The Purple Phototrophic Bacteria

### Advances in Photosynthesis and Respiration

### **VOLUME 28**

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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 organisms, 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.

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# The Purple Phototrophic Bacteria

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Cover: Four aspects of purple phototrophic bacteria, from one of their habitats through to atomic resolution structures, are superimposed on a map derived from the genome sequence of *Rhodopseudomonas palustris* CGA009 supplied by Professor Caroline Harwood, University of Washington, Seattle, USA.

Top left. Purple sulfur bacteria (*Amoebobacter purpureus*) on the shoreline of Mahoney Lake, British Columbia, Canada. Image from Professor J.T. Beatty.

Top right. Rhodobacter capsulatus streaked out on an agar plate. Image from Professor J.T. Beatty.

Bottom right. Model of a spherical chromatophore vesicle from *Rhodobacter sphaeroides* constructed by the in silico combination of atomic force microscopy, linear dichroism, electron microscopy, and X-ray crystallography data. Image from Dr. Melih Sener and Professor Klaus Schulten, prepared using VMD (Humphrey et al. (1996) J Mol Graphics 14: 33–38).

Bottom left. Structure of the reaction center complex from *Rhodobacter sphaeroides* showing the subunits and the pathway of electron transfer between cofactors. See Fig. 1, Chapter 20. Image from Professor Colin Wraight, prepared using VMD.

The camera ready text was prepared by Lawrence A. Orr, Center for Bioenergy & Photosynthesis, Arizona State University, Tempe, Arizona 85287-1604, USA.

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This book is dedicated to Roderick K. Clayton, a pioneer of photosynthesis research

# From the Series Editor

## Advances in Photosynthesis and Respiration Volume 28: The Purple Phototrophic Bacteria

I am delighted to announce the publication, in the Advances in Photosynthesis and Respiration (AIPH) Series, of *The Purple Phototrophic Bacteria*. Four distinguished authorities from three countries (UK, USA and Canada) have edited this Volume: C. Neil Hunter, the Chief Editor, Fevzi Daldal, Marion C. Thurnauer and J. Thomas Beatty. This book is produced as a sequel to Volume 2 of the Series (*Anoxygenic Photosynthetic Bacteria*), published in 1995, and edited by Robert E. Blankenship, Michael T. Madigan and Carl E. Bauer.

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- Volume 22 (2005): Photosystem II: The Light-Driven Water:Plastoquinone Oxidoreductase, edited by Thomas J. Wydrzynski and Kimiyuki Satoh, from Australia and Japan. 34 Chapters, 786 pp, Hardcover. ISBN: 978-1-4020-4249-2
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- Volume 2 (1995): Anoxygenic Photosynthetic Bacteria, edited by Robert E. Blankenship, Michael T. Madigan and Carl E. Bauer, from USA. 62 Chapters, 1331 pp, Hardcover. ISBN: 978-0-7923-3682-8
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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.' Table of Contents of Volumes 1–25 can be found at <http://www.life. uiuc.edu/govindjee/photosynSeries/ttocs.html>. Special discounts are available to members of the International Society of Photosynthesis Research, ISPR (<http://www.photosynthesisresearch.org/>). (See http://www.springer.com/ispr for more information.)

## About Volume 28: The Purple Phototrophic Bacteria

*The Purple Phototrophic Bacteria* has 48 authoritative Chapters, and is authored by 116 international authorities from 13 countries (Australia; Canada; Czech Republic; France; Germany; Israel; Italy; Japan; Netherlands; Poland; Russia; UK; and USA). It is a truly international book and the Chief Editor of this volume, C. Neil Hunter, and his three coeditors, Fevzi Daldal, Marion C. Thurnauer and J. Thomas Beatty, deserve our thanks and our congratulations for compiling this updated survey of these interesting and important organisms.

*The Purple Phototrophic Bacteria* is a comprehensive survey of all aspects of these fascinating bacteria, most metabolically versatile organisms on Earth. This volume is organized into the following sections: Physiology, Evolution and Ecology; Biosynthesis of Pigments, Cofactors and Lipids; Antenna Complexes: Structure, Function and Organization; Reaction Centre Structure and Function; Cyclic Electron Transfer Components and Energy Coupling Reactions; Metabolic Processes; Genomics, Regulation and Signaling; and New Applications and Techniques. This book is a compilation of 48 chapters, written by leading experts who highlight the huge progress made in spectroscopic, structural and genetic studies of these bacteria since 1995, when the last such book was published (Anoxygenic Photosynthetic Bacteria, Volume 2 in the Advances in Photosynthesis and Respiration Series, edited by Robert E. Blankenship, Michael T. Madigan and Carl E. Bauer; Kluwer Academic Publishers (now Springer), Dordrecht). This new volume is similarly intended to be the definitive text on these bacteria for many years to come, and it will be a valuable resource for experienced researchers, Ph.D. students, and advanced undergraduates in the fields of ecology, microbiology, biochemistry and biophysics. Scientists interested in future applications of these bacteria which could harness their potential for nanotechnology, solar energy research, bioremediation, or as cell factories, will also find the book useful.

The readers can easily find the titles and the authors of the individual chapters in the Table of Content of this book. Instead of repeating this information here, I prefer to thank each and every author by name (listed in alphabetical order) that reads like a 'Who's Who' in the field of purple phototrophic bacteria:

Maxime T.A. Alexandre; James P. Allen; Judith P. Armitage; Herbert Axelrod; Carl E. Bauer; Christoph Benning; Edward A. Berry; Robert E. Blankenship; Francesca Borsetti; Paula Braun; Per A. Bullough: Rita Casadio: Madhusudan Choudhary: Toh Kee Chua: Richard J. Cogdell: Jason W. Cooley; Julius T. Csotony; Christiane Dahl; Fevzi Daldal; Evelyne Deery; Takehisa Dewa; Timothy J. Donohue; Katie Evans; Boris A. Feniouk; Leszek Fiedor; Anthony Fordham-Skelton; Harry A. Frank; Elaine R. Frawley; Mads Gabrielsen; Alastair T. Gardiner; Toni Georgiou; Marie-Louise Groot; Marilyn R. Gunner; Wolfgang Haehnel; Deborah K. Hanson: Caroline S. Harwood: Klaas J. Hellingwerf; Johnny Hendriks; Theresa Hillon; Jonathan Hosler; Li-Shar Huang; C. Neil Hunter; Kouji Iida; J. Baz Jackson; Pierre Joliot; Michael R. Jones; Deborah O. Jung; Wolfgang Junge; Samuel Kaplan; John T. M. Kennis; Gabriele Klug; Hans Georg Koch; Jürgen Köhler; David M. Kramer; Robert G. Kranz; Alison M. Kriegel; Philip D. Laible; Jérôme Lavergne; Dong-Woo Lee; Paul A.

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It is a pleasure to note that the following 27 participants in Volume 2 have also contributed to Volume 28; they are (alphabetically): James P. Allen; Judith P. Armitage; Carl E. Bauer; J. Thomas Beatty; Robert E. Blankenship; Richard J. Cogdell; Fevzi Daldal; Harry A. Frank; Caroline S. Harwood; C. Neil Hunter; J. Baz Jackson; Pierre Joliot; Gabriele Klug; Robert G. Kranz; Paul A. Loach; Michael T. Madigan; Melvin Okamura; Pamela S. Parkes-Loach; William W. Parson; Hugo Scheer; F. Robert Tabita; Rienk van Grondelle; André Verméglio; Paulette M. Vignais; Arieh Warshel; JoAnn C. Williams; and Davide Zannoni.

It is remarkable that all three editors of Volume 2 (Carl E. Bauer, Robert E. Blankenship (Chief Editor), and Michael T. Madigan) are authors in Volume 28; and 3 of the 4 editors of Volume 28 (J. Thomas Beatty; Fevzi Daldal; and C. Neil Hunter (Chief Editor)) were authors in Volume 2.

As Volume 28 is a sequel to Volume 2, it is beneficial for the readers of the new volume to consult and cite chapters in the earlier volume; I present below authors, titles of chapters and page numbers of all the chapters in that book. Please note that this volume was published by Kluwer Academic Publishers which was later acquired by Springer, the publishers of the current volume.

### Complete List of Chapters in *Anoxygenic Photosynthetic Bacteria*, edited by R.E. Blankenship, M.T. Madigan and C.E. Bauer, Kluwer Academic Publishers, 1995

*Chapter 1*: J.F. Imhoff (1995) Taxonomy and physiology of phototrophic purple bacteria and green sulfur bacteria, pp 1-15

*Chapter 2*: M.T. Madigan and J.G. Ormerod (1995) Taxonomy, physiology and ecology of heliobacteria, pp 17–30

*Chapter 3*: B.K. Pierson and R.W. Castenholz (1995) Taxonomy and physiology of filamentous anoxygenic phototrophs, pp 31–47

*Chapter 4*: H. Van Gemerden and J. Mas (1995) Ecology of phototrophic sulfur bacteria, pp 49–85

*Chapter 5*: R.W. Castenholz and B.K. Pierson (1995) Ecology of thermophilic anoxygenic photo-trophs, pp 87–103

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*Chapter 46*: J. Gibson and C.S. Harwood (1995) Degradation of aromatic compounds by nonsulfur purple bacteria, pp 991–1003

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*Chapter 48*: J.C. Williams and A.K.W. Taguchi (1995) Genetic manipulation of purple photosynthetic bacteria, pp 1029–1065

*Chapter 49*: M. Fonstein and R. Haselkorn (1995) Physical mapping of *Rhodobacter capsulatus*: Cosmid encyclopedia and high resolution genetic map, pp 1067–1081

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*Chapter 52*: A.J. Biel (1995) Genetic analysis and regulation of bacteriochlorophyll biosynthesis, pp 1125–1134

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*Chapter 54*: J.A. Shiozawa (1995) A foundation for the genetic analysis of green sulfur, green filamentous and heliobacteria, pp 1159–1173

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*Chapter 56*: R.G. Kranz and P.J. Cullen (1995) Regulation of nitrogen fixation genes, pp 1191–1208

*Chapter 57*: J.T. Beatty (1995) Organization of photosynthesis gene transcripts, pp 1209–1219

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*Chapter 59*: G. Klug (1995) Post-transcriptional control of photosynthesis gene expression, pp 1235–1244

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*Chapter 62*: Michiharu Kobayashi and Michihiko Kobayashi (1995) Waste remediation and treatment using anoxygenic phototrophic bacteria, pp 1269–1282

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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):

- *C-4 Photosynthesis and Related CO*<sub>2</sub>*Concentrating Mechanisms* (Editors:Agepati S. Raghavendra and Rowan Sage);
- Photosynthesis: Perspectives on Plastid Biology, Energy Conversion and Carbon Metabolism (Editors: Julian Eaton-Rye and Baishnab Tripathy);

- Abiotic Stress Adaptation in Plants: Physiological, Molecular and Genomic Foundation (Editors: Ashwani Pareek, Sudhir K. Sopory, Hans J. Bohnert and Govindjee);
- The Chloroplast: Biochemistry, Molecular Biology and Bioengineering (Editors: Constantin Rebeiz, Hans Bohnert, Christoph Benning, Henry Daniell, Beverley R. Green, J. Kenneth Hoober, Hartmut Lichtenthaler, Archie R. Portis and Baishnab C. Tripathy);
- Photosynthesis In Silico: Understanding Complexity from Molecules to Ecosystems (Editors: Agu Laisk, Ladislav Nedbal and Govindjee); and
- *Lipids in Photosynthesis: Essential and Regulatory Function* (Editors: Hajime Wada and Norio Murata).

In addition to these contracted books, the following topics, among others, are under consideration:

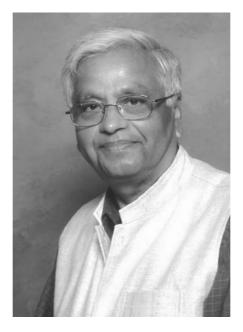
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- · Genomics, Proteomics and Evolution
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- ATP Synthase and Proton Translocation
- Interactions between Photosynthesis and other Metabolic Processes
- · Carotenoids II
- · Green Bacteria and Heliobacteria
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Readers are encouraged to send their suggestions for these and future Volumes (topics, names of future editors, and of future authors) to me by E-mail (gov@ illinois.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.

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Govindjee, Series Editor

Govindjee, born in 1932, obtained his B.Sc. (Chemistry, Biology) and M.Sc. (Botany, Plant Physiology) in 1952 and 1954, from the University of Allahabad, India, and his Ph.D. (Biophysics, under Eugene Rabinowitch), in 1960, from the University of Illinois at Urbana-Champaign (UIUC), IL, U.S.A. He is best known for his research on excitation energy transfer, light emission, primary photochemistry and electron transfer in Photosystem II (PS II). His research, with many collaborators, has included the discovery of a short-wavelength form of chlorophyll (Chl) a functioning in the Chl b-containing system, now called PS II, and of the two-light effects in Chl a fluorescence and in NADP (nicotinamide adenine dinucleotide phosphate) reduction in chloroplasts (Emerson Enhancement). Further, he has worked on the existence of different spectral fluorescing forms of Chl a and the temperature dependence of excitation energy transfer down to 4 K; basic relationships between Chl a fluorescence and photosynthetic reactions; the unique role of bicarbonate on the acceptor side of PS II. particularly in protonation events involving the Q binding region; the theory of thermoluminescence in plants; picosecond measurements on the primary photochemistry of PS II; and the use of Fluorescence Lifetime Imaging Microscopy (FLIM) of Chl a fluorescence in understanding photoprotection against excess light. His research on photosynthetic bacteria

included the observation of the absence of the Emerson Enhancement Effect (1960s); measurements on the lifetime of bacteriochlorophyll fluorescence (1970s); and the use of the bacterial reaction center structure in homology modeling of Photosystem II, particularly on its electron acceptor side (1990s). His current focus is on the 'History of Photosynthesis Research,' in 'Photosynthesis Education', and in the 'Possible Existence of Extraterrestrial Life.' He has served on the faculty of the UIUC for ~40 years. Since 1999, he has been Professor Emeritus of Biochemistry, Biophysics and Plant Biology at the same institution. His honors include: Fellow of the American Association of Advancement of Science; Distinguished Lecturer of the School of Life Sciences, UIUC: Fellow and Lifetime member of the National Academy of Sciences (India); President of the American Society for Photobiology (1980–1981); Fulbright Scholar and Fulbright Senior Lecturer; Honorary President of the 2004 International Photosynthesis Congress (Montréal, Canada): the 2006 Recipient of the Lifetime Achievement Award from the Rebeiz Foundation for Basic Biology; and the 2007 Recipient of the 'Communication Award' of the International Society of Photosynthesis Research (ISPR), presented to him at the 14th International Congress on Photosynthesis, held in Glasgow, Scotland, U.K.

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## Preface

This book follows the tradition initiated in 1963, then subsequently extended in 1978 and 1995, of summarizing our knowledge of the photototrophic bacteria in a single volume. The first book was Bacterial Photosynthesis (Howard Gest, Anthony San Pietro and Leo P.Vernon, eds), 1963, Antioch Press, Yellow Springs, Ohio. Fifteen years later, Roderick K. Clayton and William R. Sistrom edited The Photosynthetic Bacteria (1978, Plenum Press, New York), an indispensable book for any scientist in the field at that time. In 1995, Robert Blankenship, Michael Madigan and Carl Bauer edited the most complete survey of the subject, Anoxygenic Photosynthetic Bacteria. By that time, the book had been taken under the wing of the Advances in Photosynthesis Series, initiated by Govindjee, as Volume 2 (Kluwer Academic Publishers, Dordrecht), and now, in 2008, we come to volume 28, entitled The Purple Phototrophic Bacteria (Springer, Dordrecht). The word "phototrophic" is used because it has become clear that many purple bacteria are incapable of photosynthesis (synthesis of all cellular carbon components from  $CO_2$ ), although they are capable of obtaining energy in the form of ATP from light (using light-harvesting and reaction center complexes that are homologous to those of purple photosynthetic bacteria).

This latest survey of the field is restricted to the purple bacteria, and does not attempt to cover, for example, the green sulfur bacteria. There have been so many exciting developments since 1995 that the editors felt that it was sufficiently challenging to summarize thirteen years of research on the purple bacteria. This proved to be the case, and 48 chapters and more than 1000 pages were necessary to encompass the depth and breadth of the progress made in studying these fascinating organisms. Since 1995, there has been an explosion of information available from genome sequencing and related projects. The first 3-D structure of the bacterial cytochrome  $bc_1$ complex has been determined, and more structural information has been obtained for light-harvesting and reaction center membrane-protein complexes. Site-directed modifications of light-harvesting and reaction center complexes have been correlated with altered spectroscopic properties, even on a femtosecond timescale. Spectroscopic methods in general have advanced considerably since the last volume in 1995: an important example is the development of single

molecule approaches. New theoretical frameworks have had to keep pace with such technical developments. Through the use of atomic force microscopy it has been possible to examine the organization of clusters of individual light-harvesting and reaction center complexes in their native membranes. We are now beginning to see how the properties of native and modified photosynthetic complexes can be harnessed on the nanoscale for the design of biologically-inspired energy and electron transfer devices. In addition to these advances, we are reminded that many new phototrophic bacteria are still being discovered, and although it has been 45 years since the first book on these bacteria appeared, there is much that we do not know or understand. Recent publications indicate that purple phototrophic bacteria are ubiquitous on Earth, and raise questions about their contributions to global cycles of elements. Certainly, the extraordinary metabolic versatility of the purple bacteria, and their amenability to investigation by genetic, biochemical and biophysical techniques, will ensure that despite the inevitably cyclical and variable nature of science funding, there will always be compelling reasons to carry out research on the purple bacteria.

Since 1995, it has become ever easier to obtain information online, and it could be argued that the need for a book on this topic is not as compelling as it might have been thirty years ago. However, there is still much value in having a hard copy of the diverse collection of information represented by the 48 chapters of this book, compiled at this point in time and which can be held in the hand. We have attempted to impart some coherence to this project, a process helped by using the organization of the 1995 volume as a starting point. The editors have adopted a pragmatic approach to the issue of taxonomy and, in the light of the ever-changing nature of specific bacterial names, a rigid policy of using only the most recent ones has not been enforced. Thus, Rhodopseudomonas acidophila is now Rhodoblastus acidophilus, for example, but the former name still predominates in the book. Helpful lists of purple phototrophic bacteria, as well as lists of genes, enzymes, pathways, and many more attributes of these bacteria, appear throughout this book. In addition, a section is included at the end of the present volume on new applications and techniques, with the hope that perhaps some of these will form the basis of a

fifth book, several years from now. This new volume is intended to be a resource for present and future researchers in the fields of ecology, microbiology, biochemistry and biophysics, some of whom might be interested in harnessing the potential of these bacteria as cell factories, or for bioremediation, nanotechnology or solar energy research. We hope that this book will help to attract a new generation of scientists to this field. We thank the authors of all the chapters for entering into the spirit of this project, which is intended to create a lasting work of reference, and a milestone in the field, a staging post on a journey that still has a long way to run. We are grateful to various individuals who have offered advice, including Govindjee, (the Series Editor), John Golbeck (Editor of the book on Photosystem I, Volume 24 in the Series), Robert Blankenship (one of the Editors of Volume 2 in the Series) and Hugo Scheer (one of the Editors of Volume 25 that focused on Chlorophylls and Bacteriochlophylls), but above all we thank Larry Orr, whose guidance has underpinned the progress of this book. Finally the editors thank their respective families and members of their laboratories for their patience throughout the editing process.

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