SEVENTH EDITION

INTRODUCTION TO NOODERN VIROLOGY

N.J. DIMMOCK, A.J. EASTON AND K.N. LEPPARD

WILEY Blackwell

Introduction to Modern Virology

Introduction to Modern Virology

N. J. Dimmock A. J. Easton K. N. Leppard

School of Life Sciences University of Warwick Coventry

SEVENTH EDITION

WILEY Blackwell

This edition first published 2016 © 2016 by John Wiley & Sons, Ltd

First to sixth editions © 1974, 1980, 1987, 1994, 2001, 2007 by Blackwell Publishing Ltd

Registered office: John Wiley & Sons, Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial offices: 9600 Garsington Road, Oxford, OX4 2DQ, UK

The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK 111 River Street, Hoboken, NJ 07030-5774, USA

For details of our global editorial offices, for customer services and for information about how to apply for permission to reuse the copyright material in this book please see our website at www.wiley.com/wiley-blackwell.

The right of the author to be identified as the author of this work has been asserted in accordance with the UK Copyright, Designs and Patents Act 1988.

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, except as permitted by the UK Copyright, Designs and Patents Act 1988, without the prior permission of the publisher.

Designations used by companies to distinguish their products are often claimed as trademarks. All brand names and product names used in this book are trade names, service marks, trademarks or registered trademarks of their respective owners. The publisher is not associated with any product or vendor mentioned in this book.

Limit of Liability/Disclaimer of Warranty: While the publisher and author(s) have used their best efforts in preparing this book, they make no representations or warranties with respect to the accuracy or completeness of the contents of this book and specifically disclaim any implied warranties of merchantability or fitness for a particular purpose. It is sold on the understanding that the publisher is not engaged in rendering professional services and neither the publisher nor the author shall be liable for damages arising herefrom. If professional advice or other expert assistance is required, the services of a competent professional should be sought.

Library of Congress Cataloging-in-Publication Data

Dimmock, N. J. Introduction to modern virology / N. J. Dimmock, A. J. Easton, K. N. Leppard, School of Life Sciences, University of Warwick, Coventry. – Seventh edition. pages cm

Includes index.
ISBN 978-1-119-97810-7 (pbk.)
1. Virology. 2. Virus diseases. I. Easton, A. J. (Andrew J.) II. Leppard, K. N. (Keith N.) III. Title.
QR360.D56 2016
579.2–dc23

2015031818

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

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic books.

Cover design by Jeremy Tilston

Set in 10/12.5pt MeridienLTStd-Roman by Thomson Digital, Noida, India

Contents in brief

Preface		xvii
About the co	mpanion website	xix
PART I	THE NATURE OF VIRUSES	1
Chapter 1	Towards a definition of a virus	3
Chapter 2	The structure of virus particles	13
Chapter 3	Classification of viruses	30
Chapter 4	The evolution of viruses	39
Chapter 5	Techniques for studying viruses	52
PART II	VIRUS GROWTH IN CELLS	67
Chapter 6	The process of infection: I. Virus attachment and entry into cells	69
Chapter 7	The process of infection: IIA. The replication of viral DNA	86
Chapter 8	The process of infection: IIB. Genome replication in RNA viruses	105
Chapter 9	The process of infection: IIC. The replication of RNA viruses with a DNA	
	intermediate and vice versa	121
Chapter 10	The process of infection: IIIA. Gene expression in DNA viruses	
	and reverse-transcribing viruses	136
Chapter 11	The process of infection: IIIB. Gene expression and its regulation in RNA viruses	156
Chapter 12	The process of infection: IV. The assembly of viruses	179
PART III	VIRUS INTERACTIONS WITH THE WHOLE ORGANISM	199
Chapter 13	Innate and intrinsic immunity	201
Chapter 14	The adaptive immune response	218
Chapter 15	Interactions between animal viruses and cells	237
Chapter 16	Animal virus-host interactions	248
Chapter 17	Mechanisms in virus latency	261
Chapter 18	Transmission of viruses	279
PART IV	VIRUSES AND HUMAN DISEASE	293
Chapter 19	Human viral disease: an overview	295
Chapter 20	Influenza virus infection	309
Chapter 21	HIV and AIDS	327

Contents in brief

Chapter 22	Viral hepatitis	347
Chapter 23	Vector-borne infections	362
Chapter 24	Exotic and emerging viral infections	376
Chapter 25	Carcinogenesis and tumour viruses	388
Chapter 26	Vaccines and immunotherapy: the prevention of virus diseases	409
Chapter 27	Antiviral therapy	431
Chapter 28	Prion diseases	443
PART V	VIROLOGY – THE WIDER CONTEXT	459
Chapter 29	The economic impact of viruses	461
Chapter 30	Recombinant viruses: making viruses work for us	472
Chapter 31	Viruses: shaping the planet	484
Index		491

Preface			xvii
About the c	ompani	on website	xix
PART I	THE	NATURE OF VIRUSES	1
Chapter 1	Towa	rds a definition of a virus	3
	1.1	Discovery of viruses	4
	1.2	Multiplication of viruses	5
	1.3	The virus multiplication cycle	6
	1.4	Viruses can be defined in chemical terms	7
	1.5	Multiplication of bacterial and animal viruses is fundamentally similar	10
	1.6	Viruses can be manipulated genetically	11
	1.7	Properties of viruses	11
	1.8	Origin of viruses	12
	Key	points	12
	Furt	her reading	12
Chapter 2	The structure of virus particles		13
	2.1	Virus particles are constructed from subunits	13
	2.2	The structure of filamentous viruses and nucleoproteins	14
	2.3	The structure is of isometric virus particles	15
	2.4	Enveloped (membrane-bound) virus particles	24
	2.5	Virus particles with head-tail morphology	27
	2.6	Frequency of occurrence of different virus particle morphologies	28
	2.7	Principles of disassemply: virus particles are metastable	28
	Key	points	29
	Furt	her reading	29
Chapter 3	Class	ification of viruses	30
	3.1	Classification on the basis of disease	30
	3.2	Classification on the basis of host organism	31
	3.3	Classification on the basis of virus particle morphology	31
	3.4	Classification on the basis of viral nucleic acids	32
	3.5	Classification on the basis of taxonomy	34
	3.6	Satellites, viroids and prions	35
	Key	points	37
	Furt	her reading	38

Chapter 4	The evolution of viruses	39
	4.1 Mechanisms of virus evolution	40
	4.2 The potential for rapid evolution: mutation and quasispecies	40
	4.3 Rapid evolution: recombination	43
	4.4 Rapid evolution: reassortment	43
	4.5 Evolution to find a host, and subsequent co-evolution with the host	46
	Key points	51
	Questions	51
	Further reading	51
Chapter 5	Techniques for studying viruses	52
	5.1 Culturing wild virus isolates	52
	5.2 Enumeration of viruses	54
	5.3 Measuring infectious virus titres	55
	5.4 Measuring physical virus titres	57
	5.5 Detecting virus in a sample	58
	5.6 Understanding virus replication cycles	62
	5.7 Viral genetics and reverse genetics	63
	5.8 Systems-level virology	63
	Key points	65
	Questions	65
	Further reading	65
PART II	VIRUS GROWTH IN CELLS	67
Chapter 6	The process of infection: I. Virus attachment and entry into cells	69
	6.1 Infection of animal cells: the nature and importance of receptors	69
	6.2 Infection of animal cells: enveloped viruses	73
	6.3 Infection of animal cells: non-enveloped viruses	78
	6.4 Infection of plant cells	80
	6.5 Infection of bacteria	81
	6.6 Infection of cells: post-entry events	82
	6.7 Virus entry: cell culture and the whole organism	84
	Key points	84
	Questions	84
	Further reading	85
Chapter 7	The process of infection: IIA. The replication of viral DNA	86
	7.1 The universal mechanism of DNA synthesis	87
	7.2 Replication of circular double-stranded DNA genomes	90
	7.3 Replication of linear double-stranded DNA genomes that can form circles	93
	7.4 Replication of linear double-stranded DNA genomes that do not circularize	96
	7.5 Replication of single-stranded circular DNA genomes	100
	7.6 Replication of single-stranded linear DNA genomes	100
	7.7 Dependency versus autonomy among DNA viruses	103

		Contents	1)
	Key points		103
	Questions		103
	Further reading		103
Chapter 8	The process of infection: IIB. Genome replication in RNA viruses		105
	8.1 Nature and diversity of RNA virus genomes		106
	8.2 Regulatory elements for RNA virus genome synthesis		106
	8.3 Synthesis of the RNA genome of Baltimore class 3 viruses		111
	8.4 Synthesis of the RNA genome of Baltimore class 4 viruses		111
	8.5 Synthesis of the RNA genome of Baltimore class 5 viruses		115
	8.6 Synthesis of the RNA genome of viroids and hepatitis delta virus		118
	Key points		119
	Questions		119
	Further reading		119
Chapter 9	The process of infection: IIC. The replication of RNA viruses with a DNA		
	intermediate and vice versa		121
	9.1 The retrovirus replication cycle		122
	9.2 Discovery of reverse transcription		122
	9.3 Retroviral reverse transcriptase		123
	9.4 Mechanism of retroviral reverse transcription		125
	9.5 Integration of retroviral DNA into cell DNA		128
	9.6 Production of retrovirus progeny genomes		130
	9.7 Spumaviruses: retrovirus with unusual features		131
	9.8 The hepadnavirus replication cycle		131
	9.9 Mechanism of hepadnavirus reverse transcription		131
	9.10 Comparing reverse transcribing viruses		134
	Key points		134
	Questions		134
	Further reading		135
Chapter 10	The process of infection: IIIA. Gene expression in DNA viruses		400
	and reverse-transcribing viruses		136
	10.1 The DNA viruses and retroviruses: Baltimore classes 1, 2, 6 and 7		137
	10.2 Polyomaviruses		138
	10.3 Papillomaviruses10.4 Adenoviruses		142 144
	10.4 Adenoviruses 10.5 Herpesviruses		144
	10.5 Poxviruses		147
	10.7 Parvoviruses		149
	10.8 Retroviruses		150
	10.9 Hepadnaviruses		153
	10.10 DNA bacteriophages		154
	Key points		154
	Questions		155
	Further reading		155
	- around reading		. , ,

Chapter 11	The p	rocess of infection: IIIB. Gene expression and its regulation in RNA viruses	156
	11.1	The RNA viruses: Baltimore classes 3, 4 and 5	157
	11.2	Reoviruses	158
	11.3	Picornaviruses	163
	11.4	Alphaviruses	164
	11.5	Coronaviruses	166
	11.6	Negative sense RNA viruses with segmented genomes	169
	11.7	Orthomyxoviruses	169
	11.8	Arenaviruses	173
	11.9	Negative sense RNA viruses with non-segmented, single stranded	
		genomes: rhabdoviruses and paramyxoviruses	174
	Key p	points	177
	Ques	tions	178
	Furth	ner reading	178
Chapter 12	The p	rocess of infection: IV. The assembly of viruses	179
	12.1	Self-assembly from mature virion components	180
	12.2	Assembly of viruses with a helical structure	180
	12.3	Assembly of viruses with an isometric structure	184
	12.4	Assembly of complex viruses	187
	12.5	Sequence-dependent and -independent packaging of virus	
		DNA in virus particles	189
	12.6	The assembly of enveloped viruses	190
	12.7	Segmented virus genomes: the acquisition of multiple nucleic	
		acid molecules	194
	12.8	Maturation of virus particles	195
		points	196
	Ques		197
	Furth	ner reading	197
PART III	VIRUS	S INTERACTIONS WITH THE WHOLE ORGANISM	199
Chapter 13	Innat	e and intrinsic immunity	201
	13.1	Innate immune responses in vertebrates – discovery of interferon	202
	13.2	Induction of type 1 interferon responses	203
	13.3	Virus countermeasures to innate immunity	207
	13.4	TRIM proteins and immunity	209
	13.5	Intrinsic resistance to viruses in vertebrates	210
	13.6	Innate and intrinsic immunity and the outcome of infection	212
	13.7	RNAi is an important antiviral mechanism in invertebrates and plants	212
	13.8	Detecting and signalling infection in invertebrates and plants	214
	13.9	Virus resistance mechanisms in bacteria and archaea	215
		points	216
	Ques		217
	Keter	rences	217

Contents	

Chapter 14	The adaptive immune response	218
	14.1 General features of the adaptive immune system	219
	14.2 Cell-mediated immunity	221
	14.3 Antibody-mediated humoral immunity	226
	14.4 Virus evasion of adaptive immunity	232
	14.5 Age and adaptive immunity	233
	14.6 Interaction between the innate and adaptive immune systems	233
	Key points	234
	Questions	236
	Further reading	236
Chapter 15	Interactions between animal viruses and cells	237
	15.1 Acutely cytopathogenic infections	238
	15.2 Persistent infections	238
	15.3 Latent infections	241
	15.4 Transforming infections	243
	15.5 Abortive infections	243
	15.6 Null infections	244
	15.7 How do animal viruses kill cells?	244
	Key points	246
	Questions	247
	Further reading	247
Chapter 16	Animal virus-host interactions	248
	16.1 Cause and effect: Koch's postulates	248
	16.2 A classification of virus–host interactions	249
	16.3 Acute infections	252
	16.4 Subclinical infections	253
	16.5 Persistent and chronic infections	254
	16.6 Latent infections	256
	16.7 Slowly progressive diseases	257
	16.8 Virus-induced tumours	258
	Key points	259
	Questions	260
	Further reading	260
Chapter 17	Mechanisms in virus latency	261
	17.1 The latent interaction of virus and host	261
	17.2 Gene expression and the lytic and lysogenic life of bacteriophage λ	263
	17.3 Herpes simplex virus latency	270
	17.4 Epstein-Barr virus latency	274
	17.5 Latency in other herpesviruses	275
	17.6 HIV-1 latency	277
	Key points	277
	Questions	278
	Further reading	278

xi

Chapter 18	Transmission of viruses	279
	18.1 Virus transmission cycles	279
	18.2 Barriers to transmission	281
	18.3 Routes of horizontal transmission in animals	282
	18.4 Vertical transmission	285
	18.5 Vector-borne viruses and zoonotic transmission	287
	18.6 Epidemiology of virus infections	289
	18.7 Sustaining infection in populations	290
	Key points	291
	Questions	291
	Further reading	291
PART IV	VIRUSES AND HUMAN DISEASE	293
Chapter 19	Human viral disease: an overview	295
	19.1 A survey of human viral pathogens	295
	19.2 Factors affecting the relative incidence of viral disease	297
	19.3 Factors determining the nature and severity of viral disease	299
	19.4 Common signs and symptoms of viral infection	301
	19.5 Acute viral infection 1: gastrointestinal infections	302
	19.6 Acute viral infection 2: respiratory infections	304
	19.7 Acute viral infection 3: systemic spread	306
	19.8 Acute viral disease: conclusions	306
	Key points	307
	Questions	308
	Further reading	308
Chapter 20	Influenza virus infection	309
	20.1 The origins of human influenza viruses	309
	20.2 Influenza virus replication	315
	20.3 Influenza virus infection and disease	316
	20.4 Virus determinants of disease	321
	20.5 Host factors in influenza virus disease	322
	20.6 The immune response and influenza virus	323
	20.7 Anti-influenza treatment	324
	Key points	325
	Questions	326
	Further reading	326
Chapter 21	HIV and AIDS	327
	21.1 Origins and spread of the HIV pandemic	327
	21.2 Molecular biology of HIV	330
	21.3 HIV transmission and tropism	338
	21.4 Course of HIV infection: pathogenesis and disease	339

		Contents	xiii
	21.5 Immunological abnormalities during HIV infection		342
	21.6 Prevention and control of HIV infection		343
	Key points		345
	Questions		346
	Further reading		346
Chapter 22	Viral hepatitis		347
	22.1 The signs and symptoms of hepatitis		347
	22.2 Hepatitis A virus infections		349
	22.3 Hepatitis E virus infections		350
	22.4 Hepatitis B virus infections		352
	22.5 Hepatitis D virus infections		355
	22.6 Hepatitis C virus infections		356
	Key points		359
	Questions		361
	Further reading		361
Chapter 23	Vector-borne infections		362
	23.1 Arboviruses and their hosts		362
	23.2 Yellow fever virus		363
	23.3 Dengue virus		367
	23.4 Chikungunya virus		369
	23.5 West Nile virus in the USA		372
	Key points		375
	Questions		375
	Further reading		375
Chapter 24	Exotic and emerging viral infections		376
	24.1 Ebola and Marburg viruses: emerging filoviruses		377
	24.2 Hendra and Nipah viruses: emerging paramyxoviruses		381
	24.3 SARS and MERS: emerging coronaviruses		383
	24.4 Predicting the future: clues from analysis of the genomes of		
	previously unknown viruses		386
	Key points		386
	Questions		386
	Further reading		387
Chapter 25	Carcinogenesis and tumour viruses		388
	25.1 Immortalization, transformation and tumourigenesis		389
	25.2 Oncogenic viruses		390
	25.3 Polyomaviruses, papillomaviruses and adenoviruses: the small	l	
	DNA tumour viruses as experimental models		394
	25.4 Papillomaviruses and human cancer		398
	25.5 Polyomaviruses and human cancer		399
	25.6 Herpesvirus involvement in human cancers		400
	25.7 Retroviruses as experimental model tumour viruses		402
	25.8 Retroviruses and naturally-occurring tumours		404

	25.9 Hepatitis viruses and liver cancer	405
	25.10 Prospects for the control of virus-associated cancers	406
	Key points	407
	Questions	408
	Further reading	408
Chapter 26	Vaccines and immunotherapy: the prevention of virus diseases	409
·	26.1 The principles of vaccination	411
	26.2 Whole virus vaccines	412
	26.3 Advantages, disadvantages and difficulties associated with	
	whole virus vaccines	415
	26.4 Subunit vaccines	420
	26.5 Advantages, disadvantages and difficulties associated with subunit vaccines	421
	26.6 Considerations for the generation and use of vaccines	422
	26.7 Adverse reactions and clinical complications with vaccines	423
	26.8 Eradication of virus diseases by vaccination	425
	26.9 Immunotherapy for virus infections	428
	26.10 Adverse reactions and clinical complications with immunotherapy	429
	Key points	429
	Questions	430
	Further reading	430
Chapter 27	Antiviral therapy	431
	27.1 Scope and limitations of antiviral therapy	431
	27.2 Antiviral therapy for herpesvirus infections	432
	27.3 Antiviral therapy for influenza virus infections	434
	27.4 Antiviral therapy for HIV infections	435
	27.5 Antiviral therapy for hepatitis virus infections	439
	27.6 Therapy for other virus infections	440
	Key Points	441
	Questions	441
	Further Reading	442
Chapter 28	Prion diseases	443
	28.1 The spectrum of prion diseases	443
	28.2 The prion hypothesis	444
	28.3 The aetiology of prion diseases	447
	28.4 Prion disease pathogenesis	448
	28.5 Bovine spongiform encephalopathy (BSE)	451
	28.6 BSE and the emergence of variant CJD	453
	28.7 Concerns about variant CJD in the future	454
	28.8 Unresolved issues	455
	Key points	456
	Questions	456
	Further reading	456

		Contents	×
PART V	VIROLOGY – THE WIDER CONTEXT		459
Chapter 29	The economic impact of viruses		461
	29.1 The economics of virus infections of humans		462
	29.2 The economics of virus infections of animals		464
	29.3 The economics of virus infections of plants		466
	29.4 The Netherlands tulip market crash		469
	Key points		470
	Further reading		470
Chapter 30	Recombinant viruses: making viruses work for us		472
	30.1 Recombinant viruses as vaccines		473
	30.2 Recombinant viruses for gene therapy		474
	30.3 Retroviral vectors for gene therapy		476
	30.4 Adenovirus vectors for gene therapy		478
	30.5 Parvovirus vectors for gene therapy		480
	30.6 Oncolytic viruses for cancer therapy		480
	30.7 Recombinant viruses in the laboratory		482
	Key points		482
	Questions		482
	Further reading		483
Chapter 31	Viruses: shaping the planet		484
	31.1 Virus infections can give a host an evolutionary advantage		484
	31.2 Endogenous retroviruses and host biology		485
	31.3 Bacteriophage can be pathogenicity determinants for their hosts		488
	31.4 Cyanophage impacts on carbon fixation and oceanic ecosystems		488
	31.5 Virology and society: for good or ill		489
	Key points		490
	Questions		490
	Further reading		490
Index			101

Index

Preface

As before, our aim in this 7th edition of Introduction to Modern Virology is to provide a broad introduction to virology, which includes the nature of viruses, the interaction of viruses with their hosts, and the consequences of those interactions that lead to the diseases we see. In doing so, we have focused predominantly on viruses that infect humans, with some examples of viruses of other animals where they illustrate a specific point. However, in the sections covering general principles and processes of virology, we have also included bacterial and plant viruses. The revised text is aimed at undergraduate students at all levels and postgraduates who are learning virology as a new subject.

We have retained the four thematic sections that were introduced in the previous edition. These cover the fundamental nature of viruses, their growth in cells, their interactions with the host organism, and their role as agents of human disease. To complement these, we have added a fifth section that incorporates material relating to virology in a wider context. Each section contains a series of chapters that are typically focused on a topic rather than concentrating on a single virus. Inevitably, some of these topics relate to information in different parts of the book and we have included extensive cross-referencing to allow the reader to explore a broader picture than is possible within a single chapter.

The pace of discovery in the field of virology has continued unabated since the last edition. Our knowledge of the molecular detail of viruses, including their interaction with the host, has increased considerably and continues to grow. We have tried to explore the breadth of this new information while retaining a concise style. Inevitably, this has meant that we have had to choose specific examples while leaving out many others of interest, but we have tried to use examples which demonstrate broad principles as well as specific detail. There is suggested reading for those who want to follow up a subject in more depth.

The study of viruses is as topical and important as ever. The global impact of HIV and chronic hepatitis virus infections continues to be severe and, as we completed this edition, we are seeing hopeful indications of the ending of the most devastating Ebola virus outbreak ever recorded. Beyond these direct impacts on our health, viruses also continue to threaten us through effects on food supplies and our economies. Thus, a good basic understanding of viruses is important for generalists and specialists alike. Our aim in writing this book has been to try to make such understanding as accessible as possible, allowing students across the biosciences spectrum to improve their knowledge of these fascinating entities.

New to this edition

This edition contains a number of important changes and innovations. A major change has been the expansion of the consideration of immunology which now covers two chapters, one on innate immunity and the other on adaptive immunity. This reflects the growing understanding of the importance of the immune system in determining the outcome of virus infection and the contribution of the immune system to viral diseases. These chapters also consider some of the ways that viruses evade the immune response. The consideration Preface

of vaccines and antivirals has been expanded and separated into two new chapters to reflect the importance of these approaches to prevention and treatment. Virus evolution is considered in more detail than previously, and we have added new chapters on viral hepatitis, influenza, vector-borne diseases, and exotic and emerging viral infections. Finally, in the last section we have introduced three new chapters on the broader aspects of the influence of viruses on our lives, focusing on the economic impact of virus infections, the ways we can use viruses in clinical and other spheres, and the impact that viruses have on the planet and almost every aspect of our lives.

The text is supplemented throughout by information boxes of two types. These are now distinguished by different colours. One type of box provides supporting information or additional detail about the subject matter of the chapter while the other provides the experimental evidence by which selected key points were established. The aim is to assist the reader in understanding the facts but to also allow them to appreciate the nature of the evidence that underpins them.

We very much hope that the 7th edition of *Introduction to Modern Virology* will enrich the virology experience of students and teachers alike.

Finally, we would like express our thanks the staff at Wiley for their generous support throughout the production of this book.

Nigel Dimmock, Andrew Easton and Keith Leppard University of Warwick, October 2015

About the companion website

This book is accompanied by a companion website:

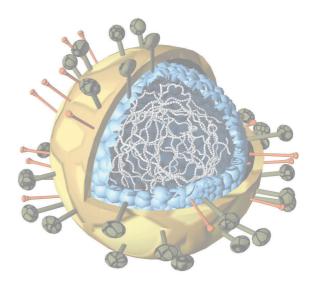
www.wiley.com/go/dimmock/virology

The website includes powerpoints of all figures from the book for downloading

Part I

The nature of viruses

- **1** Towards a definition of a virus 3
- **2** The structure of virus particles 13
- **3** Classification of viruses 30
- **4** The evolution of viruses 39
- **5** Techniques for studying viruses 52



Chapter 1

Towards a definition of a virus

Viruses occur universally, but they can only be detected indirectly. Viruses are obligate intracellular parasites that require a host within which they replicate. Although they are well known for causing disease, most viruses coexist peacefully with their hosts.

Chapter 1 Outline

- 1.1 Discovery of viruses
- 1.2 Multiplication of viruses
- 1.3 The virus multiplication cycle
- 1.4 Viruses can be defined in chemical terms
- 1.5 Multiplication of bacterial and animal viruses is fundamentally similar
- 1.6 Viruses can be manipulated genetically
- 1.7 Properties of viruses
- 1.8 Origin of viruses

Viruses are arguably the most ubiquitous and widespread group of organisms on the planet, with every animal, plant and protist species susceptible to infection. The efficiency of replication demonstrated by viruses is such that the infection of a single host can generate more new viruses than there are individuals in the host population. For example, a single human infected with influenza virus can shed sufficient virus particles to be theoretically capable of infecting the entire human population. While not every species has been examined for the presence of viruses, those that have been tested have all yielded up new virus isolates. Further, not only do viruses occur universally but each species has its own specific range of viruses that, by and large, infects only that species. In recent years, the application of new nucleic acid sequencing techniques has demonstrated that a vast array of previously unknown viruses remains to be studied.

Current estimates of the number of individual viruses on earth suggest that they considerably exceed the total number of stars in the known universe, i.e. more than 10^{23} (100 sextillion). This vast number raises questions as to what the viruses are doing there, and what selective advantage, if any, they afford to the species that host them. The answer to the first of these is the same as if the question was posed about any organism – it is simply occupying a particular environmental niche which, in the case of a virus, is another species. The answer to whether or not any benefit accrues for hosting a virus is usually not known, though the adverse effects of virus infections are all too well known. However, it is clear that, despite their adverse effects and the dramatic depictions of viruses in popular media and cinema, viruses have not made their hosts extinct.

Introduction to Modern Virology, Seventh Edition. N. J. Dimmock, A. J. Easton and K. N. Leppard. © 2016 John Wiley & Sons, Ltd. Published 2016 by John Wiley & Sons, Ltd.