

# PARASITIC PROTOZOA

*Edited by JULIUS P. KREIER.*

## II

*Intestinal Flagellates, Histomonads,  
Trichomonads, Amoeba, Opalinids,  
and Ciliates*

# Parasitic Protozoa

Volume II

*Intestinal Flagellates, Histomonads,  
Trichomonads, Amoeba,  
Opalinids, and Ciliates*

*Edited by*

*Julius P. Kreier*

Department of Microbiology  
College of Biological Sciences  
The Ohio State University  
Columbus, Ohio



ACADEMIC PRESS New York San Francisco London 1978  
A Subsidiary of Harcourt Brace Jovanovich, Publishers

COPYRIGHT © 1978, BY ACADEMIC PRESS, INC.  
ALL RIGHTS RESERVED.  
NO PART OF THIS PUBLICATION MAY BE REPRODUCED OR  
TRANSMITTED IN ANY FORM OR BY ANY MEANS, ELECTRONIC  
OR MECHANICAL, INCLUDING PHOTOCOPY, RECORDING, OR ANY  
INFORMATION STORAGE AND RETRIEVAL SYSTEM, WITHOUT  
PERMISSION IN WRITING FROM THE PUBLISHER.

ACADEMIC PRESS, INC.  
111 Fifth Avenue, New York, New York 10003

*United Kingdom Edition published by*  
ACADEMIC PRESS, INC. (LONDON) LTD.  
24/28 Oval Road, London NW1 7DX

Library of Congress Cataloging in Publication Data

Main entry under title:

Parasitic protozoa.

Includes bibliographies and indexes.

CONTENTS: v. 1. Taxonomy, kinetoplastids, and flagellates of fish. v. 2. Intestinal Flagellates, Histomonads, Trichomonads, Amoeba, Opalinids, and Ciliates. v. 4. Babesia, Theileria, Myxosporida, Microsporida, Bartonellaceae, Anaplasmataceae, Ehrlichia; and Pneumocystis.

1. Protozoa, Pathogenic. 2. Parasites. I. Kreier, Julius P. [DNLM: 1. Protozoa. 2. Protozoan infections. QX50 P223]

QR251.P24 593'.1'04524 76-13941

ISBN 0-12-426002-0 (v. 2)

PRINTED IN THE UNITED STATES OF AMERICA

# List of Contributors

Numbers in parentheses indicate the pages on which the authors' contributions begin.

- Richard A. Albach** (455), Department of Microbiology, University of Health Sciences, The Chicago Medical School, Chicago, Illinois 60612  
**Theodore Booden** (455), Department of Microbiology, University of Health Sciences, The Chicago Medical School, Chicago, Illinois 60612  
**Joe L. Griffin** (507), Division of Experimental Neuropathology, Armed Forces Institute of Pathology, Washington, D.C. 20306  
**Glenn L. Hoffman** (583), U.S. Fish and Wildlife Service, Fish Farming Experimental Station, Stuttgart, Arkansas 72160  
**B. M. Honigberg** (163, 275), Department of Zoology, University of Massachusetts, Amherst, Massachusetts 01003  
**R. E. Hungate** (655), Department of Bacteriology, University of California, Davis, California 95616  
**Jaroslav Kulda** (1), Department of Parasitology, Charles University, Viničná 7, Prague 2, 128 44, Czechoslovakia  
**L. R. McDougald** \* (139), Parasitology Research Department, Lilly Research Laboratories, Eli Lilly and Company, Greenfield, Indiana 46140  
**Eva Nohýnková** † (1), Department of Parasitology, Charles University, Viničná 7, Prague 2, 128 44, Czechoslovakia  
**W. M. Reid** (139), Department of Poultry Science, University of Georgia, Athens, Georgia 30601

\* Present address: Department of Poultry Science, University of Georgia, Athens, Georgia 30601.

† Present address: Instituté of Parasitology, Czechoslovak Academy of Sciences, Flemingovo n.2, Prague 6, 166 32, Czechoslovakia.

- Harry S. Wessenberg*** (551), Department of Biology, San Francisco State University, San Francisco, California 94132
- V. Zaman** (633), Department of Parasitology, Faculty of Medicine, University of Singapore, Sepoy Lines, Singapore 3, Singapore

## Preface

The parasitic protozoa are a large and diverse group. Many are of interest to physicians and veterinarians because they produce disease in man and his livestock. Others, which seldom produce disease, should be familiar to the practitioner of medicine and to the research scientist because they are present in the animal body and thus must be recognized to avoid a misdiagnosis, while still others, such as the intestinal and rumen protozoa, perform a useful function in the animal's economy, and their presence is an indication of health rather than disease.

I have included in these volumes protozoa parasitic in animals, such as fish and insects, which are not usually included in books on pathogenic protozoa. I did this because I believe veterinary medicine should concern itself with all species of animals, excepting man, whose care falls to the physician. From a more practical standpoint, I feel the inclusion of parasites of diverse species is appropriate in a book on protozoa of veterinary and medical interest because no matter how we set ourselves off from nature we remain a part of it, and thus we inevitably share parasites with the other species with which we live.

Because of the wide range of parasites and the volume of material available, no single author could hope to be qualified to write on all of them, thus I have chosen to have each chapter written by someone qualified in that area. This course of action, while it avoids the problems of the limitations of a single author, has problems of its own, the most serious being the variability in the author's styles and attitudes which produces unevenness in the treatment of the contributions. For this I accept responsibility as editor. For all that is good and useful in these volumes I thank the authors of the chapters and the staff of Academic Press who have aided in the production of these volumes. I also wish to thank the Army Malaria Project, whose support of my research has made it possible for me to continue my interest in protozoology.

Julius P. Kreier

# Contents of Other Volumes

## VOLUME I

Broad Classification: The Kingdoms and the Protozoans

*R. H. Whittaker*

Systematics of Parasitic Protozoa

*J. R. Baker*

Leishmania

*Avivah Zuckerman and Ralph Lainson*

*Trypanosoma (Schizotrypanum) cruzi*

*Earl H. Fife, Jr.*

Trypanosomes Causing Disease in Man in Africa

*P. de Raadt and John R. Seed*

Trypanosomes Producing Disease in Livestock in Africa

*Marian A. Soltys and Patrick T. K. Woo*

Salivarian Trypanosomes Producing Disease in Livestock

Outside of Sub-Saharan Africa

*Patrick T. K. Woo*

Nonpathogenic Trypanosomes of Mammals

*John M. Mansfield*

Trypanosomiasis of Man and Macaques in South Asia

*David Weinman*

Flagellate Parasites of Fish

*C. Dale Becker*

VOLUME III

Gregarines and Haemogregarines

*Reginald D. Manwell*

Avian Coccidia

*M. D. Ruff and W. M. Reid*

Coccidia of Mammals except Man

*Kenneth S. Todd, Jr., and John V. Ernst*

*Toxoplasma, Hammondia, Besnoitia, Sarcocystis, and  
Other Tissue Cyst-Forming Coccidia  
of Man and Animals*

*J. P. Dubey*

On Species of *Leucocytozoon, Haemoproteus,*  
*and Hepatocystis*

*A. Murray Fallis and Sherwin S. Desser*

Plasmodia of Reptiles

*Stephen C. Ayala*

Plasmodia of Birds

*Thomas M. Seed and Reginald D. Manwell*

Plasmodia of Rodents

*Richard Carter and Carter L. Diggs*

Plasmodia of Nonhuman Primates

*William E. Collins and Masamichi Aikawa*

Plasmodia of Man

*Karl H. Rieckmann and Paul H. Silverman*

**VOLUME IV**

Babesia of Domestic Animals

*D. F. Mahoney*

Babesia in Man and Wild and Laboratory-

Adapted Mammals

*Miodrag Ristic and George E. Lewis, Jr.*

*Theileria*

*S. F. Barnett*

Myxosporida

*Lawrence G. Mitchell*

Microsporidia

*Elizabeth U. Canning*

*Bartonella and Grahamella*

*David Weinman and Julius P. Kreier*

Bovine Anaplasmosis

*Miodrag Ristic*

*Aegyptianella, Eperythrozoon, and Haemobartonella*

*R. Gothe and J. P. Kreier*

Ehrlichiae

*Ronald D. Smith and Miodrag Ristic*

Pneumocystis

*Thomas M. Seed and Masamichi Aikawa*

# Contents

List of Contributors	ix
Preface	xii
Contents of Other Volumes	xiii
1. Flagellates of the Human Intestine and of Intestines of Other Species	
<i>Jaroslav Kulda and Eva Nohýnková</i>	
I. Introduction	2
II. Terminology	6
III. Retortamonadidae	8
IV. Enteromonadidae	26
V. Hexamitidae	36
VI. <i>Giardia</i> and Giardiasis	69
VII. Polymastigidae	104
VIII. Cochlosomidae	113
IX. Proteromonadidae	118
REFERENCES	127
2. <i>Histomonas meleagridis</i> and Relatives	
<i>L. R. McDougald and W. M. Reid</i>	
I. Introduction	140
II. Morphology	140
III. Taxonomic Position	142
IV. Biochemical and Antigenic Studies	143
V. Cultivation	143
VI. Host-Parasite Interactions	145
VII. Pathology	148
VIII. Epizootiology	153
IX. Diagnosis	156
X. Treatment	157
REFERENCES	159

### 3. Trichomonads of Veterinary Importance

<i>B. M. Honigberg</i>	
I. Introduction	164
II. <i>Trichomonas gallinae</i> (Rivolta)	165
III. <i>Tetratrichomonas gallinarum</i> (Martin and Robertson)	200
IV. <i>Tririchomonas foetus</i> (Riedmüller)	207
V. <i>Tririchomonas suis</i> (Gruby and Delafond)	242
VI. Lesser Trichomonads of Importance to Veterinarians	249
VII. Trichomonads from Laboratory Rodents	257
REFERENCES	258

### 4. Trichomonads of Importance in Human Medicine

<i>B. M. Honigberg</i>	
I. Introduction	276
II. <i>Trichomonas vaginalis</i> Donné	276
III. <i>Trichomonas tenax</i> (O. F. Müller)	392
IV. <i>Pentatrichomonas hominis</i> (Davaine)	406
V. <i>Trichomitus fecalis</i> (Cleveland)	421
REFERENCES	424

### 5. Amoebae

<i>Richard A. Albach and Theodore Booden</i>	
I. <i>Entamoeba histolytica</i> Schaudinn, 1903	455
II. Amoebae Other than <i>Entamoeba histolytica</i>	488
REFERENCES	497

### 6. Pathogenic Free-Living Amoebae

<i>Joe L. Griffin</i>	
I. Introduction	508
II. Life Cycles and Morphology	509
III. Taxonomic Position and Nomenclature	511
IV. Metabolic and Physiologic Characteristics	517
V. Cultivation	521
VI. Host-Pathogen Interactions	524
VII. Epidemiology and Environmental Factors	536
VIII. Diagnosis	540
IX. Treatment	541
X. Reviews and General Comments	542
REFERENCES	544

### 7. Opalinata

<i>Harry S. Wessenberg</i>	
I. Introduction	552
II. Morphology of the Trophont	555
III. Feeding and Digestion	561

IV. Mitosis	563
V. Binary Fission	564
VI. Life Cycle	567
VII. Taxonomic Position	571
VIII. Cultivation	576
IX. Geographic Distribution	576
X. Parasites and Predators of Opalines	577
REFERENCES	573
 8. Ciliates of Freshwater Fishes	
<i>Glenn L. Hoffman</i>	
I. Introduction	584
II. <i>Ichthyophthirius multifiliis</i>	584
III. <i>Chilodonella cyprini</i> (Syn. <i>Chilodon cyprini</i> )	588
IV. Sessile Peritrichs	590
V. Mobile Peritrichs	594
VI. <i>Trichophyra piscium</i>	597
VII. Facultative Parasitic Ciliates	599
VIII. <i>Hemiphrys</i> spp.	603
REFERENCES	629
 9. <i>Balantidium coli</i>	
<i>V. Zaman</i>	
I. Introduction	633
II. Morphology and Life Cycle	634
III. Taxonomic Position	641
IV. Metabolic, Biochemical, and Antigenic Characteristics	643
V. Cultivation	645
VI. Host-Parasite Interaction	646
VII. Disease Produced	647
VIII. Epidemiology	649
IX. Therapy	650
REFERENCES	650
 10. The Rumen Protozoa	
<i>R. E. Hungate</i>	
I. Introduction	655
II. The Rumen Flagellates and the More Primitive Rumen Ciliates	656
III. The More Complex Ciliates: The Entodiniomorphs	658
IV. The Nutrition and Metabolism of the Rumen Ciliates	684
V. Cultivation	687
VI. Significance of the Protozoa to the Ruminant	689
VII. Defaunation	690
REFERENCES	691
Index	697

# Flagellates of the Human Intestine and of Intestines of Other Species

*Jaroslav Kulda and Eva Nohýnková*

I.	Introduction .....	2
II.	Terminology .....	6
	A. Types of Fibrillar Structures .....	6
	B. Specific Structures and Organelles .....	7
III.	Retortamonadidae .....	8
	A. Introduction .....	8
	B. Morphology and Life Cycle .....	8
	C. Taxonomic Position .....	21
	D. Cultivation .....	22
	E. Host-Parasite Relationships .....	23
	F. Epidemiology and Epizootiology .....	25
	G. Diagnosis .....	26
	H. Treatment .....	26
IV.	Enteromonadidae .....	26
	A. Introduction .....	26
	B. Morphology and Life Cycle .....	27
	C. Taxonomic Position .....	34
	D. Cultivation .....	35
	E. Host-Parasite Relationships .....	36
	F. Diagnosis .....	36
V.	Hexamitidae .....	36
	A. Introduction .....	36
	B. Morphology and Life Cycle .....	38
	C. Taxonomic Position .....	58
	D. Cultivation .....	62
	E. Host-Parasite Interactions .....	62
	F. Epizootiology .....	66
	G. Diagnosis .....	68
	H. Treatment .....	68
VI.	<i>Giardia</i> and Giardiasis .....	69
	A. Introduction .....	69
	B. Morphology and Life Cycle .....	69
	C. Taxonomic Position .....	86

D.	Cultivation of <i>Giardia</i> .....	90
E.	Host-Parasite Interactions .....	95
F.	Epidemiology and Control of Giardiasis .....	100
G.	Diagnosis .....	102
H.	Treatment .....	103
VII.	<b>Polymastigidae</b> .....	104
A.	Introduction .....	105
B.	Morphology and Life Cycle .....	106
C.	Taxonomic Position .....	112
D.	Cultivation .....	112
E.	Host-Parasite Relationships .....	113
F.	Diagnosis .....	113
VIII.	<b>Cochlosomidae</b> .....	113
A.	Introduction .....	113
B.	Morphology and Life Cycle .....	114
C.	Taxonomic Position .....	116
D.	Host-Parasite Relationships .....	117
E.	Diagnosis .....	118
IX.	<b>Proteromonadidae</b> .....	118
A.	Introduction .....	118
B.	Morphology and Life Cycle .....	119
C.	Taxonomic Position .....	126
D.	Cultivation .....	126
E.	Host-Parasite Relationships .....	127
F.	Diagnosis .....	127
	References .....	127

## I. Introduction

Flagellates inhabiting the intestines of man and other animals are a heterogenous assemblage of organisms belonging to several orders of Zoomastigophorea. Retortamonadida, Diplomonadida, Oxymonadida, Proteromonadida and Cochlosomidae, a family of uncertain taxonomic position, are considered in this chapter. Families, genera, and important species are surveyed in Table I. Many of the intestinal flagellates belong to the order Trichomonadida and are discussed separately in Chapters 2, 3, and 4.

United in their ability to live and multiply anaerobically, intestinal flagellates differ in morphology, subcellular organization, and behavior. In the trophozoite stage all of them are equipped with flagella, fibrillar cytoskeletal components, nuclei, endoplasmic reticulum, and digestive vacuoles. Mitochondria and Golgi apparatus are absent in Retortamonadida, Diplomonadida, and Oxymonadida but are present in Proteromonadida. Their life cycles are simple and no sexual phenomena

have been observed. Trophozoites multiply typically by binary fission. In certain groups the multiplicative trophozoite stage alternates with a resting stage—the *cyst*. The cyst is enveloped by a resistant wall which is functional in transmission of the organism and its survival under unfavorable conditions.

Food is ingested by phagocytosis and pinocytosis, occurring either randomly over the protozoan surface or in specialized organelles called *cystostomes*. All intestinal "flagellates seem to depend on associated flora for both nutrition and adjustment of proper physicochemical conditions. Virtually nothing is known of their metabolism, since they are rarely obtained in a condition suitable for biochemical experiments. Very few can be maintained in culture, and those which can be are usually maintained under agnotobiotic or poorly defined conditions.

A few species are pathogenic; all pathogenic species belong to the single order Diplomonadida. Pathogenicity was also ascribed to many other flagellates, whose abundant occurrence had been found coincident with disease. However, such reports are of little significance, since convincing experimental evidence is lacking. An increase in the protozoan population is often secondary to a pathological condition of another etiology, indicating merely that the intestinal biocenosis is out of balance. Perhaps some otherwise nonpathogenic flagellates may cause symptoms at the first encounter with an unusual but susceptible host until a host-parasite equilibrium is reached. Thus the great majority of flagellates are harmless commensals. However, even these deserve consideration both from the diagnostic standpoint and for their role as constituents of a normal intestinal biocenosis.

Intestinal flagellates are acquired by the host through contaminated food and water. The host is infected either by trophozoites or cysts or both, depending on the species of parasite. Establishment of an infection is influenced by the host's diet. In mammals, a carbohydrate diet is more favorable for the intestinal flagellates than a "carnivorous" one (Hegner, 1924; Tsuchiya, 1932; Schneider, 1961b). This apparently is an indirect effect resulting from changes in the intestinal flora induced by the diet. Populations of intestinal bacteria probably are the most important factor determining the growth and reproduction of intestinal flagellates in the host (Peterson, 1960).

In a manner similar to that of other intestinal parasites, flagellates show preference for particular regions of the intestine. Most species reside in "calm corners" of the digestive tract rich in intestinal flora, where digestive processes do not take place, or at least proceed gently, namely, in the cecum of mammals and birds and the cloacal ampulla of amphibians and reptiles. A few species prefer the upper parts of the small intestine

Table I  
Survey of the Intestinal Flagellates of Vertebrates <sup>a</sup>

Taxonomic group	Genus	Hosts of the genus	Species parasitic to man	Pathogenic species	Affected host
Retortamonadidae	<i>Retortamonas</i>	Man, monkeys, cattle, sheep, rabbit, rodents, amphibians, reptiles	<i>R. intestinalis</i>	(?) <i>C. mesnili</i> (?) <i>C. gallinarum</i>	Man Quail
	<i>Chilomastix</i>	Man, monkeys, pig, horse, rabbit, rodents, poultry, amphibians, reptiles, fish	<i>C. mesnili</i>		
Diplomonadida					
Enteromonadina	<i>Enteromonas</i>	Man, monkeys, pig, rabbit, rodents, opossum, amphibians	<i>E. hominis</i>		
Enteromonadidae fam. nov.	<i>Trinitius</i>	Amphibians, reptiles, fish			
	<i>Gaviomonas</i>	Guinea pig			
Diplomonadina					
Hexamitidae	<i>Hexamita</i>	Monkeys, rodents, amphibians, reptiles, fish	<i>H. salminis</i> <i>H. parva</i> ( <i>H. nelsoni</i> )	Fish Tortoise (Oyster)	
Hexamitinae	<i>Spironucleus</i>	Poultry, rodents, amphibians, fish	<i>S. meleagridis</i> <i>S. columbae</i> <i>S. muris</i>	Turkey Pigeon Laboratory rat and mouse	
			<i>S. elegans</i>	Fish	

Giardiinae subfam. <i>Octomitus</i> nov.	<i>Giardia</i>	Rodents, amphibians Man, monkeys, cattle, goat, sheep, horse, dog, cat, rabbit, rodents, amphibians, reptiles	<i>G. intestinalis</i> (?) <i>G. bovis</i> (?) <i>G. caprae</i> (?) <i>G. cati</i> (?) <i>G. canis</i> (?) <i>G. duodenalis</i> (?) <i>G. chinillae</i>	Man Cattle Sheep Cat Dog Rabbit Chinchilla
Oxymonadida Polynastigidae	<i>Monocercomonoides</i>	Cattle, goat, rodents, amphibians, reptiles		
Proteromonadida Proteromonadidae	<i>Proteromonas</i>	Guinea pig, porcupine, amphibians, reptiles		
	<i>Karotomorpha</i>	Amphibians		
Incertae sedis Cochliosomidae	<i>Cochliosoma</i>	Domestic and wild birds, bats	(?) <i>C. anatis</i>	Turkey

<sup>a</sup> Trichomonadida is not included.