

# Contents

Preface to the third edition	xix
Acknowledgements	xx
<b>1 Parasitism: what is a parasite?</b>	<b>1</b>
1.1 Animal associations	1
1.2 Commensalism	2
1.3 Phoresis	2
1.4 Parasitism	3
1.4.1 General considerations	3
1.4.2 Metabolic dependence	3
1.4.3 Mutualism and symbiosis	6
1.4.4 Types of parasites	6
References	8
<b>2 Niches, habitats and environments</b>	<b>10</b>
2.1 Niches	10
2.2 Habitats: general comments	11
2.3 The vertebrate alimentary canal	11
2.3.1 General properties	11
2.3.2 General environmental conditions in different regions of the alimentary canal	12
2.3.3 Intestinal physiology	13
2.3.4 Physico-chemical characteristics	14
2.4 Blood	17
2.4.1 General constituents	17
2.4.2 Blood cells	18
2.5 Tissues and other habitats	18
2.6 Invertebrate habitats	19
2.7 Importance of nutritional levels of environment in parasite life cycles	19
References	20
<b>3 Protozoa: the amoebae</b>	<b>22</b>
3.1 Type example: <i>Entamoeba muris</i>	22
3.2 Ultrastructure	24
3.3 <i>Entamoeba</i> of man and other animals	25
3.3.1 <i>Entamoeba histolytica</i>	26
3.3.2 Other species of <i>Entamoeba</i>	29
3.4 Other intestinal amoebae	31

3.5	Tissue-invading soil amoebae	32
3.5.1	General account	32
3.5.2	The discovery of pathogenic soil amoebae	32
3.5.3	Species involved	32
3.5.4	Type examples: <i>Naegleria gruberi</i> and <i>N. fowleri</i>	32
3.5.5	Other <i>Naegleria</i> species	36
3.5.6	Type example: <i>Acanthamoeba castellanii</i>	36
3.6	Physiology of intestinal amoebae	37
3.6.1	Physico-chemical considerations	37
3.6.2	General metabolism	38
	References	40
	Appendix: Protozoa: abbreviated classification	42
<b>4</b>	<b>Flagellates: intestinal and related forms</b>	<b>44</b>
4.1	Classification	44
4.2	Trichomonads	45
4.2.1	General account	45
4.2.2	Particular genera of trichomonads	47
4.2.3	Particular species	47
4.3	Intestinal flagellates other than trichomonads	49
4.3.1	Minor species	49
4.3.2	Genus <i>Giardia</i>	49
4.3.3	<i>Histomonas meleagridis</i>	52
4.4	Physiology and biochemistry of intestinal flagellates	52
4.4.1	<i>In vitro</i> cultivation	52
4.4.2	Metabolism of <i>Trichomonas</i> and <i>Giardia</i>	52
	References	54
<b>5</b>	<b>Haemoflagellates</b>	<b>57</b>
5.1	Haemoflagellates as biological models	57
5.2	General account	57
5.2.1	Morphology: light microscopy	57
5.2.2	Ultrastructure	58
5.2.3	Antigenic variation	60
5.3	Morphological stages of haemoflagellates	61
5.4	Classification: Family Trypanosomatidae	62
5.5	Genus <i>Trypanosoma</i>	63
5.5.1	General account	63
5.5.2	Type example: <i>Trypanosoma lewisi</i>	64
5.5.3	Classification of mammalian trypanosomes	67
5.5.4	Trypanosomes infecting man: trypanosomiasis	68
5.5.5	Sexuality in the <i>T. brucei</i> complex	71
5.6	Genus <i>Leishmania</i>	75
5.6.1	General account	75
5.6.2	Morphology	76
5.6.3	Life cycle	78
5.6.4	Leishmaniasis: the disease	79
5.7	Physiology and biochemistry of haemoflagellates	80
5.7.1	Biochemistry of <i>Trypanosoma</i>	80
5.7.2	Biochemistry of <i>Leishmania</i> and <i>T. cruzi</i>	83
	References	84

<b>6</b>	<b>Sporozoea: gregarines and coccidia</b>	<b>88</b>
6.1	Classification	88
6.2	Subclass 1 Gregarina	89
6.2.1	General account	89
6.2.2	Morphology: light microscopy	89
6.2.3	Morphology: ultrastructure	89
6.2.4	Life cycle: <i>Gregarina garhami</i>	90
6.3	Subclass 2 Coccidia	94
6.3.1	Life cycle of typical coccidian	94
6.3.2	Morphology	96
6.3.3	Mammalian and avian coccidia	97
6.4	Tissue cyst-forming coccidia	99
6.4.1	<i>Toxoplasma gondii</i>	99
6.4.2	Genus <i>Sarcocystis</i>	104
	References	106
<b>7</b>	<b>Sporozoea: Haemosporina: malaria; basic biology</b>	<b>109</b>
7.1	General considerations	109
7.2	Subclass Coccidia: suborder Haemosporina	109
7.3	Genus <i>Plasmodium</i> : the malarial organism	110
7.3.1	History	110
7.3.2	General features of the malarial life cycle	111
7.4	Ultrastructure	115
7.4.1	Merozoite	115
7.4.2	Trophozoite	116
7.5	Genetics of <i>Plasmodium</i>	117
7.5.1	Mendelian crossing experiments	117
7.5.2	The <i>Plasmodium</i> genome	118
7.6	Biochemistry and physiology	119
7.6.1	General comments	119
7.6.2	Carbohydrate metabolism	119
7.6.3	Nucleic acid metabolism	122
7.6.4	Protein metabolism	122
	References	123
<b>8</b>	<b>Sporozoea: malaria in man and the animal kingdom</b>	<b>126</b>
8.1	Mammalian malaria	126
8.1.1	Human malaria	126
8.1.2	Simian malaria: speciation	129
8.1.3	Simian malaria: infectivity to man	131
8.1.4	Rodent malaria: <i>P. berghei</i>	132
8.2	Bird malaria	133
8.3	Amphibian malaria	135
8.4	Reptilian malaria	135
	References	135
<b>9</b>	<b>Sporozoea: Haemosporina other than Plasmodia; Piroplasmia</b>	<b>137</b>
9.1	Family Haemoproteidae	137
9.1.1	Genus <i>Leucocytozoon</i>	137
9.1.2	Genus <i>Haemoproteus</i>	138

9.2	Subclass Piroplasmia	139
9.2.1	Family Babesiidae	139
9.3	Family Theileriidae	142
9.3.1	Genus <i>Theileria</i>	142
	References	142
<b>10</b>	<b>Opalinata and Ciliophora</b>	<b>144</b>
10.1	'Opalinids' and ciliates	144
10.2	Classification	144
10.3	Subphylum Opalinata	144
10.3.1	General account	144
10.3.2	<i>Opalina ranarum</i>	145
10.4	Phylum Ciliophora	148
10.4.1	<i>Ichthyophthirius multifiliis</i>	149
10.4.2	<i>Balantidium coli</i>	150
10.4.3	Genus <i>Nyctotherus</i>	151
10.4.4	Order Entodiniomorphida	153
10.4.5	Order Hypotrichida	154
	References	154
<b>11</b>	<b>Helminth Parasites: Platyhelminthes: Monogenea</b>	<b>157</b>
11.1	Trematoda: introduction	158
11.2	Class Monogenea	159
11.2.1	Type example: <i>Polystoma integerrimum</i>	159
11.2.2	General account	164
11.2.3	Miscellaneous Monogenea	167
	References	172
<b>12</b>	<b>Trematoda: Aspidogastrea</b>	<b>175</b>
	References	176
<b>13</b>	<b>Trematoda: Digenea</b>	<b>178</b>
13.1	General morphology	178
13.2	Egg formation	184
13.2.1	General account	184
13.2.2	Structure of egg-shell	184
13.2.3	Role of Mehlis' gland	187
13.2	Trematode life cycles	188
13.3.1	Egg hatching, in water	188
13.3.2	Egg hatching, within snails	190
13.3.3	Larval forms	190
13.4	Classification	197
	References	198
<b>14</b>	<b>Digenea: Bucephalidae, Fasciolidae, Opisthorchiidae, Dicrocoeliidae</b>	<b>203</b>
14.1	Family Bucephalidae	203
14.2	Family Fasciolidae	205
14.2.1	Genus <i>Fasciola</i>	205
14.2.2	Genus <i>Fascioloides</i>	211
14.3	Family Opisthorchiidae	212

14.4	Family Dicrocoeliidae	214	
	References	216	
<b>15</b>	<b>Digenea: Plagiorchiidae, Echinostomatidae, Heterophyidae, Troglotrematidae</b>	<b>219</b>	
15.1	Family Plagiorchiidae	219	
	15.1.1 Type example: <i>Haplometra cylindracea</i>	219	
	15.1.2 Other plagiorchids in amphibia	219	
15.2	Family Echinostomatidae	221	
	15.2.1 Type example: <i>Parorchis acanthus</i>	226	
	15.2.2 Other echinostomes	228	
15.3	Family Heterophyidae	228	
	15.3.1 Type example: <i>Cryptocotyle lingua</i>	228	
	15.3.2 Other Heterophyidae	230	
15.4	Family Troglotrematidae	230	
	15.4.1 Type example: <i>Paragonimus westermani</i>	230	
	References	233	
<b>16</b>	<b>Digenea: Schistosomatidae</b>	<b>236</b>	
16.1	General account	236	
	16.1.1 Species infecting man	236	
16.2	Type example: <i>Schistosoma mansoni</i>	237	
	16.2.1 Morphology	237	
	16.2.2 Life cycle	238	
16.3	Other species attacking man	243	
	16.3.1 <i>Schistosoma haematobium</i>	243	
	16.3.2 <i>Schistosoma japonicum</i>	245	
16.4	Schistosomiasis as a world problem	245	
16.5	Type example: <i>Schistosomatium douthitti</i>	246	
	16.5.1 Morphology	246	
	16.5.2 Life cycle	248	
16.6	Unisexual infections	250	
	16.6.1 General account	250	
16.7	Hybridization in schistosomes	251	
16.8	Cercarial dermatitis: 'swimmers' itch'	251	
	References	251	
<b>17</b>	<b>Digenea: Strigeidae, Diplostomatidae, Paramphistomatidae</b>	<b>254</b>	
17.1	Families Strigeidae and Diplostomatidae	254	
	17.1.1 Type example: <i>Diplostomum phoxini</i>	254	
	17.1.2 Type example: <i>Diplostomum spathaceum</i> (the 'eye' fluke)	258	
17.2	Family Paramphistomatidae	259	
	References	261	
<b>18</b>	<b>Physiology of trematodes</b>	<b>263</b>	
18.1	Chemical composition	263	
18.2	Nutrition	263	
18.3	Energy metabolism	266	
	18.3.1 <i>Fasciola</i> spp.	266	
	18.3.2 <i>Schistosoma</i> spp.	266	

18.4	Protein metabolism	268
18.5	Lipid metabolism	269
18.6	Neurobiology	270
	References	273
<b>19</b>	<b>Cestoda: Cestodaria</b>	<b>277</b>
19.1	General account	277
19.2	Subclass Cestodaria	277
19.2.1	Amphilinidea	278
19.2.2	Gyrocotylidea	279
	References	279
<b>20</b>	<b>Eucestoda: general account</b>	<b>281</b>
20.1	Classification	281
20.2	General characteristics	282
20.2.1	General morphology	282
20.2.2	Reproductive system	285
20.2.3	Eggs and egg-envelopes (membranes)	287
20.2.4	Egg hatching	290
20.3	Life cycles	291
	References	293
<b>21</b>	<b>Eucestoda: minor orders</b>	<b>296</b>
	References	300
<b>22</b>	<b>Eucestoda: Pseudophyllidea</b>	<b>302</b>
22.1	Genus <i>Diphyllobothrium</i>	302
22.1.1	Type example: <i>Diphyllobothrium dendriticum</i>	302
22.1.2	Other Diphyllobothriidae in fish: <i>Diphyllobothrium ditremum</i>	306
22.1.3	<i>Diphyllobothrium latum</i> : the human 'broad' tapeworm	307
22.1.4	<i>Spirometra</i> spp.: 'sparganum' infections	309
22.2	The caryophyllaeid cestodes	310
22.2.1	<i>Archigetes</i> spp.	311
22.2.2	<i>Caryophyllaeus</i> spp.	311
22.3	Pseudophyllidae with progenetic plerocercoids	312
22.3.1	<i>Schistocephalus solidus</i> (Ligulidae)	312
22.3.2	<i>Ligula intestinalis</i>	316
	References	317
<b>23</b>	<b>Eucestoda: Cyclophyllidea</b>	<b>321</b>
23.1	Type example: <i>Hymenolepis diminuta</i>	321
23.2	Family Hymenolepididae	324
23.2.1	<i>Hymenolepis</i> (= <i>Vampirolepis</i> ) <i>nana</i>	324
23.2.2	<i>Hymenolepis microstoma</i>	326
23.3	Family Taeniidae	326
23.3.1	Genus <i>Taenia</i> : taeniasis and cysticercosis in man	326
23.3.2	Genus <i>Echinococcus</i> : hydatid disease	334
23.3.3	Miscellaneous Taeniidae suitable for experimental use	340
23.4	Other Cyclophyllidae	342
	References	344

<b>24</b>	<b>Physiology of cestodes</b>	<b>349</b>
24.1	General account	349
24.2	Chemical composition	351
24.2.1	General comment	351
24.2.2	Carbohydrates	352
24.2.3	Protein	352
24.2.4	Lipid	352
24.3	Carbohydrate metabolism	353
24.4	Electron transport	359
24.5	Protein metabolism	359
24.5.1	General account	359
24.5.2	Amino acid uptake	360
24.5.3	Amino acid metabolism	360
24.5.4	End-products of nitrogen metabolism	361
24.6	Lipid metabolism	361
24.7	Neurobiology	362
	References	364
<b>25</b>	<b>Nematoda: general account</b>	<b>368</b>
25.1	Classification	368
25.2	Type example: <i>Rhabditis maupasi</i>	369
25.3	General morphology of nematodes	371
25.3.1	External features	372
25.3.2	Alimentary canal	373
25.3.3	Excretory system	377
25.4	Reproduction	378
25.4.1	General account	378
25.4.2	The nematode egg-shell	379
25.4.3	Physiology of egg hatching and larval moulting	381
25.5	Body wall	383
25.5.1	Cuticle	383
25.5.2	Epidermis (hypodermis)	384
25.6	General consideration of structure and function	385
	References	385
<b>26</b>	<b>Aphasmid Nematoda</b>	<b>388</b>
26.1	Superfamily Trichuroidea	388
26.1.1	Family Trichuridae	388
26.1.2	Family Trichinellidae	389
26.1.3	Family Trichosomoididae	394
26.2	Superfamily Dioctophymatoidea	395
	References	395
<b>27</b>	<b>Phasmid Nematoda: Rhabditida, Ascaridida and Oxyurida</b>	<b>397</b>
27.1	Order Rhabditida	397
27.1.1	Family Rhabditidae	397
27.1.2	Family Strongyloididae	397
27.1.3	Genus <i>Rhabdias</i>	398
27.1.4	Genus <i>Neoaplectana</i>	400
27.2	Order Ascaridida	400

27.2.1	Superfamily Ascaridoidea	400	
27.2.2	Genus <i>Ascaris</i>	401	
27.2.3	Other Ascaridoids	404	
27.3	Order Oxyurida	407	
	References	409	
<b>28</b>	<b>Phasmid Nematoda: Strongylida</b>	<b>412</b>	
28.1	Type example: <i>Nippostrongylus brasiliensis</i> , the rat hookworm		412
28.1.1	General morphology	412	
28.1.2	Life cycle	414	
28.2	Order Strongylida	415	
28.2.1	Family Trichostrongylidae	416	
28.2.2	Family Heligmosomatidae	417	
28.2.3	Family Strongylidae	418	
28.2.4	Family Ancylostomatidae	418	
28.2.5	Family Metastrongylidae	420	
28.2.6	Family Syngamidae	420	
	References	420	
<b>29</b>	<b>Phasmid Nematoda: Spirurida</b>	<b>423</b>	
29.1	Suborder Spirurina: superfamily Filarioidea		423
29.1.1	Type example: <i>Litomosoides carinii</i>	423	
29.1.2	Filariae in dogs: <i>Dirofilaria immitis</i>	425	
29.1.3	Human filariasis	425	
29.1.4	Identification of microfilariae	430	
29.1.5	Periodicity of microfilariae	431	
29.2	Suborder Camallanina	432	
29.3	Suborder Spirurina	434	
	References	434	
<b>30</b>	<b>Physiology of nematodes</b>	<b>438</b>	
30.1	Chemical composition	438	
30.2	Respiration	440	
30.3	Carbohydrate metabolism	440	
30.3.1	Metabolism of <i>Ascaris</i>	440	
30.3.2	Other (non-filariid) species	442	
30.3.3	Metabolism of filarial worms	442	
30.4	Krebs (TCA) cycle	444	
30.5	Protein metabolism	445	
30.5.1	Proteolytic enzymes (proteases)	445	
30.5.2	Amino acid metabolism	446	
30.6	Lipid metabolism	446	
30.7	Nutrition	447	
30.7.1	Adults	447	
30.7.2	Larvae	448	
30.7.3	Filariae	448	
30.8	Neurobiology	448	
	References	448	



<b>31</b>	<b>Acanthocephala</b>	<b>451</b>
31.1	Occurrence	451
31.1.1	Host lists	451
31.1.2	Useful experimental species	451
31.2	General account	453
31.2.1	General morphology	453
31.2.2	Reproductive system	455
31.2.3	Life cycles	456
31.2.4	Classification	457
	References	457
<b>32</b>	<b>Immunoparasitology</b>	<b>460</b>
32.1	Immunity and the immune response	460
32.1.1	The adaptive immune response	460
32.1.2	Parasite antigens	463
32.1.3	Anti-parasite responses	465
32.1.4	Evasion of immunity	465
32.2	Immunity in specific host–parasite systems	466
32.2.1	Protozoa	466
32.2.2	Extra-cellular protozoa	466
32.2.3	Intra-cellular protozoa	468
32.2.4	Platyhelminthes: Trematoda (flukes)	473
32.2.5	Schistosomes	473
32.2.6	Liver flukes	476
32.2.7	Platyhelminthes: cestodes	476
32.2.8	Nematodes	477
32.3	Vaccination and diagnosis	483
32.3.1	Vaccination	483
32.3.2	Diagnosis	485
	References	486
<b>33</b>	<b><i>In vitro</i> cultivation of endoparasites: general principles; Protozoa</b>	<b>491</b>
33.1	General principles	491
33.1.1	Advances of <i>in vitro</i> culture	491
33.1.2	Terminology	491
33.1.3	Basic problems	492
33.2	Intestinal Protozoa	493
33.2.1	General account	493
33.2.2	<i>Entamoeba histolytica</i> and other intestinal amoebae	494
33.2.3	Intestinal flagellates	494
33.2.4	Intestinal ciliates	496
33.3	Blood and tissue protozoa	496
33.3.1	General account	496
33.3.2	Haemoflagellates	496
33.3.3	Malarial parasites: <i>Plasmodium</i> spp., erythrocytic stages	497
33.3.4	Malarial parasites: exo-erythrocytic forms	500
33.4	Other Sporozoea	500
	References	500

xviii | Contents

<b>34</b>	<b><i>In vitro</i> cultivation of endoparasites: helminths</b>	<b>503</b>
34.1	General account	503
34.2	Trematodes	503
34.2.1	Strigeid trematodes	503
34.2.2	Schistosomes	506
34.2.3	Other trematodes	507
34.2.4	The CAM (chorioallantoic membrane) culture technique	507
34.3	Cestodes	509
34.3.1	General account	509
34.3.2	Pseudophyllidea	509
34.3.3	Cyclophyllidea	511
34.4	Nematodes	517
34.4.1	General account	517
34.4.2	Techniques and media utilised	518
34.4.3	Trichostrongyloidea	519
34.4.4	Strongyloidea	520
34.4.5	Ascaroidea	520
34.4.6	Trichinelloidea	521
34.5	Filarioidea	521
34.5.1	General comments	521
	References	523
	Author index	527
	Subject index	534