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PARASITES AND PARASITISM

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by

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This book is dedicated to

PATRICK MANSON

who inaugurated modern parasitology,

to

ROBERT THOMSON LEIPER

who rejuvenized helminthology
in the British Empire,

and to all those
who, working under their inspiration,
have provided the information which
has made this work possible

PREFACE

NO ORGANISM is an entity unto itself; it lives as a member of a community and the life processes both of itself and of its neighbours act and interact on each other. This interaction is never of equal intensity in different species, but the more intimate it is, the more it approaches our concept of the phenomenon we call parasitism, even although no scientific definition of parasitism is possible in our present state of knowledge. It is, however, an extremely common phenomenon, and there are probably more parasitic than free-living organisms. Parasitism, however, too often has its real nature clouded by a concept of disease and is regarded subjectively rather than objectively. Accordingly, the discussion in this book attempts to disregard the anthropocentric or economic point of view and to concentrate on the biological phenomenon. Parasites of man and of his domestic animals have received much more intensive study than have other parasites, and because of that they provide better examples, and they are used as such rather than because of any medical or veterinary importance. Because a parasite lives in a living environment, an attempt has been made to show how this reacts to its presence, and how both parasite and host became adapted to each other.

No previous knowledge of parasitology is required, but the reader is assumed to have a working knowledge of biology in general—such as would be expected of an undergraduate planning to enter his final year in a biology major or one reading for a master's degree; the material has in fact been used for such a purpose during the past twenty years in this university. It is not an alternative for books which are specifically written for medical men or veterinary surgeons as it attempts to deal with principles rather than practice.

Like every other branch of biology, parasitology has its roots in morphology and systematics. The present survey has attempted to keep the study of these to minimal dimensions, not because they are unimportant but because of considerations of space. A list of annotated and selected references is appended for those whose interest would go further, and numerous diagrams attempt to replace detailed morphological descriptions.

While etymologically this book might be called 'Symbionts and Symbiosis', these words have different meanings for different writers, and it has seemed preferable to use 'Parasites and Parasitism' instead, not because the terms are more accurate but because they are better known. The words are used, however, in the wide general sense as referring to an organism which is dependent for some essential metabolic factor on another organism which is always larger than itself. The first organism may or may not harm this other organism and pathogenicity is not an essential characteristic, although the word parasite is often used as a synonym for pathogen. Pearse's term of Consor would in some respects be equally accurate, but it is too recent to be familiar to the biologist. Moreover, the original meaning of the word parasite was 'near food' and, used as it was in a social sense, it had no more connexion with pathogenicity or disease than had Symbiont or Consor. In the secondary adaptation of the word to biology it has acquired many subjective meanings, but as used here a parasite is an organism which, for some reason or other, has a compulsory association with some other living organism. A parasite is an organism which has a host.

Conventionally, living organisms have usually been grouped into two kingdoms—the plants and the animals. The plants are organisms which, by means of chlorophyll, are able to synthesize their food from inorganic chemical sources; the animals, having no chlorophyll, have to depend directly or indirectly on plants for the relatively complicated compounds on which they nourished themselves. The discovery of acellular organisms introduced complications into this simple scheme, but, at first, it was not too difficult to allot these organisms to one or another of the two kingdoms. However, as more and more became known, it became increasingly obvious that the continuance of compromise was creating more difficulties than it avoided. Moreover, the concept of acellular rather than unicellular organisms was taking shape and influencing the thinking of biologists. This concept regarded the organism as a single functioning whole which might or might not be divided into cells, each group of which performed a special function. The 'single cell' of which the 'single-celled organism' is composed is quite obviously not the equivalent of a single cell in a higher plant and metazoan animal.

The Theory of Evolution postulates the ultimate relationship of all living organisms. Nature has explored virtually all potential avenues of life and has used most sources of energy and nutrition, with a consequent development of an infinite variety of shapes and forms. It is not to be expected that any classification of living organisms would be simple or clear-cut, no matter on what basis it is constructed.

There is, however, a tendency to create a third kingdom, the Protista (to contain all the acellular organisms, whether or not they showed relationship with plants or animals), which can be distinguished from the Metaphyta, or cellular green plants, and Metazoa, or cellular animals. Within the Protista some organisms have plant characters and utilize chlorophyll as a means of applying the energy of light; others have animal characters utilizing the heat energy obtained from complicated molecules; some have both or neither. The Protista are consequently neither plants nor animals, and their bodies are not cellular. The group may even be monophyletic, and there is no evidence whatever that it is in any way an ancestral group of the higher plants or animals, although there is little doubt that all three had a common origin in proto-organisms which fed on non-living organic or inorganic material.

Accordingly, the parasites here are discussed in three groups—the Protista, or acellular organisms; the lower Metazoa, which includes the Helminths; and the higher Metazoa in which parasitism is exceptional and has originated in many different directions.

INTRODUCTION

ALTHOUGH MANY attempts have been made to formulate an accurate definition of a parasite, none has been really successful. In many cases the definition and its implications have been so completely anthropocentric as to be useless. In others they have been insufficiently comprehensive or insufficiently exclusive. As a matter of fact, our knowledge is still too fragmentary to draw any general picture of a parasite or to write any real definition. However, for our purpose we shall consider a parasite to be an organism which at some stage of its life requires some vital factor which it can obtain only from another living organism. It is true that we seldom know what makes the association compulsory, although in most cases it appears to be a nutritional factor which is deficient in some way and quite possibly this is concerned mainly with the metabolism of nitrogen.

Probably the most accurate concept of parasitism can be obtained by a consideration of how the organism feeds. To do this it is necessary to discuss nutrition and its evolution. Nutrition involves the assimilation of food elements to synthesize cell substance, to provide reserves of material, and to supply the energy required by the organism for the dissimilation or oxidation of certain foodstuffs.

The substance composing the living cell is called bioplasm; we do not know what it is, but when it is killed we call it protoplasm. During life the bioplasm is continually disintegrating mainly as the result of building and rebuilding the body and of being degraded to supply energy: it must be renewed with food from outside. In addition to water and minerals, the tissues of an animal contain fats, carbohydrates, and proteins, and it is these substances which are used up and which ultimately must be replaced. The fats and the carbohydrates are relatively simple substances; the proteins, on the other hand, are extraordinarily complex nitrogenous substances. In spite of the meagreness of our knowledge of these substances, we can be reasonably sure that the proteins of each species of animal differ from those of every other species; it is probable that this is true even for individuals of a species.

No animal can synthesize its proteins from simple inorganic substances as do plants, and so, in feeding, each animal is faced with the problem of absorbing and assimilating chemical substances different from its own which cannot be utilized directly. Accordingly, these substances must be broken down into their component parts and resynthesized into the animal's own specific fats, carbohydrates, and proteins. This is done with the aid of catalytic substances called enzymes.

When an animal, such as a human being or a farm animal, feeds, a series of complex procedures is involved. In outline the food is ingested and disintegrated mechanically. It is then mixed with various enzymes and broken into comparatively simple compounds with comparatively small molecules. These are then absorbed from the intestine by the mucosa, and at least partly resynthesized in the mucosa and liver and transferred by the blood-stream to the various organs where they are used to provide energy by being oxidized, or used to repair and replace the complex organic compounds of which the body is composed. Ultimately, the latter group is broken into relatively simple compounds and passed back to the blood-stream. There, carbon dioxide is taken up by the formed elements and exchanged in the lung for oxygen, while the other residual material is filtered out by the kidneys and discharged to the exterior. The process, therefore, consists of the following main steps:

Ingestion and fragmentation
Digestion
Absorption
Assimilation
Elimination.

While these processes are successive, they also overlap and make their recognition more difficult but more important.

The important part of this outline is to note that the first part of digestion consists of breaking down the proteins into amino-acids or simple peptides, the fats into fatty acids and glycerine, and the carbohydrates into simple sugars. These products are then absorbed by body cells and, by the action of intracellular enzymes, are reconstituted into the specific proteins, fats, and carbohydrates of the body. This second process—absorption and assimilation—is, in principle, found in all animals, whereas the first process is absent from some. The first is digestion, the second, assimilation. Animals which digest and assimilate their foods are called *Holozoic*; those which merely assimilate it are called *Saprozoic*.

A plant lives in an entirely different way from an animal. Its foodstuffs are water, carbon dioxide, and simple salts (although it can use more complicated substances). These are taken up by a marine plant by direct absorption of the dilute solutions over its entire surface. The carbon dioxide and water are combined by light with the aid of chlorophyll to form carbohydrate, and this is combined with the nitrogen salts similarly absorbed to form, first, amino-acids and, finally, proteins. In land plants the processes are similar, but there is a greater specialization of tissues. This method of nutrition, which is typical of all green plants, is called *Holophytic*.

Parasitism involves essentially a mode of nutrition in which the holozoic (or holophytic) type is either eliminated entirely or in part, or is to some extent altered. If it were not, the parasite could revert to a free life at any time; it could not be an obligate parasite. Accordingly, we must regard true parasites as saprozoic (or saprophytic) in their mode of life—at least in part.

No matter how the food is obtained, it has two main functions. The first is the synthesis of specific proteins from amino-acids. The proteins of the living protoplasm are dynamic substances, constantly in a state of flux and constantly being broken down and reformulated and end-products eliminated by the excretory organs of the body.

The second function of food is to supply the energy required by the organism for its various functions, including protein synthesis, and the carbohydrates are the main source of this energy. These are absorbed as monosaccharides and stored mainly as glycogen. Fats can also supply energy, and surplus amino-acids may be metabolized into glycogen and used to supplement the carbohydrates and fats.

The rearrangement of the food molecules into body molecules is called metabolism and is carried out by the aid of catalytic enzymes.[1]

The enzymes themselves appear to be proteins, and actually are of enormous potency, so that very small quantities can often bring about a characteristic change in an infinite amount of substrate. They are organic catalysts and are not themselves used up in the reaction, and consequently they cannot add any energy to the system. Their function is to increase the velocity of the reaction, and consequently their action must be reversible. In many cases the action is a hydrolysis—the production of simpler molecules by the addition of molecules of water (or the reverse), but also in most cases the action is very specific and enzymes will act only on their appropriate substrates. Moreover, they are generally very sensitive to heat, and not only are thermo-labile but have an optimum temperature and often an optimum hydrogen-ion concentration.

Enzymes are often combined with a prosthetic group or co-enzyme which is less complex than the enzyme itself and often has the property of specificity. Co-enzymes include substances such as the B vitamins and are not proteins.

Enzyme systems are also of great importance in accelerating the reactions which supply energy to the organism. As carbon compounds require considerable sources of energy for their synthesis, this energy can be released by their breakdown. That is why the most readily available source of animal energy is carbohydrate.

Energy is released from carbohydrates by molecular rearrangements, and the end-products of a complicated series of reactions are calories, lactic acid, alcohol, or fatty acids. This takes place irrespective of the chemicals surrounding the reactions; that is, anaerobically or aerobically—but under certain circumstances the acids can be oxidized in the presence of oxygen and more calories released; the end-products are then carbon dioxide and water.

In animals, oxidation involves the activation of the hydrogen in the substrate; in plants the oxygen is activated. When molecular oxygen acts as a hydrogen acceptor it produces hydrogen peroxide (which is a tissue poison) which in turn is decomposed into water and oxygen by an enzyme known as catalase (catalase differs from plant peroxidases in that it acts only on H_2O_2 and not on peroxidases in general). However, most of the hydrogen activated in the cell by dehydrogenases is not accepted directly by oxygen, but goes to reduce cytochrome—an iron pigment present in all cells where

[1] Enzyme comes from the Greek and means 'in yeast' and has reference to the oldest known enzyme which causes the leavening of bread by yeast. This process was called fermentation from 'ferfere'—to boil—from the similar phenomenon seen in sugar solutions which led to the production of alcohol and carbon dioxide.

oxidation takes place—and the reduced cytochrome is reoxidized by molecular oxygen by the aid of yet another enzyme—cytochrome oxidase.

Energy obtained in this way is aerobic, but the mere presence of available oxygen does not make a reaction aerobic—suitable enzyme systems must also be present.

There is an increasing body of evidence to suggest that all types of metabolism exist from a purely anaerobic, which is fatal in the presence of oxygen, through an anaerobic which simply is unable to use oxygen even if present, or through an anaerobic which can be also aerobic or micro-aerophilic, to an aerobic one which is fatal in the absence of oxygen. Some degree of anaerobiosis is fairly common, but it is usually relative rather than absolute; that is, some use is made of oxygen if available. It should also be noted that anaerobiosis postulates the ability either to dispose quickly of the metabolic end-products or to develop a tolerance to their presence. Some physiologists regard anaerobic metabolism as normal, oxidation being necessary only to destroy the poisonous end-products of the reaction. From the evolutionary point of view, it is probable that the fundamental life processes were primarily anaerobic, oxidation being secondary because free oxygen only became available after the development of chlorophyll in plants.

Aerobic metabolism is, of course, much more economic in energy than is anaerobic, and consequently more animals can live aerobically on a given quantity of food than anaerobically.

While it is quite possible that the basic alteration in external parasites lies in the specialization in their methods of obtaining food and the need for special foodstuffs, the internal parasites must have the ability either to exist in an atmosphere with a relatively low or very low oxygen tension or to extract oxygen in some special way from their environment. Most internal parasites which have been investigated have proved to be facultative anaerobes or micro-aerophils. Small size, by increasing the ratio of surface to volume, is an important physical characteristic in creatures living in an environment low in oxygen where the gas must enter the animal by diffusion through its body wall or its intestinal tract (from ingested blood, for example). The worm-like shape is an advantage in permitting the further diffusion of gases through the body fluids without the aid of a blood vascular system. These two factors may have had much to do with the development of a cylindrical or ribbon-like form in most internal parasites.

All organisms—other than green plants and some bacteria—require rather complex molecules as food. The simplest way of absorbing this food is through the surface of the body, but as only comparatively small molecules can be obtained in this way, it is necessary for these to be already preformed or for the organism to secrete extracellular enzymes which will reduce their size. These molecules must come either from other organisms which themselves feed in such a manner or from those which feed on green plants. Consequently, many different ways of obtaining food have evolved. We are concerned here only with organisms requiring complex food molecules. Ultimately, all food must come from the plant-like organisms and the simplest type of feeding in other organisms must be that which involves plant food. This in turn involves the presence of enzymes which are capable of breaking down cellulose and releasing the material in the food cell. Very few animals possess such an enzyme system, and so the most simple existing method of obtaining complex food molecules must be found in the cellulose-splitting organisms which, of course, are saprophytic. Probably the next in order of simplicity is the saprophagous one—though it may be older in the evolutionary sequence. Then would come the holozoic animals feeding (with the assistance of cellulose-splitting bacteria) on plant food in the typical herbivorous manner. This is followed by the scavenger who feeds on the dead (but undecomposed) animals or their products or excreta and by the predator who actually destroys the animals on which he feeds.

Predatism implies the immediate killing of the prey. However, there is a simple modified form of internal predatism in which the animal is finally killed but only after a period of time has elapsed. This—sometimes called parasitoidism—is the state of affairs found in many of the insects. The blood-sucking insects show another form of predatism, but in this case the victim is larger than the predator and is not necessarily killed; this can, in consequence, be called micro-predatism. Carried a stage further, this association becomes parasitism.

However, no matter how we define parasitism, it is merely one example, an extremely common one, of the universal law of eat or be eaten. Although we distinguish between predators and parasites, the effect that they have on life as a whole is remarkably similar. Predators feed on the surplus of the species, otherwise, like the parasite, they may destroy their entire food supply and so themselves. Predators are, so to speak, parasitic on the race, whereas parasites are predators on the individual. Both preserve the balance of nature.

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