TERTIARY LEVEL BIOLOGY

Physiology of Parasites

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Preface

THIS BOOK HAS BEEN DEVELOPED FROM A SHORT LECTURE COURSE GIVEN to advanced undergraduate students as part of a general introduction to the subject of parasitology for zoologists.

The book is written for the undergraduate who has no previous experience of parasitology and little background in either biochemistry or physiology. It is not a long book, and students will have to consult some of the more detailed textbooks in parasitology and physiology to gain a full understanding of the topics considered here. My objective in writing this book is to introduce the breadth of parasite physiology, leaving the reader to obtain a depth of knowledge by his own library research.

Each chapter covers a single topic or related topics in physiological parasitology, and the variable length of the chapters reflects the amount of research interest that has been generated over the last few decades. It is to be hoped that by use of this book students will develop an interest in some of the more neglected areas and be stimulated to make good some of the more glaring deficiencies in our current knowledge.

I should like to acknowledge with gratitude the assistance of my colleagues Dr J. Barrett, Dr R. A. Klein, Dr A. W. Pike and Dr R. A. Wilson for reading various chapters, and for their comments. Sincere thanks are due to Bob Duthie for his excellent line drawings and to Alison Wood for typing part of the manuscript. Special thanks go to Eileen for her typing, her encouragement and her patience.

L.H.C.

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CHAPTER ONE

INTRODUCTION

What is a parasite?

THERE ARE MANY DEFINITIONS IN THE LITERATURE THAT DESCRIBE THE intimate associations between animals of different species. Terms like parasitism, commensalism, symbiosis, mutualism, phoresy (and many others) all possess subtle nuances of meaning. There are often arbitrary distinctions between one type of association and another, and it is sometimes difficult to decide on the most appropriate terminology for a particular relationship.

In this book a simplified approach to the problem has been adopted. The term *parasite* is used to refer to those protozoans, platyhelminths, acanthocephalans and nematodes that inhabit, at some time during their life cycle, the body of another larger animal—the host. An outline classification of parasites is given at the back of the book to assist the student with the general comprehension of the text. It should not, however, be regarded as a definitive scheme of classification, and any of the more authoritative texts should be consulted for more detailed information. In general plant parasites have not been included in this book, which examines the relationships between animal parasites and their hosts at the physiological level.

The student should appreciate that the inclusion of the above groups as parasites and the exclusion of the viruses, bacteria, fungi, several minor invertebrate phyla and the arthropods is an expedient rather than an ideal. All these organisms may inhabit tissues of other organisms, and should rightfully be considered together under the term *symbiosis*, which refers simply to the act of living together. The physiological problems of these symbionts are common to all the groups that have adopted this way of life. The limited breadth of the definition of a parasite, as used in this book, is conventional, but for the future we should perhaps consider widening our horizons.

Historical perspective

Physiology, the study of living biological systems, the way they function and the way they adjust to environmental changes, is an ancient branch of the biosciences. By comparison with mammalian physiology, parasite physiology is still in its embryonic stage. During the last three to four decades there has been a gradual increase in the interest shown in this field of research, and, although our knowledge is far from complete, much has been accomplished, and the immediate future promises many exciting developments in the field.

The studies of D. F. Weinland in Germany in the early 1900s are regarded by many as the foundation stone of modern parasite physiology. His investigations of glycogen utilisation, volatile fatty acid production and fermentation in the nematode *Ascaris* provided considerable food for thought for parasitologists over the next two or three decades. During this period, physiologists focussed their attention on a small number of parasitic animals, including *Ascaris*, *Parascaris*, *Fasciola* and *Moniezia* among the metazoans, and termite flagellates, trypanosomatids, trichomonads, rumen ciliates and malaria parasites among the Protozoa.

The prime influence in the development of modern parasite physiology was the Second World War, which exposed huge numbers of individuals to the rigours of life in the tropics, inevitably including the endemic tropical parasites of man. Through the need to develop antiparasite drugs, a knowledge of the biochemistry and physiology of pathogenic parasites became an essential feature of the war effort. Since that time, the subject has become firmly established academically and as an important applied discipline; modern research now utilises both pathogenic and model parasites, and employs the armoury of techniques developed in biochemistry, molecular biology and immunology. There are, nevertheless, areas of parasite physiology that suffer from a notable lack of attention, e.g. neurophysiology, reproductive physiology and excretory physiology. Furthermore, parasitologists have disregarded many of the minor groups of parasites that exist, and have concentrated on those of immediate economic or medical importance. For the interested student, there is much to catch the imagination in the field of parasite physiology and much to be done. The recent contributions of T. Von Brand, E. Bueding, D. Fairbairn, J. F. Mueller, the late C. P. Read, J. D. Smyth and W. Trager, for example, are enormous and should serve as an encouragement to all.

The importance of parasitology to man

Why study parasitology? What is important about increasing our knowledge of parasite physiology?

Parasites inhabit man, his livestock and his crops and they reap an untold harvest of damage. It is estimated that today there are 1000 million sufferers from parasitic diseases. Many of those now infected will die prematurely, countless others will suffer from chronic, painful, debilitating or disfiguring diseases. Parasitic infection of cattle and crops reduces the food resources available for many millions of inhabitants of the Third World. The overall problem is enormous; it demands massive financial backing for research programmes into the control of parasitic diseases and the alleviation of the suffering they cause. First, however, it is necessary for us to increase our fundamental knowledge of the biology of the organisms involved.

Malaria affects 340 million people; in Africa alone, one million children die each year from this parasitic disease of the blood system. Schistosomiasis claims over 200 million sufferers, lymphatic filariasis 250 million, onchocerciasis 20 million. African trypanosomiasis is currently being diagnosed at a rate of 10,000 new cases per annum and a further 35 million people are at risk. New World trypanosomiasis (Chagas' disease) affects 10 million people in Central and South America. Amoebae, hookworms, pinworms, scabies and many other parasites take their toll of human misery. Expensive or ineffective drugs and the development of drug resistance by many parasites exacerbate this massive problem.

From a veterinary standpoint, parasitic infections of livestock dramatically reduce the production of animal protein as a source of food, over much of the globe. African trypanosomiasis of cattle, tick-borne cattle diseases (theileriasis and babesiasis) and the gastrointestinal helminths (fascioliasis, taeniasis and cysticercosis) are major tropical problems, while in the West, nematodes, liver flukes and protozoan parasites (coccidiosis and babesiasis) commonly reduce the production and quality of livestock and cause huge financial losses. On the agricultural front, large scale destruction of crop plants is brought about by infections with plant parasitic nematodes and insect pests.

The essential areas of research are chemotherapy, immunology and *in vitro* culture of parasites, so that their biology may more conveniently be studied in the laboratory. These areas depend upon a fundamental base of physiological knowledge. The World Health Organisation has recently launched a special programme of research and training in tropical parasitology, with these areas of research as stated priorities. The special programme is a long-term, multidisciplinary study of malaria, schistosomiasis, filariasis, trypanosomiasis and leishmaniasis. One aim is to encourage more parasitologists to investigate the biology of these pathogenic parasites. At present, only three out of every twenty working parasitologists are concerned with parasites of medical, veterinary or agricultural importance, and many universities teach only modest courses in parasitology, even to medical students. Some universities teach no parasitology at all.

Considerable advances in our basic knowledge of parasite physiology have been accomplished over the past three decades, yet we seem more frequently to cite what we do not know than what we know. Today's student of parasitology is in a position to rectify this situation tomorrow, and thereby to make a contribution to the improvement of the quality of life of mankind.

CHAPTER TWO

FEEDING AND NUTRITIONAL PHYSIOLOGY

Introduction

THE ECOLOGIST, CHARLES ELTON, ONCE REMARKED THAT PARASITES LIVE off their capital whereas predators live off their interest—thus suggesting that parasites maintain themselves at the expense of their hosts. In reality, there are very few examples where this conclusion is borne out by experimental observation. Parasites, in general, do not eat themselves out of a home.

The nutritional physiology of parasites is a highly complex subject. Parasites inhabit a wide variety of tissues in both invertebrate and vertebrate animals, including the alimentary canal, the blood, the nervous system, various body cavities and organs, such as the liver and the eyes. Many parasites have exceedingly complicated life cycles, involving up to three different hosts, with two or more free-living stages concerned with transmission, i.e. dispersion and infection of the next host. The transmission stages are often non-feeding phases of the life cycle (e.g. miracidia and cercariae) and there are also non-feeding parasitic larvae that are quiescent, resting stages (e.g. metacercariae). With this wide diversity of form and habitat, it becomes increasingly difficult to make general statements concerning the nutrition of parasites.

Most of the information on the nutritional physiology of parasites derives from studies on the helminth parasites that inhabit either the gut or the blood of vertebrates, and from the blood-dwelling protozoan parasites of vertebrates. These parasites inhabit a microenvironment rich in dissolved organic molecules. Rather less is known about the nutrition of parasites that live within the tissues of their host.

An important concept in the nutritional physiology of parasites, and one that we shall explore in this chapter, is the *host-parasite interface* or *interfacial space*. This is the region of contact between the parasite and its host, and is the site at which the molecular transfer of nutrients occurs. In nutritional terms the interface involves both the external surfaces and, if present, the alimentary canal of the parasite: in the majority of the parasitic nematodes the alimentary canal alone forms the nutritional interface.

In vitro culture of parasites

The culture of a parasite *in vitro* requires the parasite to be grown and maintained outside the host, in conditions that emulate its normal surroundings and support its continued development. The culture of parasites serves two main purposes: to provide parasite material for study in the absence of the host; and as a means of investigating the nutritional requirements of a parasite under completely controlled conditions. In fact, only a small number of parasites have been grown in chemically-defined conditions, containing known quantities of each nutrient. More usually, an undefined addition—such as whole serum, liver extract or yeast extract—is required for successful maintenance of the culture. There is an extensive literature on the *in vitro* culture of protozoan parasites, particularly the haemoflagellates, but rather less is known about the culture of helminth parasites.

Much of the data that we shall discuss in this chapter has been obtained from parasites that are maintained in culture, normally for short periods of time. It must be stressed that a cautious interpretation of these data is essential, since we cannot assume that events measured *in vitro* will accurately reflect the processes that take place *in vivo*. The culture of parasites *in vitro* is a powerful tool for parasitologists but, to be of any lasting service, it requires wisdom in its use.

The alimentary canal of helminth parasites

The Monogenea, Digenea and Nematoda possess an alimentary canal, which varies widely from group to group in both form and function. We shall briefly consider the morphology of the gut in these parasites, and at the same time discuss the importance of this system to the nutrition of parasites. There is no gut in the Protozoa, Cestoda or Acanthocephala.

Monogenea

The gut in the Monogenea conforms to the basic pattern of a mouth, pharynx, oesophagus and either a simple or a highly-branched blind-ending caecal system or intestine (figure 2.1). The mouth is anterior,

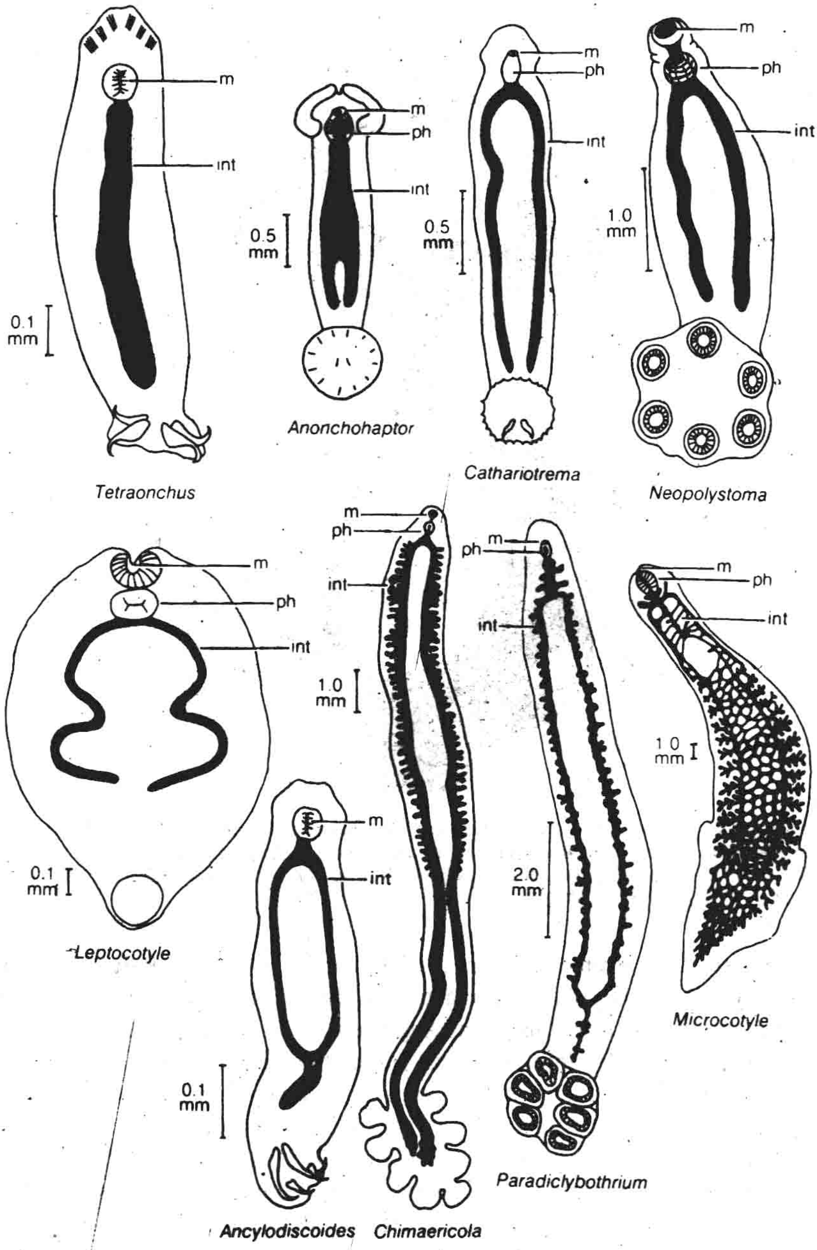

Figure 2.1 The range of form of the monogenean alimentary canal. Based on original drawings by Bychowsky (1957).
m—mouth; ph—pharynx; int—intestinal caeca.

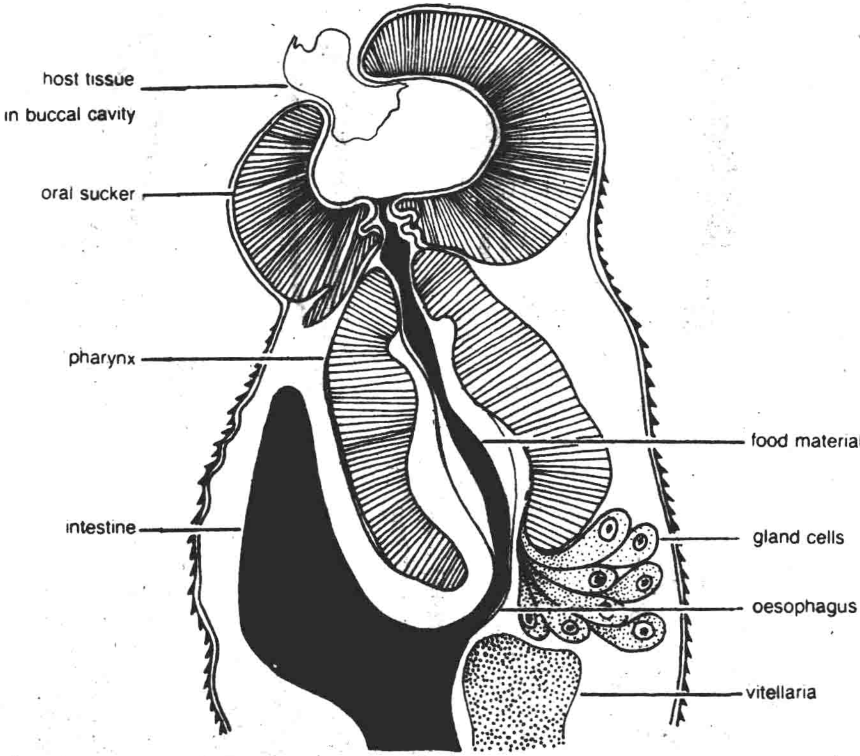

Figure 2.2 Longitudinal section through the anterior of the monogenean *Polystoma integerrimum*, showing the upper alimentary tract and associated glands.
Redrawn from an original photograph by Halton, D. W. and Jennings, J. B. (1965) *Biological Bulletin*, **129**, 257–272.

either at the extreme margin (as in *Microcotyle* and *Polystoma*), or slightly behind the anterior margin on the ventral surface—the latter representing the more usual arrangement. The mouth, which may be simple or elaborated into labia, has associated with it an oral sucker. The buccal cavity leads into the pharynx, a powerful muscular structure composed of three distinct groups of muscle fibres. Glandular structures may be associated with the pharynx (figure 2.2); *Polystoma integerrimum* produces a proteinaceous secretion from its pharyngeal glands, but this species may be unusual among the Polyopisthocotylea in the possession of pharyngeal glands, since other members of the group lack such structures. Within the Monopisthocotylea, some species possess pharyngeal glands while in others the pharynx is wholly muscular. The glandular pharynx of *Entobdella hippoglossi*, for example, reflects the extent to which the pharynx itself is used as an organ of food acquisition by being protruded through the mouth and appended to the surface of the host. In *E. hippoglossi* and *E. soleae*, the secretions from the pharyngeal glands are proteolytic.

The pharynx leads to a short oesophagus, which in some groups (Monocotylidae) is furnished with openings from glands whose function is assumed to be digestive, while in other groups (Microcotylidea and Hexabothriidae) the oesophagus is non-glandular. Little seems to be known about the function of oesophageal glands in the Monogenea.

The intestine extends from the oesophagus to the posterior region of the body and there is normally no anus. The intestine itself varies greatly in form. At its simplest it is a single tube, as in the Tetraonchidae. More usually, however, it is a bifurcated structure. In either case, a substantial degree of secondary branching may occur. According to Bychowsky, the simple form of intestine is characteristic of the smaller monogeneans, while the larger worms tend to possess the more elaborate pattern of intestine, culminating in the extensive anastamoses typical of the large marine monogeneans. Unfortunately, the relationship between the diet and the gross morphology of the monogenean intestine has attracted little attention. Somewhat more information is available, however, on the cellular structure of the gut and its relationship to worm nutrition.

The two orders of the monogenea, the Monopisthocotylea and the Polyopisthocotylea, differ distinctly in their diet. The Monopisthocotylea feed on the epidermal tissues and mucoid secretions of the host, while the Polyopisthocotylea appear to be exclusively blood feeders. This difference is reflected in the cellular construction of the intestinal epithelium, the gastrodermis. (In invertebrates the epithelial lining of the intestine is called the gastrodermis and is analagous to the mucosa of vertebrates.) The tissue and mucus feeders possess a continuous gastrodermis, whereas the sanguinivorous monogeneans are normally characterized by a *discontinuous* or *deciduous* gastrodermis in which the entire epithelium is replaced with every meal ingested—though this is not the case with *Diclidophora*. This condition is also found in some blood feeding Digenea.

There is also a divergence in the digestive processes of the two orders. The Monopisthocotylea digest their food material extracellularly within the lumen of the intestine (or, more rarely, actually outside the body, as in the case of *Entobdella*), while the digestion in the Polyopisthocotylea is both extracellular and intracellular. The digestive