Photosynthesis in Algae

Advances in Photosynthesis and Respiration

VOLUME 14

The scope of our series, beginning with volume 11, reflects the concept that photosynthesis and respiration are intertwined with respect to both the protein complexes involved and to the entire bioenergetic machinery of all life. *Advances in Photosynthesis and Respiration* is a book series that provides a comprehensive and state-of-the-art account of research in photosynthesis and respiration. Photosynthesis is the process by which higher plants, algae, and certain species of bacteria transform and store solar energy in the form of energy-rich organic molecules. These compounds are in turn used as the energy source for all growth and reproduction in these and almost all other organisms. As such, virtually all life on the planet ultimately depends on photosynthetic energy conversion. Respiration, which occurs in mitochondrial and bacterial membranes, utilizes energy present in organic molecules to fuel a wide range of metabolic reactions critical for cell growth and development. In addition, many photosynthetic organisms engage in energetically wasteful photorespiration that begins in the chloroplast with an oxygenation reaction catalyzed by the same enzyme responsible for capturing carbon dioxide in photosynthesis. This series of books spans topics from physics to agronomy and medicine, from femtosecond processes to season long production, from the photophysics of reaction centers, through the electrochemistry of intermediate electron transfer, to the physiology of whole orgamisms, and from X-ray christallography of proteins to the morphology or organelles and intact organisms. The goal of the series is to offer beginning researchers, advanced undergraduate students, graduate students, and even research specialists, a comprehensive, up-to-date picture of the remarkable advances across the full scope of research on photosynthesis, respiration and related processes.

The titles published in this series are listed at the end of this volume and those of forthcoming volumes on the back cover.

Photosynthesis in Algae

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The cover picture is a confocal scanning microscope picture of the gyres of chloroplasts in an undescribed species of *Spirogyra* which has “frills” along the margins. The light areas are putative grana (see Chapter 2). The picture was taken by Brian Gunning in false colour using a Biorad MRC-600 confocal microscope with a projection of 26 optical sections imaged at 0.4 micrometre focusing intervals with a 100x Planapo oil-immersion Zeiss lens.

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Editorial

Advances in Photosynthesis and Respiration

Volume 14: *Photosynthesis in Algae*

I am extremely delighted to announce the publication of the long-awaited *Photosynthesis in Algae* edited by Anthony Larkum, Susan Douglas and John Raven. It is Volume 14 in our Series *Advances in Photosynthesis and Respiration* (AIPH) and is a sequel to the previous thirteen volumes in the series.

Published Volumes

(1) *Molecular Biology of Cyanobacteria* (Donald R. Bryant, editor, 1994);
(2) *Anoxygenic Photosynthetic Bacteria* (Robert E. Blankenship, Michael T. Madigan and Carl E. Bauer, editors, 1995);
(3) *Biophysical Techniques in Photosynthesis* (Jan Amesz* and Arnold J. Hoff*, editors, 1996);
(4) *Oxygenic Photosynthesis: The Light Reactions* (Donald R. Ort and Charles F. Yocum, editors, 1996);
(5) *Photosynthesis and the Environment* (Neil R. Baker, editor, 1996);
(6) *Lipids in Photosynthesis: Structure, Function and Genetics* (Paul-André Siegenthaler and Norio Murata, editors, 1998);
(7) *The Molecular Biology of Chloroplasts and Mitochondria in Chlamydomonas* (Jean David Rochaix, Michel Goldschmidt-Clermont and Sabeeha Merchant, editors, 1998);
(8) *The Photochemistry of Carotenoids* (Harry A. Frank, Andrew J. Young, George Britton and Richard J. Cogdell, editors, 1999);
(9) *Photosynthesis: Physiology and Metabolism* (Richard C. Leegood, Thomas D. Sharkey and Susanne von Caemmerer, editors, 2000);
(10) *Photosynthesis: Photobiochemistry and Photobiophysics* (Bacon Ke, author, 2001);
(11) *Regulation of Photosynthesis* (Eva-Mari Aro and Bertil Andersson, editors, 2001)
(12) *Photosynthetic Nitrogen Assimilation and Associated Carbon and Respiratory Metabolism* (Christine Foyer and Graham Noctor, editors, 2002); and
(13) *Light Harvesting Antennas* (Beverley Green and William Parson, editors, 2003).

See <http://www.wkap.nl/series.htm/AIPH> for further information and to order these books. Please note that the members of the International Society of Photosynthesis Research, ISPR (<http://www.Photosynthesisresearch.org>), receive special discounts.

Photosynthesis in Algae

Algae are a fascinating group of organisms, which refuse to be classified. One may simply place them in the Protists, one of the six Kingdoms of Nature. However this ignores the fact that they are photosynthetic and are undeniably related in some way to the land plants (Plantae). It also places the algal group, which represents some of the largest organisms on the planet in a Kingdom that is typified by microscopic unicellular organisms! Of course this has not deterred workers in photosynthesis, almost all of whom will have a flask or two of algae growing somewhere in their laboratories, even though they devote their main work to higher plants. As pointed out in the Preface to this volume, it also does not prevent frequent sallies into the domain of Bacteria, to make use of the photosynthetic properties of Cyanobacteria, even though these organisms are no longer called 'algae.'

We are fortunate in having three outstanding and charming editors whose interests have allowed them a clear overview of a complex field and has allowed them to choose an excellent set of authors out of a army of great researchers in the field. Tony Larkum is basically a plant physiologist but has worked at all levels of photosynthesis from whole ecosystems such as coral reefs to genes for the light-harvesting proteins

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*deceased

of dinoflagellates and prochlorophytes. Susan Douglas is a molecular biologist who has sequenced cryptophyte genes and most recently took a major role in sequencing the three chromosomes of the relic nucleus (nucleomorph) of the cryptophyte *Guillardia theta*. John Raven is an eclectic algal physiologist, whose major contributions have been in quantifying the roles of various pathways in the carbon metabolism of algae as well as contributing prolifically to discussion on the evolution of Cyanobacteria, algae and land plants.

Knowing the editors and the topic of the specific volume are important to me. We have included brief biographies and photographs of the editors in this volume. My interest in algae dates back to the time when I was a graduate student of Robert Emerson (who himself was a student of Otto Warburg); the green alga *Chlorella* was the choice of research then. A 1957 group photograph and a shamelessly produced listing of some of our findings are given following this 'Editorial.' I have been fortunate to know Tony the most. I have been his guest once at his pleasant home in Sydney and enjoyed with him a 'walk in the ocean' that he led in Heron Island in 2001. The enjoyment of seeing the marine life there and in his laboratory has left an everlasting imprint on my mind. I have admired the work of Susan, but have yet to meet her personally. However, I met John at Urbana, Illinois, when he gave an exciting lecture wearing a Scottish kilt. (I have been too 'shy' to ever give a lecture wearing the Indian 'Kurta-Pajama and the Nehru Jacket; I could, of course, never wear a 'Dhoti' for the fear it may fall down in public.)

The various chapters in this book have beautifully covered the major aspects of photosynthesis in algae; they are written by major authorities in the field. I am pleased to see inclusion of discussions on Cyanobacteria, prochlorophytes (prokaryotes that have chlorophyll *b* as well as chlorophyll *a*) and newly discovered *Acaryochloris marina*, which possesses chlorophyll *d*. This book will serve graduate students, teachers and researchers in the areas of plant physiology, cellular and molecular biology, integrative biology, biochemistry, biophysics and global ecology.

The Scope of the Series

Advances in Photosynthesis and Respiration is a book series that provides, at regular intervals, a comprehensive and state-of-the-art account of research in various areas of photosynthesis and respiration. Photosynthesis is the process by which higher plants, algae, and certain species of bacteria transform and store solar energy in the form of energy-rich organic molecules. These compounds are in turn used as the energy source for all growth and reproduction in these and almost all other organisms. As such, virtually all life on the planet ultimately depends on photosynthetic energy conversion. Respiration, which occurs in mitochondria and in bacterial membranes, utilizes energy present in organic molecules to fuel a wide range of metabolic reactions critical for cell growth and development. In addition, many photosynthetic organisms engage in energetically wasteful *photorespiration* that begins in the chloroplast with an oxygenation reaction catalyzed by the same enzyme responsible for capturing carbon dioxide in photosynthesis. This series of books spans topics from physics to agronomy and medicine, from femtosecond (10^{-15} s) processes to season-long production, from the photophysics of reaction centers, through the electrochemistry of intermediate electron transfer, to the physiology of whole organisms, and from X-ray crystallography of proteins to the morphology of organelles and intact organisms. The intent of the series is to offer beginning researchers, advanced undergraduate students, graduate students, and even research specialists, a comprehensive, up-to-date picture of the remarkable advances across the full scope of research on bioenergetics and carbon metabolism.

Future Books

The readers of the current series are encouraged to watch for the publication of the forthcoming books:

(1) *Respiration in Archea and Bacteria.* 2 volumes (Editor: Davide Zannoni);
(2) *Chlorophylls and Bacteriochlorophylls: Biochemistry, Biophysics and Biological Function* (Editors: Bernhard Grimm, Robert J. Porra, Wolfhart Rüdiger and Hugo Scheer);
(3) *Chlorophyll a Fluorescence: A Signature of Photosynthesis* (Editors: George Papageorgiou and Govindjee);
(4) *Photosystem II: The Water/Plastoquinone Oxido-reductase in Photosynthesis* (Editors: Thomas J. Wydrzynski and Kimiyuki Satoh);
(5) *Plant Respiration* (Editors: Miquel Ribas-

Carbo and Hans Lambers);

(*6*) *Photosystem I: The NADP+/Ferredoxin Oxidoreductase in Oxygenic Photosynthesis* (Editor: John Golbeck);

(*7*) *Photosynthesis: A Comprehensive Treatise; Biochemistry, Biophysics and Molecular Biology,* 2 volumes (Editors: Julian Eaton-Rye and Baishnab Tripathy)

(*8*) *Photoprotection, Photoinhibition, Gene Regulation and Environment* (Editors: Barbara Demmig-Adams, William W. Adams III and Autar Mattoo);

(*9*) *The Structure and Function of Plastids* (Editors: Kenneth Hoober and Robert Wise); and

(*10*) *History of Photosynthesis Research* (*Editor: Govindjee*)

In addition to these contracted books, we are interested in publishing several other books. Topics under consideration are: Molecular Biology of Stress in Plants; Global Aspects of Photosynthesis and Respiration; Protein Complexes of Photosynthesis and Respiration; Biochemistry and Biophysics of Respiration; Protonation and ATP Synthesis; Functional Genomics; The Cytochromes; Laboratory Methods for Studying Leaves and Whole Plants; and C-3 and C-4 Plants.

Readers are requested to send their suggestions for these and future volumes (topics, names of future editors, and of future authors) to me by E-mail (gov@uiuc.edu) or fax (1-217-244-7246).

In view of the interdisciplinary character of research in photosynthesis and respiration, it is my earnest hope that this series of books will be used in educating students and researchers not only in Plant Sciences, Molecular and Cell Biology, Integrative Biology, Biotechnology, Agricultural Sciences, Microbiology, Biochemistry, and Biophysics, but also in Bioengineering, Chemistry, and Physics.

I take this opportunity to thank Tony Larkum, Susan Douglas, John Raven, all the authors of volume 14, Larry Orr, Jacco Flipsen, Noeline Gibson, Evan Delucia, and my wife Rajni Govindjee for their valuable help and support that made the publication of *Photosynthesis in Algae* possible.

August 15, 2003

Govindjee
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A 1957 photograph of Govindjee (3rd from the right, holding one of the Lavorels' children), Robert Emerson (1st on the left, holding another child of the Lavorels), and Ruth V. Chalmers (Emerson's assistant; 3rd from the left). Others in the photo are: Madame Mary-Jo Lavorel (2nd from left), Jean Lavorel (5th from left) and Paul Latimer (extreme right).

Govindjee

Govindjee was trained in phycology, during his M.Sc. course (1952-1954), by Professor A.K. Mittra of Allahabad University, India. From 1956-1958, Robert Emerson and his assistant Ruth V. Chalmers gave excellent training in the culture, growth, maintenance, and physiology of various algae. This included quantum yield measurements of oxygen evolution by Emerson's most precise differential two-vessel manometry (using a cathetometer to read the pressure changes as small as 0.01 mm, while the manometer was shaking). An interesting thing about Emerson's manometer was that it used a low-density, but foul-smelling iso-caproic acid as the manometer fluid! Govindjee's early research included the use of the green alga *Chlorella pyrenoidosa*, the cyanobacterium *Anacystis nidulans* (then called a blue-green alga), *Navicula minima* (a diatom), and *Porphyridium cruentum* (a red alga). Later research included the use of wild type and several Photosystem II (PS II) mutants of the cyanobacterium *Synechocystis* PCC 6803 (now fully sequenced: www.kazusa.or.jp/ cyanobase/), and the wild type and several PSII and xanthophyll cycle mutants of another green alga *Chlamydomonas reinhardtii*. The following are some of his, and co-worker's, observations: chlorophyll (Chl) *a*-670 is a part of the short-wave photosystem (now called Photosystem II) in *Chlorella* and *Navicula* (1960; E. Rabinowitch); existence of a two-light effect through Chl *a* fluorescence measurements (1960; S. Ichimura); existence of a pigment with absorption at 750 nm in *Anacystis* (1961; C. Cederstrand); existence of a new emission band in the 692-695 nm region at room temperature, when photosynthesis is saturated, or blocked, in *Porphyridium* (1963; A. Krey); in *Anacystis*, (1967, 1968; G. Papageorgiou); and in *Chlorella* (1970; J-M. Briantais); temperature dependence of Chl *a* fluorescence bands at 685 nm, 696 nm, and at 730 nm, down to 4 K, suggesting that Förster energy transfer is the most probable mechanism of energy transfer in algae (1966-1970; F. Cho); slow Chl *a* fluorescence changes related to photophosphorylation and other non-Q_A-related events (1967–1972; G. Papageorgiou, P. Mohanty); maximum quantum yield of oxygen evolution does not exceed 0.12 even in young synchronously grown *Chlorella*, in the presence of catalytic blue light and 10% CO_2, i.e., under O. Warburg's experimental conditions (1968; R. Govindjee); existence of a circadian rhythm in Chl *a* fluorescence in *Gonyaulax polyedra* (1979; B. Sweeney and B. Prezelin); heat-induces state changes (1984; P.V. Sane); bicarbonate/formate binding near D1-R257 regulates electron transfer in PSII (1996-1998); elucidating the polyphasic rise kinetics of Chl *a* fluorescence rise and the coining of the name the OJIP curve (1992-1995; R. Strasser and his coworkers); demonstrating that imaging of the lifetime of Chl *a* fluorescence is a great tool for measuring quantum yield of fluorescence, and, thus of photosynthesis even in single cells of algae (2000-2003; O. Holub, M. Seufferheld and R. Clegg); exposure of cells to forced light oscillations suggests unique regulation of attachment and de-attachment of phycobilisomes to PSII core Chl *a*-containing protein complexes (2003; L. Nedbal). See Volume 12 of AIPH Series (Editors: C. Foyer and G.Noctor) for a brief biography, Volume 13 (Editors: B. Green and W. Parson) for the story of his name, and http://www.life.uiuc.edu/govindjee/ for his publications.

Contents

Introductory Chapters

Molecular Genetics of Algae

Biochemistry and Physiology of Algae

Light-Harvesting Systems in Algae

Preface

The algae and their photosynthesis have always excited chemists and physicists. One only has to remember the great collaboration between Theodore Engelmann and Carl Zeiss in the late nineteenth century, with the now classic experiment with *Spirogyra* and the demonstration that chlorophyll was the major pigment involved in oxygen evolution (http://www.nsta.org/Energy/find/luminaries/engelmann.html); or the use of plant pigments in the first demonstration of chromatography by Mikhail Tswett in the early twentieth century (http://webserver.lemoyne.edu/faculty/giunta/tswett.html). This synergy has continued to the present time and recent advances in the crystal structure of Photosystems I and II have come about only by the judicious use of selected algae (in the widest sense, including Cyanobacteria — see below) combined with improvements in X-ray crystallography.

Mention of Cyanobacteria brings us to one of the greatest advances in biological science in recent years: the revision of the scheme of life from the six Kingdoms approach to the present acknowledgment of three great domains of Nature: the Archaea, the Bacteria and the Eukarya brought about by revolutionary studies of small subunit ribosomal RNA (ssu rRNA) by Carl Woese and others.

While this approach has its merits, it leaves books like this stranded between the 'great divide,' since the term algae, if it is valid at all (and scientists are still debating the point: some preferring 'Protists') now excludes Cyanobacteria, which are firmly placed in the Bacteria. Notwithstanding this, we know that Cyanobacteria (or at least their ancestors) gave rise to the plastids of algae by entering into endosymbiosis with several early animal protists. Thus algae and their descendants, the land plants (Plantae) are chimaeras and inherit their photosynthetic properties from their plastids, which in turn have inherited these properties largely from ancestral Cyanobacteria. *Molecular Biology of Cyanobacteria* was covered in Volume 1 of this series (edited by Don Bryant).

A second great revelation, that has come about with the invention of the electron microscope, is the fantastic diversity now revealed for the algae (and for Protists as a whole for that matter). Whereas previously there were the four great Divisions: Chlorophyta (green algae), Phaeophyta (brown algae), Rhodophyta (red algae) and Cyanophyta (blue-green algae) and with an assortment of little known unicellular algae, fine structural studies have revealed at least 12 Divisions of algae, i.e. much greater diversity than in the 'Plants' that derive from them and which usually fill our 'Plant Sciences' courses. Thus the algae are a fitting subject for a book on photosynthesis for this reason alone. However there are now even more compelling reasons.

With all the diversity locked up in the 12 or more Divisions of algae there comes a great diversity in biochemistry and physiology and the underlying genetic systems. By comparison the 'Plants' are very uniform. This especially applies to photosynthetic systems since the 'Plants' are now believed to be derived from a single branch of the green algae. Thus, in trying to understand the potential for photosynthetic systems, the algae are a 'must' for study: not only for the intellectual achievement, but also for the technological innovations that can then come about. While great strides have been made over recent years in the biotechnology of algae we are just at the beginning. Imagine a biochemical factory that will just sit there in a vat, a pond, a lake or a sea, that will take in sunlight, look after itself and convert chemicals such as carbon dioxide (and other 'wastes') into all sorts of exotic products! These advances will only come about by the judicious use of genetics and we are fortunate that we have a model algal organism that can be transformed genetically, *Chlamydomonas.* And despite the fact that there was a whole volume in this series devoted to this subject in 1998 (Volume 7, *The Molecular Biology of Chloroplasts and Mitochondria in Chlamydomonas,* edited by Jean-David Rochaix, M. Goldschmidt-Clermont and Sabeeha Merchant), there is a chapter here to bring this rapidly growing field up to date. Undoubtedly the lessons learned with *Chlamydomonas* will be applied to other algal systems, which in turn will revolutionize many aspects of the current biotechnology.

The book is divided into five sections, starting with a general look at algae and their photosynthetic machinery, the plastid. This is followed by a section on molecular biology of algae, which is perhaps the most exciting growth area of algal photosynthesis. There are then sections on biochemistry, physiology and light harvesting systems. The light harvesting systems nicely complement the material in the previous book in this series, Volume 13, *Light Harvesting Antennas* edited by Beverley Green and William Parson. The last section deals with a variety of general topics including UV inhibition, adaptation, macroalgae and symbiosis. Thus the 19 chapters in this book range over the major aspects of photosynthesis in algae in exciting treatments by major workers in the field. Cyanobacteria have not been excluded, because the editors believe that they have much to contribute to the understanding of photosynthesis in 'algae' (*sensu stricto*). As noted above, the first volume in this series *The Molecular Biology of Cyanobacteria*, edited by Don Bryant, dealt specifically with this subject, but that book is already nearly 10 years old. Furthermore there have been dramatic developments in the special group of Cyanobacteria, which possess chlorophyll *b* as well as chlorophyll *a* (the prochlorophytes) and for this reason we felt it necessary to include a chapter specifically on these Cyanobacteria (also including the newly discovered *Acaryochloris marina*, which possesses chlorophyll *d*). Also in line with the new title of this series — to include respiration — one chapter deals with carbohydrate metabolism and respiration in algae and two other chapters deal with the subject of 'chlororespiration' which is a topical area of research and was discovered in algae. Overall these chapters will be an important contribution in an area that is advancing rapidly and where there is currently a need for a clear and concise synthesis of this knowledge.

This timely book would not have come about without the painstaking work of the authors of the chapters who are to be complimented on their excellent work. We are also grateful to a number of anonymous reviewers who took the time to make comments on first drafts. Perhaps most importantly of all is the input of Govindjee and Larry Orr in shepherding the authors and editors over the many hurdles in producing a book like this and making the work not only more enjoyable but also more authoritative.

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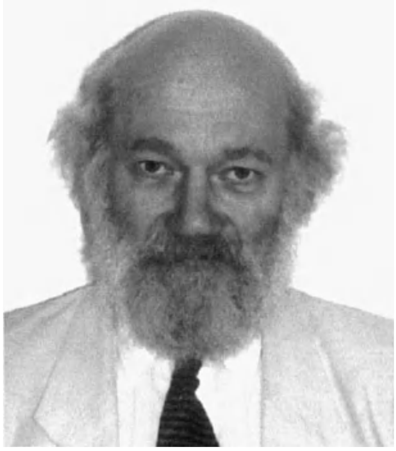
Anthony Larkum

Tony Larkum photographed in 2003 on One Tree Island, a marine station operated by the University of Sydney on the Great Barrier Reef, close to Heron Island. In the background is the old 'wet lab' where much of his experimental work has been carried out over the years.

Tony Larkum is a Professor in the School of Biological Sciences at the University of Sydney, Australia, where he has been for the past 33 years. Originally from England, he gained his doctorate in 1966 at the University Oxford, UK— under the supervision of Brian Loughman, who pioneered the use of NMR techniques for measuring phosphate in whole algal cells. His early work was on ion transport and photosynthesis in higher plants. However, on arriving in Australia, he changed his focus to marine systems (seagrasses, marine algae and corals), beckoned on by the warm, clear seas around Australia, especially on the Great Barrier Reef. He has since published three books (*Biological Science, The Web of Life*, 1974; *Biology of Seagrasses*, 1990; *Marine Cyanobacteria*, 1999), has contributed many chapters to books and published over 150 research articles in a wide range of areas, covering molecular biology, evolution, plant physiology, biochemistry and marine ecology. His early work on the vertical distribution of attached algae and the theory of complementary chromatic adaptation is still often quoted today. Over recent years he has been particularly concerned with effects of UV-B radiation on photosynthesis, coral bleaching, light-harvesting proteins in algae, evolution of photosynthesis and exotic Cyanobacteria. In the latter category the most interesting have been *Prochoron didemni* (with chlorophylls *a* and *b*) and *Acaryochloris marina* (with chlorophyll *d*). He was responsible with Roger Hiller for discovering the pcb protein, and its gene, in *Prochloron* and in showing that *Acaryochloris marina* has a similar set of genes. Most recently he has turned his attention to phylogenetic tree reconstruction in an effort to try to fathom the historical information held in the genes of Cyanobacteria and algae. As a result of this change in direction, he is currently the Deputy Director of the Sydney University Biological Informatics and Technology Centre. Further information on him and his work can be found at the following web sites: <http://www-personal.usyd.edu.au/~alark> and <http://www.bio.usyd.edu.au/SOBS/admin/staff/larkum.html>

Susan Douglas

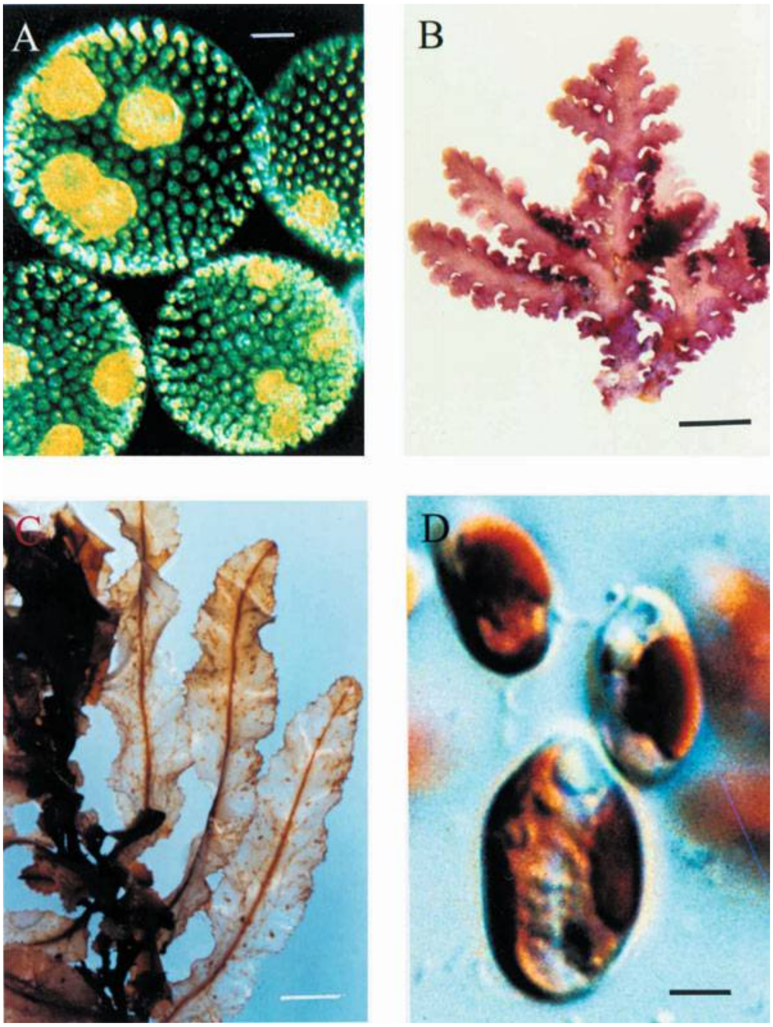
Susan Douglas obtained her M.Sc. (1980) and Ph.D. (1983) from Dalhousie University in Halifax, Nova Scotia under the supervision of Drs. Leo Vining and Ford Doolittle, respectively. She continued her doctoral interests on the evolution of plastids at the National Research Council's Institute for Marine Biosciences as a Research Associate in 1987, and is currently a Senior Research Officer at the Institute. Dr. Douglas was an associate of the Canadian Institute for Advanced Research program in Evolutionary Biology from 1991-2001 and is an adjunct professor in the Biology Department at Dalhousie University. Her research has focussed on the evolution of plastids, in particular those non-green plastids that arose by secondary endosymbiosis. This involved extensive phylogenetic analyses of plastid genomes from non-green algae and the completion of the entire plastid genome of the cryptophyte *Guillardia theta* in 1999 and the nucleomorph genome in 2001. Currently, her research is aimed at using genomics to gain a better understanding of larval development in marine fish, particularly the ontogeny of the digestive system and the role of the innate immune system in defense against pathogens. Her current work is highlighted at <http://imb-ibm.nrc-cnrc.gc.ca/research/molecbio_e.html>



John Raven: his scientific life (so far)

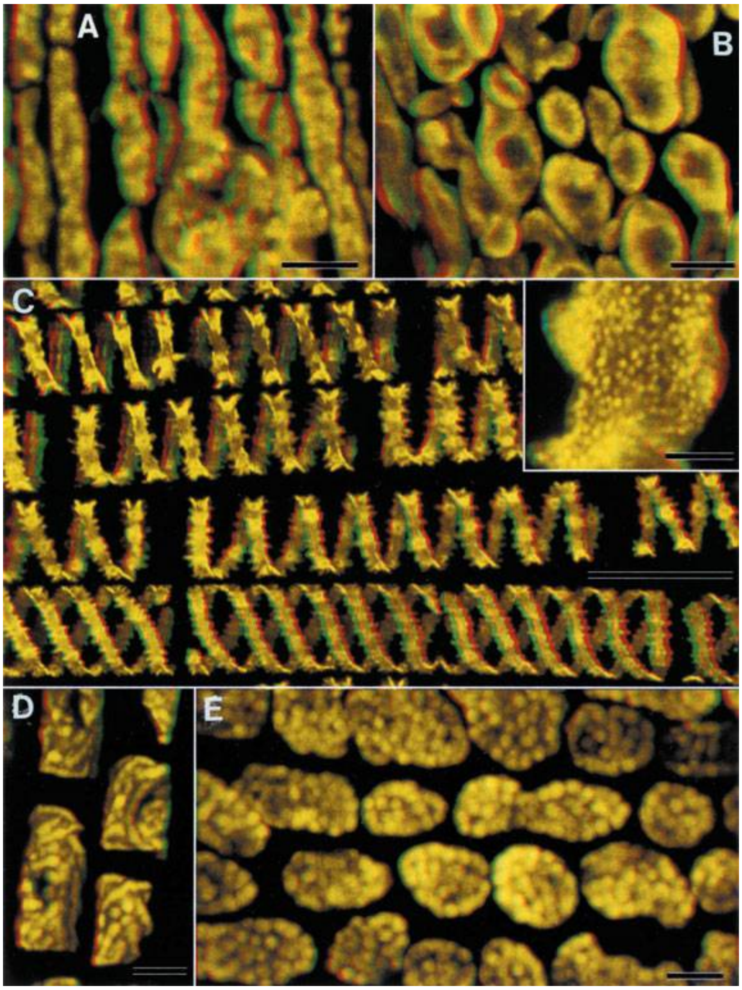
John Raven graduated from the University of Cambridge, Cambridge, UK, with a BA (1963) in Botany and a PhD (1967) in Botany/Plant Biophysics, supervised by Professor Enid MacRobbie. After post-doctoral and fixed-term lecturer posts in Cambridge he moved to the University of Dundee, where he is currently Boyd Baxter Professor of Biology. His research has involved work on higher plants as well as on algae, and embraces biophysical, biochemical, physiological ecological and evolutionary approaches to how photosynthetic organisms acquire and use resources. John has published a large number of scientific papers, has authored one book (*Energetics and Transport in Aquatic Plants*, 1984) and co-authored another (with Paul Falkowski, *Aquatic Photosynthesis*, 1997), and has received a number of awards which he feels that he, to varying degrees, deserves. He collaborates widely, and wishes to acknowledge his colleagues worldwide and his employers for the freedom they have given him to pursue his scientific interests. Some of his research publications are listed at <http://www.dundee.ac.uk/bioscience/raven.htm>

Color Plates

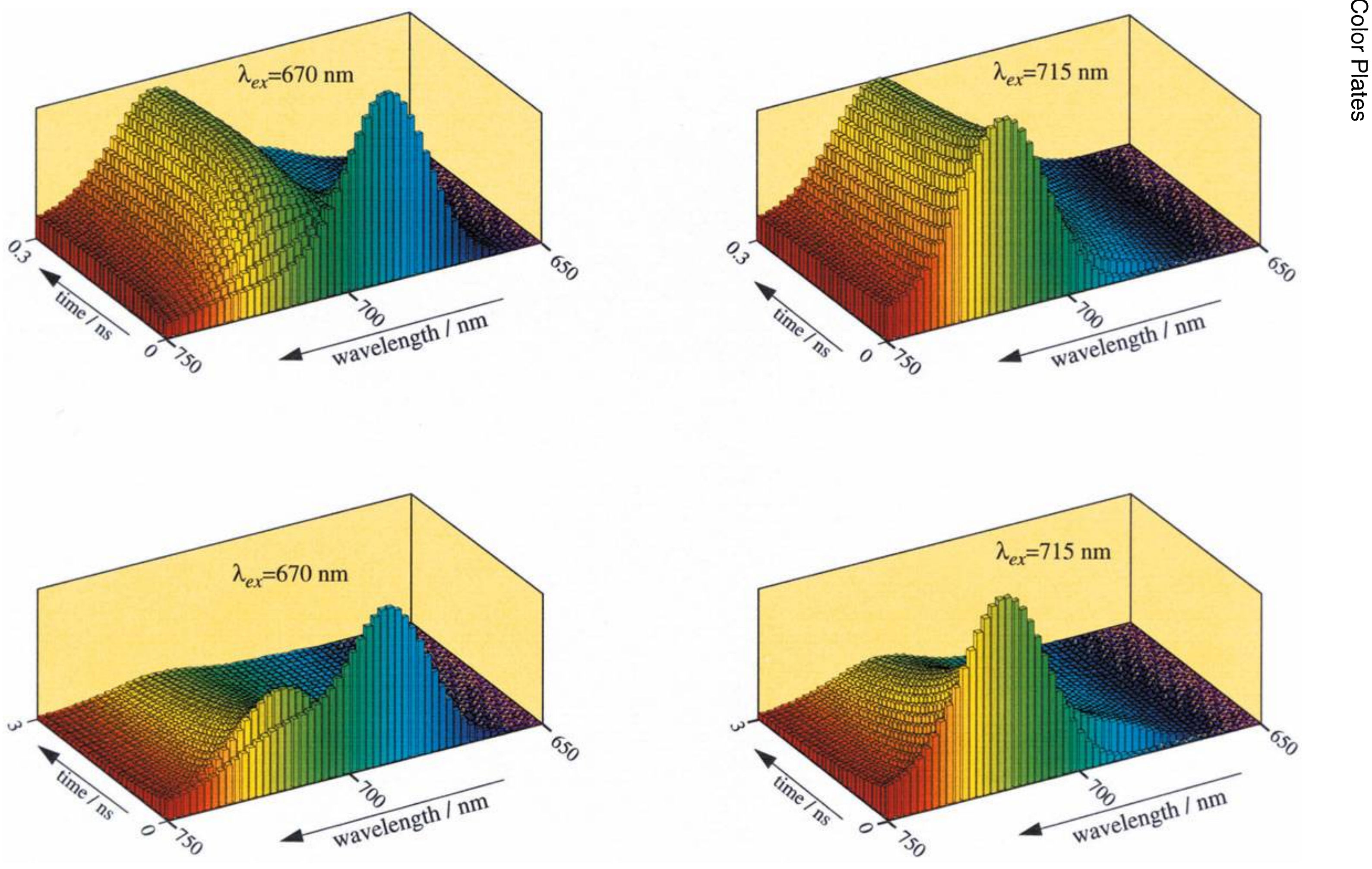


Color Plate 1. A. Colonies of the green volvocalean alga *Volvox*. Scale bar, 30 μm. B. A thallus of the red alga *Laurencia intricata.* Scale bar, 1 cm. C. Part of a thallus of the brown alga *Sargassum.* Scale bar, 1 cm. D. The cryptomonad *Cryptomonas* sp. under the light microscope. The several plastids in each cell are readily seen. The two equal flagella are not so easily seen under the light microscope. Scale bar, 2μm. Photography by M Ricketts. See Chapter 1, p. 4.

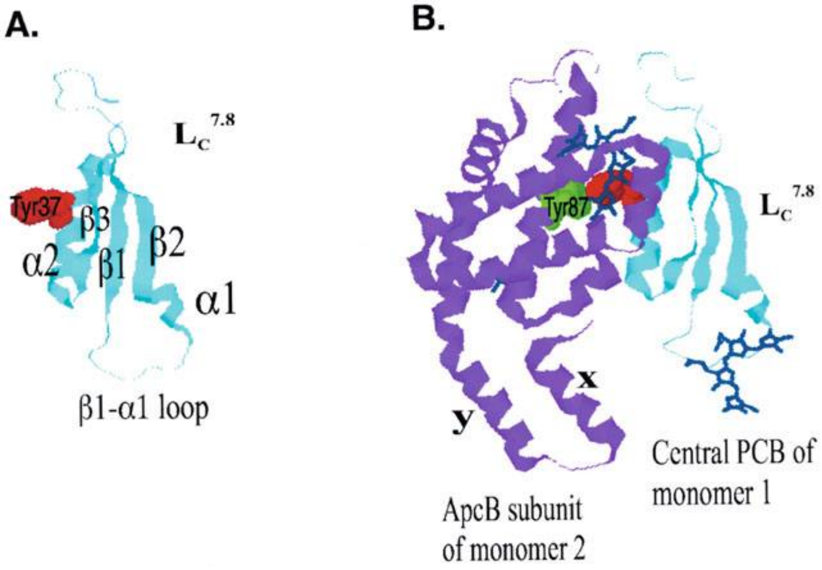
Anthony W. Larkum, Susan E. Douglas and John A. Raven (eds): Photosynthesis in Algae, pp. CP1–CP4.



Color Plate 2. Confocal images of chlorophyll fluorescence in various chlorophytes. A. *Oedogonium* (species unknown, local collection); x3,300. B. *Cladophora* (species unknown, local collection); x2,800. C. *Spirogyra* (species unknown, local collection) ×310. C.(Inset) *Spirogyra* as in C. at ×3000. D. *Klebsormidium flaccidum* (UTEX #LB2017) ×2,300. E *Nitella translucens* (Wasteneys collection) ×24000. All scale bars 5 μm except low magnification of *Spirogyra* which is 100 μm. Micrographs kindly provided by Brian Gunning: for further details and descriptions, see Gunning and Schwartz, 1999. See Chapter 2, p. 17 .



Color Plate 3. Time-resolved emission spectra (*TRES*) of the thylakoid membrane of *Ostreobium* sp. as calculated with the reaction scheme of Fig. 8 (p. 265). The *TRES* are depicted for two different excitation wavelengths and two different time scales as indicated. See Chapter 12, p. 265.



Color Plate 4. Structure of the small APC linker polypeptide ($L_C^{7.8}$) and its interactions with surrounding central phycocyanobilin chromophores covalently attached to allophycocyanin monomers 1 and 2. Panel A) Structure of the $L_C^{7.8}$ polypeptide, showing α-helices $\alpha 1$ and $\alpha 2$ and three β-sheets, $\beta 1$, $\beta 2$ and $\beta 3$. The Tyr37 amino acid residue, located on α-helix2, is depicted as space-filled atoms. The linker polypeptide is shown as a ribbon structure and colored cyan. Panel B) The same three-dimensional structure of the $L_C^{7.8}$ linker polypeptide (cyan) is shown along with its interactions with central phycocyanobilins (PCB) attached to Cys82 residues on allophycocyanin monomers 1 and 2. The PCBs of monomers 1 and 2 are colored blue and shown as stick figures. Residue Tyr37 located in α-helix2 of the linker polypeptide is shown as space-filled atoms, as is residue Tyr87 of the ApcB subunit of monomer 2. The interaction of Tyr37 (red) with Tyr87 (green) results in a conformational change between monomer 2 and its chromophore, specifically where ring B of PCB is forced in the opposite direction of Tyr87. This interaction is not found in the remaining two monomers of the APC trimer. Structures were generated using Rasmol and the PDB coordinates for APC·$L_C^{7.8}$ from the phycobilisomes of *Mastigocladus laminosus* (Reuter et al., 1999). See Chapter 14, p. 320.

Chapter 1

The Algae and their General Characteristics

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Summary

In contrast to the land plants, algae have very diverse mechanisms of photosynthesis, and especially of light-harvesting pigments and assemblages. This diversity is inherited from a great diversity of plastid types with different evolutionary histories, not withstanding the fact that all plastids appear to be derived by endosymbiosis from Cyanobacteria or their forebears. The major groups of algae are therefore related to the type of protist host and the type of plastid, and these are described. In most groups of algae it appears that the plastid has been derived by at least two serial endosymbioses. A single endosymbiosis appears to have occurred in the green algae, the red algae and the glaucocystophytes. The rich variety of types and mechanisms has given rise to many biochemical products which today form the basis of a growing biotechnology industry. Algae are important economically in many other ways. From a photosynthetic point of view the algae will be a rich source of ideas for many years to come.

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I. Introduction

Land plants have inherited from their green algal ancestors a remarkably uniform strategy for harvesting and converting light energy into chemical energy. This is based on processes using the magnesium-tetrapyrroles chlorophyll *a* (Chl *a*) and chlorophyll *b* (Chl *b*), together with a limited number of carotenoids. In eukaryotic organisms photosynthesis is carried out in cellular organelles known as plastids. Only in terms of carbon fixation has evolution brought about any changes at a cellular and plastid level; in the way in which carbon is fixed as C_3 or C_4 acids and the presence or absence of photosystems I and II in a limited number of plastid types. Using a limited range of pigments, harvesting of light energy involves the same basic mechanism throughout the land plants. In sharp contrast, the diverse assemblage of organisms grouped together under the general classification of algae, or photosynthetic protists, have evolved a great assortment of pigments and many elaborate strategies for light-harvesting and energy conversion. These 'variations on a theme' have been selected during evolution, resulting in the current diversity of form and function. However, because the algae have played a rather small direct role in the economies of the world up to the present time, they have received scant attention. Fortunately this situation is changing rapidly and is likely to change even more rapidly in the future. Biotechnology already offers a number of ways to harness products from algae and in the future this will no doubt increase. Global climate change has also provided an impetus to research on algae as solar collectors and converters of clean energy. In Japan, for example, several large laboratories working on algae have been granted funds based on carbon credits according to the Convention on Global Climate Change. Nevertheless there is still a long way to go before we can say that we really have the basic knowledge needed to understand the scope and breadth of algal photosynthesis. We hope that this book will be timely in mapping out the past work and putting forward a logical framework for future research in the area.

II. The Algae: Their Origins and Diversity

The algae, all of which carry out oxygenic photosynthesis by means of a cytoplasmic organelle, the plastid, constitute a diverse grouping of protists scattered in the crown group of protists (Fig. 1). Within the different algal groups there are non-photosynthetic sub-groups, but through close affinities with their photosynthetic cousins, they can be judged to have lost plastids secondarily. A moot point is found with the apicomplexans which are non-photosynthetic parasitic protists (e.g. *Plasmodium*, which causes malaria) in which there exists a relic plastid. These organisms are not currently placed in the algae, although their algal roots are acknowledged (Chapter 2, Larkum and Vesk).

The origin of algae occurred about 1–1.5 Ga ago by the capture of free-living oxygenic phototrophic eubacteria (most likely ancestors of present-day Cyanobacteria) by host cells that were early protists. Most workers in the field consider this endosymbiotic origin so well-supported that it is taken to be axiomatic. These host cells already possessed a mitochondrion (or mitochondrion-like organelle), whose origin was also certainly by endosymbiosis through the acquisition of a free-living α-proteobacterium. Thus the origin of algae and of mitochondriate protists was through the formation of a chimaera. And, indeed the origin of the first eukarya may also be chimaeric: from eubacterial and archaebacterial origins (Gupta and Golding, 1996). While Cyanobacteria, as prokaryotes, are not, strictly speaking, algae, they are conventionally dealt with to varying extents in texts on algae and many of the chapters in this volume consider Cyanobacteria as well as eukaryotes.

Both the origin of the plastid and the origin of the host in the chimaera which gave rise to the first algal cells are controversial. Using Ockham's razor one would seek a single origin for both. Hypothetically, a single cyanobacterium-like eubacterium would enter into symbiosis with a single kind of mitochondriate protist and from this first photosynthetic eukaryote all the other algae would arise. The majority of workers in the field broadly support such a single event (monophyly) as the origin of all primary plastids surrounded by two membranes. However, there are difficulties with this simple version especially in terms of plastid characters (Chapter 2, Larkum and Vesk). There are also difficulties that arise from the rather haphazard distribution of algae on phylogenetic trees based on small subunit rRNA or other genes. It

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Abbreviations: Chl – chlorophyll; EST – expressed sequence tags; kbp – kilobase pairs; NCBI – National Centre for Biotechnology Information, http://www.ncbi.nlm.nih.gov/; rRNA – ribosomal ribonucleic acid

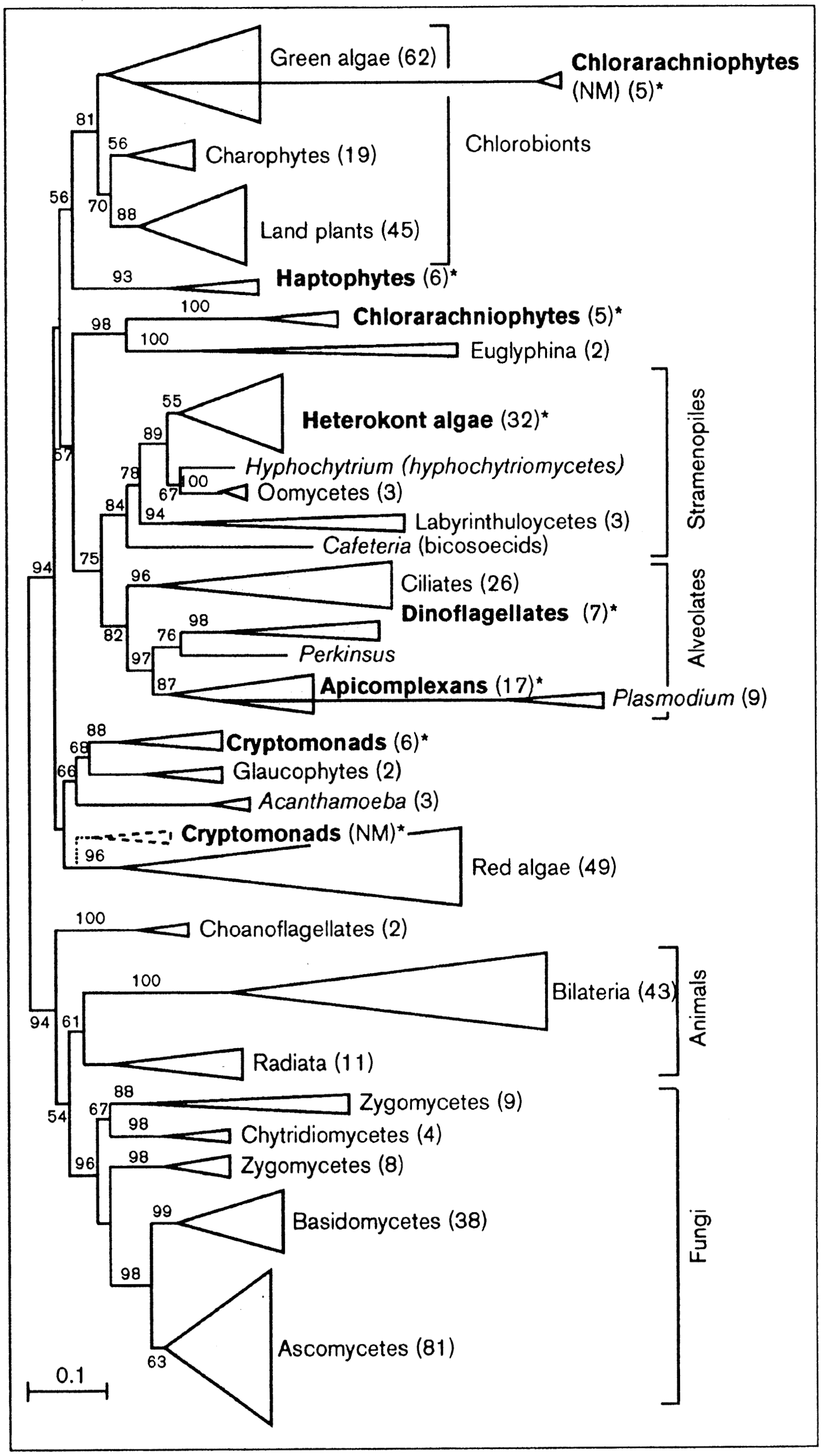

Fig. 1. Phylogenetic tree of major eukaryotic groups belonging to the crown taxa (from Douglas, 1998 with permission).

is not easy, although attempts have been made, to derive these different taxa from a single alga. However, in many of these taxa it can be argued that two serial endosymbioses occurred. The defining feature of these taxa is the presence of three or four plastid envelope membranes.

Thus in terms of a single origin of algae, the focus should be on the three groups of algae that contain only two envelope membranes where presumably a single endosymbiosis has taken place. These are the green algae (or chlorophytes), the red algae (or rhodophytes) and the glaucocystophytes (such as *Cyanophora*). The host cell in chlorophytes and glaucocystophytes may have a common origin, since in both there is clear evidence for a flagellate ancestral state. However there is no evidence for flagella in the rhodophytes and thus speculation about a single shared origin of these algae with the other two groups must surmount this and other difficulties. Furthermore there are distinct differences between the phycobiliproteins of glaucocystophytes and red algae (the red algal proteins differ significantly from those of both glaucocystophytes and Cyanobacteria ; Chapter 14, Toole and Alnutt). On the other hand, recent phylogenetic analyses based on whole plastid genomes as well as nuclear small subunit rRNA sequences argue for a common origin of red, green and glaucocystophyte algae (Moriera et al., 2000). In addition, red algae possess a Chl *a/b* protein in Photosystem I, which is found in chlorophytes and all the plastids whose origin involves two serial endosymbioses, again indicative of shared ancestry. Clearly plastids have undergone significant evolutionary changes since their endosymbiotic origin(s). Further discussion of these points is presented in Chapter 2 (Larkum and Vesk).

III. The Green, Red and Brown Algae

Classically the algae were divided into the green algae (Fig 2A), the red algae (Fig 2B) and the brown algae (Fig 2C), and, at that time, the blue-green algae which are now known to belong to the eubacteria (Engelmann, 1883, Gaidukov, 1903). Morphologically, these algae range in size from microscopic unicells to macroscopic organisms of considerable size (the brown algae include some of the tallest photosynthetic organisms in the world). This classification has stood the test of time, although the brown algae are now recognized to be part of a much larger collection of photosynthetic protists (see below). The green algae (Chlorophyta),with a few excisions such as the euglenophytes remain a monophyletic group (for review, see Graham, 1996) and the red algae (Rhodophyta) also appear to be a monophyletic group (Ragan et al., 1994). The brown algae, on the other hand, are a much more difficult group to describe and are now included in a broader group of Chl *c*-containing algae, the chromophytes (Christensen 1989). There are some dozen or more phyla or divisions within this supergroup and many ways of subdividing them and of tracing their ancestry have been suggested (van den Hoek et al., 1995; Graham and Wilcox, 2000). The chromophytes are described below.

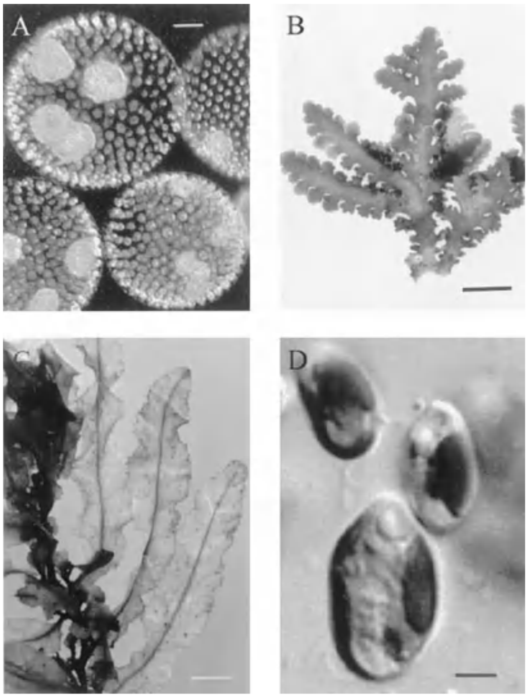

Fig. 2. A. Colonies of the green volvocalean alga *Volvox*. Scale bar, 30 μm. B. A thallus of the red alga *Laurencia intricata*. Scale bar, 1 cm. C. Part of a thallus of the brown alga *Sargassum*. Scale bar, 1 cm. D. The cryptomonad *Cryptomonas* sp. under the light microscope. The several plastids in each cell are readily seen. The two equal flagella are not so easily seen under the light microscope. Scale bar, 2μm. Photography by M Ricketts. See Color Plate 1.

IV. The Chromophytes

The chromophyte algae (Christensen, 1989) are an intriguing group of Chl *c*-containing algae whose origins are obscure, not only because they are polyphyletic but also because they represent a line of plastid descent where the plastid has been taken up at least twice by different eukaryotic hosts. In one instance, the cryptophytes, there is a relic nucleus of the primary host embedded between the two sets of plastid membranes (Greenwood, 1974; Chapter 2, Larkum and Vesk). In the remainder of the chromophyte group, no such nucleomorph remains but the presence of four membranes (heterokonts and haptophytes) and three membranes (in dinoflagellates) around the plastid indicate the occurrence of two serial endosymbioses. As mentioned above the group is also defined by having Chl *c* in addition to Chl *a,* (although this has been secondarily lost in the eustigmatophytes). However the diversity of structure of these algae is very great, ranging from flagellated unicells to macroscopic attached organisms with a large number of light-harvesting strategies and pigments (Chapters 3, 4, 12–15).

A. The Heterokonts

Within this broad group there are several well-defined groups—the phaeophytes (brown algae), bacillariophytes (diatoms), chrysophytes, xanthophytes, eustigmatophytes, synurophytes; however the overall definition is based on the type of flagella that are present and the type of cell wall and exoskeleton. The flagella are heterokont, i.e. two dissimilar flagella, one smooth and the other hairy. This classification has been known since the 19th century. However fine structural examination has provided a more comprehensive characterization: the smooth flagellum has a typical 9 + 2 microtubular structure while the second flagellum has tripartite tubular flagellar hairs, with a base, an intermediate region and a distal region (stramenopile character; Patterson, 1989). Stramenopile characterization is found in a wide range (but not all) of the so-called heterokont algae including chrysophytes, phaeophytes (brown algae), bacillariophytes (diatoms), eustigmatophytes, raphidophytes (or chloromonadophytes) and xanthophytes. A number of these algal groups are discussed below. For further information on the groups within the stramenopiles, the reader is referred to texts on algae such as van den Hoek et al. (1995) and Graham and Wilcox (2000).

1. The Phaeophytes

Brown algae have four envelope membranes and like other chromophytes contain Chl *c* in addition to Chl *a.* However, the brown algae is the only group which is consistently multicellular and produces macroscopic thalli. Recent work suggests that the brown algae are a monophyletic group. Their affinity with other chromophytes was unclear from morphological, life cycle and fine structural evidence. However recent phylogenetic tree evidence places them as a sister group with the rhaphidophytes (van de Peer, 2000).

2. The Bacillariophytes (Diatoms)

The diatoms are mostly unicellular organisms, with some colonial forms, that show no signs of motility (Round et al., 1990). Most, but not all, have a wonderfully sculpted exoskeleton made of silica (Fig 3A). This silicon frustule is synthesized in two halves and each time the cell divides a smaller frustule is formed, and sexual reproduction (or some other process which, like sexual reproduction, involves the loss and subsequent regeneration of the frustules) is generally needed to prevent a gradual decrease in the mean size of a dividing population of diatoms. Diatoms constitute a large component of the phytoplankton in both marine and fresh water bodies; so much so that geological formations are due to deposits of diatoms (diatomaceous earth) in several regions of the world. They have a light-harvesting mechanism based on Chl c_1 and c_2 and the xanthophyll, fucoxanthin (Chapter 15, Mimuro and Akimoto). The existence of diatom frustules in geological deposits is of rather recent origin (<200 Ma). It is probable that the group first appeared at an earlier time but clues as to its ultimate age are scarce. Phylogenetic trees based on small subunit rRNA gene sequences show diatoms to be basal to xanthophytes, phaeophytes, raphidophytes and chrysophytes (Daughberg and Andersen, 1997). Today, diatoms with silica frustules are so important that they dominate the deposits reaching 20% of the world's ocean floors (Falkowski and Raven, 1997), the so-called silica oceans. Diatoms are economically important as toxin-producers (e.g. *Nitzschia pungens* which causes amnesic shellfish poisoning).

B. The Haptophytes

The haptophyte algae (Green and Leadbetter, 1994; Winter and Siesser, 1994) are best known for the production of coccoliths (Fig 3D), which accounts for their other name, the coccolithophores (Fig. 3C).

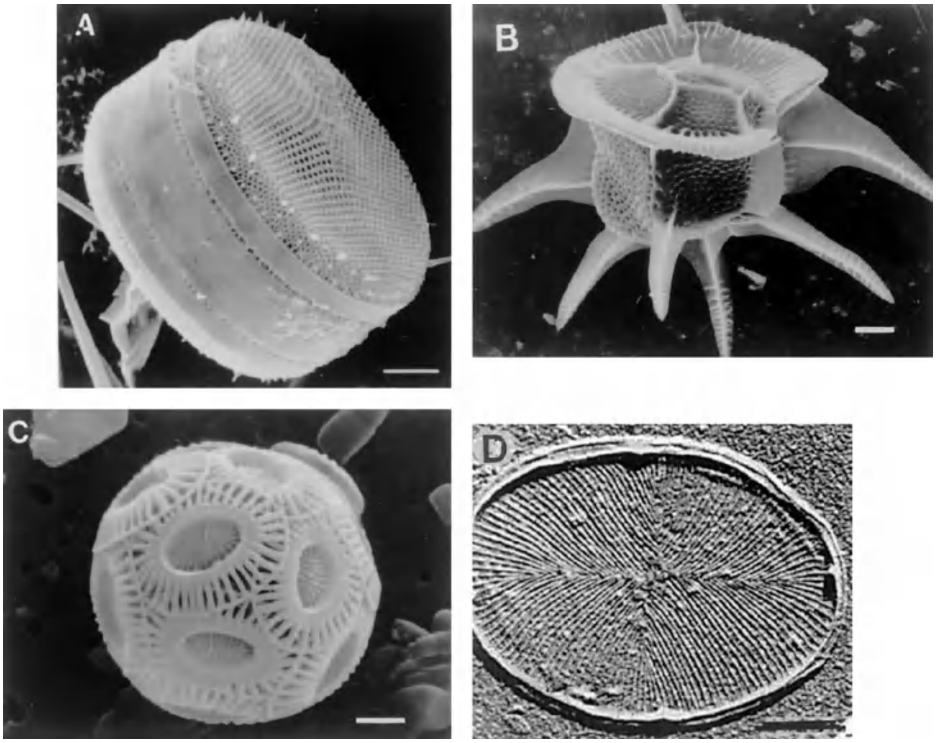

Fig. 3. A. Diatom *Thalassiosira eccentrica*. Scale bar = 10 μm. B. Dinoflagellate *Ceratocorys horrida*. Scale bar = 10 μm. C. Coccolithophorid *Emiliana huxleyi*. Scale bar = 1 μm . D. Scale or coccolith of the coccolithophorid, *Chrysochromulina sp*. Scale bar, 2 μm. The algae were visualized under the scanning electron microscope, courtesy of Dr GM Hallegraeff.

Coccoliths ('berry rocks') are sculptured scales of calcium carbonate, which form an armored protection around these single-celled algae (Winter and Siesser, 1994). These have been produced in such vast quantities in past oceans that they form large geological limestone deposits in many regions of the world. Coccocliths are recognizable from deposits of the Carboniferous Period and therefore represent some of the oldest evidence for chromophytic and other microalgae — putative fossils for green and red algae — go back much further back to 0.54–1.26 Ga (Xiao et al., 1998). The haptophytes display cellular and plastid characteristics common with the chrysophytes except for a haptonema, or attachment organ, which gives them their name. They generally have two smooth equal flagella. Haptophytes are important ecologically both because they exhibit high primary productivity and because they are responsible for toxic blooms. In the aquaculture industry many haptophytes are used as food for the growth of young prawns and other cultured marine animals.

C. The Cryptomonads

Cryptomonad algae (meaning 'hidden single' algae) have been recognized for many years (Fig. 2D). Unlike the heterokonts, these phytoflagellates possess two similar flagella (Fig 2D), and possess unique plastid characteristics (Chapter 2, Larkum and Vesk). The special interest of cryptomonads from an evolutionary point of view is that they possess a relic nucleus or 'nucleomorph' which lies between the outer and inner pairs of plastid membranes (Fig. 2D, Chapter 2, Larkum and Vesk). The nucleomorph genome encodes rRNAs distinct from those encoded by the nuclear genome and most closely related to those of red algae (Douglas et al., 1991). This small genome consists of three reduced chromosomes, now completely sequenced, that encode many proteins necessary for plastid function (Douglas et al., 2001). These data confirm that there have been two serial endosymbioses in the evolution of cryptomonads, the first giving rise to a red alga-like organism, which in turn was engulfed by a second phagotrophic flagellate host cell with affinities to *Goniomonas truncata* (McFadden et al., 1994a). Only one other group of organisms possessing nucleomorphs is known, the chlorarachniophytes (see below). These two types of organism lend credence to the idea that plastids with more than two envelope membranes arose by two (or more) serial endosymbioses. The plastids of cryptomonads also display an interesting assemblage of pigments and light-harvesting properties (Chapter 2, Larkum and Vesk).

D. The Dinoflagellates

Dinoflagellates are a unique group of unicellular chromophytic algae, whose origins are obscure and whose characteristics are quite unusual (Fig. 3B), even in terms of the high diversity of chromophytes in general (Taylor, 1987). The unique features of the plastid and its light harvesting system are described in Chapter 2 (Larkum and Vesk). The host cell is allied to the alveolate protists (Cavalier Smith, 2000), but has distinctive characteristics. Most dinoflagellates are unicellular with two distinct flagellae, which confer a characteristic whirling motion (the name 'dino' derives from the Greek word meaning 'whirling,' or 'a top')—but there are also non-flagellate forms. The two flagella emerge near each other but have very different characteristics. Dinoflagellate cysts are present in fossils, the oldest of which are found in 400 Ma Silurian deposits. Because the dinoflagellates are amongst the highest algal primary producers, they are associated with oil deposits and much effort is expended by oil companies into studying and characterizing dinoflagellate cysts as indicators of likely oil fields. Dinoflagellates are also of economic interest because they, like haptophytes, can form toxic blooms, often referred to as 'red tides,' leading to fish kills and human deaths. Toxic forms are also the basis of ciguatera, or saxitoxin, the nerve poison that accumulates in fish on coral reefs. Ciguatera poisoning—a condition which affects the nervous system—is cumulative.

V. The Chlorarachniophytes

Chlorarachnion and related green amoebae-like organisms have a nucleomorph lying between two sets of plastid membranes, as in cryptomonads. In this case, the host organism is related to filose amoebae and the plastid is related to that of green algae (Chapter 2, Larkum and Vesk). The nucleomorph contains three chromosomes and phylogenetic analysis of nucleomorph small subunit rRNA sequences indicates an origin of the primary host from a primitive green alga (McFadden et al., 1994b; van de Peer et al., 1996).

VI. The Euglenophytes

Euglena and its allies are common green or colorless flagellates found in freshwater ponds and shallow marine habitats. The host cell is allied to the kinetoplastids, protozoa which include the trypanosomes and which branch early on the evolutionary tree of protists (Bhattacharya, 1997). The host organism may therefore be one of the most primitive organisms among the algae. The plastid has three envelope membranes which has led to the suggestion that it too is the result of two serial endosymbioses (Gibbs, 1978), although no evidence of the nucleus or cytoplasm of the first host organism remains. An alternative hypothesis is that euglenoids arose by primary endosymbiosis where the cell membranes of both the host and the endosymbiont were retained (Cavalier-Smith, 1982). The plastid is most closely related to other green plastids but other evidence, such as the unusual introns in euglenophyte plastid genes, suggests an ancient origin (Chapter 2, Larkum and Vesk).

VII. Algal Genomes

The Human Genome Project has exemplified the importance and benefit of carrying out complete sequencing of the genome of an organism. Genomes for many other eukaryotic organisms (*Saccharomyces cerevisae, Drosophila melanogaster, Caenorhabditis elegans, Arabidopsis thaliana*) as well as a multitude of prokaryotic organisms are now available, making comparative genomics a reality. Unfortunately no algal nuclear genome is currently the focus of a major sequencing project; this is a major stumbling block in understanding and utilizing the genetic information locked up in the nuclei of algae. However, the complete sequence of the genome of the reduced eukaryotic nucleus of cryptomonads (Douglas et al., 2001) and EST surveys of algal protists that are underway (Gray, personal communication) should resolve this problem. On the other hand the more amenable task of sequencing the much smaller plastid genome has been accomplished in a number of algae (Table 1). While the list is reasonably long there are still a number of algae that demand attention such as the dinoflagellates, whose genomes appear to exist as single gene-encoding minicircles (Zhang et al., 1999). Nevertheless many useful conclusions can be drawn from comparative genomics of plastids (Martin et al., 1998).

VIII. Algae as Sources of Natural Products

With their high primary productivity many algae are an excellent source of specialty natural products or 'nutraceuticals.' This benefit has not been realized to a great degree by mankind but it is likely to be in future as exploitation of marine resources increases and world food supplies fail to meet demand. At present, only two types of cultivation or harvesting occur. The first is the cultivation of the unicellular green alga, *Dunaliella*, in hypersaline ponds. This alga produces excess β-carotene under high insolation and various successful enterprises around the world have been used to produce valuable supplies of β-carotene, which is used as a food colorant and nutritional supplement (Borowitzka, 1999). There are now many other examples for microalgae being cultivated as a source of natural products (Borowitzka and Borowitzka, 1988; Cohen, 1999).

The second, more commercially important aspect of algal cultivation and harvesting concerns the extraction of specific cell wall constituents from brown and red algae. In the case of brown algae, long-chain (1,4-linked) polymers of uronic acids of the sugars mannose and gulose are found and these constitute a class of natural products called alginates. These products are used in the food and cosmetic industry both as glycocolloids (gums and food stiffeners, gelling agents, etc.) and as clarifiers e. g. in brewing. In the case of red algae, shorter chain polysaccharides of 1,4- and 1,3-linked galactose with sulfate cross-linkages produce another group of glycocolloids. Agar and agarose are perhaps the most familiar of these but many more exist, the most important of which are carrageenans. They all form a very large industrial product in modern society, being used as colloids in thickening, gelling, smoothing and enhancing food and cosmetic products. The interested reader is referred to the literature for further information, especially Akatsuka (1994) and Graham and Wilcox (2000).

As a result of intense interest, several kinds of red and brown algae are cultivated for human consumption. The greatest developments have occurred in Japan, a country with a long history of seaweed cultivation and use (Ohno and Critchley 1993). Perhaps the most celebrated example is *Porphyra*, which is an essential component of *sushi* rolls. In fact, it was the discovery by a British scientist Kathleen Drew Baker, of the alternate life stage of *Porphyra*, the conchocelis phase, which led to the modern day mass cultivation of *Porphyra yezoensis* on semi-submerged rafts in Japan and elsewhere—and the erection of a statue to her on Tokyo Bay.

There is much more to algal cultivation and exploitation than can be covered in these few words. In the future the range of uses and products is likely to grow. Already pilot schemes are under way for the use of algal extracts as growth promoters in agriculture and algal turfs as bioremediators and tools to reduce eutrophication. Exciting progress is also being made in isolating antimicrobial agents from algae. In the future, it is likely that genetic engineering will see the use of algae in the production of energy and a multitude of specialty chemicals and pharmaceuticals.

IX. Concluding Remarks

This brief introduction serves to inform the reader of the great diversity that occurs within the group called the algae (defined as photosynthetic protists and their multicellular allies). It is indeed in these photosynthetic characteristics that much of the diversity of algae and their essential uniqueness are founded. However at the cellular and body plan level there is also a fascinating diversity within the algae. The interested reader is advised to go to the specialist texts that are referred to below. The following chapters will illustrate this in great detail. Chapter 2 presents details on the fine structure of algal plastids which carry the photosynthetic machinery of algae, while chapters 4, 5 and 6 explore some of the molecular biology underlying this plastid diversity. Chapter 3 looks at an intriguing and new group of Cyanobacteria, the prochlorophytes, which possess Chl *b* in addition to Chl *a*. Chapters 7 through 11 explore the biochemistry of photosynthetic carbon fixation and electron transport in algae, where many unique characteristics of algae are to be found. This is

Table 1. Plastid genomes of algae. This table was compiled from NCBI and Reith (1995).

Species	Algal Group	Size (kbp)	rRNA repeat and orientation	Repeat size kbp	Number of genes	Accession number
Cyanophora paradoxa	Glaucocystophyta	135.6	2i	12		NC_001675
Porphyra purpurea	Rhodophyta	191	2	4.8	166	NC_000925
Cyanidium caldarium	Rhodophyta	164.9	none	–	232	NC_001840
Odontella sinensis	Bacillariophyta	120	2i	7.7	141	NC_001713
Nephroselmis olivacea	Chlorophyta	200.8	2i	46	127	NC_000927
Chlorella vulgaris	Chlorophyta	150.6	none	–	111	NC_001865
Guillardia theta	Cryptophyta	121.5	2i	4.9	183	NC_000926
Euglena gracilis	Euglenophyta	143.2	3.5	5.9	108	NC_001603
Astasia longa	Euglenophyta	73.3	3.5	5.5		NC_002652
Toxoplasma gondii	Apicomplexa	35	2i	5.3	47	NC_001799
Plasmodium falciparum	Apicomplexa	35	2i	11	57	
Arabidopsis thalliana	Streptophyta	154	2i	26	139	NC_000932
Mesostigma viride	Streptophyta	118.3	2i	6	135	NC_002186
Chaetosphaeridium globosum	Charophyta	131.2	2i	12.4	124	NC–004115

i, inverse repeat

followed by four chapters (12–15) that describe the diverse range of light-harvesting strategies and pigment proteins in algae. The final chapters explore such aspects as light and UV stress (Chapter 16), adaptation to light climate (Chapter 17), photosynthesis in macroalgae (Chapter 18) and the acquisition algae for the purpose of photosynthesis by a number of animals in fascinating and economically important marine symbioses (Chapter 19, Yellowlees and Warner).

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