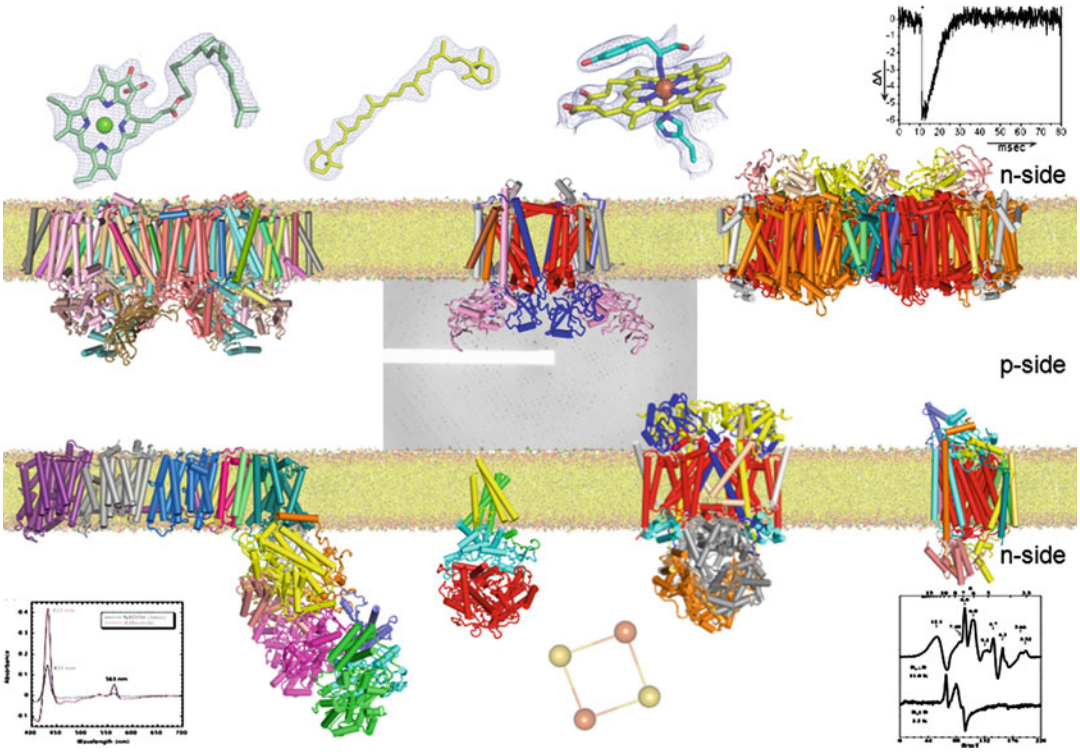
Cytochrome Complexes: Evolution, Structures, Energy Transduction, and Signaling



Experimental Information Important for Understanding Properties of Photosynthetic Cytochromes. Along the top are stick diagrams and electron density of pigments involved in light-harvesting – Chl-*a*, β-carotene, and heme of cytochrome *f* with unusual Tyr–His axial ligation (pdb, protein data base code, 4OGQ). This is followed by a flash kinetic trace of cytochrome oxidation-reduction. Along the bottom is a redox difference spectrum of the cytochrome b_6f complex, the [2Fe-2S] cluster in the Rieske iron-sulfur protein (pdb 4OGQ), and electron spin resonance spectra showing the unique $g = 12$ signal for the heme b_n–c_n couple in the cytochrome b_6f complex. In the center is an X-ray diffraction pattern of cytochrome b_6f crystals (pdb 4OGQ). **Protein structures** (*left to right*); **upper bilayer**: Photosynthetic electron transfer chain – Photosystem II (pdb 2WU2), cytochrome b_6f complex (pdb 4OGQ), Photosystem I (pdb 1JB0); **lower bilayer**: Mitochondrial electron transport chain – NDH complex (pdb 4HEA), succinate dehydrogenase (pdb 1NEN), cytochrome bc_1 complex (pdb 3CX5), cytochrome c oxidase (pdb 1V54). The lipid bilayer is a homogeneous DOPC bilayer generated with the CHARMM program. *Abbreviations*: p, n-side, electrochemically positive and negative side of the membrane (drawing by S. Saif Hasan)

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Cytochrome Complexes: Evolution, Structures, Energy Transduction, and Signaling

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From the Series Editors

Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes

Volume 41: Cytochrome Complexes: Evolution, Structures, Energy Transduction, and Signaling

We are delighted to announce the publication of Volume 41 in this series on *Advances in Photosynthesis and Respiration Including Bioenergy and Related Processes*. Oxygenic photosynthesis begins with conversion of light energy into chemical energy at two photochemical reaction centers in two separate photosystems (PS) I and II; this is followed by oxidation of water to molecular oxygen, reduction of pyridine nucleotide $NADP^+$ (nicotinamide adenine dinucleotide phosphate) to NADPH, and synthesis of ATP from ADP and inorganic phosphate by ATP synthase, the latter using the proton motive force produced across the thylakoid membrane during electron transport from water to $NADP^+$. Four protein complexes are essential for the completion of the entire process that leads to the formation of O_2, NADPH, and ATP: (1) Photosystem II (PSII); (2) Photosystem I (PSI); (3) Cytochrome (Cyt) b_6f complex; and (4) ATP synthase. Volume 22 in our Series, edited by T. Wydrzynski and K. Satoh and published in 2005, covered in great depth structure and function of PSII (Water-Plastoquinone Oxidoreductase); and volume 24, edited by J.H. Golbeck and published in 2006, did the same for PSI (Plastocyanin-ferredoxin oxidoreductase). Now, in 2016, we are fortunate to be able to present a complete structure-function description of not only Cyt b_6f complex but related complexes from mitochondria as well as from anoxygenic photosynthesis. This book (volume 41), *Cytochrome Complexes: Evolution, Structures, Energy Transduction, and Signaling*, was edited by two international authorities in biology, biochemistry, and biophysics: William A. Cramer and Toivo Kallas. In oxygenic photosynthesis, Cyt b_6f provides the link between PSII and PSI; it takes plastoquinol (PQH_2) made by PSII and reduces plastocyanin, which, in turn, is the source of electrons to reduce feredoxin (and, thus, $NADP^+$) by PSI. In addition, the cytochrome complex functions in the so-called Q cycle that is essential in generating an electrochemical proton gradient sufficient to generate the necessary ATP.

This book starts, appropriately, with a chapter by the late Derek S. Bendall, where he described the historical background of the field as well as the cytochrome notation. The book includes a discussion of the evolution of cytochromes and their functions. Students will benefit by an extensive exposure to both the experiments and the theory underlying electron transfer in proteins, as well as that of the molecular structures of cytochromes and even supercomplexes from both eukaryotes and prokaryotes. Essentially, one has, for the first time, as one would say, "*All we wanted to know about cytochromes, but could not bring ourselves to ask*." Yes, the book includes authoritative information even on macromolecular assembly, regulation, and signaling via the Cyt b_6f complex.

Because volume 41 covers an extensive subset of the cytochrome complexes that are involved not only in oxygenic photosynthesis but also in anoxygenic photosynthesis, as well as in respiration, one is confident that this book will be used in educating undergraduate and graduate students and researchers not only in plant and agricultural sciences but animal sciences as well as in microbiology. And since the book covers in depth the structure and function, the molecular biology, and the biochemistry as well as the biophysics of these cytochrome complexes (see Preface as well as Table of Contents of this book for further details), it can be used by students in molecular & cell biology, biochemistry, chemical biology, and biophysics. Further, one can see its significance in areas of agricultural and chemical engineering and in biotechnology, all of which should contribute to the significance of this book.

Authors of Volume 41

We note with great pride that the current volume is truly an international book; it has authors from 13 countries: Finland (1); France (6); Germany (10); Italy (3); Ireland (3); Israel (2); Japan (8); Lithuania (2); Poland (6); Russia (10): Switzerland (1); UK (8); and USA (25).

We begin by specifically mentioning here two authors, who are also editors of this volume: William A. Cramer of Purdue University, Indiana, USA, and Toivo Kallas of University of Wisconsin Oshkosh, Wisconsin, USA (see their biographies in this volume). Cramer's theme of research is the structure and function of membrane proteins, with a major focus on photosynthetic energy transduction via the cytochrome b_6f protein complex. We recommend that you visit his websites since they provide information on him as well as on his research: https://www.bio.purdue.edu/lab/cramer/; https://www.bio.purdue.edu/People/faculty_dm/directory.php?refID=12 Kallas's theme of research is overall photosynthesis, but in particular, electron transport through the cytochrome b_6f complex. His work has often focused on cyanobacteria; his web page is at http://www.uwosh.edu/facstaff/kallas.

There are 80 authors (including the two editors), who are experts in the field of their research, especially cytochromes. Alphabetically (by last names), they are Jean **A**lric, Eva-Mari Aro, Danas **B**aniulis, Adrian C. Barbrook, Carl E. Bauer, the late Derek S Bendall, Gabor Bernat, Edward Berry, Wojciech Bialek, Robert E. Blankenship, Elisa Bombarda, Martin **C**affrey, William A. Cramer, Fevzi **D**aldal, Miguel A. De la Rosa, Irene Díaz-Moreno, Antonio Díaz-Quintana, Timothy J. Donohue, Anne-Lise Ducluzeau, Seda **E**kici, Robert Ekiert, Lothar Esser, Giovanni **F**inazzi, Maria Luisa **G**enova, Patrice **H**amel, Shigeharu Harada, S. Saif Hasan, Florian Hilbers, Christopher J. Howe, Li-shar Huang, Saheed **I**mam, Daniel Ken Inaoka, Giles N. **J**ohnson, Toivo **K**allas, Bahia Khalfaoui-Hassani, Kiyoshi Kita, Hans-Georg Koch, Piotr Kolesinski, David Kramer, Lev I. Krishtalik, Genji Kurisu, Giorgio **L**enaz, Joseph A. Lyons, Erica L.W. **M**ajumder, Alizée Malnoë**,** Benjamin May, Yuval Mazor, I. Miliute, Jun Minagawa, Anthony L. Moore, Frank Müh, Lars Mueller, Nathan **N**elson, Robert H. Nimmo, Wolfgang Nitschke, Daniel R. Noguera, Artur **O**syczka, Jean-David Rochaix, Matthias Rögner, Marcin **S**arewicz, Georg Schmetterer, Dirk Schneider, Tomoo Shiba, Toshiharu Shikanai, Namita Shroff, Melanie A. Spero, Andrzej Szczepaniak, Petru-Iulian **T**rasnea, G. Matthias **U**llmann, Marcel Utz, Andreia F. **V**erissimo, Di **X**ia, Shinya **Y**oshikawa, Luke Young, Chang-An Yu, Sébastien **Z**appa, Fei Zhou, Francesca Zito, and Athina Zouni.

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Special 25 % discounts are available to members of the International Society of Photosynthesis Research, ISPR http://www.photosynthesisresearch.org/. See http://www.springer.com/ispr.

Future Advances in Photosynthesis and Respiration and Other Related 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):

- *Canopy Photosynthesis: From Basics to Applications* (Editors: Kouki Hikosaka, Ülo Niinemets and Niels P.R. Anten); it is already available; see < http://www.springer.com/us/book/9789401772907>
- *Photosynthesis and Climate Change* (working title) (Editor: Joy K. Ward)

- *Cyanobacteria* (Editor: Donald Bryant)
- *Leaf Photosynthesis* (Editors: William W. Adams III and Ichiro Terashima)
- *Photosynthesis in Algae* (Editors: Anthony Larkum and Arthur Grossman)
- *Plant Respiration* (Editor: Guillaume Tcherkez)

In addition to the above contracted books, the following topics are under consideration:

- Algae, Cyanobacteria: Biofuel and Bioenergy
- Artificial Photosynthesis
- ATP Synthase: Structure and Function
- Bacterial Respiration II
- Carotenoids II
- Evolution of Photosynthesis
- Green Bacteria and Heliobacteria
- Interactions between Photosynthesis and other Metabolic Processes
- Limits of Photosynthesis: Where do we go from here?
- Photosynthesis, Biomass and Bioenergy
- Photosynthesis under Abiotic and Biotic Stress

If you have any interest in editing/coediting any of the above listed books, or being an author, please send an e-mail to Tom Sharkey (tsharkey@msu.edu) and/or to Govindjee (gov@illinois.edu). Suggestions for additional topics are also welcome.

Instructions for writing chapters in books in our series are available by sending e-mail requests to one or both of us; they may also be downloaded from Govindjee's website http://www.life.illinois.edu/govindjee as the fourth item under "Announcements" on the main page.

Acknowledgments

We take this opportunity to thank and congratulate William A. Cramer and Toivo Kallas for their outstanding editorial work; they have indeed done a fantastic job, not only in editing but also in organizing this book for all of us, and for their highly professional dealing with the reviewing process. We thank all the 81 authors of this book (see the list given earlier); without their authoritative chapters, there would be no such volume. We give special thanks to S. Koperundevi of SPi Global, India, for directing the typesetting of this book; her expertise has been crucial in bringing this book to completion. We owe Jacco Flipsen, Andre Tournois, and Ineke Ravesloot (of Springer) thanks for their friendly working relation with us that led to the production of this book.

March 15, 2016

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Series Editors

Govindjee is the founding series editor of *Advances in Photosynthesis*, as it was called then, with volume 1 (*The Molecular Biology of Cyanobacteria*, 1994). In addition to being co-series editor (with Tom Sharkey) since volume 31 (The Chloroplast: Basics and Applications, 2010), he has coedited (1) Volume 19 (*Chlorophyll a Fluorescence: A Signature of Photosynthesis*, 2004); (2) Volume 20 (*Discoveries in Photosynthesis*, 2006); (3) Volume 29 (*Photosynthesis In Silico: Understanding Complexity from Molecules to Ecosystems*, 2009); and (4) Volume 40 (*Non-Photochemical Quenching and Energy Dissipation in Plants, Algae and Cyanobacteria*, 2014).

Govindjee, who uses one name only, has been Professor Emeritus of Biochemistry, Biophysics, and Plant Biology at the University of Illinois at Urbana- Champaign (UIUC), since 1999. His short evolving biography can be found in each volume of *Advances in Photosynthesis and Respiration*, and other information on him and his activities is available at his website http://www.life.illinois.edu/govindjee. An interview for Annual Reviews Inc., by Don Ort, is available at https://www.youtube.com/watch?v=cOzuL0vxEi0. His recent publications are listed at http://www.life.illinois.edu/govindjee/recent_papers.html, and earlier publications since 1955 are at http://www.life.illinois.edu/govindjee/pubschron.html.

Govindjee was trained in Plant Physiology (1952–1956) by Shri Ranjan (a student of Felix Frost Blackman of UK), in Biology and Biochemistry of Photosynthesis (1956–1958) by Robert Emerson (a student of the Nobel laureate Otto Warburg), and in Biophysics of Photosynthesis (1958–1961) by Eugene Rabinowitch (a postdoc student of the Nobel laureate James Franck). After his Ph.D. in Biophysics in 1960 from the UIUC, he has learned many concepts and techniques from many others including Louis N.M. Duysens (Leiden, The Netherlands); C. Stacy French (Stanford, California, USA); Herbert S. Gutowsky (Urbana, Illinois, USA); Bessel Kok (Baltimore, Maryland, USA); Jean Lavorel (Gif-syur-Yvette, France); Gregorio Weber (Urbana, Illinois); and Horst Witt (Berlin, Germany).

Govindjee's discoveries, with his coworkers and graduate students, include the participation of chlorophyll (Chl) *a* (in what we now call Photosystem (PS) II); proof of the existence of two light reactions in NADP reduction, and in Chl a fluorescence; temperature dependence of excitation energy transfer down to 4° K in algae and cyanobacteria; molecular understanding of both the fast and slow Chl a fluorescence (both prompt and delayed) changes—that includes participation of membrane potential, pH gradient, "traffic jam" in PSI, and the so-called state changes; first picosecond measurements on the primary photochemistry of PSI and PSII; unique role of bicarbonate in electron transfer and protonation events at the Q_B binding site; first comprehensive theory of thermoluminescence in plants; and the first use of lifetime of Chl a fluorescence measurements in understanding photoprotection in plants.

Govindjee's activities include, besides research on "Light Reactions of Photosynthesis," honoring others (Robert Blankenship; Bob Buchanan; Andre Jagendorf; Wolfgang Junge; Hartmut Lichtenthaler; George Papageorgiou; William Ogren; Vladimir Shuvalov; and Diter Von Wettstein; see Govindjee's website) in the field, as well as participating in writing and editing obituaries and tributes (Lou Duysens; Colin Wraight; Al Bassham; Rene Marcelle; V.S.R. Rama Das; Prasanna Mohanty; Jalal Aliyev; Al Frenkel; and Andy Benson). In addition, he enjoys lecturing on the history of photosynthesis research and in teaching photosynthesis by having students act as molecules and demonstrating the path of electrons in photosynthesis by having them enact a drama. He has had many honors, but he cherishes five of them dearly: 2006 Lifetime Achievement Award of the Rebeiz Foundation for Basic Biology; 2007 Communication Award of the International Society of Photosynthesis Research; 2008 Liberal Arts & Sciences Lifetime Achievement Award of UIUC; 2015 Dr. B.M. Johri Memorial Award for Excellence in Plant Biology, from the Society of Plant Research, India; and a 2016 Distinguished Alumnus Award from his High School (Colonelganj Inter College) in Allahabad. In addition, he has enjoyed what others have written on him at his 75th and 80th birthdays (see Photosynth Res **93**:1–5 (2007); **94**: 153–178 (2007); **100**: 49–55 (2009); **116**: 107–110; 111–144 (2013); **122**: 113–119); also see <https://www.linkedin.com/pulse/govindjee-living-legend-i-met-dr-ravi-sharma>. (To see this site, click on "living-legend".) A rather useful effort in teaching others is through the article "Photosynthesis Web Resources" <http://www.life.illinois.edu/govindjee/photoweb/>. Also see a collection of education books at http://www.life.illinois.edu/govindjee/g/Books.html. He is always delighted to respond to questions on both photosynthesis research and education (e-mail: gov@illinois.edu).

Thomas D. (Tom) Sharkey obtained his Bachelor's degree in Biology in 1974 from Lyman Briggs College, a residential science college at Michigan State University, East Lansing, Michigan, USA. After 2 years as a research technician, Tom entered a Ph.D. program in the Department of Energy Plant Research Laboratory at Michigan State University under the mentorship of Klaus Raschke and finished in 1979. Postdoctoral research was carried out with Graham Farquhar at the Australian National University, in Canberra, where he coauthored a landmark review on photosynthesis and stomatal conductance. For 5 years he worked at the Desert Research Institute, Reno, Nevada. After Reno, Tom spent 20 years as Professor of Botany at the University of Wisconsin in Madison. In 2008, Tom became Professor and Chair of the Department of Biochemistry and Molecular Biology at Michigan State University. Tom's research interests center on the exchange of gases between plants and the atmosphere and carbon metabolism of photosynthesis. The biochemistry and biophysics underlying carbon dioxide uptake and isoprene emission from plants form the two major research topics in his laboratory. Among his contributions are measurement of the carbon dioxide concentration inside leaves, an exhaustive study of short-term feedback effects in carbon metabolism, and a significant contribution to elucidation of the pathway by which leaf starch breaks down at night. In the isoprene research field, Tom is recognized as the leading advocate for thermotolerance of photosynthesis as the explanation for why plants emit isoprene. In addition, his laboratory has cloned many of the genes that underlie isoprene synthesis and he has published many important papers on the biochemical regulation of isoprene synthesis. Tom's work has been cited over 21,000 times according to Google Scholar in 2015. He has been named an Outstanding Faculty member by Michigan State University and in 2015, he was honored, and named as a University Distinguished Professor. Tom has coedited three books, the first on trace gas emissions from plants in 1991 (with Elizabeth Holland and Hal Mooney), volume 9 of this series (with Richard Leegood and Susanne von Caemmerer) on the *Physiology of Carbon Metabolism of Photosynthesis* in 2000, and volume 34 (with Julian Eaton-Rye and Baishnab C. Tripathy) entitled *Photosynthesis*: *Plastid Biology*, *Energy Conversion and Carbon Assimilation*. Tom has been co-series editor of this series since volume 31.

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Preface

Why study cytochrome complexes? An answer is provided by the range of subtopics in the book, "evolution, structures, energy, and signaling," which are described in the book title. Studies on the cytochrome family of proteins encompass a uniquely wide area of basic and applied research. Research in this field utilizes a range of theoretical and computational approaches, as well as a broad cross section of experimental techniques. Understanding obtained on the structure and function of the cytochromes and cytochrome complexes utilizes an extraordinary range of experimental approaches, including computational biology, genetics, macromolecular biochemistry, molecular biology, physics of charge transfer reactions, structure analysis using x-ray and electron diffraction, and ultrafast spectroscopy.

As reflected in the book title, the information and understanding gained in the field has an influence on a wide range of subjects, including evolution, mechanisms of membrane-based respiratory and photosynthetic energy transduction, theory of charge transfer in proteins, structure-function of large hetero-oligomeric membrane proteins, including lipid-protein interactions, and transmembrane signaling.

A special aspect of cytochromes, cytochrome complexes, as well as other proteins involved in bioenergetics and charge transfer is that they allow function to be quantitatively analyzed. Thus, in this group of proteins, it is possible to determine that a protein or protein complex is functional before committing a large amount of time to crystallization and analysis of structure. Dating back to the 1988 Nobel Prize in Chemistry, given to J. Deisenhofer, H. Michel, and R. Huber for determination of the crystal structure of the bacterial photosynthetic reaction center, the majority of the crystal structures of hetero-oligomeric membrane proteins obtained in the subsequent 10 years were of energy-transducing proteins. Of these, a substantial fraction involved cytochrome complexes.

The Logic of the Collection The book starts with an Introduction by Derek Bendall describing cytochrome notation, which is connected to the history of the field, focusing on research in England in the pre-World War II era. An *ab initio* "start with the beginning" logic then leads to a discussion of the evolution of cytochromes and hemes. Before presentation of the many individual cytochrome systems, the fundamentals of the theory of electron transfer in proteins are presented, followed by an extensive description of the molecular structures of cytochromes and cytochrome complexes from eukaryotic and prokaryotic sources, including those derived from photosynthetic reaction centers. The presentation of atomic structure information has a major role in these discussions, including the relatively new subject of "supercomplexes." This structure information has a major niche in the broad field of membrane structure-function. Expanding the perspective beyond structure-function applied to charge transfer and energy storage, the problems of protein and macromolecule assembly, regulation, and signaling, including transmembrane signaling, which have conceptual connections to central areas of biochemistry, biophysics, and cell biology, are considered. Regarding subjects related to cutting-edge areas of biology and plant biology, the up-to-date presentation of the topics of *Regulation* and *Signaling* is noted here.

The broad extent of fundamental intellectual and research areas that are represented in this book makes it a useful resource for teaching of academic courses and presentation of seminars on fundamental and broad aspects of biological energy transduction to advanced undergraduates and graduate students with interests in biology, biochemistry, biological engineering, chemistry, and biophysics.

As a last entry to the Introduction to this book, we note, sadly, the passing of Derek S. Bendall and Bernard L. Trumpower, whose achievements in this field are substantial and of fundamental importance. The Remembrances in this volume that are dedicated to them are of historical importance and note their many contributions to the subjects discussed herein.

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Editors

William A. Cramer (WAC) received a B.S. (Physics, 1959) from the Massachusetts Institute of Technology (MIT), Boston, Mass., USA. From MIT, WAC went to the University of Chicago, where he obtained his M.S. in Physics; he initially worked and published in muon physics and birefringence of muscle proteins, and obtained a Ph.D. in Biophysics (1965), studying with R.B. Uretz. Subsequently, he carried out postdoctoral studies on photosynthetic electron transport with Warren L. Butler at the University of California/San Diego. He is currently the Henry Koffler Distinguished Professor in the Department of Biological Sciences at Purdue University, West Lafayette, Indiana. His research is focused on the relationship between structure and function of membrane proteins, including those involved in photosynthetic energy transduction. He is an authority on the cytochrome (cyt) b_6f complex, a hetero-oligomeric lipoprotein complex in the cytochrome *bc* family that functions in the photosynthetic and respiratory electron transport chains. The b_6f complex generates a major fraction of the transmembrane electrochemical potential and proton gradient; it is also responsible for significant generation of superoxide, and for a unique redox-controlled mechanism of transmembrane signaling that activates a kinase responsible for phosphorylation of the light-harvesting chlorophyll protein. Cramer also studies the membrane-mediated mechanism of cellular import of bacterial cytotoxins.

Some of the conceptual and experimental bases for his chapters in this book have been discussed in the 1991 textbook by him and the late David B. Knaff, entitled *Energy Transduction in Biological Membranes,* published by Springer-Verlag, as well as reviews on the cytochrome complex and the mechanism of cytotoxin import, including those in the Annual Reviews (Biophysics, Biochemistry, Plant Biology, and Genetics). WAC has served as the Chair of the Gordon Research Conferences on Photosynthesis (1990) and Bioenergetics (2001). He has served as the Chair of the Bioenergetics

Subgroup, and as the Program Chair (1996), of the National Meeting (1996) of the American Biophysical Society. He has been a recipient of the Charles F. Kettering Award of the American Society of Plant Physiology for "Excellence in Photosynthesis" (1996), a Guggenheim Fellow (1992), and is a Fellow of the Alexander von Humboldt Foundation and of the Biophysical Society.

Toivo Kallas is a Distinguished Professor of Microbial Genetics and Biotechnology at the University of Wisconsin (UW) – Oshkosh, USA. He holds a B.A. from Carleton College, Minnesota, and a Ph.D. in Microbiology from the University of Oregon where he worked with Richard Castenholz on thermophilic cyanobacteria. He did postdoctoral work with Germaine Cohen-Bazire (Stanier), Institut Pasteur (Paris, France), on aerobic nitrogen fixation by unicellular cyanobacteria and with Richard Malkin, University of California (UC), Berkeley, on the cytochrome b_6f electron transfer complex of photosynthesis. He spent sabbaticals with Francis-André Wollman and Catherine de Vitry, Institut Biologie Physico-Chimique (Paris, France), on regulation and electron transfer kinetics in *Chlamydomonas* and cyanobacteria and Michael Sussman, UW Madison Biotechnology Center, on proteomics of silica cell wall biogenesis in diatoms. His research at UW Oshkosh has focused on electron transfer proteins, energy transduction, gene expression, and metabolic engineering of cyanobacteria. Some 80 undergraduate students, 24 Master's students, and several postdoctoral and visiting scientists have participated in this research funded by grants from the US National Science Foundation, US Department of Agriculture, UW Oshkosh, and UW WiSys Technology Foundation.

Over the past several years, Kallas, Matthew Nelson (UW Oshkosh), and Eric Singsaas (Natural Resources Research Institute, University of Minnesota, Duluth, USA) have worked on metabolic engineering of cyanobacteria and photobioreactor design to convert solar energy and waste CO_2 into high-value isoprene-terpene bioproducts and biofuels. This project has reached several milestones, and the team recently founded Algoma Algal Biotechnology (AABT), a limited liability company (LLC), to develop both biomass conversion and microalgal carbon capture as avenues for sustainable hydrocarbon production. Kallas has published two detailed authoritative reviews on the cytochrome *bf* complex for the *Advances in Photosynthesis and Respiration* series (volumes 1 and 34) and has coedited (with Anne Ruffing, of Sandia National Labs, Albuquerque, New Mexico, USA) a recent special issue on Cyanobacteria, the Green *E. coli* for *Frontiers in Bioengineering and Biotechnology.* He co-organized (with Jack Meeks, UC Davis) the 2007 Cyanobacterial Workshop and has co-organized two Midwest-Southeast Photosynthesis Conferences (in 2001 and

2010). His current work on CO_2 capture, isoprene production, and AABT business development is funded by Small Business Technology Transfer (STTR) Phase I and IB grants from the US National Science Foundation and a supplement from the UW Center for Technology Commercialization. Further information on Toivo Kallas is available at his website http://www.uwosh.edu/facstaff/kallas.

Remembrances

Remembering Professor Derek S. Bendall

The distinguished biochemist Derek S. Bendall, whose last written scientific work is presented in this volume, passed away in December 2014 at the age of 84 years. We would like to contribute to a celebration of Derek's life with personal reflections on Derek and his scientific legacy and our experiences working closely with him on a collaborative project.

Derek's research passion was redox reactions of biological systems, a topic that he pursued for nearly 60 years. In particular, he was fascinated by the problem of how solar energy is transduced into chemical energy in green plants, and on the mechanism of photosynthetic oxygen evolution. His research journey began with his scientific training as an undergraduate in Cambridge in the UK, where he was awarded a first class degree in 1953. His evolving interests in photosynthesis led him to studies of plant microsomes and mitochondria for a dissertation project with Robin Hill in the Biochemistry Department. He was awarded a Ph.D. in 1957 from Cambridge University and then spent a year working in Louvain, Belgium, where he studied methods for preparing mammalian mitochondria fractions for characterization. Derek then worked for the Nyasaland Tea Association in both Africa and Cambridge before becoming a demonstrator (1960) and lecturer (1965) in the Biochemistry Department in Cambridge. His early work demonstrated that mitochondria have a cytochrome oxidase, and he analyzed cytochromes in chloroplasts. He studied the cycling of electron transfer around photosystem I, and how this helps to protect against the effects of rapid changes in light level. Under this condition, electrons are transferred from the plastoquinone pool or terminal oxidase rather than photosystem I to reduce backup of photosynthetic electron transfer.

The mechanism of biological electron transfer and, in particular, transient protein-protein interactions mediating such reactions was of special interest to him, and he edited and contributed to an excellent book on the subject, entitled *Protein Electron Transfer*, which was published in 1996 before Derek's official "retirement." For Jonathan Worrall, this book holds special memories and was a source of continuous background reading during his Ph.D. and early postdoc years. It was with great pleasure therefore that upon attending a meeting in Denmark focused on transient protein-protein interactions, Jonathan was awarded the poster prize and received from Derek a signed copy of his book.

Not content to follow retirement in the traditional sense, Derek joined Chris Howe's laboratory in the Biochemistry Department in Cambridge, where he continued earlier collaborative work that they had started on various projects. He continued studies on protein targeting in cyanobacteria, and in particular on the distribution of photosystem proteins in the membrane, following up earlier studies in which they had found evidence for the localization of some proteins in the cytoplasmic membrane. In addition he continued his interest in weak protein-protein interactions, particularly those of the electron transfer complex formed between cytochrome *f* and plastocyanin.

His interest in cytochromes attracted him to a mysterious cytochrome c_6 homologue, encoded in the genome of several land plants and algae, but possessing a more negative redox potential than its bacterial counterparts. To distinguish this homologue from the bacterial proteins, Derek suggested that it should be named cytochrome c_{6A}. We worked with Derek to initially characterize the crystal structure of cytochrome c_{6A} in reduced and oxidized forms. Derek's driving enthusiasm to understand why cytochrome c_{6A} possessed a redox potential some 250 mV lower than bacterial cytochrome c_6 proteins led to further collaboration with us and to experimental support for a mechanism of redox potential control by the interactions of side chains around the heme. The chapters presented in this book written with his long-term collaborator, Chris Howe, describe his last work on cytochrome c_{6A}.

Derek was also involved in translational projects during his retirement. He worked on renewable energy projects using cyanobacteria, studying direct electron transport from cyanobacteria and algal cells onto electrodes to make direct photovoltaic devices. He was also involved in engineering cyanobacteria to explore terminal oxidases in the process of direct electron transfer.

Derek had a long-standing interest in tea, both as a tea-drinker connoisseur and as a subject for scientific investigation. He studied the biochemical processes of tea fermentation, and his work, including preparation and characterization of catechol oxidase, resulted in several reports on the fermentation process. His passion for botany was also expressed in his activities as a keen gardener.

Through our work with Derek on the cytochrome c_{6A}, we had an opportunity for extensive interactions that involved hypothesis formulation and testing, and these were stimulating interactions. We were struck by Derek's knowledge and scientific imagination, by his gentle character and modest nature. Like many other colleagues, we feel very fortunate to have had the opportunity to work with him and to have benefited from these interactions.

For further information and references to Bendall's key papers. see C.J. Howe, P.R. Rich and M. Ubbink (2015) Derrek Bendall (1930–2015) Photosynth Res 124: 249–252.

March 15, 2016

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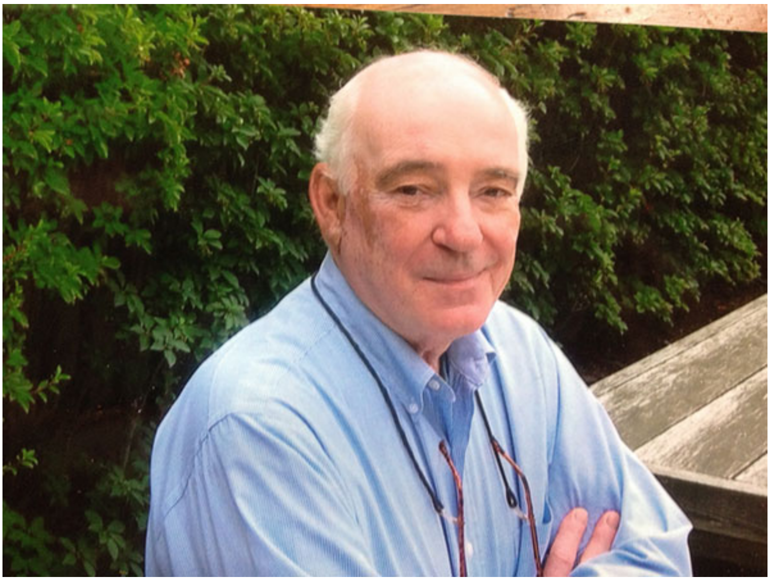

Remembering Professor Bernard L. Trumpower

The news that Bernard had passed away on the Christmas day of 2014 spread rapidly among his friends, colleagues, former Ph.D. students, and postdocs. Together with the personal sorrow that inevitably comes with such a message, I immediately felt struck by the gap created within our scientific community. “Bernie,” as we used to call him, when I had the privilege to work as a postdoc in his laboratory, was clearly a leading figure in the field of bioenergetics for many years. Here, I can only try to give an account of his fundamental contributions to our understanding of the structure and function of the mitochondrial cytochrome bc_1 complex.

Bernard L. Trumpower studied Chemistry at the University of Pittsburgh and completed his Ph.D. in Biochemistry at St. Louis University, Missouri, USA, in 1969, where he worked with Robert E. Olson on the biosynthesis of ubiquinone-9. During his postdoctoral studies with Efraim Racker at Cornell University, Ithaca, N.Y. (1969-1972), he became acquainted with the membrane protein complexes of the oxidative phosphorylation system that use ubiquinone as a substrate. This set the stage for his successful career of more than 40 years studying the structure and function of the cytochrome bc_1 complex that made him a leader in the field of Molecular Bioenergetics.

In 1972, when Bernard was appointed Assistant Professor of Biochemistry at Dartmouth Medical School, the molecular mechanism of this central complex of the respiratory chain was still enigmatic. Early on, he had realized the key role of the Rieske iron-sulfur protein, and the usefulness of specific inhibitors for studying the intricate mechanism of the enzyme. This allowed him to provide decisive experimental proof for the proton-motive Q-cycle, soon after Peter Mitchell published this hypothesis for the redox-driven proton translocation by the cytochrome bc_1 complex in 1975. Shortly after Bernard was promoted to Associate Professor in 1978, he published a series of landmark papers showing the activation of cytochrome bc_1 complex function by reconstitutively active Rieske iron-sulfur protein (Trumpower and Edwards 1979), establishing the use of Electron Paramagnetic Resonance (EPR) spectroscopy with Tomoko Ohnishi to study catalytic intermediates (Ohnishi and Trumpower 1980, Trumpower et al. 1980), and introducing novel ubiquinone analogues as specific inhibitors of the cytochrome bc_1 complex (Bowyer and Trumpower 1980). When he became a full Professor of Biochemistry at Dartmouth in 1983, he was just performing groundbreaking functional studies together with Gebhard von Jagow using myxothiazol, the first representative of another new class of specific inhibitors. In a classical experiment, later known as the "double-kill," they were able to demonstrate unambiguously and characterize functionally the two distinct ubiquinone-binding sites of the cytochrome bc_1 complex, thereby confirming a central postulate of the proton-motive Q-cycle hypothesis (von Jagow et al. 1984).

Following Efraim Racker's pledge "*Don't waste clean thinking on dirty enzymes*." Bernard developed simple and efficient protocols to purify cytochrome bc_1 complexes from mitochondria and bacterial membranes still applied today that were among the first to demonstrate the usefulness of the now widely used detergent dodecyl-maltoside to purify membrane protein complexes (Ljungdahl et al. 1987). This paved the way for a series of important studies on the kinetic properties of the bacterial enzyme seminal to understanding central aspects of the proton-motive Q-cycle.

Again leading the field, Bernard recognized soon the enormous potential of molecular biology that became widely applicable in the 1980s. In his quest to understand all aspects of structure and function of the cytochrome bc_1 complex, he spent time with Gerry Fink at Harvard University (Cambridge, Massachusetts) to learn yeast genetics. Using this powerful approach, Bernard's laboratory subsequently cloned several genes of all so-called supernumerary subunits of the complex from yeast mitochondria and characterized their function by genomic deletion and structure/function studies (see Zara et al. (2009) for a review). Exhaustive site-directed mutagenesis of the Rieske iron-sulfur protein were a straightforward extension of his early work and led to the identification of the functionally critical domains (Graham et al. 1993).

Returning to the roots of his early research, Bernard then used the X-ray structures of the cytochrome bc_1 complex that finally became available in the late 1990s as a guide for fundamental studies to understand the molecular basis of the proton-motive Q-cycle. Intrigued by the fact that the structures showed the cytochrome bc_1 complex to be a constitutive dimer, he indeed defined a functional role for this remarkable structural feature (Covian and Trumpower 2008).

In the years before retirement and becoming Professor Emeritus from the Dartmouth Medical School in 2013, he also dived into an important medical aspect demonstrating the societal impact of his research: The molecular target of the widely used antimalarial Atoquavone is the ubiquinol oxidation site of the cytochrome bc_1 complex. Bernard applied his profound knowledge on structure and function of enzymes, to design quinone derivatives binding to this site that are less susceptible to drug resistance (Hughes et al. 2011).

The groundbreaking research contributions by Bernard L. Trumpower were honored through a number of national and international awards including the Humboldt Prize in 1984 and the Merit Award of the National Institute of Health (NIH) in 1994. He served the scientific community in many ways, as editor of several leading biomedical journals, member of NIH Study Sections, and organizer of a number of major national and international conferences.

Reaching far beyond the dry facts that can be documented in a list of his publications, Bernard had a truly lasting impact as a guide and a role model for his students and young colleagues. Never content with a superficial answer, he taught us to stay focused, to be thorough, persistent, and self-critical. I will never forget that when we finally reached a conclusion in an intense and controversial scientific discussion, his next sentence would usually start with "But . . . " to express that there is always another side of the problem to explore.

For me, his unconditional quest for perfection best characterizes Bernard not only as a scientist. It can be experienced nicely by looking at the series of wonderful photographs he made after his retirement (https://www.dartmouth.edu/~grnhouse/brout.php) showcasing the beauty and elegance of orchids.

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