

Contents

List of contributors

ix

Introduction

1

Laura A. Katz and Debashish Bhattacharya

Part I

5

1 Current perspectives on high-level groupings of protists

7

Alastair G.B. Simpson and David J. Patterson

Part II Evolutionary genomics of eukaryotic microbes

31

2 Comparative genomics of *Plasmodium* species

33

Jane M. Carlton

3 The genomes of dinoflagellates

48

Jeremiah D. Hackett and Debashish Bhattacharya

4 Ciliate genome evolution

64

Casey McGrath, Rebecca Zufall, and Laura A. Katz

5 Molecular evolution of Foraminifera

78

Samuel S. Bowser, Andrea Habura, and Jan Pawłowski

6 Photosynthetic organelles and endosymbiosis

94

M. S. Sommer, S. B. Gould, O. Kawach, C. Klemme, C. Voß, U.-G. Maier, and S. Zauner

7 Genome evolution of anaerobic protists: metabolic adaptation via gene acquisition

109

Jan O. Andersson

8 Horizontal and intracellular gene transfer in the Apicomplexa: The scope and functional consequences

123

Jinling Huang and Jessica C. Kissinger

Part III Analyses of complete genomes

137

9 The nuts and bolts of sequencing protist genomes

139

Daniella C. Bartholomeu, Neil Hall, and Jane M. Carlton

10 Comparative genomics of the trypanosomatids	155
<i>Kenneth D. Stuart and Peter J. Myler</i>	
11 The genome of <i>Entamoeba histolytica</i>	169
<i>C. Graham Clark</i>	
12 Genome reduction in Microsporidia	181
<i>Patrick J. Keeling</i>	
13 Nucleomorphs: remnant nuclear genomes	192
<i>Oliver Kawach, Maik S. Sommer, Sven B. Gould, Christine Voß, Stefan Zauner, and Uwe-G. Maier</i>	
14 Genomic insights into diatom evolution and metabolism	201
<i>E. Virginia Armbrust, Tatiana A. Rynearson, and Bethany D. Jenkins</i>	
15 The <i>Dictyostelium</i> genome – a blueprint for a multicellular protist	214
<i>Pauline Schaap</i>	
Index	227

List of contributors

Jan O. Andersson

Institute of Cell and Molecular Biology
Uppsala University
Biomedical Center
Box 596
S-751 24, Uppsala
Sweden

E. Virginia Armbrust

Marine Molecular Biotechnology Laboratory
School of Oceanography
University of Washington
Seattle, Washington 98195
USA

Daniella Bartholomeu

The Institute for Genomic Research
9712 Medical Center Drive
Rockville, MD 20850
USA

Debashish Bhattacharya

Department of Biological Sciences and
Roy J. Carver Center for Comparative Genomics
446 Biology Building
University of Iowa
Iowa City, IA 52242
USA

Samuel S. Bowser

Laboratory of Cell Regulation
Wadsworth Center
New York State Department of Health
P.O. Box 509
Albany, NY 12201
USA

Jane Carlton

The Institute for Genomic Research
9712 Medical Center Drive
Rockville, MD 20850
USA

C. Graham Clark

Department of Infectious and Tropical Diseases
London School of Hygiene and Tropical Medicine
Keppel Street, London, WC1E 7HT
UK

Sven Gould

University of Marburg
Cell Biology, Karl-von-Frisch Strasse
D-35032 Marburg
Germany

Andrea Habura

Laboratory of Cell Regulation
Wadsworth Center
New York State Department of Health
P.O. Box 509
Albany, NY 12201
USA

Jeremiah D. Hackett

Woods Hole Oceanographic Institution
Biology Department
Mail Stop 32
Woods Hole, MA 02543
USA

Neil Hall

The Institute for Genomic Research
9712 Medical Center Drive
Rockville, MD 20850
USA

Jinling Huang

Department of Biology
East Carolina University
Greenville, NC 27858
USA

Bethany D. Jenkins

Department of Cell and Molecular Biology
Graduate School of Oceanography
University of Rhode Island
316 Morrill Hall
45 Lower College Road
Kingston, Rhode of Island 02881
USA

Laura A. Katz

Department of Biological Sciences
Smith College
Northampton, MA 01063
USA

Oliver Kawach

University of Marburg
Cell Biology, Karl-von-Frisch Strasse
D-35032 Marburg
Germany

Patrick J. Keeling

Canadian Institute for Advanced Research
Botany Department
University of British Columbia
3529-6270 University Boulevard
Vancouver, BC, V6T 1Z4
Canada

Jessica Kissinger

Department of Genetics and Center for
Tropical and Emerging Global Diseases
Paul D. Coverdell Center
500 D.W. Brooks Drive
Athens, GA 30602-7394
USA

C. Klemme

University of Marburg
Cell Biology, Karl-von-Frisch Strasse
D-35032 Marburg
Germany

Uwe-G. Maier

University of Marburg
Cell Biology, Karl-von-Frisch Strasse
D-35032 Marburg
Germany

Casey Mc Grath

Department of Biological Sciences
Smith College
Northampton, MA 01063
USA

Peter J. Myler

Seattle Biomedical Research Institute
307 Westlake Ave N, Suite 500
Seattle, WA, 98109-5219
and
Department of Pathobiology and
Division of Biomedical and
Health Informatics
University of Washington
Seattle, WA 98195
USA

David J. Patterson

Marine Biological Laboratory
Woods Hole, MA 02543
USA

Jan Pawlowski

Department of Zoology and Animal Biology
University of Geneva
Sciences III 30, Quai Ernest-Ansermet
CH-1211 Geneva 4
Switzerland

Tatiana A. Rynearson

University of Rhode Island
South Ferry Road
Narrangan Sett, RI, 02882
USA

Pauline Schaap

School of Life Sciences
University of Dundee
MSI/WTB complex
Dow Street, Dundee,
DD1 5EH
UK

Alastair G. B. Simpson

Canadian Institute for Advanced Research
Program in Evolutionary Biology and
Department of Biology
Dalhousie University
Halifax, Nova Scotia, B3H 4J1
Canada

Maik Sommer

University of Marburg
Cell Biology, Karl-von-Frisch Strasse
D-35032 Marburg
Germany

Kenneth D. Stuart

Seattle Biomedical Research Institute
307 Westlake Ave N, Suite 500
Seattle,
WA, 98109-5219
and
Department of Pathobiology
University of Washington
Seattle, WA 98195
USA

Christine Voß,

University of Marburg
Cell Biology, Karl-von-Frisch Strasse

D-35032 Marburg
Germany

Stefan Zauner

University of Marburg
Cell Biology, Karl-von-Frisch Strasse
D-35032 Marburg
Germany

Rebecca Zufall

Department of Biology and Biochemistry
University of Houston
Houston, TX 77204

prokaryotic microorganisms (i.e. prokaryotes), defined as organisms that are neither plants, animals, nor fungi, are essential to many aspects of human health and the environment. These organisms represent at least 1200 million years of evolution, comprise the bulk of eukaryotic lineages, and include members with many key evolutionary innovations. Furthermore, because plants, animals, and fungi arose independently from within microbial groups, elucidating the origins and nature of developments within eukaryotic microorganisms are necessary to understand fully the evolution of these macroscopic lineages. Hence, genomic studies of eukaryotic microbes are vital to understanding the biodiversity of life on Earth.

Genomes from eukaryotic microbes challenge the principles of genome evolution that have resulted mainly from studies of a few plant and animal groups. Examples of such discoveries, many of which are documented in this volume, include genome strand polarity in kinetoplastids (including *Leishmania*, *Trypanosoma* and *L. smithi*), chromatin packaging in ciliates, and extrachromosomal DNA as a catalyst for the cumulative spread of selfish genes through. As genomes have been studied from an increasing fraction of the diverse tree of eukaryotic life, we are confident that many more novel genomic features are yet to be discovered. A wealth of knowledge will result from answering questions of mechanisms underlying, and the implications of, genome evolution in these taxa.

Unraveling the principles of genome evolution in microbial eukaryotes is, however, a daunting task because so little is known about their basic biology. This challenge is being met, in part, by

advances in DNA sequencing technologies that have made the often large genomes of eukaryotic microbes more accessible. High-throughput genomics alleviates the reliance on model systems to understand basic biology, and technological advances in genomics enables the full sequencing of numerous genomes from microbial eukaryotes. Whereas early studies largely focused on pathogens with relatively reduced genome sizes, larger genomes from free-living microbial eukaryotes are now (or will soon be) complete (e.g. *Trichomonas thermophilus* ciliate, *Thalassiosira pseudonana* (dinoflagellate), *Dictyostelium discoideum* (cellular slime mold), *Candida albicans* (yeast), and algae). The availability of these data promises to revolutionize our understanding of eukaryotic genomes, as well as the physiology, systematics, and basic biology of eukaryotes in general.

Goals of this volume

Our intention with this edited volume is to convey a basic understanding of genomes and evolution to microbial eukaryotes to a wide-spectrum audience, including genomic scientists, evolutionary biologists, microbiologists, and ecologists. The chapters in this book focus on evolutionary genomics, but also provide a basic understanding of microbial diversity. The contributing authors were chosen because of their leadership in their fields. Many of the authors contributed to a National Science Foundation-funded workshop entitled "Frontiers in Genomics: Insights into Prokaryotic Evolutionary Biology" that was convened at the University of Iowa from June 19 to 21, 2001, and