The Structure and Function of Plastids

Advances in Photosynthesis and Respiration

VOLUME 23

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 crystallography 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.

The Structure and Function of Plastids

Edited by

Robert R. Wise
University of Wisconsin, Oshkosh, WI, USA

and

J. Kenneth Hoober
Arizona State University, Tempe, AZ, USA

Springer

A C.I.P. Catalogue record for this book is available from the Library of Congress.

ISBN 978-1-4020-6570-5 (PB)
ISBN 978-1-4020-4060-3 (HB)
ISBN 978-1-4020-4061-0 (e-book)

Published by Springer,
P.O. Box 17, 3300 AA Dordrecht, The Netherlands.

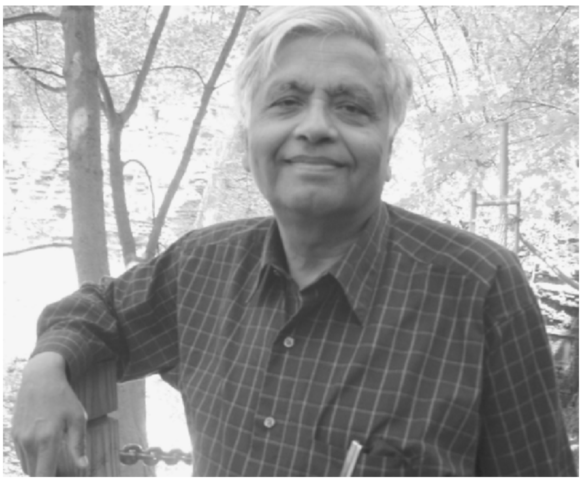
www.springer.com

Cover illustration:
Flower and leaves of the Garden Nasturtium (*Tropaeolum majus* L.) by Jim L. Bowman,
Bowman Images—Visual Imagination (http://bowco.com/images)

Printed on acid-free paper

From the Series Editor

Advances in Photosynthesis and Respiration, Volume 23



I am delighted to announce the publication, in *Advances in Photosynthesis and Respiration* (AIPH) Series, of **The Structure and Function of Plastids**, a book covering the central role of plastids for life on earth. It deals with both the structure and the function of the unique organelles, particularly of chloroplasts. Two distinguished authorities have edited this volume: Robert R. Wise of University of Wisconsin at Oshkosh, Wisconsin, and J. Kenneth Hoober of Arizona State University, Tempe, Arizona. Two of the earlier AIPH volumes have included descriptions of plastids: Volume 7 (The Molecular Biology of Chloroplasts and Mitochondria in *Chlamydomonas*, edited by Jean David Rochaix, Michel Goldschmidt-Clermont and Sabeeha Merchant); and Volume 14 (Photosynthesis in Algae, edited by Anthony Larkum, Susan Douglas and John Raven).

The current volume follows the 22 volumes listed below.

Published Volumes (1994–2005)

- *Volume 1:* ***Molecular Biology of Cyanobacteria*** (28 chapters; 881 pages; 1994; edited by Donald A. Bryant, from USA; ISBN: 0-7923-3222-9);
- *Volume 2:* ***Anoxygenic Photosynthetic Bacteria*** (62 chapters; 1331 pages; 1995; edited by Robert E. Blankenship, Michael T. Madigan and Carl E. Bauer, from USA; ISBN: 0-7923-3682-8);
- *Volume 3:* ***Biophysical Techniques in Photosynthesis*** (24 chapters; 411 pages; 1996; edited by the late Jan Amesz and the late Arnold J. Hoff, from The Netherlands; ISBN: 0-7923-3642-9);
- *Volume 4:* ***Oxygenic Photosynthesis: The Light Reactions*** (34 chapters; 682 pages; 1996; edited by Donald R. Ort and Charles F. Yocum, from USA; ISBN: 0-7923-3683-6);
- *Volume 5:* ***Photosynthesis and the Environment*** (20 chapters; 491 pages; 1996; edited by Neil R. Baker, from UK; ISBN: 0-7923-4316-6);
- *Volume 6:* ***Lipids in Photosynthesis: Structure, Function and Genetics*** (15 chapters; 321 pages; 1998; edited by Paul-André Siegenthaler and Norio Murata, from Switzerland and Japan; ISBN: 0-7923-5173-8);
- *Volume 7:* ***The Molecular Biology of Chloroplasts and Mitochondria in Chlamydomonas*** (36 chapters; 733 pages; 1998; edited by Jean David Rochaix, Michel Goldschmidt-Clermont and Sabeeha Merchant, from Switzerland and USA; ISBN: 0-7923-5174-6);
- *Volume 8:* ***The Photochemistry of Carotenoids*** (20 chapters; 399 pages; 1999; edited by Harry A. Frank, Andrew J. Young, George Britton and Richard J. Cogdell, from USA and UK; ISBN: 0-7923-5942-9);
- *Volume 9:* ***Photosynthesis: Physiology and Metabolism*** (24 chapters; 624 pages; 2000; edited by Richard C. Leegood, Thomas D. Sharkey and Susanne von Caemmerer, from UK, USA and Australia; ISBN: 0-7923-6143-1);
- *Volume 10:* ***Photosynthesis: Photobiochemistry and Photobiophysics*** (36 chapters; 763 pages; 2001; authored by Bacon Ke, from USA; ISBN: 0-7923-6334-5);
- *Volume 11:* ***Regulation of Photosynthesis*** (32 chapters; 613 pages; 2001; edited by Eva-Mari Aro

and Bertil Andersson, from Finland and Sweden; ISBN: 0-7923-6332-9);

- *Volume 12:* ***Photosynthetic Nitrogen Assimilation and Associated Carbon and Respiratory Metabolism*** (16 chapters; 284 pages; 2002; edited by Christine Foyer and Graham Noctor, from UK and France; 0-7923-6336-1);
- *Volume 13:* ***Light Harvesting Antennas*** (17 chapters; 513 pages; 2003; edited by Beverley Green and William Parson, from Canada and USA; ISBN: 0-7923-6335-3);
- *Volume 14:* ***Photosynthesis in Algae*** (19 chapters; 479 pages; 2003; edited by Anthony Larkum, Susan Douglas and John Raven, from Australia, Canada and UK; ISBN: 0-7923-6333-7);
- *Volume 15:* ***Respiration in Archaea and Bacteria: Diversity of Prokaryotic Electron Transport Carriers*** (13 chapters; 326 pages; 2004; edited by Davide Zannoni, from Italy; ISBN: 1-4020-2001-5);
- *Volume 16:* ***Respiration in Archaea and Bacteria 2: Diversity of Prokaryotic Respiratory Systems*** (13 chapters; 310 pages; 2004; edited by Davide Zannoni, from Italy; ISBN: 1-4020-2002-3);
- *Volume 17:* ***Plant Mitochondria: From Genome to Function*** (14 chapters; 325 pages; 2004; edited by David A. Day, A. Harvey Millar and James Whelan, from Australia; ISBN: 1-4020-2339-5);
- *Volume 18:* ***Plant Respiration: From Cell to Ecosystem*** (13 chapters; 250 pages; 2005; edited by Hans Lambers, and Miquel Ribas-Carbo, 2005; from Australia and Spain; ISBN: 1-4020-3588-8);
- *Volume 19:* ***Chlorophyll a Fluorescence: A Signature of Photosynthesis*** (31 chapters; 817 pages; 2004; edited by George C. Papageorgiou and Govindjee, from Greece and USA; ISBN: 1-4020-3217-X);
- *Volume 20:* ***Discoveries in Photosynthesis*** (111 chapters; 1210 pages; 2005; edited by Govindjee, J. Thomas Beatty, Howard Gest and John F. Allen, from USA, Canada and Sweden (& UK); ISBN: 1-4020-3323-0);
- *Volume 21:* ***Photoprotection, Photoinhibition, Gene Regulation, and Environment*** (21 chapters; 500 pages; 2005; edited by Barbara Demmig-Adams, William W. Adams III and Autar K. Mattoo, from USA; ISBN: 1-4020-3564-0); and
- *Volume 22:* ***Photosystem II: The Light-Driven Water:Plastoquinone Oxidoreductase.*** (34 chapters; 820 pages; 2005; edited by Thomas J. Wydrzynski and Kimiyuki Satoh, from Australia and Japan; ISBN: 1-4020-4249-3).

Further information on these books and ordering instructions can be found at <http://www.springeronline.com> under the Book Series "Advances in Photosynthesis and Respiration". Special discounts are available for members of the International Society of Photosynthesis Research, ISPR (<http://www. photosynthesis-research.org/>).

The Structure and Function of Plastids

The Structure and Function of Plastids, Volume 23 in the *Advances in Photosynthesis and Respiration* Series, provides a comprehensive look at the biology of plastids, the multifunctional biosynthetic factories that are unique to plants and algae. Fifty-nine international experts, from 11 countries, have contributed an excellent "Dedication" and 27 chapters that cover all aspects of this large and diverse family of plant and algal organelles. The book is divided into five sections: (I) **Plastid Origin and Development** (5 chapters); (II) **The Plastid Genome and its Interaction with the Nuclear Genome** (5 chapters); (III) **Photosynthetic Metabolism in Plastids** (4 chapters); (IV) **Non-Photosynthetic Metabolism in Plastids** (6 chapters); and (V) **Plastid Differentiation and Response to Environmental Factors** (7 chapters). Each chapter includes an integrated view of plant biology from the standpoint of the plastid. The book is intended for a wide audience, but is specifically designed for advanced undergraduate and graduate students and scientists in the fields of photosynthesis, biochemistry, molecular biology, physiology, and plant biology. This book, edited by Bob Wise and Ken Hoober, is a very important addition to the already published books in the AIPH Series.

The Structure and Function of Plastids begins with *a dedication* by Brian Gunning (of Australia) Friederike Koenig (of Germany) and Govindjee (USA) to the early pioneers. This dedication ends by honoring Wilhelm Menke, who had coined the word "thylakoids" in 1961. I provide below some of the names, mentioned in this dedication (arranged here by the year of birth of those mentioned):

- Anthony van Leewenhoeck (1632–1723) described chloroplasts without naming them
- Nehemiah Grew (1641–1712) may have indeed seen chloroplasts

- Franz Julius Ferdinand Meyen (1804–1840) described “chlorophyll granules” (or “corpuscules”)
- Hugo von Mohl (1805–1872) provided detailed description of “chlorophyll granules” (“Chlorophyllkörner”)
- Nathanael Pringsheim (1823–1894) used the term “Stroma” for the non-green part of “Chlorophyllkörner”
- Eduard Strasburger (1844–1912) used the word “Chloroplast” for chloroplast
- Arthur Meyer (1850–1922) used the term “Grana” and distinguished between “Autoplasten” (what we call chloroplasts); “Chromoplasten” (chromoplasts); “Trophoplasten” (reserve storing plastids); and “Anaplasten” (leucoplasts)
- Constantin Sergeevich Mereschkowsky* (1855–1921) provided a detailed hypothesis of endosymbiosis (* also spelled as Konstantin Sergejewicz Mereschkovsky)
- Andreas Franz Schimper (1856–1901) described three types of plastids (“Chloroplastiden”, “Leukoplastiden”, and “Chromoplastiden”); stated that “Chloroplastiden” resembled cyanobacteria

Twenty-seven chapters, in order of appearance, are (authors names are in parentheses):

(1) The Diversity of Plastid Form and Function (Robert R. Wise, USA);
(2) Chloroplast Development: Whence and Whither (J. Kenneth Hoober, USA);
(3) Protein Import into Plastids: Who, When, and How? (Ute C. Vothknecht and Jürgen Soll, both from Germany);
(4) Origin and Evolution of Plastids: Genomic View on the Unification and Diversity of Plastids (Naoki Sato, Japan);
(5) The Mechanism of Plastid Division: The Structure and Origin of The Plastid Division Apparatus (Shin-ya Miyagishima and Tsuneyoshi Kuroiwa, USA and Japan);
(6) Expression, Prediction and Function of the Thylakoid Proteome in Higher Plants and Green Algae (Klaas van Wijk, USA);
(7) The Role of Nucleus- and Chloroplast-Encoded Factors in the Synthesis of the Photosynthetic Apparatus (Jean-David Rochaix, Switzerland);
(8) Plastid Transcription: Competition, Regulation, and Promotion by Plastid- and Nuclear-Encoded Polymerases (A. Bruce Cahoon, Yutaka Komine and David B. Stern, all from USA);
(9) Plastid-to-Nucleus Signaling (Åsa Strand, Tatjana Kleine and Joanne Chory, from Sweden and USA);
(10) Trace Metal Utilization in Chloroplasts (Sabeeha Merchant, USA);
(11) Light/Dark Regulation of Chloroplast Metabolism (Shaodong Dai, Kenth Johansson, Hans Eklund and Peter Schürmann, of USA, Switzerland and Sweden);
(12) Chlororespiratory Pathways and their Physiological Significance (Peter J. Nixon and Peter R. Rich, both from UK);
(13) CO_2 Concentrating Mechanisms (Sue G. Bartlett, Mautusi Mitra and James V. Moroney, all from USA);
(14) Synthesis, Export, and Partitioning of the End Products of Photosynthesis (Andreas P.M. Weber, USA);
(15) Chlorophyll Synthesis (Robert D. Willows, Australia);
(16) Carotenoids (Abby J. Cuttriss, Joanna L. Mimica, Barry J. Pogson and Crispin A. Howitt, all from Australia);
(17) Lipid Synthesis, Metabolism and Transport (Peter Dörmann, Germany);
(18) Amino Acid Synthesis in Plastids (Muriel Lancien, Peter J. Lea and Ricardo A. Azevedo, from UK and Brazil);
(19) Sulfur Metabolism in Plastids (Elizabeth A.H. Pilon-Smits and Marinus Pilon, both from USA);
(20) Regulation and Role of Calcium Fluxes in the Chloroplast (Carl Hirschie Johnson, Richard Shingles and William F. Ettinger, all from USA);
(21) The Role of Plastids in Ripening Fruits (Florence Bouvier and Bilal Camara, both from France);
(22) Fate and Activities of Plastids During Senescence (Karin Krupinska, Germany);
(23) The Kleptoplast (Mary E. Rumpho, Farahad P. Dastoor, James R. Manhart and Jungho Lee, from USA and Korea);
(24) The Apicoplast (Soledad Funes, Xochitl Pérez-Martínez, Adrián Reyes-Prieto and Diego González-Halphen, all from Mexico);
(25) The Role of Plastids in Gravitropism (Maria Palmieri and John Z. Kiss, both from USA);
(26) Chloroplast Movements in Response to Environmental Signals (Yoshikatsu Sato and Akeo Kadota, both from Japan) and
(27) Oxygen Metabolism and Stress Physiology (Barry A. Logan, USA).

A List of Selected Books

Volume 20 of the AIPH Series (Discoveries in Photosynthesis, edited by Govindjee, J.T. Beatty, H.Gest and J.F. Allen) contains a recently published time-line on oxygenic photosynthesis covering its many aspects, including research on the functional work on chloroplasts (see Govindjee and D. Krogmann (2004) "Discoveries in oxygenic photosynthesis (1727–2003): a perspective". Photosynth Res **80**: 15–57). In addition, this book contains a historical perspective by Andrew Staehelin: "Chloroplast structure: from chlorophyll granules to supra-molecular architecture of thylakoid membranes" (Photosynth Res **76**: 185–196, 2003).

Plastids have been at the heart of plant biology and several books have been written on them. Bob Wise, Ken Hoober and I have selected to list some of these books that have influenced research in the field of *plastids*. They are listed chronologically. From the students' point of view, the book by J.K. Hoober (1984), and by U.C. Biswal, B. Biswal and M.K. Raval (2003) are most suitable in providing a basic background of the field of plastids.

- T.W. Goodwin (ed.) (**1966**) Biochemistry of Chloroplasts, Volume 1. Proceedings of a NATO Advanced Study Institute held at Aberystwyth, UK, August, 1965. Academic Press, London and New York
- T.W. Goodwin (ed.) (**1967**) Biochemistry of Chloroplasts, Volume 2. Proceedings of a NATO Advanced Study Institute held at Aberystwyth, UK, August, 1965. Academic Press, London and New York
- J.T.O. Kirk and R.A.E. Tilney-Bassett (**1967**) The Plastids, their Chemistry, Structure, Growth and Inheritance. WH Freeman and Co., London
- B.E.S. Gunning and M.W. Steer (**1975**) Ultrastructure and the Biology of Plant Cells . Edward Arnold, London
- J. Barber (ed.) (**1976**) The Intact Chloroplast (Topics in Photosynthesis, Vol. 1) Elsevier Scientific Pub. Co., Amsterdam and New York
- G. Akoyunoglou and J-H. Argyroudi-Akoyunoglou (**1978**) Chloroplast Development: Proceedings of the International Symposium on Chloroplast Development held on the Island of Spetsai, Greece, July 9–15, 1978. Elsevier/North-Holland Biomedical Press, Amsterdam and New York
- J.T.O. Kirk and R.A.E. Tilney-Bassett (**1978**) The Plastids, their Chemistry, Structure, Growth, and Inheritance, 2nd edition. Elsevier/North Holland Biomedical Press, Amsterdam and New York
- J. Reinert (**1980**) Chloroplasts (in Results and Problems in Cell Differentiation, Vol. 10). Springer-Verlag, Berlin
- J.A. Schiff and H. Lyman (eds.) (**1982**) On the Origins of Chloroplasts. Elsevier/North-Holland, Amsterdam and New York
- M.A. Tribe and P. Whittaker (**1982**) Chloroplasts and Mitochondria (Institute of Biology's Studies in Biology, No. 31), 2nd edition. Edward Arnold, London
- N.R. Baker and J. Barber (eds.) (**1984**) Chloroplast Biogenesis. Elsevier Science Pub. Co., Amsterdam
- B. Halliwell (**1984**) Chloroplast Metabolism: The Structure and Function of Chloroplasts in Green Plants. Clarendon Press, New York and Oxford University Press, Oxford
- J.K. Hoober (**1984**) Chloroplasts. Plenum Press, New York
- J.R. Ellis (ed.) (**1984**) Chloroplast Biogenesis (Seminar Series/Society for Experimental Biology, No. 21) Cambridge University Press, Cambridge and New York
- J.H. Argyroudi-Akoyunoglou and H. Senger (**1999**) The Chloroplast: From Molecular Biology to Biotechnology. Kluwer Academic Publishers (now Springer), Dordrecht
- U.C. Biswal, B. Biswal and M.K. Raval (**2003**) Chloroplast Biogenesis from Proplastid to Gerontoplast. Kluwer Academic Publishers (now Springer), Dordrecht
- S.G. Moller (ed.) (2004) Plastids (in Annual Plant Reviews, Vol. 13). Blackwell Publishing, Oxford, U.K.

A Useful Compact Disc (CD)

A very useful CD that should be helpful to students of "Plastids" is*: Plant Cell Biology on CD, Part 1* (ISBN 0-9751682-0-7); it was produced by Brian Gunning, of the Research School of Biological Sciences, Australian National University, Canberra, Australia. It is a two-CD set containing more than 1000 images covering an introduction to plant cells, mitochondria, plastids and peroxisomes, designed as a source of information for students and a resource for teachers. It is probably the largest collection of images of plastids ever assembled for these purposes, including most kinds of light and electron microscopy, diagrams and numerous time-lapse movies, organized in a user-friendly menu-driven interface. Further details are available at: www.plantcellbiologyonCD.com.

Future AIPH Books

The readers of the current series are encouraged to watch for the publication of the forthcoming books (not necessarily arranged in the order of future appearance):

- *Chlorophylls and Bacteriochlorophylls: Biochemistry, Biophysics, Functions and Applications* (Editors: Bernhard Grimm, Robert J. Porra, Wolfhart Rüdiger and Hugo Scheer);
- *Photosystem I: The Light-Driven Plastocyanin: Ferredoxin Oxidoreductase* (Editor: John Golbeck);
- *Biophysical Techniques in Photosynthesis. II* (Editors: Thijs J. Aartsma and Jörg Matysik);
- *Photosynthesis: A Comprehensive Treatise; Physiology, Biochemistry, Biophysics and Molecular Biology, Part 1* (Editors: Julian Eaton-Rye and Baishnab Tripathy); and
- *Photosynthesis: A Comprehensive Treatise; Physiology, Biochemistry, Biophysics and Molecular Biology, Part 2* (Editors: Baishnab Tripathy and Julian Eaton-Rye)

In addition to these contracted books, we are already in touch with prospective Editors for books on the following topics:

- *Molecular Biology of Cyanobacteria. II*
- *Protonation and ATP Synthases*
- *Genomics and Proteomics*
- *Anoxygenic Photosynthetic Bacteria. II*
- *Sulfur Metabolism in Photosynthetic Systems*
- *Global Aspects of Photosynthesis and Respiration*
- *Molecular Biology of Stress*
- *Artificial Photosynthesis*
- *Chloroplast Bioengineering*

Readers are encouraged to send their suggestions for future volumes (topics, names of future editors, and of future authors) to me by email (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.

Acknowledgments

First of all, I thank Achim Trebst as his emails have been a constant source of inspiration to continue our projects. I take this opportunity to thank Ken Hoober and Bob Wise for their outstanding and painstaking editorial work for this volume. I also thank Brian Gunning and Friederike Koenig for their excellent contributions to the “Dedication”, and most importantly to all other 56 authors of volume 23: without their authoritative chapters, there would be no such volume.

I owe Jacco Flipsen and Noeline Gibson (both of Springer) special thanks for their friendly working relation with us that led to the production of this book. Thanks are also due to Jeff Haas (Director of Information Technology, Life Sciences, University of Illinois at Urbana-Champaign, UIUC) and Evan DeLucia (Head, Department of Plant Biology, UIUC) for their support. Larry Orr constantly provides us with guidance regarding the rules and the format of our Series that started in 1994. All the members of my immediate family (my wife Rajni Govindjee; our daughter Anita, her husband Morten Christiansen, and our grand-daughter Sunita; our son Sanjay, his wife Marilyn, and our grandsons Arjun and Rajiv) have been very supportive during the preparation of this and other books in the AIPH Series. I also thank Arvind Sohal (of Techbooks, in New Delhi, India) and André Tournois (of Springer) for their contribution towards the production of this volume.

September 14, 2005

Govindjee
Series Editor, *Advances in Photosynthesis and Respiration*
University of Illinois at Urbana-Champaign,
Department of Plant Biology
Urbana, IL 61801-3707
email: gov@uiuc.edu;
URL: http://www.life.uiuc.edu/govindjee

Contents

Preface

The very origin of the plastid is clouded in mystery, even though the evidence is clear that the wide diversity of plastids is a historical consequence resulting from a single event, in which an evolving eukaryotic cell captured a photosynthetic prokaryotic cell. The product of this event—all algae and plants, the primary producers in all ecosystems—was one of the major outcomes of evolution. Core metabolic processes such as amino acid and fatty acid synthesis, and the ability to synthesize secondary products such as carotenoids, enzyme cofactors and antioxidants, were provided by the prokaryotic endosymbiont. ATP formation via oxidative phosphorylation was provided by another, earlier endosymbiont. The principal contributions of the eukaryotic nucleus, which was derived from an Archean organism, were the mechanisms of expression of the nuclear genome—nuclear transcription and cytosolic translation. Somehow, this latter organism was able to co-opt the genetic information of the respiratory and photosynthetic prokaryotes for its own use. Thus, the endosymbiotic events, first to produce the mitochondrion and then the plastid, were essential for the development of modern, complex organisms.

Most of the volumes in this series emphasize mechanisms related to photosynthesis or respiration. We all recognize that photosynthesis in the chloroplast is the most fundamental process in biology and provides the major foodstuff on which almost all organisms depend for survival. However, the plastid is, in addition, essential for many other processes, which are highlighted in this volume. For instance, the herbicide glyphosate, although not an inhibitor of photosynthesis, is highly toxic to all photosynthetic organisms. This is because glyphosate inhibits aromatic amino acid synthesis, an essential but non-photosynthetic function of plastids. We considered the ability of the plastid to provide these other, important functions worthy of attention. An astonishing feature of this volume is the phenomenal amount of research that has been done over the past several decades to understand these other, non-photosynthetic plastid functions.

It has been almost 40 years since John T.O. Kirk and Richard A.E. Tilney-Bassett published the first comprehensive treatment of plastid biology: "The Plastids: Their Chemistry, Structure, Growth and Inheritance", 1967, W.H. Freeman. While photosynthesis and chloroplasts (and indeed each of the topics covered in this volume) have received their due attention in the ensuing four decades, no single volume has brought together the amazing variety of plastid types and the remarkable diversity of plastid functions. We felt it was time for a modern synthesis of plastid biology and it was with this goal in mind we selected the topics and authors for this volume. We sought to produce a volume that is comprehensive without being encyclopedic; complete but readable; synthetic with even a touch of thought-provoking speculation, where warranted; a book that both beginning and experienced plant scientists will want to read, not one that will only reluctantly be referred to when absolutely necessary.

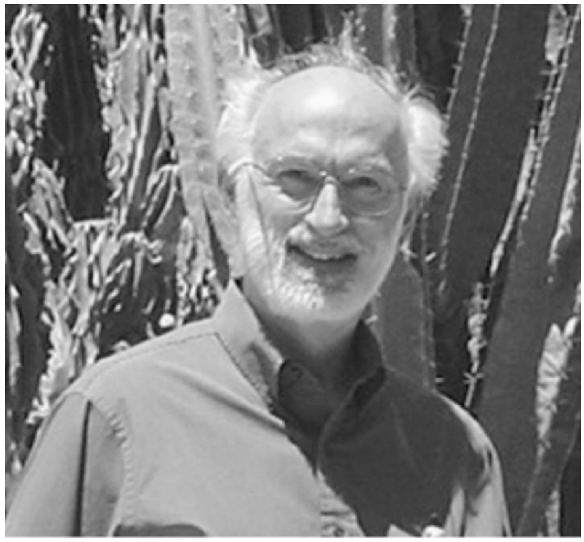
First, and foremost, we thank our 57 co-authors who have given their time and expertise to the writing of the chapters contained herein. Without them this volume would not have been possible. (For details, see the *Table of Contents* and *From the Series Editor*.) We hope that the scope of this volume will provide a framework in which new studies of the plastid can be launched and anyone interested in research in plastid biology would do well to start with the information provided by these authors. We also wish to thank senior series editor Govindjee as his efforts and vision have been instrumental in bringing this project to completion.

Robert R. Wise
Department of Biology
University of Wisconsin, Oshkosh, WI 54901
Telephone: 1-920- 424-3404
Fax: 1-920- 424-1101
Email: wise@uwosh.edu

J. Kenneth Hoober
School of Life Sciences
Arizona State University
Tempe, AZ 85287
Fax: 1-480-965-6899
Email: khoober@asu.edu

Robert R. Wise

Bob Wise is a professor of plant physiology at the University of Wisconsin at Oshkosh. His research interests are the biochemistry and bioenergetics of plant stress and plant cell ultrastructure. He graduated from the University of Wisconsin at Stevens Point in 1977 with a B.Sc. in Biology. It was there under the direction of Joseph B. Harris he was introduced to the world of plant cell ultrastructure and began a life-long interest in all matters plastidal. Discovering, and devouring, J.T.O. Kirk and R.A.E. Tilney-Bassett's 1967 seminal volume "The Plastids" was a decisive experience in his undergraduate education. In 1986 he earned his Ph.D. from the Botany Department of Duke University, Durham, North Carolina. For his dissertation he studied reactive oxygen species generation during chilling in the light under the direction of the late Aubrey W. Naylor. Postdoctoral work at the University of Illinois at Urbana-Champaign in the laboratory of Donald R. Ort (funded by the United States Department of Agriculture and the McKnight Foundation) included studies of the bioenergetics of chilling stress, the pattern of carbon fixation in leaves during drought stress, and the diurnal regulation of photosynthesis under both laboratory and field conditions. He joined the Biology Department at the University of Wisconsin at Oshkosh in 1993 and has conducted research in and taught plant physiology, plant anatomy and electron microscopy. He very much enjoys teaching at every collegiate level from large, freshman-level biology lectures to small, advanced graduate level seminars. Both undergraduate and graduate students play large roles in his research program. He spent the 2001/2002 academic year on sabbatical in the laboratory of Thomas D. Sharkey in the Botany Department at the University of Wisconsin at Madison investigating the response of photosynthesis to high temperature stress and the central role played by the thylakoid membrane in the sensing and signaling of heat stress in laboratory and field-grown plants. That collaboration continues. Elucidating the proteome of heat-stress-induced plastoglobuli is a current focus of his research program. Further information can be found at his web page (http://www.uwosh.edu/departments/biology/wise/wise.html). He can be reached by e-mail at: wise@uwosh.edu.



J. Kenneth Hoober

Ken Hoober started his scientific career as an undergraduate in chemistry and then received a Ph.D. degree in 1965 in biochemistry from the University of Michigan in Ann Arbor. His graduate work involved characterization of unique proteins synthesized during differentiation of the epidermis of neonatal rats in the laboratory of Isadore Bernstein. He then spent 15 months as a postdoctoral fellow with Stanley Cohen at Vanderbilt University in Nashville, Tennessee, working on the biochemical effects of epidermal growth factor. During a 2-year postdoctoral fellowship at the Rockefeller University in New York City with Philip Siekevitz and George Palade, he began working on chloroplast development in the green alga *Chlamydomonas reinhardtii*, his first introduction to the chloroplast, photosynthesis and plants. He obtained his first faculty position in 1968 in the Department of Biochemistry at Rutgers Medical School in New Jersey. In 1971 he moved with his chairman, Gerhard Plaut, to the Department of Biochemistry at Temple University School of Medicine in Philadelphia. He rose through the ranks and in 1989 became chairman of the department. An exceptional opportunity in 1987 was the experience working with Diter von Wettstein, Gamini Kannangara and Simon Gough at the Carlsberg Laboratories in Copenhagen, Denmark, during which he contributed to elucidation of the mechanism of glutamate 1-semialdehyde aminotransferase. In 1991, he accepted an offer to become chair of the Department of Botany at Arizona State University in Tempe. Several years later the departmental name was changed to Plant Biology. Perhaps the justification of being offered this position was derived from his monograph *Chloroplasts* that was published by Plenum Press in 1984. Although he knew little about plants, writing this book formed the basis of his knowledge about the plastid. At Arizona State University, he was accepted as a member of the world-renowned Center for the Study of Early Events in Photosynthesis. As a result of interactions with members of the Center, he received a legitimate education in photosynthesis. His research has emphasized assembly of the major light-harvesting complexes as probes for biogenesis of thylakoid membranes. He was one of the first to characterize ribosomes of chloroplasts and describe their differences from cytosolic ribosomes, and was the first to establish that the apoproteins are synthesized on cytosolic ribosomes. He established that in *Chlamydomonas* the apoproteins are initially integrated into the membranes of the chloroplast envelope. The well-established need for chlorophyll *b* was revealed as a requirement for import and retention of the apoproteins in the chloroplast envelope and that, most significantly, chlorophyll *a* and chlorophyll *b* accept different structures in the protein as ligands during assembly of the chlorophyll-protein complexes. In 2004, he retired from the faculty but continued working as a Research Professor. As a scientist, he has cherished the opportunities to travel internationally to conferences and meet many of the other investigators with similar interests, some of whom are authors of chapters in this volume. Further information can be found on his web page (URL: http://sols.asu.edu/faculty/khoober.php). He can be reached by email at: khoober@asu.edu.

A Dedication to Pioneers of Research on Chloroplast Structure

In his famous paper proposing that plastids had an endosymbiotic origin, Constantin Sergeevich Mereschkowsky (1855–1921) presented a delightful mind picture:

> Let us imagine a palm tree, growing peacefully near a spring, and a lion, hiding in the brush nearby, all of its muscles taut, with bloodthirsty eyes, prepared to jump upon an antelope and to strangle it. The symbiotic theory, and it alone, lays bare the deepest mysteries of this scene, unravels and illuminates the fundamental principle that could bring forth two such utterly different entities as a palm tree and a lion. The palm behaves so peacefully, so passively, because it is a symbiosis, because it contains a plethora of little workers, green slaves (chromatophores) that work for it and nourish it. The lion must nourish itself. Let us imagine each cell of the lion filled with chromatophores, and I have no doubt that it would immediately lie down peacefully next to the palm, feeling full, or needing at most some water with mineral salts.

(Über Natur und Ursprung der Chromatophoren im Pflanzenreiche. Biol. Centralbl. **25**: 593–604, 1905; annotated English translation by W. Martin and K.V. Kowallik, Eur. J. Phycol. **34**: 287–295, 1999)

The First Observations

Some historians have taken a discourse by the English physician Nehemiah Grew (1641–1712, Fig. 2, shown later) as a starting point of our knowledge of chloroplast structure. He read his communication *A Discourse on the Colours of Plants* to the Royal Society of London, UK, on May 3, 1677, telling how he extracted the green pigment of leaves with olive oil and noted its different colors when held up to a candle. However, it is another passage in his text that has aroused conjecture (see Fig. 1).

Did he see chloroplasts with the compound microscope that he used for his pioneering work on plant anatomy, and describe them as a "precipitate" in the cells? If he did, he did not elaborate when some five years later he compiled and republished revisions of his earlier books and lectures on anatomy (written between 1671–1677) in the form of his master work *The Anatomy of Plants, with an Idea of a Philosophical History of Plants* (1682, see No. 11 of The Sources of Science, Johnson Reprint Corporation, New York and London, 1965). Although this volume included magnificent drawings, many of which stand up well alongside the most modern scanning electron micrographs in their depiction of cellular patterns, there are no illustrations of intracellular components.

The claim of Grew's contemporary and correspondent, Anthony van Leeuwenhoek (1632–1723, Fig. 2), to be the first to describe chloroplasts (not, of course, using that word) is on more solid ground. He made his own single-lens microscopes in spare time from his trade as a draper and a job as Chamberlain with the town council, and over a period of 50 years starting in August 1673 sent a series of letters from his home in Delft, The Netherlands, to the Royal Society of London. Among his numerous discoveries, his "little animalcules" (the name Protozoa was not coined until 1817) are the best known. Clifford Dobell published a detailed account of van Leeuwenhoek's life and work in 1932, 300 years after his birth, having learned Old Dutch to do so (C. Dobell, *Anthony van Leeuwenhoek*

> 14. §. I ſuppoſe therefore, That not only *Green*, but all the *Colours* of *Plants*, are a kind of *Precipitate*, reſulting from the concurrence of the *Saline Parts* of the *Aer*, with the *Saline* and *Sulphurious Parts* of the *Plant*; and that the *Subalkaline*, or other like *Saline Part* of the *Aer*, is concurrent with the *Acid* and *Sulphurious Parts* of *Plants*, for the *Production* of their *Verdure*; that is, as they ſtrike altogether into a *Green Precipitate*.

Fig. 1. Extract from Chapter 1 of *A Discourse on the Colours of Plants* (from page 271 of *The Anatomy of Plants*).

Fig. 2. Nehemiah Grew (left) and Anthony van Leeuwenhoek (right). Source: Mikroskopie: Entwicklungen im 19. Jahrhundert und ihre Anfänge im 17. Jahrhundert at http://www.biologie.uni-hamburg.de/b-online/d01/01f.htm, accessed on June 15, 2005.

and his Little Animals, Swets and Zeitlinger, 1932). Letter number 6, dated 7 September, 1674, narrates how van Leeuwenhoek took water samples from the Berkelse Mere and found floating in it "some green streaks, spirally wound serpent-wise, and orderly arranged, after the manner of the copper or tin worms which distillers use to cool their liquors as they distil over. The whole circumference of these streaks was about the thickness of a hair of one's head . . . All consisted of very small green globules joined together: and there were many small green globules as well". There is little doubt that he had resolved the chloroplast of *Spirogyra*, and possibly the glistening starch sheaths around its pyrenoids (described again by Jean-Pierre Vaucher in 1803 and named as such by Friedrich Karl Johann Schmitz (1882, *Die Chromatophoren der Algen*, Max Cohen and Sohn, Bonn). It was the first structure to be recognized within a plant cell.

van Leeuwenhoek's next observation was incidental, but again it is plain that he saw chloroplasts, this time in a higher plant. In September 1678 many people in his home district were stricken with fever, and suspected a red dust that colored their shoes when they walked through grassy meadows, indicating, they thought, "infected, fiery air". van Leeuwenhoek examined the dust, which was probably spores of a rust-fungus, and saw that they came out of the grass and turned red upon exposure to the air ". . . whereas these same globules, when they lie enclosed in the pores are green". van Leeuwenhoek probably used the word "pores" in the same sense as his other correspondent at the Royal Society, Robert Hooke (1635–1703, *Micrographia*, Dover Publications (1961, New York) facsimile reproduction of the 1665 original). Certainly Dobell considered that the "pores" must have been leaf *cells,* and that van Leeuwenhoek had taken green chloroplasts to be precursors of the rust spores.

Long after Dobell's studies, a search of van Leeuwenhoek's letters stored in the Royal Society's strong room in London revealed that several were accompanied by packages of material. One such (letter of 17 October, 1687) was a sample of an algal mat which he had dried in front of his fire. Some of it retained its green color, and he had recorded seeing filaments with green globules *one sixth* [the volume] *of a globule of blood*, i.e., about 4 μm in diameter. When Brian Ford re-examined this historic material with modern techniques he found that the algae *Cladophora*, *Cosmarium*, *Vaucheria* and *Rhizoclonium*, as well as a number of diatoms, were still identifiable (*The Leeuwenhoek Legacy*, Biopress and Farrand Press, Bristol and London, 1991). Again it is apparent that van Leeuwenhoek had seen algal chloroplasts.

Discovery of Grana and Stroma

Physiology advanced relative to microscopy in the 18th century, and few discoveries relating to the structure of chloroplasts were recorded. Two examples that have come down to us are Bonaventura Corti's (1729–1813) well known observation of green particles streaming around *Chara* cells (1774), and Andrea Comparetti's (1745–1801) study of *green grains in plant cells*, in which he saw grains of starch (page 11, *Prodromus de fisica vegetabile*, Padua, 1791) (quotation from A. Trécul, cited later).

Ludolph Christian Treviranus (1779–1864), Charles Francois Brisseau de Mirbel (1776–1854), Kurt Polycarp Joachim Sprengel (1766–1833), George Wahlenberg (1781–1851), Johann Heinrich Friedrich Link (1767–1851) (who isolated and chemically analyzed starch grains), Pierre Jean François Turpin (1775–1840), Johann Jacob Paul Moldenhawer, Henri Dutrochet (1776–1847, proponent of the cell theory considerably before Schleiden and Schwann) and François Vincent Raspail (1794–1878, credited with founding the discipline of histochemistry) were among those who described green corpuscles in plants in the early decades of the 19th century. Brief biographies of many of these pioneers are given by Henry Harris in *The Birth of the Cell* (Yale University Press, New Haven, 1999). Even in this early period there were some indications that the "green corpuscles" might be complex structures. Thus Treviranus may have detected particles within chloroplasts (see T.E. Weier, cited below). Also, following his first descriptions in 1807 and 1814, Link wrote that the "green corpuscles are sometimes composite, that is to say, large corpuscles sometimes contain smaller ones . . . " (para 44, *Grundlehren der Kräuterkunde*, Berlin, 1837, translated from A. Gris, cited below).

Link's extraordinary pupil, Franz Julius Ferdinand Meyen (1804–1840) also saw composite green corpuscles. He graduated in medicine in 1826, published books on algae and plant anatomy (*Phytotomie*, Haude and Spener, 1830), then took the advice of Alexander von Humboldt (after whom the famous Humboldt Foundation is named) and voyaged around the world for three years—just ahead of that other voyager, Charles Darwin. On his return to Germany he published a multi-volume account of his discoveries, including first descriptions of the *Radiolaria* and still-cited articles on amphibians of South America and Borneo and plants of China and Oahu. He became a Professor in Berlin in 1834 and resumed studies of plant anatomy while carrying on his professorial duties as well as practicing medicine. Between then and his early death in 1840 he published books on plant physiology (3 volumes), secretion, plant geography, cultivated plants, embryology and fruiting in plants, and plant pathology—an astonishing output. In between he gave *Saccharomyces* its name and engaged in fierce arguments with Matthias Jakob Schleiden (1804–1881) on cell theory and the chemist Justus von Liebig (1803–1873) on plant physiology and the chemistry of humus (see P. Werner and F.L. Holmes, *Justus Liebig and the Plant Physiologists*. J. History of Biol. **35**: 421–441, 2002). Set against this frenzied activity his contribution to the world of chloroplasts may seem minor, yet in his book *Phytotomie* he too reported chlorophyll granules or corpuscles. The name "chlorophyll" was by then in use, having been coined in 1818 by the French pharmacists Pierre-Joseph Pelletier (1788–1842) and Joseph Bienaimé Caventou (1795–1877). Of more significance, in his 3-volume *Neues System der Pflanzenphysiologie* (1837; Haude and Spener, Berlin), Meyen described cases in which chlorophyll grains appeared as bodies with dark spots on a light background (reported by T. Elliott Weier in Cytologia **7**: 504–509, 1936 and Bot. Rev. **4**: 497–530, 1938). Further, in respect of *Vallisneria*, he wrote about the existence of a substratum for the green component (reported by Arthur Gris, cited below). His early glimpse of inhomogeneity of chloroplast contents (setting aside starch grains) preceded the now familiar nomenclature of grana and stroma by nearly fifty years.

Hugo von Mohl (1805–1872; Fig. 3) was another medical graduate who turned to natural science and made many contributions to the study of plant cells, including descriptions of cell division and his introduction of the word "protoplasm" (1846, independently of Purkinje's use of the word in 1840). Earlier he had provided detailed descriptions of "Chlorophyllkörner" or "chlorophyll granules" (*Untersuchungen über anatomische Verhältnisse des Chlorophylls*. Dissertation, W. Michler, University of Tübingen, Germany, 1837), and in due course presented them as components of the protoplasm. He extracted the green pigment from them and examined the residue with a variety of stains, concluding that it was a vesicular, proteinaceous material in which the chlorophyll was somehow distributed non-uniformly (H. von Mohl, *Über den Bau des Chlorophylls* Bot. Zeit. **13**: 89–99, 105–115, 1855). It was not clear, however, whether the pigmented spots had something to do with starch deposition or were the result of pathological changes. There followed prolonged debates on heterogeneity versus homogeneity, and if the former, whether the chlorophyll was randomly distributed, or in fibrils, granules or vesicles.

Two contributions in French interrupted the otherwise almost complete domination of the field by German microscopists. Both gave valuable surveys of the earlier literature, and both authors saw minute spots of concentrated pigment in chloroplasts. Jean Baptiste Arthur Gris (1829–1872) (*Recherches microscopiques sur la chlorophylle*, Ann. Sci. Nat. Bot. Ser **IV**, **7**: 179–219, 1857) looked at many species, e.g., the shade orchids *Phajus* (with grains of chlorophyll that are *very*

Fig. 3. Hugo von Mohl (top left; from http://www.biologie.uni-hamburg.de/b-online/e01/01f.htm), Nathanael Pringsheim (top right; provided by by E. Höxtermann), Andreas Franz Wilhelm Schimper (bottom left; scanned in from K. Mägdefrau: Geschichte der Botanik, Gustav Fischer Verlag Stuttgart 1973, page 221) and Constantin Sergeevich Mereschkowsky (bottom right; provided by E. Höxtermann).

granular) and *Acanthophippium* (with *finer granules* in the chlorophyll grains), and *Colocasia* (with *chlorophyll grains containing granules, some mobile, some immobile*). He decolorized *Phajus* chloroplasts with ether and was still able to see internal granulation, and went on to conclude that chlorophyll grains are *albumino-graisseux* in nature, i.e., lipoprotein in modern parlance. Some of his illustrations (monochrome) are reproduced in Fig. 4. Auguste Adolphe Lucien Trécul (1818–1896) (*Des formations vésiculaires dans les cellules végétales*, Ann. Sci. Nat. Bot. Ser IV, **8**: 20–163, 205–382, 1858) reviewed all known categories of "vesicle" at great length, including chlorophyll and starch grains. He described chlorophyll grains that contain *granular points of stronger color*. Like Gris, he published exquisite drawings of chloroplasts and chromoplasts (but in color); some of the former are reproduced in Fig. 4. Schimper (see later) described Trécul's work as the first thorough study in the field. The current state of knowledge did not allow Gris or Trécul to attach any significance to the deeply pigmented spots they saw in chlorophyll grains, and their work has not received as much credit as the later studies of Schimper and Meyer, both of whom were able to place their observations in a broader context, and who are heavily cited because they introduced new and useful terminology.

Trécul and many others employed the word *vesicle* (vésicule, Bläschen) as a convenient diminutive. Nowadays it implies a small intracellular compartment with a bounding membrane but at first it referred simply

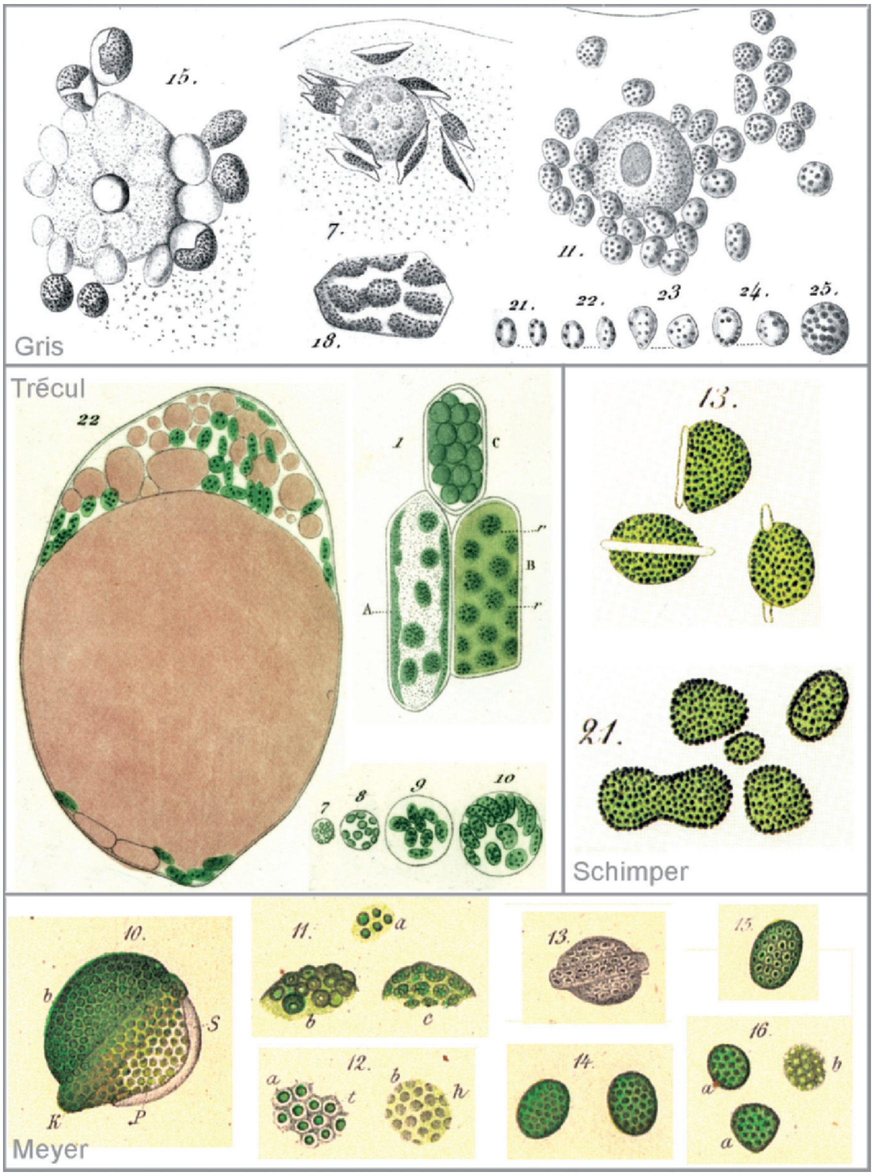


Fig. 4. Grana in chloroplasts, 1857–1885. (Top): from A. Gris (1857, see text for details); 15—*Solanum tuberosum* stem cell with nucleus surrounded by "spheres coated with green granular material"; 7—*Phajus grandiflorus*, cell from green bulb; 18—*Hydrangea hortensia* mesophyll; 11—*Vanilla planifolia* leaf cell; 21–25—stages of chloroplast development in *Sempervivum tectorum*. (Center left): from A. Trécul (1858, see text for details); 22—*Solanum nigrum* fruit cell; 1—*Lepanthes cochlearifolia*, stages of development A-B-C, with cell B showing "more granular" green bodies; 7–10—developmental stages of young fruit of *Solanum nigrum* (22). (Center right): from Schimper (1885, see text for details); 13—the orchid *Goodyera*; 21– the moss *Polytrichum*, described as having "prominent grana". (Bottom): from Meyer (1883, see text for details); 10–15 *Acanthophippium*; 16—*Vallisneria*; 10—chloroplast from green tuber; k crystalloid, s starch, p granum (dated 1 April 1882); 11—successive stages of swelling of grana in water; 12—effects of "Chlorallösung" (the clearing agent chloral hydrate) on grana; 13—after extraction with alcohol; 14—chloroplasts from leaf tissue; 15—grana in leaf chloroplast, swollen by uptake of water; 16—a) internal planes of focus, b) surface focus.

to a distinctive, observable unit which could, according to context, be what was later termed a "cell" or else something from which a cell might develop. It was much used by another pioneer of chloroplast biology, Carl Wilhelm von Nägeli (1817–1891), who made extensive studies of starch grains and developed the concept of growth by interpolation of new molecules between existing ones (intussusception). He also detected a distinct surface component of chlorophyll grains and provided the first documentation of their division (1846), using cells of *Nitella* and other algae. Carl Sanio (1832–1891) extended Nägeli's observation on division of chloroplasts to flowering plants in 1864, though the process had been seen in mosses, hornworts and horsetails earlier. Sanio is better known for elucidating the origin and activity of the cambium; his description (without any illustrations) of chloroplast division appeared more or less as an aside in a study of phloem development (Bot. Zeit. **22**: 193–200, 1864). There are remarkably few, if any, subsequent descriptions of chloroplast division in higher plants until 1936 (Seikan Kusunoki and Yoshio Kawasaki, Cytologia **7**: 530–534, 1936). Division of chloroplasts remains as one of the most fundamental processes in the life of plants, yet for higher plants it has very seldom been observed in the sense of continuous monitoring, though of course presumed stages have been photographed and molecular aspects analyzed.

The great physiologist and historian, of the plant sciences, Julius Sachs (1832–1897) was another who extracted chlorophyll, commenting that it can be removed without altering the dimensions of the ground substance, which remains as a solid, minutely vacuolated body (see Conway Zirkle, *The structure of the chloroplast in certain higher plants*, Amer. J. Bot. **13**: 301–341, 1926). In his *History of Botany 1530–1860* (Russell and Russell, New York, 1890, reissued 1967) Sachs pointed out that many advances in microscope technique were made by the biologists of the mid 19th century, notably von Mohl and von Nägeli, and that those who came after were able to build upon these advances. Thus it was that many key publications appeared in the period 1881–1885, which should have, but did not, settle the questions that had arisen about the distribution of chlorophyll in chloroplasts.

Nathanael Pringsheim (1823–1894, Fig. 3) extended the experiments on extraction of chlorophyll that had been done by Gris, von Mohl and Sachs. He described the pigment-free residue as a spongy or trabecular structure whose meshes are normally occupied by the chlorophyll (*Ueber Lichtwirkung und Chlorophyllfunction in der Pflanze*, Jahrb. Wiss. Bot. **12**: 288–437, 1881). One year later he gave us the word "stroma": "*Ich habe ferner gezeigt, dass die farblose Grundmasse, die ich ein für alle Mal als das Gerüst **(Stroma)** der Chlorophyllkörper bezeichnen will, eine schwammartige Structur besitzt…*" (*Ueber Chlorophyllfunction und Lichtwirkung in der Pflanze*, Jahrb. Wiss. Bot. **13**: 377–490, 1882).

Next, Andreas Franz Wilhelm Schimper (1856–1901, Fig. 3), who in his later career became better known as a plant geographer, encapsulated much preceding work by establishing a logical nomenclature based on the Greek word *Plastikos*, meaning formed, or moulded (*Ueber die Entwickelung der Chlorophyllkörner und Farbkörper*, Bot. Zeit. **41**: 105–112, 121–130, 137–146, 153–162, 1883). He wrote: "*Ich werde sie als Plastiden bezeichnen, und zwar nenne ich die Chlorophyllkörper Chloroplastiden, die Stärkebildner und alle hierher gehörigen farblosen Gebilde Leukoplastiden und die Farbkörper Chromoplastiden*". This sentence (page 108) follows an introductory review of preceding observations and in it Schimper names the green types *Chloroplastiden*, the colorless types (usually with starch) *Leukoplastiden*, and the non-green colored types as *Chromoplastiden*. The category of plastid that we now know as amyloplasts was not separated as a subset of Schimper's "Leukoplastiden" until much later. Schimper followed up with a book-sized issue of the Jahrbücher für Wissenschaftliche Botanik, *Untersuchungen über die Chlorophyllkörper und die ihnen homologen Gebilde*, **16**: 1–247, 1885, including five plates, two of which are in color. His Plate 3 is readily available in the form of the frontispiece of J.T.O. Kirk and R.A.E. Tilney-Bassett's comprehensive book *The Plastids* (1967; Freeman, New York). Two of his figures, showing chloroplasts with grana, are reproduced in Fig. 4.

Schimper's other major contribution was to see that large plastids (chloro- and chromo-) develop from small leucoplasts in egg cells and meristematic cells, and in essence to propound the genetic continuity of plastids and the absence of their *de novo* formation in the protoplasm. In these conclusions he concurred with Friedrich Schmitz (cited above in connection with van Leeuwenhoek), who had made continuous observations of chloroplast division and development from spores and zygote stages in algae. In 1893, Andrei Sergeevitch Famintzin (1835–1918), one of the founders of Russian plant physiology, demonstrated that "Chlorophyllkörner" persist as small, shriveled structures in seeds, and that those in the seedlings develop from them, further establishing the uninterrupted continuity of plastids (*Über Chlorophyllkörner der Samen und Keimlinge*, Mélanges biologiques. T. **XIII**. St. Petersburg, 1893). Confirmation that chloroplasts can carry genetic traits awaited the rediscovery of Mendel's results and subsequent work of Erwin Baur (1875–1933) on non-Mendelian inheritance in the *albomarginata* form of *Pelargonium zonale* (Z. Indukt. Abstamm. Vererbungsl. **1**: 330–351, 1909). Moreover Schimper surmised that chloroplasts might be symbionts, though this was merely an aside written in a footnote in his 1883 paper (page 112, see W. Martin and K.V. Kowallik, Eur. J. Phycol. **34**: 287–295, 1999). The idea was later developed in detail by Constantin Sergeevich Mereschkowsky (1855–1921, Fig. 3) (Biol. Centralblatt **25**: 593–604, 1905—for translation see W. Martin and K.V. Kowallik, cited above and quoted at the very beginning of this *dedication*—and Biol. Centralblatt **30**: 278–303, 321–347, 353–367, 1910).

Knowledge of another class of cellular inclusion, chondriosomes (one of many names for them), was growing during this period, and some of the ideas on genetic continuity of plastids became clouded by uncertainty about the distinctions between mitochondria (as they came to be called) and small leucoplasts in meristematic cells. Conway Zirkle (1895–1972) clarified this situation and distinguished "plastid primordia" from mitochondria (Amer. J. Bot. **14**: 429–445, 1927). Eventually Siegfried Strugger (1906–1961) (Naturwiss. **37**: 166–167, 1950) applied the term "proplastid", signifying a sub-category of leucoplast which can multiply in dividing cells and mature into other forms of plastid when cell progeny leave meristems and differentiate. Pierre Dangeard (1862–1947) expressed the relatedness of members of the plastid family by classifying them as part of the overall "plastidome" (Comptes Rendus Acad. Sci. **169**: 1005–1009, 1919)—an early use of the currently fashionable "-ome" suffix.

In his 1885 publication Schimper described chloroplasts as a colorless stroma with numerous "vacuoles" filled with green, viscous substance. He saw this basic organization in chloroplasts of flowering plants, pteridophytes and bryophytes, and was able to refer to the green components as "grana", this new term having been introduced by Arthur Meyer (1850–1922) in 1883. Meyer's critical review, including many black and white and colored figures on three plates, discussed observations on "Autoplasten" (= chloroplasts); "Chromoplasten" (= chromoplasts); "Trophoplasten" (= reserve-storing plastids); and "Anaplasten" (= leucoplasts) (*Das Chlorophyllkorn in chemischer, morphologischer und biologischer Beziehung. Ein Beitrag zur Kenntnis des Chlorophyllkornes der Angiospermen und seiner Metamorphosen*, pp. 1–91. Leipzig: Arthur Felix). On page 24 (lines 6–10, para 2), in relation to observations on the shade plant *Acanthophippium*, he defines "Grana" as follows: "*Es wäre die Klärung dieses Punktes von Wichtigkeit, weil im Falle der Farblosigkeit der Grundsubstanz die Auffassung gerechtfertigt erschiene, dass die grünen Körner, welche wir der Kürze halber* '***Grana***' *nennen wollen, aus unserem Chlorophyll beständen, und dass dieses in der übrigen Masse des Autoplasten nicht weiter vorkäme*". Here, he gives the green bodies he has seen the name *Grana* "for convenience". His drawings clearly show grana (e.g., Fig. 11–16 on his plate 1, reproduced in Fig. 4). He demonstrated that they are constitutive components of chloroplasts, and not transient products of metabolism.

Schimper's terminology soon became widely accepted, for instance in his widely-used textbook *Das kleine botanische Practicum* (Gustav Fischer, Jena, 1884). Eduard Strasburger lists the three main categories of plastid ("Chromatophoren") under their former and new names, and points out that they are closely related and can change into one another: "*Wir können alle drei Gebilde als Chromatophoren zusammenfassen und weiter die Chlorophyllkörper, Farbkörper und farblosen Stärkebildner als Chloroplasten, Chromoplasten und Leukoplasten unterscheiden. Diese Gebilde sind nahe verwandt und können ineinander übergehen*". His three terms (*Chloroplasten*, *Chromoplasten* and *Leukoplasten*) are close to our modern terminology, but the leucoplasts of that time included categories which we now distinguish as proplastids (see above), amyloplasts and etioplasts (this term was introduced by J.T.O. Kirk and R.A.E. Tilney-Bassett in *The Plastids*, cited above, page 64), with leucoplasts as currently understood being a collective term for a multitude of different sizes and shapes of plastid which have in common the attributes of little or no pigment and occurrence in non-dividing cells, but still with the ability to re-differentiate into other forms of plastid.

Towards the Modern Era

Despite the clarity with which grana and stroma had been demarcated by 1885, a long period of comparative stagnation ensued. A view of the cell as a unit containing homogeneous colloidal material gained the upper hand, and in textbooks up to 1935, chloroplasts were generally regarded as homogeneous too. Grana were relegated to the status of artefacts arising from preparation methods (for accounts of this period, see Conway Zirkle (Amer. J. Bot. **13**: 301–341, 1926) and Eugene Rabinowitch, *Photosynthesis and Related Processes,* **1:** Chapter 14, 1945, Interscience Publishers, New York).

The climate of opinion concerning grana began to change in the mid-1930s. J. Doutreligne produced the first photomicrographs of grana in chloroplasts in 1935 (*Note sur la structure des chloroplastes*, Proc. Kon. Ned. Akad. Weten. Amst. **38**: 886–896, 1935). It seems strange that it should have taken so long for photomicrography to be employed in this field—its first

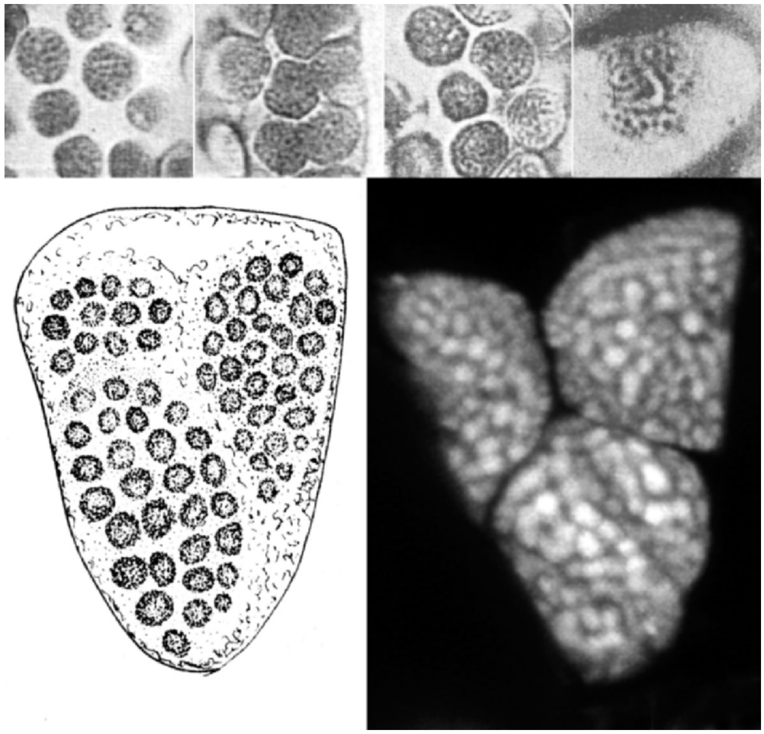


Fig. 5. Top row, first 3 photographs: a selection of the first photomicrographs of grana in chloroplasts, from Doutreligne (1935, see text for details); left to right: *Vallisneria*, *Mnium* and *Cabomba*, respectively; top far right photograph: part of a chloroamyloplast from *Pellionia*, with grana displayed in a very thin film over the surface of a starch grain, from Jungers and Doutreligne (1943, see text). These micrographs are copied here at approximately the same magnification as in the original papers, the image of *Pellionia* is at a magnification of 1400x. Lower left: A mesophyll cell of the shade plant *Pellionia* containing three chloroplasts with large grana (Fig. 4 from Weier 1938, see text); Lower right: a confocal fluorescence micrograph of a similar *Pellionia* cell by one of us (BG).

use in tissue anatomy was no less than 90 years earlier (O. Breidbach, *Representation of the microcosm—the claim for objectivity in 19th century scientific microphotography*. J. History Biol. **35**: 221–250, 2002). Doutreligne's images were especially convincing because she used colored filters to vary the contrast between the grana and the stroma, and because they included living photosynthetic tissue of water plants, free of potential damage from preservatives. She published another paper during the war (*Sur la localisation de la chlorophylle*, La Cellule **49**: 407–418, 1943) which included a perceptive footnote saying it is *piquant* to note that the combination of achromatic objective (with low numerical aperture) and eyepiece lenses used by some proponents of homogeneous chloroplasts would have been incapable of resolving objects smaller than 0.8 μm, which could well have contributed to their failure to see grana; she herself used a much better objective lens of numerical aperture 1.32.

In the year after Doutreligne's paper appeared, Emil Heitz (1892–1965, discoverer of heterochromatin) submitted two papers (Ber. Dtsch. Bot. Ges. **54**: 362–368, 1936 and Planta **26**: 134–163, 1937) containing unequivocal micrographs from very many species, and including "face" and "side" views of grana that led him to include the words "oriented chlorophyll-discs" (*Gerichtete Chlorophyllscheiben*) in his titles. He added an Addendum to his Planta paper in which he confirmed the appearance of grana as disc-shaped in living material using fluorescence microscopy. In the same year T.E. Weier (Cytologia **7**: 504–509) compared living and preserved (by various methods) chloroplasts and amyloplasts of the shade plant *Pellionia*, confirming the existence of grana (see Fig. 5). His other paper in 1936 (Amer. J. Bot. **23**: 645–652) contained equally convincing views of grana in beet chloroplasts, but he still allowed that healthy plants could have both grana-containing and homogeneous chloroplasts.

Other approaches had been used before the images described above removed doubts about the reality of grana. Birefringence of chloroplasts was discovered by G.W. Scarth in 1924 and was further investigated by others, including A. Frey-Wyssling and W. Menke, in the 1930s. Infiltration with glycerol abolished the birefringence, indicating that it arises from structural layering. Menke and H.-J. Küster elaborated by studying dichroism of gold impregnated chloroplasts, inferring the existence of submicroscopic laminae (Protoplasma **30**: 283–290, 1938), and Menke and E. Koydl succeeded with ultra-violet microscopy to visualize them directly (Naturwiss. **27**: 29–30, 1939). Almost concomitantly G. Kausche and H. Ruska obtained the first electron micrographs of whole mounts (Naturwiss. **28**: 303–304, 1940), with further progress having to await the end of the war and development and application of more refined methods of specimen preparation such as vacuum drying and shadow casting (S. Granick and K. Porter, Amer. J. Bot. **34**: 545–555, 1947; E. Steinmann, Exper. Cell Res. **3**: 367–372, 1952), osmic acid fixation and ultra-thin sectioning (G. Palade, cited in Granick (1955, reference below), 1952; J.B. Finean, E. Steinmann and F.S. Sjöstrand, Exper. Cell Res. **5**: 557–559, 1953; E. Steinmann and F.S. Sjöstrand, Exper. Cell Res. **8**: 15-23, 1955), and the advent of glutaraldehyde as a fixative for chloroplasts (B. Gunning, J. Cell Biol. **24**: 79–93, 1965). The architectural details of the membranes in grana were elucidated by W. Wehrmeyer (Planta **62**: 272–293, 1964), J. Heslop-Harrison (Sci. Prog. Oxf. **54**: 519–541, 1966) and D. Paolillo (J. Cell Sci. **6**: 243–255, 1970) using a variety of techniques of electron microscopy and reconstruction. The early literature of electron microscopy of chloroplasts is well covered by S. Granick (Encyclopedia of Plant Physiology **1**: 507–564, 1955, Springer, Berlin), and L.A. Staehelin takes the story forward to the supra-molecular architecture of thylakoids (Photosynth. Res. **76**: 185–196, 2003).

It is appropriate to end this dedication to some of the pioneers of chloroplast structure by honoring Wilhelm Menke, with whom one of us (FK) worked for several years. It is he who, in 1961, coined the term "thylakoids" for "membrane sacs" (*Über die Chloroplasten von* Anthoceros punctatus. Z. Naturforsch. **16b**: 334–336). He wrote: "*Da die Beschreibung der Lamellar-Struktur der Chloroplasten mit Hilfe des bisher verwendeten Begriffs* '*in sich geschlossene Doppellamellen*' *umständlich ist, und weil diese morphologisch und funktionell bedeutsamen Strukturelemente wohl eine eigene Bezeichnung verdienen, werde ich sie in Zukunft Thylakoide nennen*". In English (as translated freely), it is: "Since the term 'self-contained double lamellae' which is currently used to describe the lamellar structure of the chloroplasts is long and complicated and since these morphologically and functionally important structural elements may well deserve a proper term, I will call them in future 'thylakoids', an expression coming from the Greek language meaning sac-like." (Also see W. Menke (1962) *Structure and chemistry of plastids*. Annu. Rev. Plant Physiol. **13**: 27–44; W. Menke (1990) *Retrospective of a botanist*. Photosynth. Res. **25**: 77–82).

Acknowledgments

We thank Bob Wise and Ken Hoober for inviting us to present this historical dedication and Ekkehard Höxtermann for help with the Pringsheim papers and for portraits of Pringsheim and Mereschkowsky. BG thanks the Plant Cell Biology Group, RSBS, Australian National University for a Visiting Fellowship to enable him to work in the Group in an Emeritus capacity. G thanks the University of Illinois at Urbana-Champaign for library and office facilities.

Brian Gunning (Corresponding author)
Research School of Biological Sciences
Australian National University
Canberra, ACT 2601, Australia
email: brian.gunning@anu.edu.au

Friederike Koenig
Department of Biology and Chemistry
University of Bremen
28334 Bremen, Germany
email: fkoenig@uni-bremen.de

Govindjee
Department of Plant Biology and
Department of Biochemistry
University of Illinois at Urbana-Champaign
Urbana, IL 61801
email: gov@life.uiuc.edu

Color Plates