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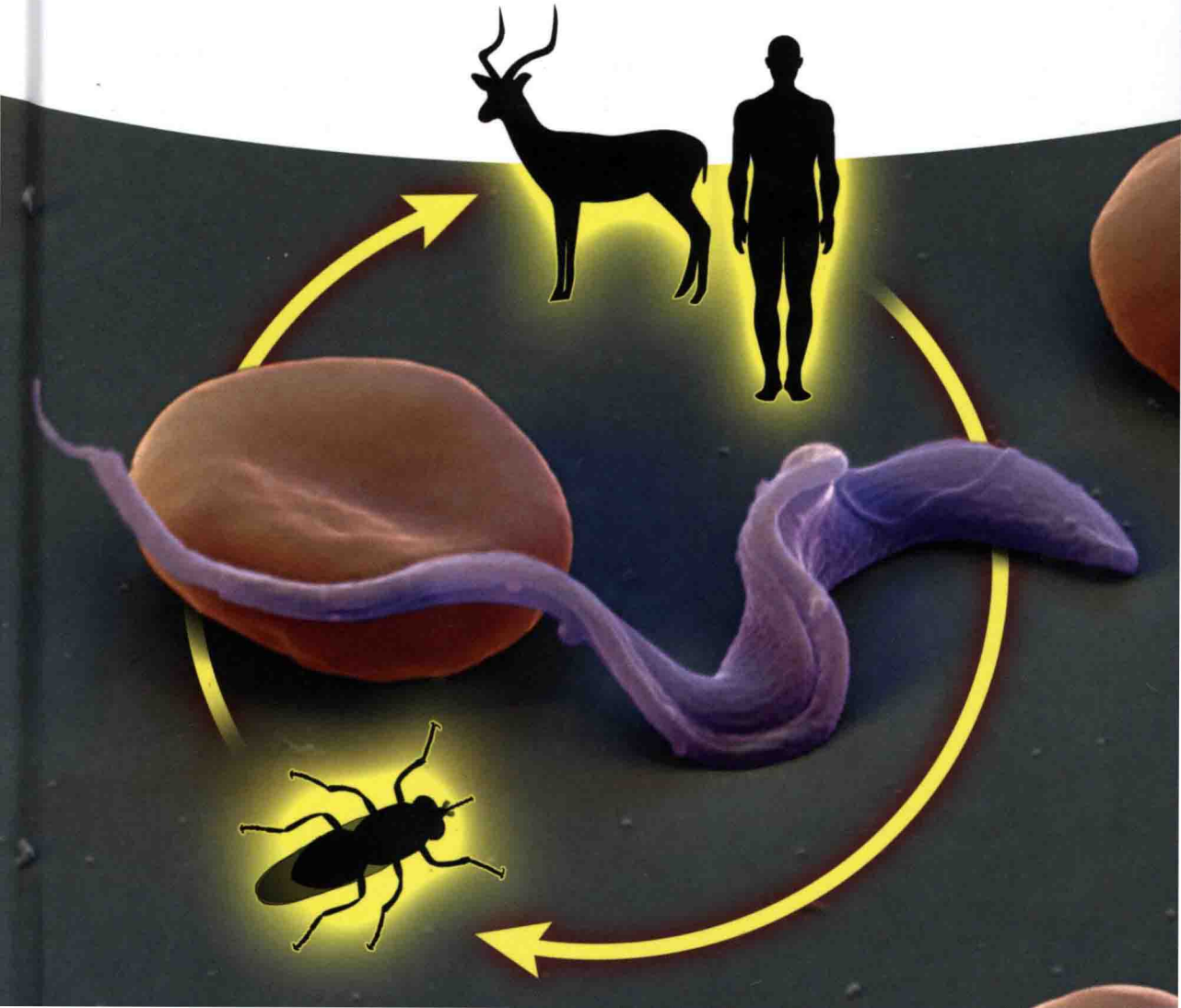
R. Lucius, B. Loos-Frank, R. P. Lane, R. Poulin,
C. W. Roberts, and R. K. Grencis

The Biology of Parasites



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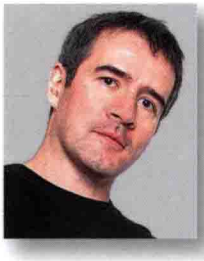
Filling the gap for a textbook combining classical parasitology with the latest research results from cell and molecular biology, this unique volume covers each class of animal parasites, including all major human parasites, and features a large introductory section focusing on their evolution and ecology. 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 leishmanaisis. 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.*

ISBN 978-3-527-32848-2

www.wiley-vch.de

Lucius • Loos-Frank • Lane
Poulin • Roberts • Grencis

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Robert Poulin, Craig W. Roberts, and Richard K. Grencis

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The Biology of Parasites

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WILEY-VCH
Verlag GmbH & Co. KGaA

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

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>.

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. Grencis

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 utlize 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

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