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Editorial

Celebrating the millennium: historical highlights of photosynthesis research, Part 3

Govindjee[1,*], John F. Allen[2] & J. Thomas Beatty[3]
[1]*Departments of Biochemistry and Plant Biology, and the Center of Biophysics and Computational Biology, University of Illinois, 265 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801-3707, USA;* [2]*Plant Biochemistry, Center for Chemistry and Chemical Engineering, Lund University, Box 124, 221 00 Lund, Sweden;* [3]*Department of Microbiology and Immunology, University of British Columbia, Room 300, 6174 University Blvd, Vancouver, BC, V6T 1Z3 Canada;* **Author for correspondence (e-mail: gov@uiuc.edu; fax: +1-217-244-7246)*

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Abstract

This paper introduces the third and final part of the 'millennium celebrations of historical highlights of photosynthesis research.' Part 1 (308 pages) was published in October 2002 as Vol. 73 of the journal *Photosynthesis Research*, and Part 2 (458 pages) was published in July 2003 as Vol. 76. Here, we recognize particularly the work of three major contributors to our understanding of photosynthesis: Roger Stanier (1916–1982); Germaine Cohen-Bazire (Stanier) (1920–2001); and William Arnold (1904–2001). We also introduce the historical papers contained in this volume; consider the legacy of Alfred Nobel (1833–1896); and identify Nobel prizes of special relevance to understanding the capture, conversion, and storage of light energy in both anoxygenic and oxygenic photosynthesis.

> 'If I have seen further, it is by standing upon the shoulders of giants.'
> – Isaac Newton (1642–1727),
> letter to Robert Hooke, 5 February 1675

The beginnings of the history issues of photosynthesis research

The idea of compiling a history of photosynthesis research arose more than 20 years ago when one of us (G) sent out a one-page letter to a limited number of photosynthesis researchers. The letter (Appendix A) had the goal of publishing an informal historical newsletter, which would include birthdays of distinguished colleagues. To our good fortune, this idea has evolved to culminate in three published volumes of *Photosynthesis Research*. We thank our distinguished colleague and master historian Howard Gest for his initiative, constant support, guidance and many contributions on the history of photosynthesis research, including three articles in this issue. Without Howard, we would never have seen these history issues in print. The time Howard and Govindjee spent together, in planning these issues, in July 2001 in San Diego, California, was crucial to the success of these historical volumes. The great charm, hospitality, historical insight and the wonderful anecdotes provided by Andy Benson during this visit added to the pleasure that Howard and Govindjee took in initiating this project (see Figure 1).

In continuation of Parts 1 and 2, celebrating the millennium

This issue is the third in a series that was originally intended to consist of a single journal issue, but

Figure 1. From left to right: Howard Gest, Andy Benson and Govindjee. Photo taken in La Jolla (California) in July 2001 by Rajni Govindjee.

Figure 2. Roger Stanier (*right*) and Norbert Pfennig (*left*). This photo was taken at the second International Symposium on Phototrophic Prokaryotes held in 1976 in Dundee. Pfennig is a prominent scientist widely acclaimed for his contributions to the microbiology of anoxygenic phototrophs (green and purple). This photo is a courtesy of Howard Gest.

which was expanded because of the enthusiastic response. Parts 1 and 2 contain editorials that note key discoveries in photosynthesis research, from its roots in the early 18th century to the application of spectroscopy and molecular genetics in the late 20th century (Govindjee and Gest 2002; Govindjee et al. 2003). Some of these discoveries are featured in historical and personal perspectives of Parts 1 and 2, and this style continues in this issue. Part 1 has 308 pages and 38 articles, the latter distributed under four headings: 'Introduction' (8 articles); 'Anoxygenic photosynthesis' (7 articles); 'Oxygenic photosynthesis' (22 articles); 'Photosynthesis Laboratories' (1 article). Part 2 has 462 pages and 39 papers; the distribution of papers is almost the same in the first two categories as in Part 1, but has 7 papers under 'Photosynthesis Laboratories and Research around the world,' and 17 under 'Oxygenic photosynthesis.' A unique feature of Part 3 is the inclusion of papers on the history of the X-ray crystal structures of reaction centers of photosynthetic bacteria, Photosystem II and Photosystem I, and of the cytochrome $b6/f$ complexes.

Special recognitions

The editorial of Part 1 of these history issues described the work of Martin Kamen and Robert Emerson. Martin Kamen (1913–2002) was the co-discoverer (with Samuel Ruben) of ^{14}C. Robert Emerson (1903–1959) was the discoverer, with William Arnold, of the concept of the 'photosynthetic unit,' and of the Emerson enhancement that later led to the current two-light reaction scheme of photosynthesis. The editorial of Part 2 recognized Cornelis B. van Niel (1897–1985), a pioneer of the physiology of purple phototrophic bacteria; Robert Hill (1899–1991), discoverer of the 'Hill reaction,' and of the 'Z-scheme' of photosynthesis; and Eugene Rabinowitch (1901–1973), a master thinker of all aspects of photosynthesis. Additionally in Part 2, special tribute was paid to Louis N.M. Duysens. His work on excitation energy transfer, the first observation of 'P' (which turned out to be the reaction center), and the evidence for the series scheme of photosynthesis, obtained in collaboration with Jan Amesz (1934–2001), is a cornerstone of our current understanding of photosynthesis.

In Part 3, we herein recognize Roger Stanier (Figure 2), Germaine Cohen-Bazire (Stanier) (Figure 3), and William Arnold (Figure 4).

Roger Yate Stanier (1916–1982) and Germaine Cohen-Bazire (Stanier) (1920–2001)

One of the outcomes of Roger Stanier's 1952 visit to the Institut Pasteur in Paris, during a sabbatical leave of absence from the University of California, Berkeley (UCB), was that he later married Germaine Cohen-Bazire (then a member of Jacques Monod's group) and they became a renowned scientific team.

Stanier (BA 1936, University of British Columbia) was a Canadian citizen. He did his PhD thesis (on the biology of *Cytophaga* and bacterial classification; 1942, Stanford University) with Cornelis B. van Niel (1897–1985), by whom he was strongly influenced

Figure 3. Two photographs of Germaine Cohen-Bazire (Stanier). *Left*: courtesy of Janet Stanier. *Right*: courtesy of Nicole Tandeau de Marsac.

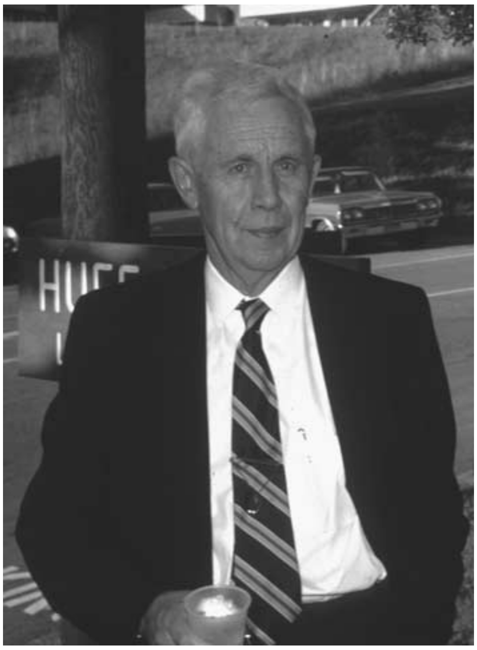

Figure 4. William Archibald Arnold. Photo taken by Govindjee in the late 1970s.

(see Govindjee et al. 2003). Stanier's rise to prominence began in 1947, when he took up a faculty position at UCB and started research on a variety of topics (Stanier 1980). Stanier's wide range of interests was underlain by his drive to integrate prokaryotes into a general understanding of cell biology. For example, some of Stanier's stellar contributions were: a clear exposition of the fundamental differences between prokaryotic and eukaryotic microbes (Stanier and van Niel 1962; Stanier 1970); promoting the recognition of 'blue-green algae' as prokaryotes and popularizing the name cyanobacteria (Stanier and Cohen-Bazire 1977); co-authoring a textbook ('The Microbial World') that was for decades THE microbiology text, in large part because of Stanier's imprint – manifested by the breadth and depth of coverage, and clarity of writing. The first edition of this textbook (1957) included Michael Doudoroff and Edward A. Adelberg as co-authors, and the fifth edition (1986) included Stanier as a posthumous author.

Perhaps because of van Niel's influence, Stanier was slow to accept the early evidence that purple phototrophic bacteria do not split water but instead use 'cyclic photophosphorylation' to produce ATP (Frenkel 1954), with reducing power (NAD[P]H) provided by dark reactions. Questions first arose from Hans Gaffron's early experiments (Gaffron 1933; see comments in Stanier et al. 1959) and Stanier finally agreed that '. . .van Niel had been wrong and Hans Gaffron had been right. . .' (Stanier 1980), characteristically after experiments done by Stanier and colleagues (Stanier et al. 1959). Nevertheless, confusion about the fundamental differences between these two types of photosynthesis persisted in the literature, as noted by Gest (1993).

In 1967, Stanier was appointed as director of the Laboratoire de Cytophysiologie de la Photosynthèse of the CNRS (Centre National de la Recherche

Scientifique) in Gif-sur-Yvette, near Paris, and Cohen-Bazire accepted a permanent position as a senior scientist in the neighboring Laboratoire de Photosynthèse (de Kouchkovsky 2002). They moved to the Institut Pasteur in 1971, where Stanier headed the Unité de Physiologie Microbienne and was succeeded by Cohen-Bazire upon his death in 1982. Stanier's research during the last decade of his life, with Cohen-Bazire, Rosmarie Rippka, Nicole Tandeau de Marsac and others, was focused on the biology and taxonomy of cyanobacteria (Stanier and Cohen-Bazire 1977; Stanier 1980).

Stanier was influential in starting the International Symposium on Phototrophic Prokaryotes, the first meeting of which was hosted by Gerhard Drews (with help from Norbert Pfennig, shown in Figure 2) at Freiburg, Germany (Guerrero 1999). This meeting has been held at a variety of venues at 3-year intervals, with the 2003 symposium held in Tokyo, Japan, and the next meeting scheduled for 2006 in France.

Germaine Bazire (who changed her surname to Cohen-Bazire after her first marriage, and later used the surname Stanier) received her early education in Toulouse, France, and did her PhD thesis (1950) on bacterial fermentations with Jacques Monod (1917–1976) at the Institut Pasteur. She stayed on as a postdoc in Monod's group and contributed to the development of the concepts of induction and repression of enzyme synthesis (regulation of gene expression; Monod et al. 1951, 1952). Monod shared the Nobel Prize for Physiology or Medicine in 1965 with his Insitut Pasteur colleagues François Jacob and André Lwoff, 'for their discoveries concerning genetic control of enzyme and virus synthesis.'

After Cohen-Bazire began her postdoctoral work around 1953 at UCB, Stanier introduced her to phototrophic bacteria and she used her training to do the first studies of genetic regulation of photosynthesis in purple bacteria. Cohen-Bazire was among the first to use mutants to study the function of photosynthetic pigments (Griffiths et al. 1955). Her landmark paper (Cohen-Bazire et al. 1957) on the repressive effects of oxygen concentration and light intensity on the synthesis of the photosynthetic apparatus in purple phototrophic bacteria continues to be cited by researchers in this very active field (see Bauer, this issue; and Kaplan 2002). She also worked on the structure and composition of phycobilisomes in cyanobacteria, and on chromatic adaptation (Glazer and Cohen-Bazire 1971; Bryant and Cohen-Bazire 1981). Cohen-Bazire became an expert electron microscopist and her micrographs helped lead to our current understanding of the membrane architecture of thylakoids in cyanobacteria, 'chromatophores' (intracytoplasmic membranes) in purple phototrophic bacteria and chlorosomes in green phototrophic bacteria (Cohen-Bazire and Kunisawa 1960; Cohen-Bazire et al. 1964; Guglielmi and Cohen-Bazire 1984).

Starting at UCB, and continuing after her return to the Institut Pasteur in 1971, Cohen-Bazire established herself as a world leader in the ultrastructure and physiology of cyanobacteria. She headed the Unité de Physiologie Microbienne from 1982 until her retirement in 1988, when it was named the Unité des Cyanobacteries.

William Archibald Arnold (1904–2001)

In 1996, Govindjee, Robert S. Knox and Jan Amesz honored William (Bill) Archibald Arnold with a 319-page special issue of *Photosynthesis Research* (Govindjee et al. 1996). It started with the following words:

> It was Arnold's experimental and theoretical acumen as an undergraduate student of the great experimentalist of photosynthesis Robert Emerson, then an assistant Professor of Biophysics at Caltech, that led in 1932 to the concept of a photosynthetic unit – that of a large number of chlorophyll molecules feeding an enzymatic conveyor belt. . . . Thus, the division into light harvesting (the antenna) and photochemistry (the reaction center) was born.

Arnold had called the photosynthetic unit the 'chlorophyll unit.' Jack Myers (1994) has paid special tribute to Bill Arnold, and given him special credit for this discovery of 1932. However, Arnold (1991) was modest, stating 'Emerson put my name on these papers as co-author (see Emerson and Arnold 1932a, b). I was only an undergraduate student.' We note that he was only one year younger than Emerson: before he received his BS, he had worked for four years with S.J. Barnett (Head of the Physics Department at the University of California at Los Angeles) on the Earth's magnetic field.

Arnold was a discoverer of many phenomena in photosynthesis, and a scientist of few, but clear and simple words; he believed in precision, simplicity and above all brevity. He once told Govindjee 'scientists should be asked to write on stone; then, they will publish less.' Arnold's shortest published sentence is: 'It does.' He also coined the word 'fission' for atomic fission. He believed that 'discoveries are made because we follow our scientific curiosities' (Arnold 1991); he stated that he entered biology under the influence of Robert Emerson; he was earlier a student of Physics/Astronomy at Cal Tech. With these beginnings, Arnold went on to make many discoveries in photosynthesis:

- Earliest measurements, using calorimetry, showing that the minimum quantum requirement for oxygen evolution was not 4, but 8–12 (presented in his 1936 PhD thesis at Harvard, but published only in 1949 (Arnold 1949) because he had earlier convinced himself that the value 4 (of Otto Warburg) must be the correct number (Malkin and Fork 1996).
- The very first concept of the mechanism of excitation energy transfer that was to be the precursor of the current Förster theory (with Robert Oppenheimer; see Knox 1996). This was followed by evidence of excitation energy transfer from phycocyanin to chlorophyll *a* (Arnold and Oppenheimer 1950); he stated (Arnold 1991) that he did this work because Emerson asked him 'to see if the energy absorbed by phycocyanin was transferred to chlorophyll or was phycocyanin doing photosynthesis.'
- After Louis (Lou) N.M. Duysens' thesis (see Govindjee et al. 2003), Arnold and Eleanor S. Meek (1956) were the first to measure excitation energy transfer, using the concept of depolarization of fluorescence.
- Arnold (1991; also see Arnold 1960) wrote, 'One plans an experiment to find something and then finds something else.' For example, Bernard Strehler (1925–2001) and Arnold (1951) planned an experiment to discover 'ATP production by chloroplasts,' but instead discovered 'delayed light emission' that became a non-invasive probe of Photosystem II (Strehler 1996).
- Arnold and Sherwood (1957) discovered thermoluminescence (glow curves) in plants, that turned out to be another powerful probe of Photosystem II. The theory behind its mechanism was later explained by DeVault and one of us (G) in collaboration with Arnold (see DeVault et al. 1983; Vass and Govindjee 1996; Vass 2003).
- The solid-state nature of the primary photochemistry of photosynthesis was established when Arnold and Clayton (1960) observed the first step of photosynthesis (oxidation of the reaction center P) at liquid helium temperature (see Mauzerall 1996).
- Arnold and Azzi (1971) discovered 'electroluminescence' in chloroplasts.

Readers may also consult Herron (1996) for a daughter's perspective; Duysens (1996) for a discussion of Arnold's inspiring experiments; Lavorel (1996) for the importance of luck in Science; and Pearlstein (1996) for his personal reflections. Arnold is clearly one of the founding fathers of a physical basis of photosynthesis.

Contents of Part 3

> 'The physicist Leo Szilard once announced to his friend Hans Bethe that he was thinking of keeping a diary: "I don't intend to publish it: I am merely going to record the facts for the information of God." "Don't you think God knows the facts?" Bethe asked. "Yes," said Szilard. "He knows the facts, but he does not know this version of the facts."'
> – Freeman Dyson, Disturbing the Universe (Preface)

In almost all the papers of the three historical issues of *Photosynthesis Research* celebrating the millennium, the goal was to give authors the leeway to present their 'version of the facts,' in the spirit of Leo Szilard's humorous insight. However, all papers were refereed and edited. As in Parts 1 and 2, most papers are illustrated with photographs of scientists. In alphabetical order, we list below the authors of Part 3, along with the general topic of their papers: James P. Allen (X-ray crystal structure of the reaction center of a photosynthetic bacterium); James Barber (structure and organization of Photosystem II); Carl Bauer (regulation of photosystem synthesis in a photosynthetic bacterium); Derek Bendall (cytochrome *f*); Britton Chance (the 'stop-flow' method); Richard Cogdell, H. Hashimoto and A.T. Gardiner (structures of purple bacterial light-harvesting complexes); William Cramer (structure of cytochrome $b6/f$); Anthony Crofts (the Q cycle); Richard Dilley (localized proton gradients); R. John Ellis (chaperones); Jack Fajer (chlorophyll photochemistry); Petra Fromme and Paul Mathis (structure and function of Photosystem I reaction center); Howard Gest (a tribute to Sam Ruben); Howard Gest and Robert Blankenship (time-line of discoveries in anoxygenic photosynthesis); Ashish Ghosh (the Rabinowitch laboratory);

Govindjee (lists of international conferences, symposia volumes and edited books on photosynthesis); Govindjee and David Krogmann (discoveries in oxygenic photosynthesis); Edith Camm and Beverley Green (the naming of light-harvesting proteins); Roger Hangarter and Howard Gest (pictorial demonstrations in photosynthesis); Günter Hauska (isolation of Cyt *b6/f* complex); Wolfgang Junge (energy coupling and the structure and function of ATP synthase); Anastasios Melis and T. Happe (green algal hydrogen research; a follow-up of a paper by Peter Homann in Part 2); John Olson (the Fenna–Mathews–Olson protein); John Olson and Robert Blankenship (evolution of photosynthesis); Jerry Rosenberg (a tribute to James Franck); Hans Rurainski (the conference at the Airlie House in 1963); Masateru Shin (ferredoxin–NADP reductase); Robert Tabita (carbon dioxide fixation); Sam Wildman, Ann Hirsch, S.J. Kirchanski and Don Spencer (questions on the structure of chloroplasts); Horst Witt (3-D crystals and X-ray structural analysis of Photosystems I and II); Carl Woese (The story of Archea); Tom Wydrzynski (NMR measurements related to Mn changes during oxygen evolution); and Lion Xiong and Richard Sayre (engineering the chloroplast-encoded proteins of *Chlamydomonas*).

Photosynthesis and the legacy of Alfred Nobel

The will of Dr Alfred Nobel (1833–1896) was drawn up on 27 November 1895 and, translated from Swedish, contains a section incorporated in the statutes of the Nobel Foundation, established on 29 June 1900:

> The whole of my remaining realizable estate shall constitute a fund, the interest on which shall be annually distributed in the form of prizes to those who, during the preceding year, shall have conferred the greatest benefit on mankind. . . . one part to the person who shall have made the most important discovery or invention within the field of physics; one part to the person who shall have made the most important chemical discovery or improvement; one part to the person who shall have made the most important discovery within the domain of physiology or medicine; one part to the person who shall have produced in the field of literature the most outstanding work of an idealistic tendency; and one part to the person who shall have done the most or the best work for fraternity between nations, for the abolition or reduction of standing armies and for the holding and promotion of peace congresses. . . . It is my express wish that in awarding the prizes no consideration whatever shall be given to the nationality of the candidates, but that the most worthy shall receive the prize, whether he be a Scandinavian or not.

Few would dispute that this quotation demonstrates remarkable idealism and breadth of vision. For example, at that time, the end of the nineteenth century, its last sentence was considered by some to be unpatriotic, and it met with considerable public criticism. Today, it is clear that explicit exclusion of nationality was essential for the Nobel prizes to acquire their unique status. We suggest that Nobel's reasonable perspective and concern for rigor meant that photosynthesis as the primary, life-sustaining process it is, went unnoticed, or more likely, could reasonably be subsumed into chemistry. After all, Nobel was, himself, a chemist.

Today we might expect photosynthesis to come squarely into any broad and humanitarian world-view such as Nobel's. But if the context of photosynthesis is physiology, it is plant and microbial physiology, not the sort of physiology with which the Karolinska Institute for Medical Research was, and is, concerned. What, precisely, Nobel had in mind under '. . .the domain of physiology or medicine. . .' is a matter for Nobel scholars and historians, but we note that 'physiology' comes first, and its conjunction with 'medicine' is 'or'; not 'and,' as often supposed. We suggest that there are perhaps half a dozen discoveries in photosynthesis that might have 'conferred the greatest benefit on mankind' in the broad domain of physiology.

Let us briefly consider whose work on photosynthesis might have qualified in the early part of the 20th century, especially if the Foundation had interpreted Nobel's will, and his intentions, more widely. Timiriazeff (1843–1920) was a Russian physiologist who measured the action spectrum of photosynthesis and the absorption spectrum of chlorophyll. He concluded that chlorophyll was required for photosynthesis, and made the far-reaching conclusion that absorption of light by chlorophyll causes its redox transformation. In retrospect, we might conclude that Timiriazeff's contributions were at least as deserving of recognition as were the recipients of several prizes in both Chemistry and Physiology or Medicine up until the year of his death. To take another example, Engelmann (1843–1909) demonstrated that photosynthetic oxygen evolution occurs in chloroplasts of the alga *Spirogyra*, and also obtained an

Figure 5A. Photographs of selected Nobel laureates (1915–1965). *Top row* (*from left to right*): Richard Wilstätter (1915, Chemistry); James Franck (1925, Physics); Hans Fischer (1930, Chemistry). *Middle row* (*from left to right*): Otto Warburg (1931, Physiology or Medicine); Paul Karrer (1937, Chemistry); Richard Kuhn (1938, Chemistry). *Bottom row* (*from left to right*): Severo Ochoa (1959, Physiology or Medicine); Melvin Calvin (1961, Chemistry); Robert Woodward (1965, Chemistry).

action spectrum, based on the positively aerotactic behavior of bacteria. Engelmann's was clearly a fundamental discovery in physiology, broadly defined. In 1903, Tswett (1872–1919) invented the technique of chromatography, undoubtedly a major contribution to Chemistry, and used it to separate chlorophylls and carotenoids. F.F. Blackman (1866–1947) showed that photosynthesis is composed of 'light' and 'dark' reactions, which clearly relates to physiology, although not directly of humans. The deep implications of this discovery continued well into the 20th century, and inspired, amongst others, the pioneering work of Emerson and Arnold.

A 'science-in-fiction' play and novel by Djerassi and Hoffman (2001) is based on the supposition that one Nobel Prize in Chemistry might have been awarded posthumously. The play concerns questions of priority in a fundamental discovery for photosynthesis

Figure 5B. Photographs of selected Nobel laureates (1966–1997). *Top row* (*from left to right*): George Porter (1967, Chemistry); Wreyford Norrish (1967, Chemistry); Peter Mitchell (1978, Chemistry). *Middle row* (*from left to right*): Johann Deisenhofer (1988, Chemistry); Hartmut Michel (1988, Chemistry); Robert Huber (1988, Chemistry). *Bottom row* (*from left to right*): Rudolph Marcus (1992, Chemistry); Paul Boyer (1997, Chemistry); John Walker (1997, Chemistry).

and chemistry as a whole, the discovery of oxygen (see also Lane 2002).

One chemical discovery that led directly to at least two Nobel prizes was that of carbon-14 (^{14}C). This radioactive isotope of carbon was used not only to explore the pathway of carbon dioxide fixation in photosynthesis, but also for radiocarbon dating. The latter application was recognized with the 1960 Chemistry prize to Willard Frank Libby, of University of California, Los Angeles, 'for his method to use carbon-14 for age determination in archaeology, geology, geophysics, and other branches of science.' Because of the extraordinarily wide importance of their discovery of ^{14}C, not just for photosynthesis, we imagine that a Chemistry prize to Martin Kamen (1913–2002) and Sam Ruben (1913–1943) would have caused little controversy, and wonder whether the tragic early death of Ruben in 1943 (see Benson 2002; Gest, this issue) may have influenced the outcome of such an obvious nomination, surely one that many chemists must have considered at that time.

We end by showing portraits of some of the Nobel laureates (Figures 5A and B) whose work had direct or indirect relationship to photosynthesis. Appendix B provides another list of Nobel prizes, also related to photosynthesis. Appendix C is an example of a Nobel presentation speech.

Concluding remarks

Our understanding of photosynthesis provides a part of the foundation for large-scale endeavors dedicated to genomic and proteomic approaches, and these will undoubtedly have huge impact on the way in which future photosynthesis research is done (see Vol. 78, No. 3 (2003) of *Photosynthesis Research*, a special issue on 'Proteomics' edited by Robert (Rob) L. Burnap and Willem (Wim) F.J. Vermaas, at http://www.kluweronline.com/issn/0166-8595/current). The first complete, annotated genome sequence of a photosynthetic organism was of the cyanobacterium *Synechocystis* PCC6803 (Kaneko et al. 1996), and the latest is of the purple phototrophic bacterium *Rhodopseudomonas palustris* (Larimer et al. 2004). The first plant genome sequence (of *Arabidopsis thaliana*; for the current status, see http://www.arabidopsis.org/info/agicomplete.jsp) is already transforming plant biology. We suggest that this enormous increase in information will allow novel approaches and discoveries, the significance of which will depend, not only on other new technologies, but on the prior discoveries described in these history issues of *Photosynthesis Research*.

We began this article with Isaac Newton's famous quotation about the privileged position of the scientist who is first to see further than others before him. We end with another quotation from Newton. As great as we believe the achievements described in these history issues to have been, time alone will tell their true significance. We should not forget that even the most synoptic history of a rapidly moving field is, at best, an interim report. We hope future generations of students will remember too, that their view of the world will have had an origin and an evolution, and that their contributions may, if they are fortunate, one day become part of someone else's history. That is both the limit of ambition, and yet the noblest aspiration, for any scientist.

> 'I seem to have been only like a boy playing on the seashore, and diverting myself in now and then finding a smoother pebble or a prettier shell than ordinary, whilst the great ocean of truth lay all undiscovered before me.'
> – Isaac Newton (1642–1727),
> Memoirs of Newton, Vol. 2, Ch. 27, ed. David Brewster (1855)

Acknowledgments

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Figure 6. John F. Allen. Photo by Sarah Allen.

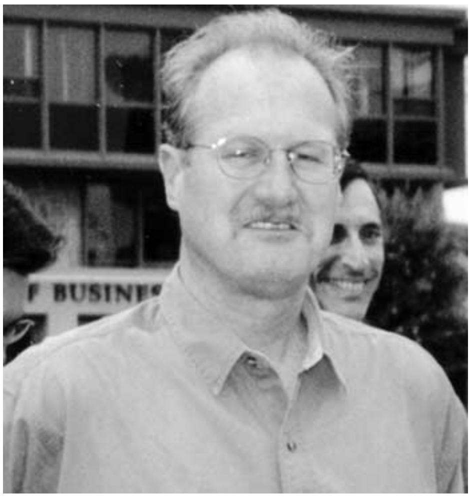
Figure 7. J. Thomas Beatty at the 2003 Gordon Conference on Photosynthesis. Photo by Govindjee.

John F. Allen and J. Thomas Beatty in Figures 6 and 7, respectively.

Appendix A. A 1981 newsletter

Restricted distribution (it was distributed to about 50 researchers; the result remains to be published).

HISTORY OF PHOTOSYNTHESIS NEWSLETTER
Vol. 0; No. 1; October, 1981 Issue
Present correspondent: Govindjee, Department of Botany, University of Illinois, 289 Morrill Hall, 505 S. Goodwin Avenue, Urbana, IL 61801, USA
A mimeographed newsletter on 'History of Photosynthesis' will appear at irregular intervals. To receive a copy, you are required to provide any historical note(s) on photosynthesis research before 1961, and on scientists who have worked in this area, based on authentic sources (newspaper clippings, research papers, letters, your notes, etc.) or anecdotes (based on direct experience, your 'grapevine' stories picked up from your colleagues, teachers, students, etc., or at parties).

I would like to hear anecdotes or obtain historical notes on the reasons why the late Professor Otto Warburg continued to obtain high quantum yield (1/4) of O_2 evolution in photosynthesis. This topic is planned for the Vol. 1 of our newsletter.

A historical note on Emerson enhancement effect

The first published record, to my knowledge, of Emerson enhancement effect in O_2 evolution was an abstract at a National Academy of Science meeting, in 1956 (R. Emerson, R. Chalmers, C. Cederstrand, and M. Brody, Science, 123 (3199) 20 April 1956, p 673). It states, 'If the low-intensity beam of measured energy is supplemented by a more intense (unmeasured) beam, then the efficiency of the small increment of measured light remains nearly constant out to 685 mμ, even at a temperature of 26 °C. [Note: the abstract had mentioned earlier that the efficiency as a function of wavelength (of the measured light) dropped by 50% between 650 and 685 nm at 20 °C.] The supplementary beam is effective whether it is made up of a mixture of longer and shorter wavelengths, or whether it includes only red light of wavelengths longer than 650 mμ' – Supplied by correspondent Govindjee on 26 October 1981.

Birthdays of distinguished colleagues

November 4: Cornelis Bernardus van Niel
November 14: Daniel Israel Arnon
December 6: William Archibald Arnold
December 13: Charles Stacy French
April 8: Melvin Calvin
April 22: Lawrence Rogers Blinks
July 10: Jack Edgar Myers
July 24: Britton Chance
August 27: Martin David Kamen
Congratulations and many happy returns.

Appendix B. Some Nobel prizes relevant to photosynthesis

1915 (Chemistry): Richard Martin Willstätter (1872–1942); (Germany) (Munich University, Munich, Germany) '*for his researches on plant pigments, especially chlorophyll*.'

1930 (Chemistry): Hans Fischer (1881–1945); (Germany) (Technische Hochschule (Institute of Technology) Munich, Germany) '*for his researches into the constitution of haemin and chlorophyll and especially for his synthesis of haemin*.'

1931 (Physiology or Medicine): Otto Heinrich Warburg (1883–1970); (Germany) (Kaiser-Wilhelm-Institut (now Max-Planck-Institut) für Biologie, Berlin-Dahlem, Germany) '*for his discovery of the nature and mode of action of the respiratory enzyme*.'

1937 (Chemistry): Walter Norman Haworth (1883–1950); (UK) (Birmingham University, Birmingham, UK) '*for his investigations on carbohydrates and vitamin C*,' Paul Karrer (1889–1971); (Switzerland) (University of Zurich, Zurich, Switzerland) '*for his investigations on carotenoids, flavins and vitamins A and B2*.'

1937 (Physiology or Medicine): Albert von Szent-Györgyi Nagyrapolt (1893–1986); (Hungary) (Szeged University, Szeged, Hungary) '*for his discoveries in connection with the biological combustion processes, with special reference to vitamin C and the catalysis of fumaric acid*.'

1938 (Chemistry): Richard Kuhn (1900–1967); (Germany, born in Vienna, Austria) (University of Heidelberg; Kaiser-Wilhelm-Institut (now Max-Planck-Institut) für Medizinische Forschung, Heidelberg, Germany) '*for his work on carotenoids and vitamins*.' (Caused by the authorities of his country to decline the award but later received the diploma and the medal.)

1953 (Physiology or Medicine): Hans Adolf Krebs (1900–1981); (UK, born in Hildesheim, Germany) (Sheffield University, Sheffield, UK) '*for his discovery of the citric acid cycle*'; Fritz Albert Lipmann (1899–1986) (USA, born in Koenigsberg, then

Germany) (Harvard Medical School; Massachusetts General Hospital, Boston, Massachusetts, USA) '*for his discovery of co-enzyme A and its importance for intermediary metabolism*.'

1961 (Chemistry): Melvin Calvin (1911–1997); (USA) (University of California, Berkeley, California, USA) '*for his research on the carbon dioxide assimilation in plants*.'

1967 (Chemistry): Manfred Eigen (Germany) (Max-Planck-Institut für Physikalische Chemie, Göttingen, Germany); Ronald George Wreyford Norrish (1897–1978); (UK) (Institute of Physical Chemistry, Cambridge, UK); George Porter (1920–2002) (UK) (Royal Institution of Great Britain, London, UK) '*for their studies of extremely fast chemical reactions, effected by disturbing the equlibrium by means of very short pulses of energy*.'

1978 (Chemistry): Peter D. Mitchell (1920–1992); (UK) (Glynn Research Laboratories, Bodmin, UK) '*for his contribution to the understanding of biological energy transfer through the formulation of the chemiosmotic theory*.'

1988 (Chemistry): Johann Deisenhofer (Germany, born in Aarhus, Denmark) (Howard Hughes Medical Institute, Chevy Chase, Maryland, USA; University of Texas Southwestern Medical Center at Dallas, Dallas, Texas, USA); Robert Huber (Germany) (Max-Planck-Institut für Biochemie, Martinsried, Germany); Hartmut Michel (Germany) (Max-Planck-Institut für Biophysik, Frankfurt-am-Main, Germany) '*for the determination of the three-dimensional structure of a photosynthetic reaction centre*.'

1992 (Chemistry): Rudolph A. Marcus (USA, born in Montreal, Canada) (California Institute of Technology Pasadena, California, USA) '*for his contributions to the theory of electron transfer reactions in chemical systems*.'

1997 (Chemistry): Paul D. Boyer (USA) (University of California, Los Angeles, California, USA); John E. Walker (UK) (MRC Laboratory of Molecular Biology, Cambridge, UK) '*for their elucidation of the enzymatic mechanism underlying the synthesis of adenosine triphosphate (ATP)*'; Jens C. Skou (Denmark) (Aarhus University, Aarhus, Denmark) '*for the first discovery of an ion-transporting enzyme, Na+, K+-ATPase*.'

1999 (Chemistry): Ahmed H. Zewail (Egypt and USA) (California Institute of Technology, Pasadena, California, USA) '*for his studies of the transition states of chemical reactions using femtosecond spectroscopy*.'

Appendix C. A Nobel presentation speech

As an exercise in clarity, accuracy, and eloquence, we present extracts from the address by Lars Ernster at the awards ceremony of 1978, From 'Nobel Lectures,' Chemistry 1971–1980, World Scientific Publishing, Singapore: 'The Nobel Prize in Chemistry 1978, presentation speech by Professor Lars Ernster of the Royal Academy of Sciences (*Translation from the Swedish text*):

Your Majesties, Your Royal Highnesses, Ladies and Gentlemen, Green plants and other photosynthetic organisms derive energy directly from sunlight – the ultimate source of energy for all life on earth – and utilize this energy to convert carbon dioxide and water into organic compounds. Other organisms, including all animals and many bacteria, are dependent for their existence on organic compounds which they take up as nutrients from their environment. Through a process called cell respiration these compounds are oxidized by atmospheric oxygen to carbon dioxide and water with a concomitant release of energy.

Both respiration and photosynthesis involve a series of oxidation–reduction (or electron-transport) reactions in which energy is liberated and utilized for the synthesis of adenosine triphosphate (ATP) from adenosine diphosphate (ADP) and inorganic phosphate. These processes are usually called oxidative and photosynthetic phosphorylation. Both processes are typically associated with cellular membranes. In higher cells, they take place in special, membrane-enclosed organelles, called mitochondria and chloroplasts, while, in bacteria, both processes are associated with the cell membrane.

ATP serves as a universal energy currency for living cells. This compound is split by a variety of specific enzymes and the energy released is used for various energy-requiring processes. The regeneration of ATP by way of oxidative and photosynthetic phosphorylation thus plays a fundamental role in the energy supply of living cells.

The above concepts had been broadly outlined by about the middle of the 1950s, but the exact mechanisms by which electron transport is coupled to ATP synthesis in oxidative and photosynthetic phosphorylation remained unknown. Many hypotheses were formulated, most of which postulated the occurrence of 'energy-rich' chemical compounds of more or less well-defined structures as intermediates between the electron-transport and ATP-synthesizing systems. Despite intensive efforts in many laboratories, however, no experimental evidence could be obtained for these hypotheses. In addition, these hypotheses did not provide a rational explanation for the need for a membrane in oxidative and photosynthetic phosphorylation.

At this stage, in 1961, Peter Mitchell put forward his chemiosmotic hypothesis. The basic idea of this hypothesis is that the enzymes of the electron-transport and ATP-synthesizing systems are localized in the membrane with a well-defined orientation and are functionally linked to a vectorial transfer of positively charged hydrogen ions, or protons, across the membrane. Thus, electron transport will give rise to an electrochemical proton gradient across the membrane which can serve as a driving force for ATP synthesis. A requisite for the establishment of a proton gradient is, of course, that the membrane itself is impermeable to protons, which explains the need for an intact membrane structure in oxidative and photosynthetic phosphorylation.

The chemiosmotic hypothesis was received with reservation by many workers in the field which is, in a way, understandable, since it was unorthodox, fairly provocative, and based on little experimental evidence. Perhaps due to just these features, however, the hypothesis stimulated a great deal of activity; and it can be stated without exaggeration that during the last decade the chemiosmotic hypothesis has been the dominating issue in the field of bioenergetics both in the literature, at scientific meetings and, not least, in laboratories all over the world. As a result, a great deal of experimental data has been accumulated, both from Mitchell's own laboratory – there mostly in collaboration with Dr Jennifer Moyle – and from other places, which strongly supports the hypothesis. In fact, the basic postulates of the chemiosmotic hypothesis are today generally regarded as experimentally proven, thus making it a fundamental theory of cellular bioenergetics.

Dr. Mitchell,

With ingenuity, courage and persistence you have innovated one of the classical fields of biochemistry. Your chemiosmotic theory has meant a breakthrough that has opened up new insights into the fundamental problems of bioenergetics. The details may need completion and adjustment; but the edifice you have raised will stand.

It is my great pleasure and privilege to convey to you the congratulations of the Royal Swedish Academy of Sciences on your outstanding achievements and to ask you to receive the Nobel Prize for Chemistry of 1978 from the hands of His Majesty the King.

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