

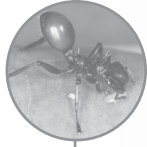
Cambridge University Press

978-0-521-19028-2 - Parasitism: The Diversity and Ecology of Animal Parasites: Second Edition

Timothy M. Goater, Cameron P. Goater, Gerald W. Esch

Frontmatter

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# Parasitism

The Diversity and Ecology of Animal Parasites

SECOND EDITION

Reflecting the enormous advances made in the field over the past 10 years, this text synthesizes the latest developments in the ecology and evolution of animal parasites against a backdrop of parallel advances in parasite systematics, biodiversity, and life cycles. It has been thoroughly revised to meet the needs of a new generation of parasitology students, whether their interest is in ecology, conservation biology, evolution, immunology, or health sciences.

Balancing traditional approaches in parasitology with modern studies in parasite ecology and evolution, the authors present basic ecological principles as a unifying framework to help students understand the complex phenomenon of parasitism. Richly illustrated with over 300 figures, the text is accompanied by case study boxes designed to help students appreciate the complexity and diversity of parasites and the scientists who study them. This unique approach, which is presented clearly and with a minimum of jargon and mathematical detail, encourages students to think generally and conceptually about parasites and parasitism.

**Timothy M. Goater** is Professor and former Chair in the Biology Department at Vancouver Island University, British Columbia, Canada. During the past 20 years he has taught courses in introductory biology, parasitology, ecological parasitology, invertebrate zoology, and entomology. His research interests focus on the population and community ecology of parasites.

**Cameron P. Goater** is Associate Professor and former Chair in the Department of Biological Sciences at the University of Lethbridge, Alberta, Canada. His parasitological research roots are in the community ecology of helminths of waterfowl on the Canadian prairies, and over the past 15 years he has taught courses in introductory biology, invertebrate biology, field biology, and symbiotic interactions. His current research interests are in the experimental ecology of helminth–host interactions.

**Gerald W. Esch** is Charles M. Allen Professor of Biology at Wake Forest University, North Carolina, USA, where he has taught for 47 years. He is widely regarded to be one of the world's leading ecological parasitologists, and served as Editor of the *Journal of Parasitology* for 19 years.

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[More information](#)

### **Advance praise for *Parasitism: The Diversity and Ecology of Animal Parasites, Second Edition***

“Their approach is synthetic, refreshingly original and effectively blends coverage of long-standing fundamentals of parasitology with modern advances in the field.”

Janine N. Caira, University of Connecticut, USA

“This is an extremely well written book that does an excellent job of integrating conceptual and organismal aspects of parasitology.”

Dale H. Clayton, University of Utah, USA

“There is a wealth of detail for well-selected examples, building on the rich experience of the authors as top-notch researchers and educators.”

Mark R. Forbes, Carleton University, Canada

“*Parasitism* gives the student both the systematic and zoological background to understand parasitology and the ecological and evolutionary context to understand why it is important. . . As a team, their approach is clear and scholarly, with many important updates since the first edition.”

Kevin D. Lafferty, US Geological Survey, University of California, Santa Barbara, USA

“This new edition will be a wonderful resource for teachers of undergraduate parasitology courses. The well-illustrated and easy-to-read text is unrivalled at the moment and will be a great tool to turn on a new generation of young minds to the wonders of parasitic organisms. A true parasitological tour de force!”

Robert Poulin, University of Otago, New Zealand

“A well-organized integration of the diversity of ideas and methods that characterize this new field of parasite ecology. The style is easily readable, the details extraordinary, and the story is told from the perspective of evolutionary thought. . . even the pros will learn from this book.”

Michael V. K. Sukhdeo, Rutgers University, USA

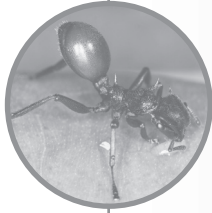
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## The Diversity and Ecology of Animal Parasites

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TIMOTHY M. GOATER

Vancouver Island University, British Columbia, Canada

CAMERON P. GOATER

University of Lethbridge, Alberta, Canada

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*We dedicate this book to our students,  
past, present, and future*

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Frontmatter

[More information](#)

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Frontmatter

[More information](#)

## CONTENTS

<i>List of boxes</i>	<i>page</i> ix		
<i>Foreword by John C. Holmes</i>	xi		
<i>Preface and acknowledgments</i>	xiii		
<b>1 Introduction</b>	1		
1.1 Encounters with parasites	1		
1.2 Scope	2		
1.3 Terminology	5		
1.4 Overview	10		
<b>2 Immunological aspects of parasitism</b>	16		
2.1 General considerations	16		
2.2 Vertebrate immunity	21		
2.3 Invertebrate immunity	31		
2.4 Ecological immunology	34		
<b>3 Protista: the unicellular eukaryotes</b>	40		
3.1 General considerations	40		
3.2 Form and function	41		
3.3 Biodiversity and life-cycle variation	43		
3.4 Phylogenetic relationships and classification	80		
<b>4 Microsporida: the intracellular, spore-forming fungi</b>	86		
4.1 General considerations	86		
4.2 Form and function	86		
4.3 Development and general life cycle	88		
4.4 Biodiversity and life-cycle variation	88		
4.5 Phylogenetic relationships and classification	93		
<b>5 Myxozoa: the spore-forming cnidarians</b>	96		
5.1 General considerations	96		
5.2 Form and function	97		
5.3 Development and general life cycle	97		
5.4 Biodiversity and life-cycle variation	100		
		5.5 Phylogenetic relationships and classification	106
		<b>6 Platyhelminthes: the flatworms</b>	113
		6.1 General considerations	113
		6.2 Temnocephalidea	114
		6.3 Udonellida	115
		6.4 Aspidobothrea	115
		6.5 Digenea	116
		6.6 Monogenea	145
		6.7 Gyrocotylidea	152
		6.8 Amphilinidea	153
		6.9 Eucestoda	153
		6.10 Phylogenetic relationships and classification	169
		<b>7 Acanthocephala: the thorny-headed worms</b>	179
		7.1 General considerations	179
		7.2 Form and function	179
		7.3 Nutrient uptake and metabolism	186
		7.4 Development and general life cycle	188
		7.5 Biodiversity and life-cycle variation	191
		7.6 Phylogenetic relationships and classification	192
		<b>8 Nematoda: the roundworms</b>	199
		8.1 General considerations	199
		8.2 Form and function	199
		8.3 Nutrient uptake and metabolism	208
		8.4 Development and general life cycle	209
		8.5 Biodiversity and life-cycle variation	211
		8.6 Phylogenetic relationships and classification	237
		<b>9 Nematomorpha: the hairworms</b>	244
		9.1 General considerations	244
		9.2 Form and function	244

Cambridge University Press

978-0-521-19028-2 - Parasitism: The Diversity and Ecology of Animal Parasites: Second Edition

Timothy M. Goater, Cameron P. Goater, Gerald W. Esch

Frontmatter

[More information](#)

## viii Contents

9.3	Development and general life cycle	246		
9.4	Biodiversity and ecology	247		
9.5	Phylogenetic relationships and classification	249		
<b>10</b>	<b>Pentastomida: the tongue worms</b>	252		
10.1	General considerations	252		
10.2	Form and function	252		
10.3	Nutrient uptake and metabolism	256		
10.4	Development and general life cycle	256		
10.5	Biodiversity and life-cycle variation	258		
10.6	Phylogenetic relationships and classification	260		
<b>11</b>	<b>Arthropoda: the joint-legged animals</b>	263		
11.1	General considerations	263		
11.2	Crustacea	264		
11.3	Chelicerata	289		
11.4	Hexapoda	308		
11.5	Phylogenetic relationships and classification	328		
<b>12</b>	<b>Parasite population ecology</b>	335		
12.1	General considerations	335		
12.2	Terminology and general approaches	336		
12.3	Introduction to parasite population ecology	337		
<b>13</b>	<b>Parasite community ecology</b>	356		
13.1	General considerations	356		
13.2	Introduction to parasite community ecology	357		
13.3	The structure of parasite infra-communities: restricted niches	361		
13.4	The structure of parasite communities: species richness	368		
<b>14</b>	<b>Parasite biogeography and phylogeography</b>		379	
14.1	General considerations		379	
14.2	Historical biogeography		380	
14.3	Ecological biogeography		386	
14.4	Applied aspects of parasite biogeography and phylogeography		389	
<b>15</b>	<b>Effects of parasites on their hosts: from individuals to ecosystems</b>		396	
15.1	General considerations		396	
15.2	Effects of parasites on host individuals		396	
15.3	Effects of parasites on host populations		411	
15.4	Effects of parasites on host communities and ecosystems		422	
<b>16</b>	<b>Evolution of host–parasite interactions</b>	432		
16.1	General considerations	432		
16.2	Parasite-mediated natural selection and evolution	432		
16.3	Genetic structure of parasite populations	441		
16.4	Introduction to host–parasite coevolution	446		
<b>17</b>	<b>Environmental parasitology: parasites as bioindicators of ecosystem health</b>	459		
17.1	General considerations	459		
17.2	Parasites as effect indicators of pollutant stress	460		
17.3	Parasites as environmental sentinels	470		
	<i>Glossary</i>		477	
	<i>Index</i>		489	

*The color plates are located between pages 248 and 249.*



Cambridge University Press

978-0-521-19028-2 - Parasitism: The Diversity and Ecology of Animal Parasites: Second Edition

Timothy M. Goater, Cameron P. Goater, Gerald W. Esch

Frontmatter

[More information](#)

## BOXES

1.1	A brief historical perspective of parasitology: pioneering scientists and their ground-breaking parasitological discoveries	page 4		
1.2	Parasite systematics: a phylogenetics primer	11		
2.1	Immunology: a terminology primer	18		
3.1	A plastid in apicomplexans: a promise for new drug therapies?	43		
3.2	Protists as hosts for microbial symbionts	44		
3.3	Giardiasis: epidemiology and pathogenesis of beaver fever	48		
3.4	Pathogenesis, epidemiology, and diagnosis of Chagas' disease	53		
3.5	Relapse and recrudescence in malaria	68		
3.6	Diagnosis of human malaria	74		
3.7	Classification of the Protista	81		
4.1	<i>Nosema ceranae</i> : an emerging pathogen of European honey bees	89		
4.2	Classification of the Microsporida	94		
5.1	Pathogenesis and epizootiology of whirling disease caused by <i>Myxobolus cerebralis</i>	101		
5.2	Proliferative kidney disease and solving the PKX organism mystery: an orphan parasite of bryozoans finds a taxonomic home in the Myxozoa	106		
5.3	Classification of the Myxozoa	108		
6.1	'Getting in': host location, recognition, and penetration by trematode miracidia	123		
6.2	'Getting out': the enigma of egg release in the human schistosomes	138		
6.3	Classification of the Platyhelminthes	172		
7.1	Acanthocephalans: masters of phenotypic manipulation	180		
7.2	Sexual selection in the Acanthocephala	188		
7.3	Classification of the Acanthocephala	194		
7.4	Phylogeny of the Acanthocephala and the evolution of parasitism		195	
8.1	Evolution of nematode life-cycle plasticity: developmental switching in <i>Strongyloides</i> spp.		213	
8.2	Entomopathogenic nematodes and their microbial symbionts: tapping their chemotherapeutic potential		216	
8.3	Transmammary transmission in hookworms		225	
8.4	<i>Wolbachia</i> spp.: endosymbiotic bacteria in filariid nematodes		234	
8.5	Classification of the Nematoda		239	
10.1	Pentastomids: masters of immunoevasion		254	
10.2	Fossil pentastomes from the Cambrian era suggest an alternative phylogenetic hypothesis		259	
10.3	Classification of the Pentastomida		261	
11.1	Astonishing metamorphosis in pennellid copepods and rhizocephalan barnacles		280	
11.2	On acorns, ticks, and mice: the epidemiology of Lyme disease		297	
11.3	A mite-y ecological and economic problem: <i>Varroa destructor</i> of honey bees		303	
11.4	Fly maggots as agents of lethal parasitism		322	
11.5	Parasite's web of death! Manipulation of spider web-building behavior by an insect parasitoid		326	
11.6	Classification of the Arthropoda		329	
13.1	Host immunity and parasite infracommunity structure: new evidence for an old hypothesis		366	
15.1	'Berry ants': parasite-induced fruit mimicry in neotropical rainforests		407	

Cambridge University Press

978-0-521-19028-2 - Parasitism: The Diversity and Ecology of Animal Parasites: Second Edition

Timothy M. Goater, Cameron P. Goater, Gerald W. Esch

Frontmatter

[More information](#)**x** List of boxes

- |   |   |
|---|---|
| <p>15.2 The politics of parasitism: sea lice, aquaculture, and the decline of salmon populations in coastal British Columbia 412</p> <p>15.3 Avian malaria determines the distributions, biodiversity, and community structure of Hawaii's native birds 423</p> <p>16.1 Parasite-mediated natural selection on the human HbS gene 433</p> | <p>16.2 Parasites, sex, and the Red Queen: castrating trematodes maintain sexual reproduction in New Zealand snails 449</p> <p>17.1 <i>Ribeiroia</i> and the complexity of amphibian deformities: a multidisciplinary approach to understanding the possible link to eutrophication 466</p> |
|---|---|

Cambridge University Press

978-0-521-19028-2 - Parasitism: The Diversity and Ecology of Animal Parasites: Second Edition

Timothy M. Goater, Cameron P. Goater, Gerald W. Esch

Frontmatter

[More information](#)

## FOREWORD

The ability of parasites to cause disease has always been an important reason to study them, and the teaching of parasitology has almost always been stimulated by conditions conducive to disease, such as war or climate change. Currently, zoonotic diseases emerging from altered ecosystems, or carried by arthropod vectors spreading their ranges due to climate changes, supply that stimulation. However, most of us who teach, or have taught, parasitology have chosen that topic because of the fascinating life cycles of many parasites and their complex interactions with their hosts. Much of that fascination stemmed from learning how parasites can affect the population dynamics of their hosts, or the behavior of the hosts, or even the evolution of their hosts. In addition, that fascination was based on how much parasites could tell us about the life of their hosts, such as their diet, travels, or evolution. Or even of the earth itself – some of the earliest evidence for continental drift was the similarity in parasites of amphibians in Africa and South America. Examples of all of these influences are provided in this book.

Many of the systems that parasitologists have used to show these fascinating features have become relatively easy to study due to new techniques, such as those in genomics and proteomics, which have provided new and more powerful ways to study systematics, evolution, and host–parasite relationships. This has attracted the attention of biologists with a wide variety of backgrounds, so that much of the very interesting work done on host–parasite systems recently has been done by those trained in other specialties, such as ecology, behavior, neurophysiology, and evolutionary biology. Very few of the students in senior-level parasitology courses will go on for further study in parasitology, but many more will go on for

further study in other biological specialties. Our courses, books, readings, and other materials used in our classes should be chosen to expose those students to the usefulness of parasites in investigations in their chosen fields.

This book is the best I have seen for that purpose. The authors have provided a wide-ranging review of the diversity of parasites, emphasizing those which provide examples of the insights provided by the use of the new techniques or examples of how parasites can provide new and exciting insights into other aspects of biology. One of the best features of this book is that it emphasizes the complexity of host–parasite systems, with full recognition that most of the outcomes are markedly dependent on the conditions in which that system is embedded. This emphasis on complexity starts with a chapter on immunity, which is the best and most succinct coverage I have ever seen of those aspects of immunity that are important in host–parasite interactions. This emphasis is most apparent in the most integrative chapters – those on the influence of parasites on their hosts, and parasite evolutionary ecology.

This is the book I would have loved to have been available when I was teaching. But, of course, it could not have been written then. Most of the more provocative insights, and especially the evidence for complexity and conditional outcomes of host–parasite encounters, have come in the past two decades since I retired. The field of parasitology has become increasingly fascinating, and its implications for other fields of biology more significant, in those two decades. Enjoy this book, as I have, and see where it leads you.

**John C. Holmes**

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Frontmatter

[More information](#)

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Frontmatter

[More information](#)

## PREFACE AND ACKNOWLEDGMENTS

In this second edition, we stay true to the philosophical approach that was adopted in the first. Thus, we continue to see a need for a single text with dual focus on the diversity *and* ecology/evolution of parasites. At the core, we feel that an ideal strategy for senior undergraduate and beginning graduate students to understand and appreciate breakthroughs in parasite ecology is through a solid understanding of parallel advances in parasite diversity, life-cycle variation, systematics, and functional morphology. By way of example, we suggest that an understanding of the role of falciparum malaria in determining the worldwide distribution of the human sickle-cell gene, and thus the role of parasites in mediating natural selection (Chapter 16), comes from an understanding of life-cycle variation, functional morphology, and biodiversity of the apicomplexans (Chapter 3). Likewise, real understanding of the evidence in support of the parasite hypothesis for the evolution and maintenance of sexual reproduction in molluscs (Chapter 16) comes from a detailed understanding of variation in life cycles and life histories of the platyhelminths (Chapter 6). This dual focus, under one cover, is the hallmark of this text.

Our aim is to provide students with a synthetic understanding of the biodiversity, ecology, and evolution of animal parasites. Thus, throughout most of the text, we unabashedly take a parasite-centered view of the phenomenon of parasitism. Yet, we also aim to provide insights on the nature of the host–parasite interaction itself. It is for this reason that following a brief introductory chapter, we provide an overview of vertebrate and invertebrate immunity, and the new discipline of ecological immunology. We turn again and again to the importance of fundamental immunological principles throughout the text.

There are now nine biodiversity chapters (Chapters 3–11). We have added chapters on the Myxozoa, Microsporida, and Nematomorpha,

reflecting developments in their systematics, and their value as models in parasite ecology and evolution. By necessity, the ‘phylogenetic relationships and classification’ sections for all of the diversity chapters have been updated, adopting the most current molecular-based taxonomic schemes. The protist chapter in particular has been completely revised from the first edition, reflecting the monumental changes in protist systematics. New text boxes that highlight key areas of development, and the scientists behind them, are integrated into each of these chapters. New life cycle diagrams and dozens of new photographs and micrographs have also been incorporated. A color plate section has been added, showcasing dramatic photographs of parasites in or on their hosts.

Armed with a solid background in parasite biodiversity, systematics, and functional biology, Chapters 12–17 cover advances in the ecology and evolution of parasites. The titles and content of these chapters have been completely revised from the first edition, reflecting in part, the interests and backgrounds of the new authors. Yet the substantial revisions also reflect the pace of development in methodologies and in overall approaches that have matured the field over the past decade. While some of these developments have confirmed earlier ideas, others have revolutionized our understanding of even the most fundamental aspects of the parasitic way of life. Thus, the incorporation of new model host–parasite interactions that are amenable to manipulation in the laboratory and field have provided key insights into how parasite populations are regulated and how they are distributed among hosts in space and time (Chapter 12). Studies at the community level (Chapter 13) have also benefited from rigorous empirical approaches involving key model systems where the composition of component species can be manipulated. In Chapter 14, we see how advances in molecular biology, genomics, and remote sensing have

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Frontmatter

[More information](#)

transformed our understanding of parasite biogeography and phylogeography. Coverage in Chapter 15 is focused on the diverse manner in which parasites can affect the biology of their hosts, whether it is at the level of the host individual, or on the structure of entire host ecosystems. Again, key advances stemming from empirical, hypothesis-testing approaches involving selected model systems have markedly advanced our understanding of the magnitude of these effects, and their underlying mechanisms. The focus in Chapter 16 takes the next logical step, covering the manner in which parasites affect the evolutionary and coevolutionary trajectory of their hosts. We conclude the text by summarizing the nature of the parasite/human/habitat interface, and how the multidisciplinary field of environmental parasitology (Chapter 17) can assist in interpreting the nature of host–parasite interactions in the face of anthropogenic change.

As with all projects of this scope, this book is a collaborative effort. We extend sincere thanks to the authors of the first edition, Al Bush, Jackie Fernández, and Dick Seed for their initial vision and dedication. Several of their line drawings and photographs, incorporating the image-editing skills of Maggie Bush, have been retained here. Numerous colleagues offered valuable suggestions on specific sections/chapters, especially Carter Atkinson, Mark Blaxter, Katharina Dittmar, Eric Hoberg, Jens Høeg, Kayla King, David Marcogliese, Jim Mertins, Beth Okamura, George Poinar, John Webster, Chris Whipps, and Stephen Yanoviak. We also appreciate the insightful comments John Holmes provided for several chapters. Several of our former students, especially Martin Anglestad, Melissa Beck, Aaron Jex, Chelsea Matisz, Phillip Morrison, Vanessa Phillips, Brad van Paridon, and Chris Whipps helped to review and edit chapters. Their perspectives helped clarify and focus our efforts.

This revision contains many new drawings, as well as new photographs and micrographs. Bill Pennell spent many hours of his retirement taking several new photographs, as well as editing countless others. Doug

Bray and Brad van Paridon took several of the new scanning electron micrographs. We thank our colleagues for contributing extensive new data figures, photographs, and micrographs for the new edition. Their generous contributions are acknowledged in the figure captions. John Sullivan is especially thanked for sharing several of his photographs from his excellent parasitological resource, *A Color Atlas of Parasitology*. Several new life-cycle diagrams and line drawings are incorporated into this edition, thanks to Chelsea Matisz, Lisa Esch McCall, and Danielle Morrison. Danielle, in particular, is thanked for her patience and dedication in preparing, labeling, and editing many of the new figures and photographs.

Vancouver Island University is thanked for providing Tim Goater the sabbatical and professional development funds that enabled this revision to take shape. Special thanks also to Mike Steele, David Marcogliese, and Herman Eure for providing office space during his sabbatical, as well as Eric Demers, Larissa Nelson, Wendy Simms, and Jane Watson for their enthusiastic encouragement throughout the project. Likewise, Cam thanks Dean Chris Nicol and Chair Brent Selinger for moral support and teaching relief during the peak phases of this revision, and colleagues Doug Bray, Doug Colwell, Andy Hurly, Joe Rasmussen, and Brian Wisenden for their constant support. Cam also extends thanks to Barb Johnson and staff at Waterton Lakes National Park for access to their cabin during key writing phases. Most sincere thanks also to Lori Goater for her monumental patience and support and to Ben and Ali for frequently reminding their dad, and their uncle, that parasite ecologists come in all ages.

Our primary editor, Katrina Halliday and her assistant, Megan Waddington at Cambridge University Press are thanked for all of their help addressing our many queries and, especially, for their patience and devotion to seeing this project to its completion.

**Timothy M. Goater**  
**Cameron P. Goater**

## About this edition

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The first edition of our book was published in 2001. Al Bush, Jackie Fernández, and Dick Seed were co-authors, along with myself. Sadly, Al died in 2010. Further, Jackie stepped aside to raise two sons and Dick retired from his faculty position at the University of North Carolina-Chapel Hill. As the only original author that was still active professionally, it became my responsibility to recruit new co-authors. Given the overall theme and target audience of the text, my choice fell upon brothers, Tim and Cam Goater. Tim was a former Ph.D. student of mine at Wake Forest University, and Cam was a former Ph.D. student with Clive Kennedy at the University of Exeter. Both brothers were mentored by Al Bush at Brandon University in Manitoba, Canada. Tim and Cam have extensive experience teaching senior undergraduate

courses in parasitology and ecology, and Cam extends his teaching perspectives to the mentoring of graduate students. Both have diverse and complementary research backgrounds that, together, span most areas of modern parasitology.

Throughout the writing of both editions, I maintained my duties as Editor of the *Journal of Parasitology*, as well as my teaching. Mrs. Vickie Hennings, my Editorial Assistant for the Journal, continued her responsibilities while I was occasionally subsumed by the book. Cindy Davis and Zella Johnson, both long-term secretaries for the Department of Biology at Wake Forest University, are thanked for their help as well. I especially express my appreciation to Ann for being such a marvelous 'listener' and for her constant support from the book's inception.

**Gerald W. Esch**