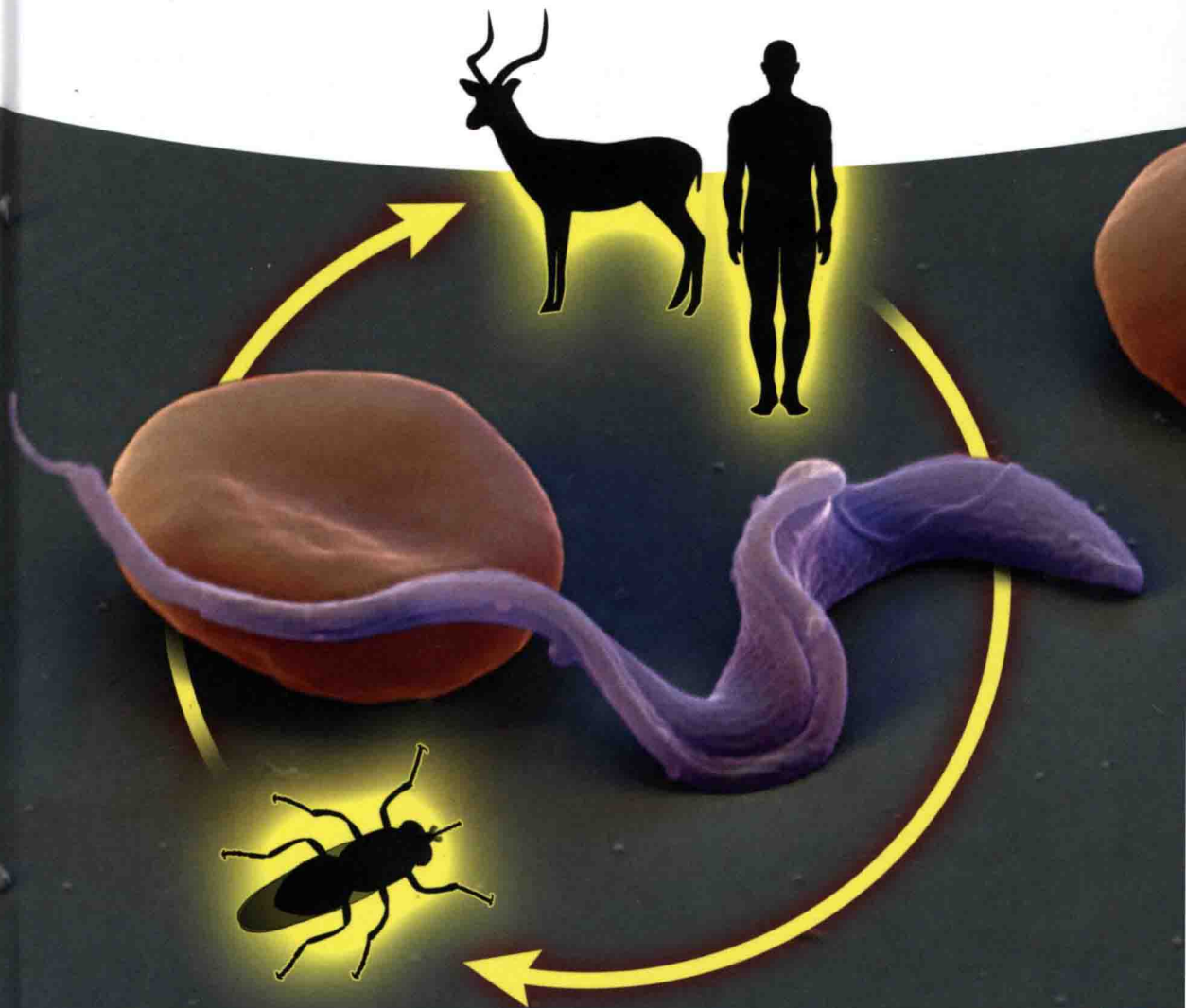


R. Lucius, B. Loos-Frank, R. P. Lane, R. Poulin,
C. W. Roberts, and R. K. Grensis

The Biology of Parasites



Filling the gap for a textbook combining classical parasitology with the latest research results from cell and molecular biology, this unique volume covers each class of animal parasites, including all major human parasites, and features a large introductory section focusing on their evolution and ecology. Immunological aspects are covered in detail and 250 study questions with solutions are included for self-study.

Based on a successful German textbook, this edition has been completely rewritten and restructured with the help of outstanding researchers and lecturers from the UK and New Zealand, making it the first choice for those parasitology students planning to stay in research in academia or industry.



Richard Lucius heads the department of Molecular Parasitology at Humboldt-Universität zu Berlin (Germany). His work concentrates on the interaction between parasites and their host's immune system. He is bearer of the Leuckart medal of the German Society

of Parasitology and of the Behring-Bilharz medal.



Brigitte Loos-Frank is emeritus Professor for Parasitology at Universität Hohenheim (Germany). Since the 1990s, she has studied the life cycles of *Dicrocoelium dendriticum* and other trematodes as well as of cestodes of the genus *Mesocestoides* and *Taenia*. She has also worked on the biology

of lung mites and other arthropod mammalian parasites.



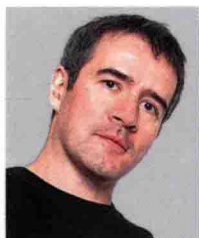
Richard Lane was formerly Director of Science at the Natural History Museum, London (UK). As a medical entomologist he studied the transmission of several insect-borne diseases, especially leishmaniasis. He has also been Head of the Vector Biology Unit at the

London School of Hygiene and Tropical Medicine and Head of International Health at the Wellcome Trust.



Robert Poulin is Professor of Zoology at the University of Otago (New Zealand). His research group focuses on broad questions in parasite ecology and evolution. He was awarded the Hutton Medal from the Royal Society of New Zealand and the Wardle Medal from the Canadian Society of

Zoologists for his outstanding contribution to parasitology.



Craig W. Roberts is Professor of Parasitology at the University of Strathclyde, Glasgow (UK). His current research concentrates on (i) the interaction of *Toxoplasma gondii* and *Acanthamoeba* with their host and how this knowledge can be exploited for vaccines design

and new antimicrobials and (ii) the influence of sex and pregnancy associated hormones on immunity.



Richard Grencis is Professor of Immunology at the University of Manchester. His research has focused on immune responses to parasites, especially intestinal nematodes. He was awarded the Wright Medal from the British Society for Parasitology for his outstanding contribution to

Parasitology and he serves as co-editor-in-chief of the journal *Parasite Immunology*.

**Lucius • Loos-Frank • Lane
Poulin • Roberts • Grensis**

The Biology of Parasites

WILEY
CH

*Richard Lucius, Brigitte Loos-Frank, Richard P. Lane,
Robert Poulin, Craig W. Roberts, and Richard K. Grensis*

With contributions of guest authors

Nina Papavasiliou, Rockefeller University, New York, USA

John Boothroyd, Stanford University, Stanford, USA

Kai Matuschewski, Humboldt Universität zu Berlin, Berlin, Germany

The Biology of Parasites

Translated by Renate FitzRoy and Ron Shankland

WILEY-VCH
Verlag GmbH & Co. KGaA

Authors

Prof. Dr. Richard Lucius

Humboldt University
Institute of Biology
Philippstr. 13
10115 Berlin
Germany

Prof. Dr. Brigitte Loos-Frank

University of Hohenheim
Department of Parasitology
Emil Wolff-Straße 34
70599 Stuttgart
Germany

Prof. Dr. Richard P. Lane

Stonewall Holt
The Street
EX13 7RW Kilminster, Devon
United Kingdom

Prof. Dr. Robert Poulin

University of Otago
Zoology Department
Great King Street
Dunedin 9054
New Zealand

Prof. Dr. Craig W. Roberts

University of Strathclyde
Strathclyde Institute of Pharmacy and
Biomedical Sciences (SIPBS)
161 Cathedral Street
G4 0RE Glasgow
United Kingdom

Prof. Dr. Richard K. Grencis

University of Manchester
Life Sciences/AV Hill Building
Oxford Road
M13 9PT Manchester
United Kingdom

Translators

Renate FitzRoy

MSc Transl & Technology
26 Cairnhill Gardens
KY16 8QX St. Andrews
United Kingdom

Ron Shankland

Kevron Translations
Erlenweg 2
69509 Mörlenbach
Germany

Cover

Trypanosoma brucei SEM image © eye of
science, Meckes & Ottawa GbR.

■ All books published by **Wiley-VCH** are carefully produced. Nevertheless, authors, editors, and publisher do not warrant the information contained in these books, including this book, to be free of errors. Readers are advised to keep in mind that statements, data, illustrations, procedural details or other items may inadvertently be inaccurate.

Library of Congress Card No.: applied for

British Library Cataloguing-in-Publication Data

A catalogue record for this book is available from the British Library.

Bibliographic information published by the Deutsche Nationalbibliothek

The Deutsche Nationalbibliothek lists this publication in the Deutsche Nationalbibliografie; detailed bibliographic data are available on the Internet at <<http://dnb.d-nb.de>>.

© 2017 Wiley-VCH Verlag GmbH & Co. KGaA, Boschstr. 12, 69469 Weinheim, Germany

All rights reserved (including those of translation into other languages). No part of this book may be reproduced in any form – by photoprinting, microfilm, or any other means – nor transmitted or translated into a machine language without written permission from the publishers. Registered names, trademarks, etc. used in this book, even when not specifically marked as such, are not to be considered unprotected by law.

Print ISBN: 978-3-527-32848-2

ePDF ISBN: 978-3-527-69855-4

ePub ISBN: 978-3-527-69856-1

Mobi ISBN: 978-3-527-69857-8

Cover Design Formgeber, Mannheim, Germany

Typesetting SPi Global, Chennai, India

Printing and Binding Markono Print Media Pte Ltd, Singapore

Printed on acid-free paper

This is a completely revised and updated version of the second edition of “R. Lucius and B. Loos-Frank: Biologie von Parasiten” (ISBN 978-3-540-37707-8, Springer-Verlag, Berlin, Heidelberg).

*Richard Lucius, Brigitte Loos-Frank,
Richard P. Lane, Robert Poulin,
Craig W. Roberts, and Richard K. Grensis*

The Biology of Parasites

Preface

Parasitism is a specialized way of life, pursued by organisms that have evolved to thrive at the expense of a living host. Therefore, in a broad sense, all pathogens like viruses, bacteria, or eukaryotic infectious agents are parasites and thus share many common features. However, they also have important differences. For example, viruses and bacteria are genetically less complex and employ different strategies for exploiting a host, leading to different disease syndromes. As a consequence, different scientific fields have emerged, of which the discipline of parasitology is one that deals with eukaryotic pathogens, namely, protozoa, worms, and arthropods. Parasites, in this narrower sense, are a huge burden to mankind, with billions of infected people, mainly in tropical developing countries with relatively poor hygiene. Along with their medical and veterinary importance, parasites have a fascinating biology, which is the theme of this book. *The Biology of Parasites* is based on an earlier German book (Lucius & Loos-Frank (2008), Springer Verlag, Heidelberg), which has been extended and updated by the current team of authors.

The living host is a very particular niche; it is not a neutral place at all. Parasites are involved in a constant struggle with their hosts, who strive to rid themselves of the unwanted company, deploying all sorts of mechanisms against them. These range from defensive behavior to the effector molecules and cells of a complex immune system. In spite of such defenses, an extraordinary number of animals have adopted parasitism as a mode of life; some specialists believe that >50% of animal species are parasites or have at least a parasitic phase in their life cycle. It seems that the parasitic lifestyle is so rewarding that it has been worth the great effort parasites have made to develop most intriguing means of locating their hosts, survive within or on them, produce offspring, and ensure that the next generation reaches a new host. To exploit a host, parasites may change their morphology beyond all recognition: they may trick and cheat by disguising themselves or manipulate their host's cellular pathways or even their behavior. Because of these extraordinary, bizarre, or seemingly "otherworldly" abilities, parasites have always fascinated biologists and captured the attention of the general public.

The antagonistic relationship between pathogens and their hosts drives the evolution of both adversaries in a profound manner. This arms race has affected the evolution of some of the most important processes of life, for example, sexual reproduction and the immune system. It also shaped the genomes of both parties

to a degree that we have only recently discovered. Indeed, new molecular techniques developed in past few decades have opened an extraordinary range of perspectives on the interplay between eukaryotic parasites and their hosts. Genome projects have cast light on the peculiarities of parasite genomes. For example, we have learned that many protozoans and worms have undergone a reductive evolution in their genomes, especially with regard to those functions they have appropriated from their host, while other areas have been expanded, such as those needed for the manipulation of the host. This explosion in genomic knowledge has also provided us with the tools to discover and describe precisely parasite-specific metabolic pathways. It has also facilitated the dissection of molecular mechanisms used by parasites to detect host cues, invade host cells, or cope with immune effector mechanisms. This information has already allowed and will hopefully further allow us to design specific measures against parasites and their vectors, ranging from strategies to prevent infection, such as vaccines and pesticides, to drug development. However, it is not the sole goal of parasitologists to fight diseases, as worthy as that is, but to understand the intricacies of the parasitic lifestyle and to put them into a broader biological context. This greatly contributes to our wider understanding of key biological processes, such as evolution, ecology, and generation of biodiversity. Last but not least, the simple wonder and awe the extraordinary biology of parasites instills in us makes their study worthwhile in its own right.

This book is designed to provide advanced information to students of biology, medicine, or veterinary medicine and to interested lay persons. An introductory chapter on general parasitology, addressing crosscutting topics of parasitology, is followed by specific chapters on the biology of protozoan parasites, parasitic worms, and parasitic arthropods. The focus is on parasites of medical or veterinary importance, as these are best known from intensive research and are of the widest interest, although we also highlight parasites with interesting biological adaptations to emphasize those traits most typical of the parasitic lifestyle. To be concise, we discuss particular species as representatives of their taxon, while related parasites are briefly mentioned or treated in tabular form. Inevitably, the book cannot cover the entire field of parasitology. It does not give detailed treatment of the therapy or control of parasitic infections, parasite ecology, or evolutionary parasitology. Likewise, we have sparingly mentioned marine parasites or parasitoids and their interesting biologies. To cover cutting-edge topics, we have invited three renowned guest authors to contribute concise information from their field of research, namely, John Boothroyd (parasite–host interplay of *Toxoplasma*), Kai Matuschewski (vaccine development against the malaria parasite *Plasmodium*), and Nina Papavasiliou (new developments in trypanosome research).

We are thankful to many colleagues from different fields of parasitology and beyond for their helpful discussions. We thank specifically those who provided images of parasites or illustrative research data, in particular Oliver Meckes and Nicole Ottawa from *eye of science* for fascinating electron microscope pictures, Prof. Egbert Tannich for images of amoebae, and Dr. Heiko Bellmann for photos

of arthropods. We gratefully acknowledge the permission of the Departments of Parasitology of University of Hohenheim and of Humboldt University to utilize pictures from their archives. The life cycles and other drawings are based on the painstaking work of Flavia Wolf, Dr. J. Gelnar, and Hanna Zeckau, which is gratefully acknowledged. A heartfelt thank-you goes to Christine Nowotny for her most professional help with the organization of the manuscript and illustrations. This work would not have been possible without the continuous support of Dr. Gregor Cicchetti and Dr. Andreas Sendtko and their team from the publisher Wiley-VCH, which is gratefully acknowledged.

September 2016

Richard Lucius
Berlin

Contents

Preface *XI*

1	General Aspects of Parasite Biology	1
	<i>Richard Lucius and Robert Poulin</i>	
1.1	Introduction to Parasitology and Its Terminology	2
1.1.1	Parasites	2
1.1.2	Types of Interactions Between Different Species	5
1.1.2.1	Mutualistic Relationships	5
1.1.2.2	Antagonistic Relationships	6
1.1.3	Different Forms of Parasitism	10
1.1.4	Parasites and Hosts	11
1.1.5	Modes of Transmission	16
	Further Reading	17
1.2	What Is Unique About Parasites?	18
1.2.1	A Very Peculiar Habitat: The Host	18
1.2.2	Specific Morphological and Physiological Adaptations	22
1.2.3	Flexible Strategies of Reproduction	27
	Further Reading	29
1.3	The Impact of Parasites on Host Individuals and Host Populations	30
	Further Reading	37
1.4	Parasite–Host Coevolution	38
1.4.1	Main Features of Coevolution	38
1.4.2	Role of Alleles in Coevolution	42
1.4.3	Rareness Is an Advantage	45
1.4.4	Malaria as an Example of Coevolution	46
	Further Reading	50
1.5	Influence of Parasites on Mate Choice	51
	Further Reading	57
1.6	Immunobiology of Parasites	58
1.6.1	Defense Mechanisms of Hosts	60
1.6.1.1	Innate Immune Responses (Innate Immunity)	60
1.6.1.2	Acquired Immune Responses (Adaptive Immunity)	62

1.6.1.3	Scenarios of Defense Reactions Against Parasites	63
1.6.1.4	Immunopathology	67
1.6.2	Immune Evasion	68
1.6.3	Parasites as Opportunistic Pathogens	72
1.6.4	Hygiene Hypothesis: Do Parasites Have a Good Side?	74
	Further Reading	76
1.7	How Parasites Alter Their Hosts	77
1.7.1	Alterations of Host Cells	78
1.7.2	Intrusion into the Hormonal System of the Host	79
1.7.3	Changing the Behavior of Hosts	82
1.7.3.1	Increase in the Transmission of Parasites by Bloodsucking Vectors	83
1.7.3.2	Increase in Transmission Through the Food Chain	83
1.7.3.3	Introduction into the Food Chain	88
1.7.3.4	Changes in Habitat Preference	92
	Further Reading	93
2	Biology of Parasitic Protozoa	95
	<i>Richard Lucius and Craig W. Roberts</i>	
2.1	Introduction	97
	Further Reading	98
2.2	Metamonada	99
2.2.1	<i>Giardia lamblia</i>	99
	Further Reading	102
2.3	Parabasala	102
2.3.1	<i>Trichomonas vaginalis</i>	103
2.3.2	<i>Tritrichomonas foetus</i>	106
	Further Reading	106
2.4	Amoebozoa	107
2.4.1	<i>Entamoeba histolytica</i>	108
2.4.2	<i>Entamoeba dispar</i>	114
2.4.3	Other <i>Entamoeba</i> Species	114
2.4.4	Further Intestinal Amoebae	115
2.4.5	<i>Acanthamoeba</i>	115
	Further Reading	116
2.5	Euglenozoa	117
2.5.1	Cell Biology and Genome	118
2.5.2	Phylogeny	121
2.5.3	<i>Trypanosoma brucei</i>	121
2.5.4	<i>Trypanosoma congolense</i>	131
2.5.5	<i>Trypanosoma vivax</i>	132
2.5.6	<i>Trypanosoma evansi</i>	133
2.5.7	<i>Trypanosoma equiperdum</i>	133
2.5.8	<i>Trypanosoma cruzi</i>	134
2.5.9	<i>Leishmania</i>	141

2.5.9.1	Development	142
2.5.9.2	Morphology	143
2.5.9.3	Leishmaniosis	143
2.5.9.4	Cell and Immune Biology	143
2.5.10	<i>Leishmania tropica</i>	148
2.5.11	<i>Leishmania donovani</i>	150
2.5.12	<i>Leishmania braziliensis</i> and <i>Leishmania mexicana</i>	151
	Further Reading	151
2.6	Alveolata	153
2.6.1	Apicomplexa	155
2.6.1.1	Development	155
2.6.1.2	Morphology	157
2.6.1.3	Cell Biology	160
2.6.2	Coccidea	165
2.6.2.1	<i>Cryptosporidium parvum</i>	166
2.6.2.2	<i>Eimeria</i>	169
2.6.2.3	<i>Eimeria tenella</i>	174
2.6.2.4	<i>Eimeria bovis</i>	175
2.6.2.5	<i>Isospora</i> and <i>Cyclospora</i>	175
2.6.2.6	<i>Toxoplasma gondii</i>	176
2.6.2.7	<i>Neospora caninum</i>	186
2.6.2.8	<i>Sarcocystis</i>	187
2.6.3	Haematozoa	190
2.6.3.1	<i>Plasmodium</i>	190
2.6.3.2	<i>Plasmodium vivax</i> , a Causative Agent of Tertian Malaria	199
2.6.3.3	<i>Plasmodium ovale</i> , a Causative Agent of Tertian Malaria	200
2.6.3.4	<i>Plasmodium malariae</i> , the Causative Agent of Quartan Malaria	200
2.6.3.5	<i>Plasmodium falciparum</i> , the Causative Agent of Malignant Tertian Malaria or Malaria tropica	201
2.6.3.6	<i>Plasmodium</i> species of Monkeys, Rodents, and Birds	210
2.6.4	Piroplasms	211
2.6.4.1	<i>Babesia</i>	211
2.6.4.2	<i>Theileria</i>	214
2.6.5	Ciliophora	218
2.6.5.1	<i>Balantidium coli</i>	219
2.6.5.2	<i>Ichthyophthirius multifiliis</i>	219
2.6.5.3	<i>Trichodina</i>	221
	Further Reading	222
3	Parasitic Worms	225
	Brigitte Loos-Frank and Richard K. Grencis	
3.1	Platyhelminths	228
3.1.1	Digenea	230
3.1.1.1	Development	230

3.1.1.2	Morphology	232
3.1.1.3	Adults	234
3.1.1.4	Systematics and Evolutionary History	237
3.1.1.5	<i>Schistosoma</i>	238
3.1.1.6	<i>Leucochloridium paradoxum</i>	248
3.1.1.7	<i>Diplostomum spathaceum</i>	248
3.1.1.8	<i>Fasciola hepatica</i>	251
3.1.1.9	<i>Opisthorchis felineus</i>	254
3.1.1.10	<i>Paragonimus westermani</i>	257
3.1.1.11	<i>Dicrocoelium dendriticum</i>	259
	Further Reading	262
3.1.2	Cestoda	263
3.1.2.1	Development	265
3.1.2.2	Evolution and Origin of Life Cycles	266
3.1.2.3	Morphology	266
3.1.2.4	Genome	269
3.1.2.5	Diphyllbothriidea	269
3.1.2.6	<i>Mesocestoides</i>	272
3.1.2.7	Cyclophyllidea	272
3.1.2.8	<i>Moniezia expansa</i>	273
3.1.2.9	<i>Hymenolepis diminuta</i>	274
3.1.2.10	<i>Rodentolepis nana</i> (<i>Hymenolepis nana</i>)	275
3.1.2.11	Taeniidae	277
3.1.2.12	<i>Taenia saginata</i>	281
3.1.2.13	<i>Taenia solium</i>	282
3.1.2.14	<i>Taenia asiatica</i>	282
3.1.2.15	<i>Hydatigera taeniaeformis</i>	283
3.1.2.16	<i>Echinococcus</i>	283
3.1.2.17	<i>Echinococcus granulosus</i>	283
3.1.2.18	<i>Echinococcus multilocularis</i>	285
3.1.2.19	<i>Echinococcus vogeli</i> and <i>Echinococcus oligarthrus</i>	286
	Further Reading	287
3.2	Acanthocephala	288
	Further Reading	293
3.3	Nematoda	294
3.3.1	Development	295
3.3.2	Morphology	297
3.3.3	Dorylaimea	300
3.3.3.1	<i>Trichinella spiralis</i>	300
3.3.3.2	<i>Trichuris trichiura</i>	305
3.3.4	Chromadorea	306
3.3.4.1	<i>Strongyloides stercoralis</i>	306
3.3.4.2	<i>Ancylostoma duodenale</i> and <i>Necator americanus</i>	308
3.3.4.3	<i>Angiostrongylus cantonensis</i>	311
3.3.4.4	<i>Haemonchus contortus</i>	312

3.3.4.5	<i>Dictyocaulus viviparus</i>	315
3.3.4.6	<i>Ascaris lumbricoides</i>	315
3.3.4.7	<i>Ascaris suum</i>	318
3.3.4.8	<i>Toxocara canis</i>	318
3.3.4.9	<i>Anisakis simplex</i> and <i>Anisakis</i> spp.	320
3.3.4.10	<i>Dracunculus medinensis</i>	321
3.3.4.11	<i>Enterobius vermicularis</i>	323
3.3.4.12	Filariae	325
3.3.4.13	<i>Wuchereria bancrofti</i> and <i>Brugia malayi</i>	326
3.3.4.14	<i>Onchocerca volvulus</i>	330
3.3.4.15	<i>Loa loa</i> and <i>Dirofilaria immitis</i>	334
3.3.4.16	Rodent Models of Filariasis	334
	Further Reading	335
4	Arthropods	337
	Brigitte Loos-Frank and Richard P. Lane	
4.1	Introduction	338
4.1.1	Vector Concepts	340
4.1.2	Impact of Bloodfeeding	343
	Further Reading	343
4.2	Acari – Mites and Ticks	344
4.2.1	Morphology	346
4.2.2	Development	347
4.2.3	Anactinotrichida (= Parasitiformes)	347
4.2.3.1	Mesostigmata	347
4.2.3.2	<i>Dermanyssus gallinae</i>	348
4.2.3.3	<i>Varroa destructor</i>	348
4.2.3.4	Metastigmata (= Ixodida or Ixodoidea, Ticks)	350
4.2.3.5	Development	353
4.2.3.6	Tick Bites and Saliva	353
4.2.3.7	Ixodidae – Hard Ticks	354
4.2.3.8	Argasidae (Soft Ticks)	358
4.2.3.9	Tick-Borne Diseases	359
4.2.4	Actinotrichida (= Acariformes)	361
4.2.4.1	Prostigmata = Actinedida = Trombidiformes	362
4.2.4.2	Trombiculidae – Harvest Mites, Chiggers	363
4.2.4.3	Astigmata = Acaridida = Sarcoptiformes	364
	Further Reading	365
4.3	Crustacea	366
4.3.1	<i>Argulus foliaceus</i>	367
4.3.2	<i>Sacculina carcini</i>	368
	Further Reading	370
4.4	Insecta	370
4.4.1	Phthiraptera – Lice	374
4.4.2	“Mallophaga” – Chewing Lice	375

4.4.3	Anoplura – Sucking Lice	375
4.4.3.1	<i>Pediculus humanus capitis</i>	377
4.4.3.2	<i>Pediculus humanus humanus</i>	378
4.4.3.3	<i>Pthirus pubis</i>	378
4.4.3.4	Disease Transmission by Lice	379
4.4.4	Heteroptera – True Bugs	380
4.4.5	Triatominae – Kissing Bugs	380
4.4.6	Cimicidae – Bedbugs	382
4.4.6.1	<i>Cimex lectularius</i>	383
4.4.7	Siphonaptera – Fleas	384
4.4.7.1	Biology and Development	384
4.4.7.2	Morphology	385
4.4.7.3	<i>Pulex irritans</i>	387
4.4.7.4	<i>Ctenocephalides</i> : Cat and Dog Fleas	387
4.4.7.5	<i>Tunga penetrans</i> – Jiggers	388
4.4.7.6	Disease Transmission by Fleas	388
4.4.8	Diptera – Flies	390
4.4.8.1	Lower Diptera	390
4.4.8.2	Ceratopogonidae – Biting Midges, No-see-ums, Punkies	391
4.4.8.3	Disease Transmission	393
4.4.8.4	Culicidae – Mosquitoes	394
4.4.8.5	Disease Transmission	398
4.4.8.6	Simuliidae – Blackflies	401
4.4.8.7	Phlebotominae – Sandflies	404
4.4.8.8	Brachycera	408
4.4.8.9	Tabanidae – Horse Flies	408
4.4.8.10	Muscidae – House and Stable Flies	410
4.4.8.11	Calliphoridae – Blowflies, Screwworms	413
4.4.8.12	Oestridae – Bot or Warble Flies	413
4.4.8.13	Glossinidae – Tsetse Flies	415
4.4.8.14	Hippoboscidae, Nycteribiidae, Streblidae – Louse Flies, Keds and Bat Flies	418
	Further Reading	419

Answers to Test Questions 423

Chapter 1 423

Chapter 2 426

Chapter 3 429

Chapter 4 431

Index 435