. There was little advance in parasitology during the medieval period, although there was a great increase in the prevalence of helminth and arthropod parasites due to insanitary conditions and ineffective treatment. Up to 1200 A.D. the important advances in helminthology, including clinical descriptions of urinary schistosomiasis and filarial elephantiasis, were made by Arabic and Persian physicians. Avicenna described the morphology and symptomatology of the beef tapeworm, *Ascaris*, pinworm, and Guinea worm. He also differentiated between anthelmintics and purgatives, and recommended a pretreatment fluid diet and a post-treatment purge. The only important advances in the last half of this period were made by Jean de Brie, who in 1379 discovered the liver fluke, *Fasciola hepatica*, in the bile ducts of sheep and described the associated liver rot; and by Gessner, who recognized human infection with *Cysticercus cellulosæ* in 1558.

Period of helminthic identification and classification (1601-1850 A.D.). During the seventeenth century few advances in parasitology were made. *Diphyllobothrium latum* was described by Plater in 1603, *Cysticercus bovis* by Wepfer in 1675, and the animal nature of hydatid cysts and cysticerci by Redi in 1684.

Sikkartus in 1698 published a treatise on anthelmintics, and Audry in 1700 first assigned pathologic importance to the parasitic worms. Free-living protozoa were recognized by van Leeuwenhoek in 1676, although the compound microscope in its simplest form had been invented in 1609.

In the eighteenth and in the first half of the nineteenth century many species of worms and arthropods were identified, and systems of classification were formulated. Mongin removed *Loa loa* from the human eye in 1770; Pallas discovered *Macracanthorhynchus hirudinaceus* in 1781; Goeze differentiated *Tænia saginata* and *Tænia solium*, recognized the cestode nature of the hydatid cyst, discovered the kidney worm, *Dioctophyme renale*, and made the first accurate description of *Trichuris trichiura* in 1782; Bremser identified *Moniliformis moniliformis* in 1811; Owen described the larval *Trichinella spiralis* in 1835; Dubini discovered the hookworm, *Ancylostoma duodenale*, in 1838; and Busk found *Fasciolopsis buski* in 1843.

Several attempts to classify the parasitic worms were made during this period. Linnaeus in 1771 gave accurate descriptions of the helminthic parasites and a classification of the principal groups. Zeder in 1800 presented the taxonomy of roundworms, flukes, tapeworms, and acanthocephalic worms. Rudolphi in 1808 gave the present scientific names to the phyla NEMATOIDEA and ACANTHOCEPHALA and to the classes CESTOIDEA and TREMATODA, and Lamarck in 1818 placed the leeches in the class HIRUDINACEA, NOW HIRUDINEA.

Period of helminthic life cycles, medical protozoology, and arthropod vectors (1851-1920 A.D.). In this period discoveries of the past were consolidated, new discoveries were made, the life cycles of many important worms were elucidated, knowledge of protozoan parasites was acquired, and the role of arthropod vectors was established. The new discoveries among the worms included: *Schistosoma hæmatobium* by Bilharz in 1851, the microfilaria of *Wuchereria bancrofti* by Demarquay in 1863, the adult *Wuchereria bancrofti* by Bancroft in 1876, *Paragonimus westermani* by Kerbert in 1878, the larval *Diphyllobothrium erinacea* by Manson in 1882; *Acanthocheilonema perstans* by Manson in 1891, *Onchocerca volvulus* by Leuckart in 1893, and *Necator americanus* by Stiles in 1902.

This period was chiefly concerned with investigations of the life cycles of various parasitic worms. Steenstrup in 1842 recognized cercariae as larval flukes and disclosed the alternation of hosts. Küchenmeister in 1851 showed that cysticerci were larval stages of tapeworms. Von Siebold in 1852 established the life history of *Echinococcus granulosus* in cattle and dogs. Leuckart between 1855 and 1884 described the life cycles of *Trichinella spiralis, Tænia saginata, Strongyloides stercoralis,* and *Enterobius vermicularis*. Fedtschenko in about 1870 reported the larval existence of *Dracunculus medinensis* in species of *Cyclops*. Grassi in the years 1878 to 1880 described the free-living generations of *Strongyloides stercoralis* and contributed to our knowledge of the life cycles of *Hymenolepis nana, Dipylidium caninum,* and *Moniliformis moniliformis*. Thomas in 1883 gave a detailed description of the life cycle of *Fasciola hepatica*. Looss between 1898 and 1911 established the cutaneous route of infection and the migration through the host of *Ancylostoma duodenale* and *Strongyloides stercoralis*. Leeper in the years 1915 to 1918 proved that *Schistosoma hæmatobium* and *S. mansoni* required snails as intermediate hosts. Japanese investigators between 1910 and 1920 evolved the life cycles

of *Clonorchis sinensis*, *Paragonimus westermani*, and *Fasciolopsis buski*. Ransom and Hall in 1915 traced the life cycle of *Gongylonema pulchrum* and Janicki and Rosen that of *Diphyllobothrium latum*. Stewart in 1916 and Ransom and Foster in 1917 demonstrated the lung migration of *Ascaris lumbricoides* in the host.

This period marked the rise of medical protozoology and the discovery of a number of pathogenic protozoa. Among the first recognized protozoan parasites were: *Trichomonas vaginalis* by Donné in 1836, *Entamœba gingivalis* by Gros in 1849, *Balantidium coli* by Malstem in 1856, *Giardia lamblia* by Lambl in 1859, and *Trichomonas hominis* by Davaine in 1860. In 1875 Lösch confirmed Lambl's earlier observations of the presence of motile amebae in patients with diarrhea. In 1880 Laveran observed the malarial plasmodia. In 1900 Leishman discovered *Leishmania donovani*, the cause of kala-azar; in 1901 Forde found *Trypanosoma gambiense*, the parasite producing African sleeping sickness; and in 1907 Chagas detected *Trypanosoma cruzi*, the etiologic agent of American trypanosomiasis.

Although certain arthropods had been recognized since early times as ectoparasites, their role as vectors of other parasites and in spreading bacterial, fungal, and viral diseases was not established until Melnikov in 1869 found the larval stages of *Dipylidium caninum* in the dog louse. Manson in 1878 showed that the mosquito *Culex pipiens fatigans* was the insect vector of *Wuchereria bancrofti*, and Smith and Kilborne demonstrated in 1893 that ticks were the transmitting agents of Texas fever in cattle. Ross traced the development of an avian malarial parasite in the mosquito in 1898, and Reed and his co-workers proved the transmission of yellow fever by *Aedes ægypti* in 1900. Subsequently other arthropods were found to be vectors of diseases: the tsetse fly in African sleeping sickness in 1903, the tick in spirochetal relapsing fever in 1905, the reduviid bug in American trypanosomiasis in 1907, and the body louse in epidemic typhus fever in 1909.

Period of preventive and therapeutic parasitology (1921-1961). Studies of the life cycles of parasites paved the way for epidemiologic investigations and the institution of preventive measures involving the destruction of insect vectors, reservoir hosts, and molluscan intermediate hosts. Preventive and therapeutic campaigns of international scope, which have been financed by foundations such as the Rockefeller Foundation or developed under the World Health Organization, have accomplished much in reducing the prevalence of parasitic diseases, particularly malaria, African sleeping sickness, and hookworm disease. Physiologic, biochemical, and pathologic investigations of the parasites have led to advances in therapy and prevention. Effective chemotherapeutic agents have been developed for many diseases and are used in combination with supplementary surgical, dietary, and hygienic therapy. The development of new and potent insecticides has aided the control of vectors.

The early studies in immunity were chiefly directed toward evolving serologic diagnostic tests and elucidating taxonomic relationships. The precipitin test was first used in 1904, the complement-fixation test in 1906, and the cutaneous test in 1911. Improvements in these tests and the development of new tests are constantly being made. Immunization with its attendant problems has occasioned detailed studies in the mechanism of natural and acquired immunity. The interrelationships of nutrition, age, premunition, and residual immunity have been subjects of much investigation.

PARASITES AND PARASITISM

Types of Parasites. In general, **parasitism** includes any reciprocal association in which one species depends upon another, but in its usual medical usage it is an association in which one animal, the host, is injured in some degree through the activities of the other animal, the parasite. This association may be accidental and temporary or fixed and permanent. In **symbiosis** there is a permanent association of two organisms that cannot exist independently, protection or other advantages being provided for one or both; in **mutualism** both symbiotic organisms are benefited; and in **commensalism** one partner is benefited and the other is unaffected, a commensal being an organism living on or within another but not acting as an injurious parasite. The term parasite is ordinarily applied to a weaker organism that obtains food and shelter from another and derives all the benefit from the association. The host may show no noticeable harmful effects or may suffer from a wide range of functional and organic disturbances. There is such a wide range of parasitic types that it is difficult to draw a sharp distinction between a permanent parasite and a temporary resident such as a biting insect.

Various descriptive names denote special types or functions of parasites. An **ectoparasite** lives on the outside and an **endoparasite** within the body of the host. Parasites are termed **facultative** when they are capable of leading both a free and parasitic existence, and **obligate** when they are completely dependent upon the host. An **incidental** parasite is one that establishes itself in a host in which it does not ordinarily live. An **occasional** or **periodic** parasite seeks its host intermittently to obtain nourishment. **Temporary** parasites are free-living during part of their existence, while **permanent** parasites remain on or in the body of the host from early life until maturity, sometimes for their entire life. **Pseudoparasites** are artifacts mistaken for parasites. **Coprozoic** or spurious parasites are species that have passed through the alimentary tract without infecting the host.

Nomenclature. Animal parasites are classified according to the International Code of Zoological Nomenclature. Each parasite belongs to a phylum, class, order, family, genus, and species. At times the further divisions of subclass, suborder, superfamily, subfamily, and subspecies are employed. The names are Latinized, and the scientific designation is uninominal for subgenera and higher groups, binominal for species, and trinominal for subspecies. In this textbook the names of the phyla, classes, and orders of the various parasites follow the listings in the Fourth Edition of Zoological Names.[4]

The law of priority obtains as to the oldest available name, even if only a portion of the parasite or its larva has been described. To be valid a generic name must not have been given already to another genus of animals. The names of genera and species are printed in italics; the generic name begins with a capital, and the specific name with a small letter. The name of the author is written without italics and without punctuation after the name of the parasite. The date follows the author's name separated by a comma, e.g., *Dientamœba fragilis* Jepps and Dobell, 1918. When a species is transferred to another genus or when the specific name is combined with another generic name, the name of the original author is placed in parentheses and the name of the author of the new combination follows the parentheses, e.g., *Ancylostoma duodenale* (Dubini, 1843) Creplin, 1845.

The family name ends in "idæ," the superfamily in "oidea," and the subfamily in "inæ." The terminations of certain divisions are indicated by the following examples:

Division	Example
Phylum	Platyhelminthes
Class	Trematoda
Order	Prosostomata
Suborder	Distomata
Superfamily	Fascioloidea
Family	Fasciolidæ
Genus	*Fasciola*
Species	*Fasciola hepatica*

Classification. Animal parasites may be divided into two main groups, protozoa and metazoa. The former are unicellular organisms. The latter are multicellular animals, the cells of which are differentiated to perform special functions but are dependent upon one another for their existence. The metazoan cell differs in structure and function from the protozoan cell in the absence of differentiation into ectoplasm and endoplasm, in reproduction by mitotic division only, and in the structure of the nucleus.

Animal parasites are legion. They are represented throughout the animal kingdom, and some classes are entirely parasitic, e.g., SPOROZOA, CESTOIDEA, and TREMATODA. The distribution of parasites in 12 phyla of the animal kingdom is indicated in Table 1. The parasitic species are chiefly confined to the PROTOZOA, PLATYHELMINTHES, NEMATOIDEA, ACANTHOCEPHALA, and ARTHROPODA.

Parasites also have been classified from the standpoint of epidemiology. Kozar separates parasites into three classes according to their ability to parasitize man and lower mammals: (1) zooparasites, in which the parasites are highly specific for animals but man is completely insusceptible (absolute), or the parasites may be less highly specific for animals, and man occasionally susceptible (relative); (2) anthropoparasites, in which the parasites are highly specific for man, but animals are completely insusceptible (absolute), or the parasites may be less highly specific for man, and animals occasionally susceptible (relative); and (3) anthropozooparasites, in which the parasites have approximately equal specificity for man and animals.[3] Garnham divides zoonoses of parasites into two groups: (1) enzoonoses, a very limited group in which man is essential for the life cycle of the parasite, e.g., *Tænia solium* and *T. saginata*; and (2) parazoonoses, an important but unstable and changeable group that includes many parasites with which man is only accidentally involved.[1]

Geographic Distribution of Parasites. Several conditions govern the geographic distribution of parasites. Their endemicity depends upon the presence and habits of a suitable host, upon easy escape from the host, and upon environmental conditions favoring survival outside the host. Consequently, diseases due to parasites are most prevalent in the tropics. Parasites with simple life cycles are more likely to have a cosmopolitan distribution than those with complicated life cycles, because of their relative independence of the effects of environmental factors such as temperature and humidity.

Table 1. Distribution of Parasites in the Animal Kingdom

Phylum	Class	Parasitic Species	Human Parasites
Protozoa	Sarcodina	Many	+
	Ciliata	Many	+
	Mastigophora	Many	+
	Sporozoa	All	+
Coelenterata		Few	−
Porifera		Rare	−
Arthropoda	Insecta	Very many	+
	Arachnida	Very many	+
	Crustacea	Many	−
Platyhelminthes	Cestoidea	All	+
	Trematoda	All	+
	Turbellaria	Few	−
Nemertea		Few	−
Nematoidea		Very many	+
Acanthocephala		All	+
Nematomorpha		All (larva)	?
Annelida		Rare	+
Mollusca		Few	−
Chordata		Rare	−

Hosts. The range of a parasite is confined to the habitat of its host. Parasites restricted to a single species of host generally have a more limited range than those that infect several species.

Socio-economic factors. Economic and social conditions affect the distribution of the parasites of man. Customs considered financially profitable may be hygienically unsound. Thus, irrigation projects and the use of night soil in agriculture provide facilities for parasitic infection. Inadequate individual and community sanitation, low standards of living, promiscuous deposition of excreta, overcrowding, and ignorance favor the spread of parasitic diseases. Raw or insufficiently cooked food may be a source of disease, if infected by parasites or contaminated by night soil, polluted water, or infected food handlers. Religious rites such as immersion in heavily contaminated water may be responsible for the transmission of parasites. Migrations of populations have tended to spread parasitic disease throughout the world. The importation of the Negro to the Western Hemisphere was accompanied by hookworm disease and schistosomiasis. Immigrants from the Baltic countries introduced the fish tapeworm into North America.

Climate. Although many important species of parasites have a world-wide distribution, tropical countries, where optimal conditions of temperature and humidity are present, are most favorable for the survival, larval development, and transmission of parasites. The short summer season in the temperate zones prevents the development of many species that require high temperatures during their larval stages, thus establishing zones of distribution according to latitude. Warm tem-

peratures, however, do not always favor the existence of parasites. Intense dry heat or direct sunlight may destroy the larval forms. On the other hand, low temperatures arrest the development of ova and larvae and may even destroy them. Temperature indirectly affects the distribution of parasites by limiting the range of animal hosts. Likewise moisture, which depends upon temperature, latitude, and topography, governs the distribution of parasites. Not only is moisture essential for the development of free-living larvae, but it is also necessary for the propagation of intermediate hosts, such as arthropods, snails, and fishes. Even in the tropics, dry plateaus, because of lack of humidity, are practically free from parasites except resistant species or those that are transferred directly from host to host.

Vital Requirements of Parasites. Free-living animals require protection from enemies and a favorable environment in order to carry on unimpeded the bodily functions of digestion, excretion, respiration, and reproduction. The requirements of parasites do not differ essentially from those of free-living animals, except for modifications necessary for existence in their hosts. Biochemical knowledge of the vital requirements of parasites has increased notably in the last 25 years. Their chemical composition, metabolism, and nutritive requirements are intricately interwoven. Parasites often lack the necessary equipment for digesting or synthesizing raw food material, and deficient enzyme systems usually force the parasite to depend upon the host for predigested food.

Parasites require moisture. An adequate supply is assured within the host, but during the free-living existence of the parasite inadequate moisture will either prove fatal or prevent larval development. Likewise, temperature exerts an important influence upon parasites, some of which are susceptible to slight variations. Each species has an optimal temperature for its development. Higher or lower temperatures often prove detrimental.

Evolution of Parasites. The present relationship between parasite and host has gradually evolved throughout the ages. While no instance of a sudden change from a free-living to a parasitic existence has been recorded, evolution has produced so many gradations of parasitic existence that no sharp line can be drawn between occasional parasites and allied free-living species. In the earliest stages of parasitic existence the host acted simply as a vehicle of transportation. Later the parasite became dependent upon the host for food, and finally it reached the degenerate state of consuming the tissues of the host. Naturally, adaptation of a free-living organism to an endoparasitic existence demands more adjustment than is required for an ectoparasitic existence. Whether endoparasitism evolved directly from ectoparasitism or from commensalism and symbiosis is unknown. In any event, the process has produced far-reaching changes in the parasite and in its life history and has affected the life of its host.

Changes in the parasite. The dependent existence of the parasite has brought about structural changes in both adult and larval forms. Organs no longer necessary have atrophied and others useful for a parasitic existence have developed. The more specialized endoparasites show the greatest changes. The loss of enzyme systems essential for the nutrition of free-living animals, a deficiency supplied by the host, has rendered obligatory a parasitic or at least a symbiotic existence.

Retrogressive Changes. The most marked retrogressive changes are found in the organs of locomotion and alimentation. Although in many instances the