Unravelling the algae

the past, present, and future of algal systematics

Edited by
Juliet Brodie
Jane Lewis

THE Systematics ASSOCIATION
The LINNEAN SOCIETY of London
A living forum for biology
NATURAL HISTORY MUSEUM
THE BRITISH PHYCOLOGICAL SOCIETY
CRC

The Systematics Association Special Volume Series 75

Unravelling the algae

the past, present, and future of algal systematics

The Systematics Association Special Volume Series

Series Editor

Alan Warren

Department of Zoology, The Natural History Museum
Cromwell Road, London SW7 5BD, UK

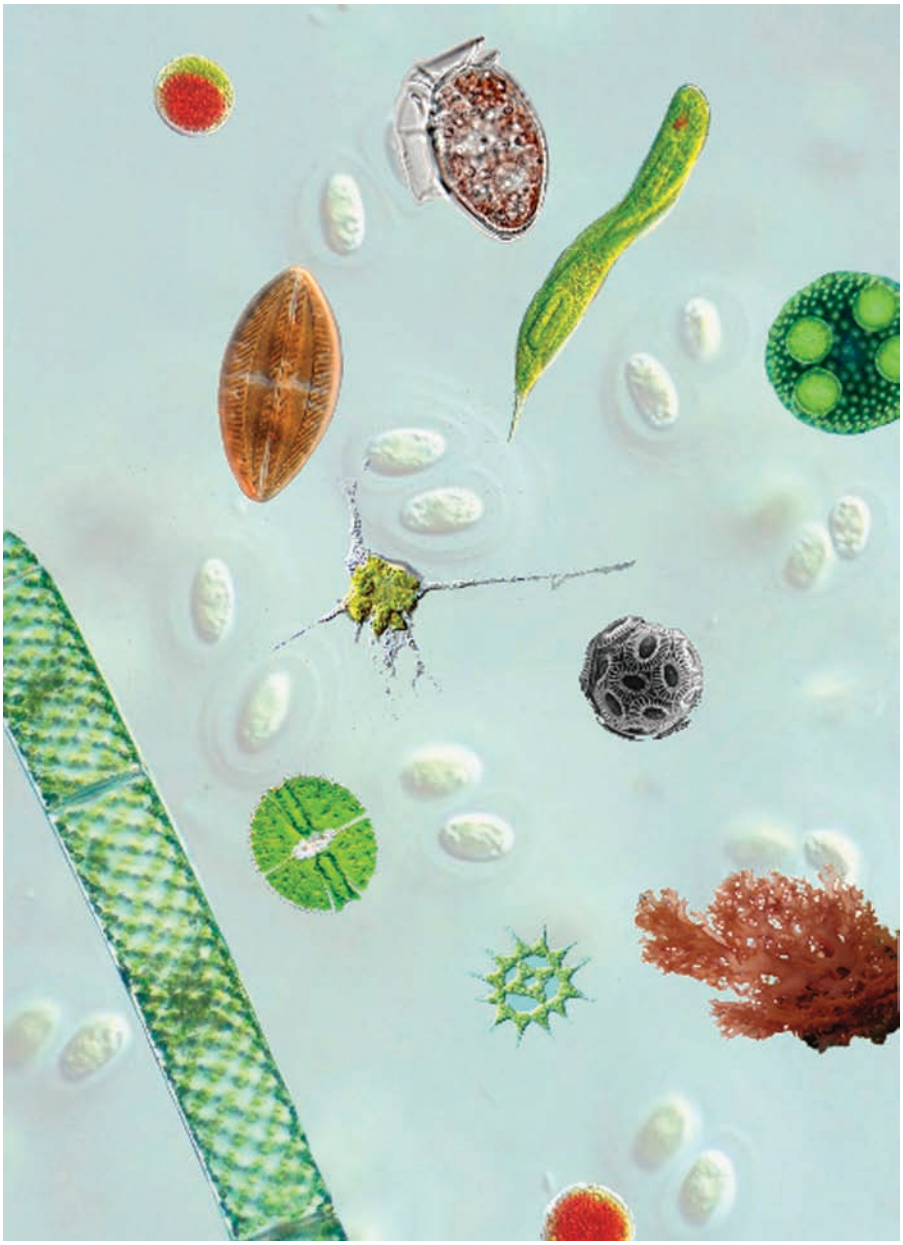
The Systematics Association promotes all aspects of systematic biology by organizing conferences and workshops on key themes in systematics, publishing books and awarding modest grants in support of systematics research. Membership of the Association is open to internationally based professionals and amateurs with an interest in any branch of biology including palaeobiology. Members are entitled to attend conferences at discounted rates, to apply for grants and to receive the newsletters and mailed information; they also receive a generous discount on the purchase of all volumes produced by the Association.

The first of the Systematics Association's publications *The New Systematics* (1940) was a classic work edited by its then-president Sir Julian Huxley, that set out the problems facing general biologists in deciding which kinds of data would most effectively progress systematics. Since then, more than 70 volumes have been published, often in rapidly expanding areas of science where a modern synthesis is required.

The *modus operandi* of the Association is to encourage leading researchers to organize symposia that result in a multi-authored volume. In 1997 the Association organized the first of its international Biennial Conferences. This and subsequent Biennial Conferences, which are designed to provide for systematists of all kinds, included themed symposia that resulted in further publications. The Association also publishes volumes that are not specifically linked to meetings and encourages new publications in a broad range of systematics topics.

Anyone wishing to learn more about the Systematics Association and its publications should refer to our website at http://www.systass.org

Other Systematics Association publications are listed after the index for this volume.



Frontispiece showing the diversity of the algae developed by Reen Pilkington from images contributed by authors

The Systematics Association Special Volume Series 75

Unravelling the algae

the past, present, and future of algal systematics

Edited by

Juliet Brodie

Natural History Museum

London, UK

Jane Lewis

University of Westminster

London, UK

CRC Press

Taylor & Francis Group

Boca Raton London New York

CRC Press is an imprint of the

Taylor & Francis Group, an **informa** business

CRC Press
Taylor & Francis Group
6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

Printed in the United States of America on acid-free paper
10 9 8 7 6 5 4 3 2 1

International Standard Book Number-13: 978-0-8493-7989-5 (Hardcover)

Table of Contents

Foreword

This is a fascinating and challenging book about a group of diverse living organisms that span the whole course of evolution. Numerous and extremely widely distributed across the planet, they are titans in the global control of the biosphere and have been main players and drivers in environmental change. Yet most of us don't even know of their existence, let alone their crucial importance to everyday life in the 21st century. So what more appropriate time for this publication than during the Tercentenary of Linnaeus, the scientist who first persuaded the world of natural historians that providing every distinct organism with a name was not only the foundation of scientific understanding but also of the progress of human economy. Linnaeus not only named names but was a pioneer in natural economy, and if alive today I am sure would play the stock market in the burgeoning enterprise of algal products. Every child lucky enough to visit the ocean will discover seaweeds, and almost certainly partake of their products. They will enjoy ice cream, snack on processed food, and use a growing number of everyday items, including antibiotics, all of which depend on organic chemicals extracted from these strange slippery plants. A rainbow of green, brown, and red living colour and a myriad of shapes and forms have sown the seeds of wonder, exploration, ecology, and taxonomy in many youngsters. Some such individuals at the start of their scientific careers and other well-established scientists have helped craft this wonderful book. Now in the laboratory and using new technologies like chromatography and genetic fingerprinting (both pioneered using alginates), their innermost secrets of ancestry and phylogeny are being revealed.

In addition to the macroscopic seaweeds, there are legions of minute algae whose intricate beauty is revealed only under the microscope, and with magnifications now probing the bounds of the atom, the information to hand is encyclopaedic. Information there to hone our understanding of life on earth and the staggering magnitude algae have played across evolutionary time. The happy band of phycologists already know that in their strange world, enslavement of once free-living organelles helped produce more complex cells and more complex organisms with greater capabilities. The minutiae of change have allowed the construction of the world's first stromatolites, solar-powered, self-repairing sea defences, and the shape of more massive things to come. There are reefs that are home to thousands of different fishes and other animals.

Extremophiles thrive where other life forms cannot exist, in heat and impossible concentrations of toxic chemicals. Single cells that gained a new individuality of purpose became eggs or sperm, and thus the carriers of diverse genes that shook up evolution, and stirred it with the lust of sex. Whiplash flagella or the sensual rhythm of beating cilia speed gametes to their chosen mates. The Oceans were not enough—the land was their final goal.

In our knowledge of the algae, the subject of this book, lie the answers to many important questions science has dreamed of answering for decades, so it should take pride of place in your library. A *vade mecum* for the future, which can only make us wonder what else this diverse group have hidden in and around their genes. I was very proud when one of my grandchildren was named Luca. The **L**ast **U**niversal **C**ommon **A**ncestor of all living things, whose descendants helped charge the biosphere with free oxygen trying and testing new armamentaria of antioxidants, enzymes, and substrates that are as important to us today as they were almost 4 billion years ago. Half bacteria, half alga, half plant, half animal, we do not know. But one day we will, and that is the excitement of this book.

Professor David Bellamy

Preface

The chapters in this book came about as a result of a two-day symposium in 2006 "Unravelling the algae: the past, present and future of algal molecular systematics," which was convened in order to review the state of the subject and assess the impact of molecular tools on the taxonomy of virtually all the different algal groups and to produce a volume setting out this material. The symposium included 16 talks by invited speakers, all of whom (sometimes with assistance of coauthors) contributed papers to the book. In reviewing the symposium and putting the material together for the book, we were keen to fill a gap we identified and were pleased that the chapter on the euglenophytes was so very willingly contributed by the chapter's authors during the production of the book. The symposium also attracted 27 posters, which also covered almost all the algal groups, and topics were diverse, ranging from the general to the specific, covering macroalgae to ultraplankon and from phylogenies to the development of identification tools using molecular techniques. The meeting also provided the opportunity for some lively discussion that allowed participants to debate issues as they arose and to speculate on the shape of the future. A common thread throughout the talks and an overwhelming outcome from the resulting discussions was that a range of traditional and molecular approaches are required coupled with other techniques including the use of transmission electron microscopy in order to support interpretation.

We were able to run this symposium because of the generous support of the Systematics Association, Linnean Society, British Phycological Society, and the Natural History Museum and the support of the publisher, CRC. These organisations play a crucial role in the advancement of science via their sponsorship and resources, and this should never be underestimated. We were able to create this timely and unique book because of the intellect and generosity of time and materials from the authors, some of whom also peer reviewed other chapters, and many of whom supplied the illustrations for the book cover and the frontispiece. It was their tremendous spirit of endeavour that enabled us to achieve the goals of this project.

Acknowledgments

The Systematics Association, Natural History Museum, London (NHM), Linnean Society, British Phycological Society, CRC Press, and Abgene all provided sponsorship or support for the meeting. We acknowledge the assistance of Mandy Walton, Elinor and Sarah Rowing (University of Westminster), Julie Gray and Barbara Rinkel (NHM) for administrative, technical, and secretarial support and the students and staff of both institutions who assisted in the smooth running of the symposium. Artistic inspiration was provided by Reen Pilkington. Chapters were peer reviewed by Margaret Clayton, Katharine Evans, Paul Hayes, Lucien Hoffmann, Max Hommersand, David John, Marina Montresor, Gianfranco Novarino, Øjvind Moestrup, Barry Leadbeater, Fabio Rindi, and Max Taylor. We thank them for the efforts in improving the manuscripts. We also had excellent advice from members of the Systematics Association Council, in particular Alan Warren the Systematics Association Special Volumes Series Editor and Colin Hughes the Treasurer. We also had the support of two book proposal reviewers, Barry Leadbeater and Wytze Stam. We would also like to thank the production team at CRC, in particular John Sulzycki, Pat Roberson and Amy Rodriguez for their work. Finally, we are indebted to all the authors for their contributions and for enabling us to meet our manuscript submission deadline.

The Editors

Juliet Brodie is a senior researcher in marine algae at the Natural History Museum, London. She graduated from the University of Bristol with a degree in botany and zoology and has studied macroalgae for over 25 years. Her doctoral research was undertaken in Galway (the National University of Ireland) and focused on life histories, crossing studies, morphology, and photoperiodic responses of red algae. She continued as a postdoctoral researcher with the Smithsonian Institution, USA, undertaking taxonomic studies on tropical red algae. She embraced molecular techniques in the early days of their use in algal taxonomy and notably applied them to *Porphyra*, a large, economically important, taxonomically problematic genus of red algae. She is a leading authority in the world on the taxonomy of this genus and has co-authored a book on the subject. She specialises in molecular systematics, taxonomy, and ecology of red algae, and her experience covers many different parts of the world. Her other interests include the biodiversity and conservation of marine algae.

Jane Lewis is the Dean of the School of Biosciences at the University of Westminster. She graduated from the University of Wales, Bangor with a degree in marine biology and oceanography and since has studied microalgae for some 25 years. Her doctoral research was carried out in Scotland at the Scottish Marine Biological Association and Royal Holloway and Bedford New College (University of London), and was focused on the ecology of harmful algal blooms, particularly dinoflagellates. Studies of this nature crucially depend on accurate identification of potentially harmful species, and so her interest in microalgal taxonomy began. Her studies of dinoflagellates include a particular focus on the cyst stage of the life cycle, including their role in the ecology of harmful algal blooms and their use in the interpretation of the fossil record. Establishing cyst–theca relationships and working with *Alexandrium* species have, more recently, led to the application of molecular techniques in her research. However, she still favours "knowing" the organisms she is working on and encourages students to become proficient in microscopic as well as molecular techniques.

Contributors

Andrew E. Allen
Département de Biologie
Ecole Normale Supérieure
Paris, France

Robert A. Andersen
Provasoli-Guillard National Center for Culture of Marine Phytoplankton
Bigelow Laboratory for Ocean Sciences
West Boothbay Harbor, Maine

Chris Bowler
Cell Signalling Laboratory
Stazione Zoologica
Napoli, Italy
and
Département de Biologie
Ecole Normale Supérieure
Paris, France

Juliet Brodie
Department of Botany
Natural History Museum
London, United Kingdom

Thomas Cavalier-Smith
Department of Zoology
University of Oxford
Oxford, United Kingdom

Federica Cerino
Stazione Zoologica A. Dohrn
Naples, Italy
and
Department of Marine Sciences
Polytechnic University of Marche
Ancona, Italy

Niels Daugbjerg
Department of Phycology
Biological Institute
University of Copenhagen
Copenhagen, Denmark

Olivier de Clerck
Phycology Research Group
Ghent University
Ghent, Belgium

Bruno de Reviers
Département Systématique et Evolution
Muséum National d'Histoire Naturelle
Paris, France

Charles F. Delwiche
Cell Biology and Molecular Genetics
University of Maryland at College Park
College Park, Maryland

Stefano G.A. Draisma
Nationaal Herbarium Nederland
Universiteit Leiden Branch (NHN-L)
Phanerogams and Cryptogams of the Netherlands and Europe (PCNE)
Leiden, The Netherlands

Bente Edvardsen
Department of Biology
University of Oslo
Oslo, Norway

Nermin Adel El Semary
Department of Botany and Microbiology
University of Helwan
Cairo, Egypt

Katharine M. Evans
Royal Botanic Garden
Edinburgh, Scotland

Mark A. Farmer
Department of Cellular Biology
University of Georgia
Athens, Georgia

John D. Hall
Cell Biology and Molecular Genetics
University of Maryland at College Park
College Park, Maryland

Paul K. Hayes
School of Biological Sciences
University of Bristol
Bristol, United Kingdom

Ken-ichiro Ishida
Graduate School of Life and Environmental Sciences
University of Tsukuba
Tsukuba, Japan

Uwe John
Alfred Wegener Institute
Bremerhaven, Germany

Frederik Leliaert
Phycology, Research Group
Ghent University
Ghent, Belgium

Jane Lewis
School of Biosciences
University of Westminster
London, United Kingdom

Christine A. Maggs
School of Biological Sciences
Medical Biology Centre
Queen's University Belfast
Belfast, United Kingdom

David G. Mann
Royal Botanic Garden
Edinburgh, Scotland

Linda K. Medlin
Alfred Wegener Institute
Bremerhaven, Germany

Katja Metfies
Alfred Wegener Institute
Bremerhaven, Germany

Øjvind Moestrup
Department of Phycology
Biological Institute
University of Copenhagen
Copenhagen, Denmark

Jeanine L. Olsen
Department of Marine Benthic Ecology and Evolution
Centre for Ecological and Evolutionary Studies
University of Groningen
Haren, The Netherlands

Shuhei Ota
Graduate School of Natural Science and Technology
Kanazawa University
Kanazawa, Japan

Thomas Pröschold
Scottish Association for Marine Science
Culture Collection of Algae and Protozoa
Dunstaffnage Marine Laboratory
Dunbeg by Oban, Scotland

Florence Rousseau
Département Systématique et Evolution
Université Pierre et Marie Curie (Paris VI)
Paris, France

Patricia Sánchez-Baracaldo
School of Biological Sciences
University of Bristol
Bristol, United Kingdom

Richard E. Triemer
Department of Plant Biology
Michigan State University
East Lansing, Michigan

Heroen Verbruggen
Phycology Research Group
Ghent University
Ghent, Belgium

David M. Williams
Department of Botany
Natural History Museum
London, United Kingdom

Akinori Yabuki
Graduate School of Life and Environmental Sciences
University of Tsukuba
Tsukuba, Japan

Adriana Zingone
Stazione Zoologica A. Dohrn
Naples, Italy

Abbreviations

18S	Small subunit of the ribosomal operon
26S	Large subunit of the ribosomal operon
5.8S rDNA	Ribosomal DNA located between the SSU and LSU rDNA
ADP	Adenosine diphosphate
AFLP	Amplified fragment length polymorphism
ALL	Alariaceae, Lessoniaceae, Laminariaceae
ARB	Software for handling genetic data, named for "arbor," Latin for tree
ATP	Adenosine triphosphate
atpB	Gene coding for beta subunit of ATPase
BOLD	Barcode of Life Data System
bp	Base pair
CBC	Compensatory base changes
CCAP	Culture collection of algae and protozoa
CCM	Carbon concentrating mechanism
CCMP	Center for Culture of Marine Phytoplankton
CCW	Counterclockwise
CFB	Cytophaga-Flavobacterium-Bacteroides
CM	Cytoplasmic membrane
cox1	Mitochondrial cytochrome with oxidase subunit 1
CPS	Carbomyl phosphate synthase
CW	Clockwise
DNA	Deoxyribonucleic acid
DO	Directly opposite
DSOS	Dictyotales, Sphacelariales, Onslowiales, Syringodermatales
DSP	Diarrhoeic shellfish poisoning
ER	Endoplasmic reticulum
EST	Expressed sequence tag
F	Phenylalanine
FA	Fatty acid
FBA	Fructose 1,6-bisphosphate
GAPDH	Glyceraldehyde 3-phosphate dehydrogenase
GTPase	Guanine triphosphate
ICBN	International Code of Botanical Nomenclature
ICZN	International Code of Zoological Nomenclature
IM	Inner membrane
IPC	Internal periplast component
ITS	Internal transcribed spacers
ITS-1	Internal transcribed spacer region 1 located between SSU and 5.8S rDNA
ITS-2	Internal transcribed spacer region 2 located between 5.8S and LSU rDNA
KT boundary	Cretaceous–Tertiary boundary
LBA	Long-branch attraction
LGT	Lateral gene transfers
LHC	Light-harvesting complex
LINEs	Long interspersed nuclear elements