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Minireview

Time line of discoveries: anoxygenic bacterial photosynthesis

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Abstract

A time line of important research relating to anoxygenic photosynthetic organisms is presented. The time line includes discoveries of organisms, metabolic capabilities, molecular complexes and genetic systems. It also pinpoints important milestones in our understanding of the structure, function, organization, assembly and regulation of photosynthetic complexes.

Abbreviations: BChl – bacteriochlorophyll; Bph – bacteriopheopytin; EPR – electron paramagnetic resonance; GTA – gene transfer agent; P – photoactive pigment; RC – reaction center; TCA – tricarboxylic acid cycle

Introduction

Why list scientific discoveries in a time line? There are at least four answers. A time line is a condensed history showing how understanding of a particular problem or science blossoms from its ‘roots.’ Secondly, it reveals, more or less at a glance, how basic discoveries lead to new findings in ever-increasing detail. Thirdly, it should remind us that at many stages of a time line, scientists must have erroneously believed that ‘breakthroughs’ they experienced during their most productive years represented advanced understandings that would not be greatly altered by subsequent research. Fourthly, it instills deservedly greater respect for the efforts and insights of our predecessors. Although their names are frequently not mentioned, their fundamental discoveries are usually discussed at the beginning of seminars, before the speaker plunges into molecular and other details. Interested readers are also referred to a general timeline of photosynthesis by Huzisige and Ke (1993). A time line of discoveries in oxygenic photosynthesis is presented by Govindjee and David Krogmann (this issue).

In the time line, names of organisms are given as they appeared in original publications. Appendix A lists alternative names of some anoxyphototrophs that have been prominent in research over the past 50 years. Some important events in the general history of bioenergetics research are also included in the time line to serve as ‘mileposts.’ References are divided into two sections. Appendix B contains general references, which are primarily secondary sources and are included as an entry to the primary literature. The section labeled as ‘References’ refers to specific landmark papers that are cited in the text. Not all entries in the time line have cited references, but a combination of the cited and general references should permit the interested reader to find primary reports for any of the milestones listed in the time line.

As requested by the editors, a photograph of the authors is shown in Figure 1.

Beginnings (1873–1876)

Sir E. Ray Lankester (1847–1929) was a prominent biologist who did research on a wide variety of

Figure 1. Photograph of the authors: Howard Gest (left), Robert Blankenship (right). Photo taken at the Arizona State University, Tempe, Arizona, in February 2002.

organisms, from protozoa to mammals. Lankester made the first observations of purple photosynthetic bacteria in enrichment cultures, associated with the decay of organic matter (e.g., dead worms) in water. In 1876 he noted red-colored 'crusts' resembling the colored films that form on the sides of a bottle of Burgundy wine. Lankester designated the pigmented bacteria as '*Bacterium rubescens*' and made preliminary attempts to characterize the pigment, which he called 'bacteriopurpurin.'

1883

Theodor W. Engelmann (1843–1909) reported that in a dispersed spectrum, cells of the purple '*Bacterium photometricum*' accumulated at specific wavelengths, including a band in the infrared. Failure to detect production of O_2 led him to doubt that the organism was truly photosynthetic, at least as the process was then defined (Engelmann 1883). Subsequent research by Engelmann in 1888 led him to conclude that 'bacteriopurpurin is a true chlorophyll.' S. Winogradsky later identified Engelmann's culture as a mixture of *Chromatium* species (Winogradsky 1888).

1884

Dr Charles MacMunn, an Irish physician, discovers cytochromes in a variety of animal tissues, but eminent chemists believe he is merely observing breakdown products of hemoglobin (see 1925).

1887

Erwin von Esmarch (1855–1915), a medical bacteriologist, isolates a spiral-shaped bacterium from a dry mass, originating from a sample of Berlin tap-water in which a dead mouse had decayed. He grew the bacterium as a heterotroph and named it *Spirillum rubrum*. In 1907, Molisch concluded that it was a nonsulfur purple photosynthetic bacterium and renamed the bacterium *Rhodospirillum rubrum* (see 1907).

1888

S. Winogradsky, discoverer of chemoautotrophy, describes purple sulfur bacteria (including *Chromatium*) that develop on the illuminated side of a 'Winogradsky column.' To prepare the column, a large glass cylinder is packed with mud mixed with organic matter, $CaCO_3$, $CaSO_4$, and overlain with lake, pond or ditch water. The column is incubated in a north window, where it receives adequate illumination (Winogradsky 1888).

1907

Hans Molisch (1856–1937) pioneered in isolating and describing a number of species of nonsulfur purple bacteria in pure culture, including *Rhodonostoc capsulatum*, later renamed *Rhodopseudomonas capsulatus* (Molisch 1907). He demonstrated conclusively that O_2 is not produced by such organisms, and also discovered the photoheterotrophic growth mode. Molisch separated two pigments from purple bacteria, retaining the name 'bacteriopurpurin' for the red pigment. He designated the green pigment 'bacteriochlorin.'

1912

G.A. Nadson describes the green bacterium *Chlorobium limicola*, which was later isolated and studied in pure culture by van Niel (1932).

1925

David Keilin, in Cambridge, UK, rediscovers cytochromes. Keilin spent his entire career working on cytochromes, examining their redox behavior and distribution in a wide variety of cell types.

1929

K. Lohmann, C.H. Fiske and Y. Subbarow isolate and characterize ATP.

1931

Keita Shibata publishes ‘Carbon and Nitrogen Assimilation’ (1931). Shibata’s theory of photosynthesis assumed the photodissociation of water and he also proposed a general interpretation of the metabolism of anoxygenic photosynthetic bacteria that was very similar to Cornelis B. van Niel’s scheme. It is very likely that Shibata and van Niel developed their hypotheses independently.

1932

From his studies on purple sulfur bacteria, van Niel (1897–1985) concludes that:

> For the process of photosynthetic carbon dioxide assimilation (or reduction) we may then say that the reaction
>
> $$CO_2 + 2H_2A = CH_2O + H_2O + 2A$$
>
> requires various and special compounds of hydrogen for various and special organisms. From which it follows that the photosynthetic activity of the chlorophyll-bearing organisms, in which H_2A represents H_2O, represents only one very special instance of a group of possible photosynthetic activities. This would mean that the purple sulphur bacteria can use H_2S as a hydrogen donor, but cannot use H_2O. (van Niel 1932).

Robert Emerson and William Arnold publish two landmark papers in photosynthesis, demonstrating that most chlorophylls do not directly carry out photosynthesis. They proposed the concept of the photosynthetic unit, which consists of all the pigments that cooperate to carry out photosynthesis and the enzymes that do the actual chemistry. While these experiments were carried out with the oxygen-evolving green alga *Chlorella*, the concept of the photosynthetic unit is essential for the later development of the concept of separable antenna and reaction center complexes in both oxygenic and anoxygenic photosynthetic organisms (Emerson and Arnold 1932a, b; also see Clayton 2002).

1933

F.M. Muller demonstrates that purple sulfur bacteria can grow photosynthetically under anaerobic conditions in media containing simple organic carbon sources in the absence of oxidizable inorganic sulfur compounds. Growth was accompanied by production or utilization of CO_2, depending on the ‘redox level’ of the organic substrate. With lactate, pyruvate, succinate or malate, there was a net production of CO_2; with butyrate, growth required addition of CO_2.

1936–1938

Starting in 1936, Harland Wood and colleagues obtain evidence showing that heterotrophic propionic acid bacteria utilize CO_2 for formation of C_4 dicarboxylic acids (via $C_1 + C_3$ condensation). This was the first evidence that incorporation of CO_2 into organic compounds was not limited to photosynthetic or chemosynthetic autotrophs. Wood’s research paved the way for later characterization of carbon metabolism in C_4 plants (sugar cane, maize, etc.).

Hans A. Krebs describes the tricarboxylic acid cycle, otherwise known as the citric acid cycle or the Krebs cycle. This is the primary metabolic machinery that furnishes the reducing power for energy-yielding respiration of many kinds of cells.

Otto Warburg and W. Christian discover FAD (Flavin adenine dinucleotide) and explain the basic roles of NAD and NADP in metabolism.

1940

Samuel Ruben and Martin Kamen discover ^{14}C. In earlier (frustrating) attempts to trace the path of carbon in photosynthesis, they used short-lived ^{11}C (see H. Gest, this issue). The use of ^{14}C as a tracer played a major role in elucidation of metabolic mechanisms (including the Calvin/Benson cycle) and also led to the ^{14}C radiocarbon method for dating archaeological and historical artefacts. See also Benson (2002).

1944

C.B. van Niel publishes an extensive study on characteristics (general physiology and pigments) of nonsulfur purple species that later became major experimental organisms for exploring bacterial photosynthesis, including *Rps. capsulatus*, *Rhodopseudomonas sphaeroides*, and *Rsp. rubrum* (van Niel 1944).

1949

H. Gest and M.D. Kamen discover light-dependent production of H_2 and N_2 fixation by *Rsp. rubrum.* Subsequent studies revealed that many anoxygenic phototrophs have N_2 fixation capacity (Gest and Kamen 1949; Kamen and Gest 1949), and that *Rsp. rubrum* can use H_2 and CO_2 (as sole carbon source) for photoautotrophic growth in a synthetic medium (Ormerod et al. 1961). Both light-dependent H_2 formation and N_2 reduction were found to be catalyzed by the same enzyme complex, nitrogenase.

1952

In his doctoral degree thesis, L.N.M. Duysens describes a powerful approach to understanding the effects caused by illumination of photosynthetic cells, difference spectroscopy (see a photograph of the cover page of this classical thesis in Govindjee et al. 2003; see pp. 6 and 7). His experiments with *Rsp. rubrum* revealed that one prominent effect corresponded to 'photo-oxidation' of a cytochrome (Duysens 1952). In his thesis Duysens discovered absorption changes in a fraction of BChl, and named it 'P' for pigment, for example, P870.

1953

L.P. Vernon discovers the presence of large quantities of cytochrome *c* in *Rsp. rubrum* cells grown photosynthetically under anaerobic conditions.

Helge Larsen's PhD thesis on photosynthetic green sulfur bacteria describes conditions for optimal growth of *C. limicola and C. thiosulfatophilum*, and compares their distinguishing characteristics. Quantum yield measurements with various inorganic electron donors indicated a minimum quantum number of about 8.

1954

J. Postgate observes cytochrome in the strict anaerobe *Desulfovibrio desulfuricans*. This finding led to research of great import for understanding the energy metabolism of anaerobic organisms that use inorganic terminal oxidants such as sulfate.

Albert Frenkel discovers that membrane fragments obtained by disruption of *Rsp. rubrum* cells (see 1959) can rapidly phosphorylate ADP when illuminated anaerobically in the absence of electron donors or acceptors (Frenkel 1954).

1957

G. Cohen-Bazire, W.R. Sistrom, and R.Y. Stanier systematically investigate the overall effects of light and O_2 on synthesis of BChl and carotenoids in *Rps. sphaeroides* and *Rsp. rubrum.* This work provided basic guidelines for later biochemical and molecular biological analysis of regulatory mechanisms that control photopigment production in purple bacteria (Cohen-Bazire et al. 1957).

1959

Prior to the 1959 report of Tuttle and Gest (1959), the photopigments of purple photosynthetic bacteria were believed to be localized in small intracellular 'organelles' called 'chromatophores,' as first demonstrated by Pardee et al. (1952). They found, however, that lysis of *Rsp. rubrum* cells did not release free chromatophores. Lysis yielded pigmented membranes capable of photophosphorylation of ADP. It became evident that '*in vivo* the photosynthetic apparatus of the photosynthetic bacteria is associated with the cytoplasmic membrane and/or membranous extensions in the cytoplasm of the cell.'

A.A. Krasnovsky proposes that the pigments in green photosynthetic bacteria are organized as oligomeric complexes (Krasnovsky and Pakshina 1959). This organizational model is finally confirmed in the 1980s (Smith et al. 1983).

R. Clinton Fuller and Martin Gibbs show that purple bacteria contain the Calvin–Benson cycle of carbon fixation (Fuller and Gibbs 1959).

1960

Clayton and Smith report on the *Rps. sphaeroides* blue-green mutant R-26, which became a preferred strain for research in many biophysical laboratories and the source of the reaction center preparations used for many spectroscopic and structural studies

(Clayton and Smith 1960). For more details, see Clayton (2002).

1962

L.E. Mortenson and colleagues isolate and describe a low redox potential Fe protein obtained from extracts of the anaerobe *Clostridium pasteurianum*, and name it ferredoxin. The protein is required as an electron carrier in N_2 fixation and in the conversion of pyruvate to acetyl $CoA + CO_2 + H_2$. Various ferredoxins were soon recognized as important redox catalysts in photosynthetic and other kinds of metabolic processes. Historical aspects are discussed in Mortenson (1963) and Lovenberg (1974).

John Olson discovers the bacteriochlorophyll *a* antenna protein, later renamed as the FMO (Fenna: Matthews: Olson) protein in green sulfur bacteria (Olson and Romano 1962). See also Olson, this issue.

1963

W.R. Sistrom, B.M. Ohlsson and J. Crounce isolate the first mutant with a defective photosystem. The mutant PM-8 was found among the survivors of ultraviolet light-irradiated cells (Sistrom et al. 1963). It showed no gross changes in photopigment synthesis, was able to grow under semi-aerobic conditions, but could not grow anaerobically with light as the energy source. PM-8 exhibited none of the reversible light-induced absorbancy changes detectable in the wild-type parental strain. Later research showed that membranes of the mutant lacked three protein components associated with reaction center BChl.

Wim Vredenberg and L.N.M. Duysens analyze fluorescence in *Rps. rubrum* and propose that energy transfer in photosynthetic bacteria can take place from one photosynthetic unit to the next, giving rise to the concept of 'puddle' and 'lake' organization of antenna systems (Vredenberg and Duysens 1963).

The first international symposium on bacterial photosynthesis was held in Yellow Springs, Ohio. Investigators from a number of countries met to exchange information at this informal meeting sponsored by the C.F. Kettering Foundation. The proceedings of the meeting were published in 'Bacterial Photosynthesis,' edited by H. Gest, L.P. Vernon and A. San Pietro, Antioch Press, Yellow Springs, Ohio, 1963. The 77 participants in the meeting included almost all of the leading investigators of bacterial photosynthesis, as well as a number of prominent researchers of oxygenic photosynthesis. Also see Vernon (2003).

R.K. Clayton proposes the name 'reaction center' to describe the complex that catalyzes light-driven photosynthetic electron transfer. Early efforts to isolate this complex were carried out by Clayton by photodegradation or chemical oxidation of the antenna pigments, leaving behind the more robust reaction center (Clayton 1963). See also Clayton (2002).

C. Sybesma and J. Olson carry out the first quantitative studies of energy transfer efficiency in green sulfur bacteria (Sybesma and Olson 1963).

1964

G. Cohen-Bazire and coworkers describe the unique structures observed in electron micrographs of green sulfur bacteria, and refer to them as '*chlorobium vesicles*,' later designated as 'chlorosomes' (Cohen Bazire et al. 1964).

1966

M.C.W. Evans, B.B. Buchanan and D.I. Arnon propose a new CO_2 reduction cycle to account for photoautotrophy in *Chlorobium* (Evans et al. 1966). Accordingly, two ferredoxin-linked carboxylation reactions facilitate reversal of reactions of the tricarboxylic acid (TCA) cycle, permitting conversion of CO_2 to acetyl-CoA. In 1966, evidence for operation of the 'reductive TCA cycle' was incomplete. Subsequent research, notably by Sirevåg (1995), provided the missing evidence. See also Ormerod (2003).

Don DeVault and Britton Chance report the temperature-independent photooxidation of cytochromes in *Chromatium vinosum*, the first evidence for quantum mechanical tunneling processes in any biological system (DeVault and Chance 1966).

Drews and Giesbrecht (1966) publish a description of *Rhodopseudomonas viridis*, which later was used as the source of material to obtain reaction center crystals to solve the 3D structure (see 1984).

1968

D.W. Reed and R.K. Clayton report the isolation of a photosynthetic reaction center complex from *Rps. sphaeroides* (Reed and Clayton 1968).

W. Parson uses kinetic spectroscopy on chromatophore membranes of *C. vinosum* to establish that P870 oxidation is the primary reaction in bacterial photosynthesis, and that a cytochrome is oxidized as $P870^+$ is rereduced (Parson 1968). See also Parson (2003).

1969

J.B. Jackson and A. Crofts utilize potassium diffusion potentials to calibrate the carotenoid bandshift as a measure of membrane electrical potential (Jackson and Crofts 1969).

1970

A. Borisov and V. Godik determine fluorescence lifetime of bacteriochlorophyll in purple bacterial membranes (Borisov and Godik 1970). See also Borisov (2003).

1971

June Lascelles and David Wertlieb describe mutants of *Rps. sphaeroides* that produced large amounts of BChl and carotenoids under highly aerobic conditions in darkness (Lascelles and Wertleib 1971). They concluded that 'the insensitivity of the mutants to O_2 repression is due to defects in the regulatory system which controls formation of the enzymes concerned in pigment synthesis.'

R.C. Fuller and coworkers report highly enriched, photochemically active membrane preparation from green sulfur bacteria (Fowler et al. 1971).

George Feher reports extensive characterization of the composition and properties of the *Rps. sphaeroides R-26* reaction center complex (Feher 1971).

1972

Les Dutton and coworkers discover the T_0 spin-polarized triplet EPR signal from photosynthetic bacteria (Dutton et al. 1972). M. Thurnauer, J.J. Katz and J. Norris, later in 1975, explain the spin polarization in terms of the radical pair theory, which establishes that the electronic state that precedes electron transfer is an excited singlet state (Thurnauer et al. 1975).

Oelze and Drews suggest adoption of the term 'intracytoplasmic membrane' to describe the invaginated membrane system that houses the photosynthetic apparatus in purple bacteria (Oelze and Drews 1972). Intracytoplasmic membrane had been used earlier by Marr and co-workers to describe the structures in which the respiratory enzymes of *Azotobacter agilis* (Pangborn et al. 1962) and the BChl of *Rsp. rubrum* (Holt and Marr 1965) are localized. See also Drews and Niederman (2002).

1973

Colin Wraight and R. Clayton determine the absolute quantum yield of photochemistry in isolated reaction centers from purple bacteria to be 1.0 (Wraight and Clayton 1973).

1974

Barry Marrs discovers a genetic recombination system in *Rps. capsulata* (Marrs 1974). Gene transfer is mediated by a 'bacteriophage-like' entity called 'gene transfer agent' (GTA). GTA later proved to be very useful for mapping the location and order of photosynthesis genes. See also Marrs (2002).

B.K. Pierson and R.W. Castenholz report on a 'phototrophic, gliding, filamentous bacterium of hot springs, *Chloroflexus aurantiacus*.' This bacterium is the most thermophilic of known anoxyphototrophs. Some strains can grow at 70 °C (Pierson and Castenholz 1974).

1975

William Parson and coworkers observe the optical transients P_F and P_R states in reaction centers from purple bacteria using nanosecond optical spectroscopy. These states are later identified as the charge-separated state $P870^+$ BPh^- and the triplet state of P870, respectively (Parson et al. 1975). See also Parson (2003).

First picosecond spectroscopic studies on reaction centers from purple bacteria are carried out by Parson and coworkers and independently by Dutton, Rentzepis and colleagues. These studies establish that bacteriopheophytin is an early electron acceptor (Kaufmann et al. 1975; Rockley et al. 1975). See also Parson (2003).

R. Fenna and B. Matthews determine the X-ray structure of the bacteriochlorophyll *a* protein, now known as the Fenna–Matthews–Olson or FMO protein, using protein provided by J. Olson. This was the first X-ray structure of a photosynthetic pigment-protein (Fenna and Matthews 1975). See also Olson, this issue.

Extraction and reconstitution experiments by Melvin Okamura, George Feher and coworkers show that ubiquinone is the first stable electron acceptor in reaction centers from *Rps. sphaeroides* (Okamura et al. 1975).

E. Broda publishes 'The Evolution of the Bioenergetic Processes' (Broda 1975). His analysis considered bioenergetic mechanisms in all forms of life, and the literature coverage was extensive. Broda's 'conversion hypothesis' proposed that many aerobic non-photosynthetic prokaryotes descended from purple photosynthetic bacteria and that 'membrane bound photosynthetic electron flow chains were converted to respiratory chains.'

1976

Barry Marrs and coworkers clones the photosynthesis gene cluster using illegitimate recombination between an R plasmid and the chromosome of *Rps. capsulatus* (Yen and Marrs 1976). See also Marrs (2003).

1977

Colin Wraight and André Vermeglio independently discover the two electron gate in reaction centers from *Rps. sphaeroides* (Verméglio 1977; Wraight 1977). See also Verméglio (2002).

T. Monger and W. Parson deduce elements of the membrane organization of antenna complexes in *Rps. sphaeroides* from triplet quenching experiments (Monger and Parson 1977).

1978

K. Sato and K. Harashima report the presence of BChl *a* in certain marine aerobic heterotrophic bacteria that are unable to grow anaerobically with light as the energy source. From subsequent research it appears that such organisms can use light as a supplementary energy source under certain conditions; see Harashima et al. (1989). More recently, organisms of this kind have been designated as 'aerobic anoxygenic phototrophic bacteria' (Beatty 2002), and found to make up a significant portion of the marine microbial community in some ocean surface locations (Kolber et al. 2000).

Andrew Staehelin and coworkers carry out freeze fracture electron microscopic analysis of chlorosomes from *C. aurantiacus* and propose a detailed structural model (Staehelin et al. 1978).

V. Shuvalov and coworkers identify bacteriochlorophyll as the first electron acceptor in purple bacterial photosynthesis (Shuvalov et al. 1978).

1979

T. Swarthoff and J. Amesz prepare a highly enriched reaction center particle from the green sulfur bacterium *Prosthecochloris aestuarii* (Swarthoff and Amesz 1979).

1981

H. Zuber and coworkers determine the complete protein sequence of an LH1 (light-harvesting) antenna protein from *Rsp. rubrum* (Brunisholz et al. 1981).

1983

JoAnn Williams and coworkers determine the gene sequence for reaction center proteins from *Rb. sphaeroides* (Williams et al. 1983).

H. Gest and J. Favinger isolate *Heliobacterium chlorum*, the first representative of the Gram positive heliobacteria family (Gest and Favinger 1983). The heliobacteria contain a novel form of BChl (BChl *g*) that is closely related to chlorophyll *a*. Heliobacteria are also distinctive in that the reaction center is of the Photosystem I type and its protein moiety consists of a single homodimeric polypeptide (see 1992–1993).

Beverly Pierson and Philip Thornber prepare reaction centers from the green filamentous bacterium *C. aurantiacus* (Pierson and Thornber 1983).

1984

John Hearst's research group publishes the nucleotide sequence of the reaction center and LH1 structural genes of *Rhodobacter capsulatus* (Youvan et al. 1984). This work gave clues about the membrane structure (i.e., transmembrane segments) and similarities to reaction center apoproteins of plants (Hearst and Sauer 1984).

Johann Deisenhofer and colleagues report electron density and chromophore structure of the reaction center complex from *Rps. viridis* (Deisenhofer et al. 1984). The structure of the complete protein complex is published shortly thereafter (Deisenhofer et al. 1985). This is the first structure at atomic (3 Å) resolution of a protein complex from a biological membrane. See also Allen (2004).

Michael Madigan isolates the 'mildly thermophilic' *Thermochromatium tepidum*, whose optimal growth temperature is 50 °C. This bacterium contains a novel LHI photopigment complex that absorbs maximally near 920 nm (Madigan 1984). See also Madigan (2003).

1985

R.C. Fuller and coworkers identify reaction center from *H. chlorum* and establish that the primary donor is BChl *g* absorbing at 800 nm (Fuller et al. 1985). Further work establishes that the reaction center is of Type I (Prince et al. 1985).

1987

Douglas Youvan and E. Bylina construct the first site-directed mutants of bacterial reaction centers (Bylina and Youvan 1987).

George Feher and colleagues crystallize the reaction center of *Rb. sphaeroides* R-26 and determine its structure (Allen et al. 1987). See also Allen, this issue.

1988

J. Deisenhofer, R. Huber and H. Michel awarded the Nobel Prize in Chemistry for determination of the structure of the photosynthetic reaction center, the first integral membrane protein to have its structure determined at high resolution.

1989

J. Trost and R. Blankenship prepare reaction centers from *Heliobacillus mobilis*. The purified complex contains only a single type of polypeptide, which later work establishes to be a protein homodimer (Trost and Blankenship 1989).

Paddock et al. (1989) propose proton donors to Q_B in reaction centers from *Rb. sphaeroides*. Subsequent work leads to the outline of a proton pathway (Ädelroth et al. 2001).

1992–1993

Gene sequence of reaction center proteins was obtained for *C. limicola* and *H. mobilis*, establishing that these reaction centers are a homodimer of two identical core proteins (Büttner et al. 1992; Liebl et al. 1993).

1993

F. Widdel and coworkers discover photoautotrophic growth of purple bacteria on CO_2 with Fe^{2+} as the electron donor (Widdel et al. 1993) This growth mode has significant implications for hypotheses of early life on Earth, and could explain the deposition of banded-iron formations in an assumed anoxic biosphere in Archean times.

1994

Carl Bauer and coworkers discover photoactic behavior of *Rhodospirillum centenum*. Colonies of the bacterium on agar move toward a light source whose spectrum overlaps the *in vivo* IR absorbancy bands of BChl (positive phototaxis) (Ragatz et al. 1994). Visible light that includes the 590 nm band of BChl and absorbancy maxima of carotenoids (475–550 nm) causes negative phototaxis.

C. Bauer's research group publishes a detailed mutational analysis of BChl biosynthesis genes that later proved to be important in identifying chlorophyll biosynthesis genes of cyanobacteria and plants (Bollivar et al. 1994). See also Bauer (this issue).

1995

Richard Cogdell and colleagues determine the X-ray crystal structure of the LH2 antenna complex from *Rhodopseudomonas acidophila* (McDermott et al. 1995). See also R. Cogdell et al. (this issue).

1999

Aartsma and coworkers report spectroscopic studies on single molecules of the LH2 antenna complex from purple bacteria (van Oijen et al. 1999).

2000

Phylogenetic analysis of photosynthesis genes by Bauer's research group suggests that purple bacteria contain the most ancient Mg-tetrapyrrole biosynthesis genes (Xiong et al. 2000). Later work by Raymond and coworkers establishes that horizontal gene transfer has played a major role in the evolutionary development of photosynthesis (Raymond et al. 2002).

Kobayashi and coworkers identify the primary electron acceptor of green sulfur bacteria as a chlorophyll a derivative (Kobayashi et al. 2000).

A.S. Lang and J.T. Beatty report that the structural gene sequence and organization of the *Rb. capsulatus* 'gene transfer agent' (GTA) are similar to that of double-stranded DNA phages, but that expression of these genes is regulated by a cellular two-component signal transduction system (Lang and Beatty 2000). GTA structural gene-like clusters were found in other α-proteobacteria, suggesting a long evolutionary history of GTA-like elements and this group of bacteria (Lang et al. 2002).

Acknowledgment

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Appendix A

The names of anoxygenic photosynthetic bacteria are given in the time line as they appeared in original publications. During the recent past, some over-zealous taxonomists have proposed changing the names of many organisms that were, and still are, important in experimental research. This unfortunate development is discussed in several papers by one of the authors (HG), most recently in Gest (2001) and by Nimis (2001). As an aid to those who may be perplexed by the apparent multiplication of different names for the same organism in the recent literature, original and alternative names of a number of anoxyphototrophs are given below.

For those interested in further historical details, a list of reference sources is appended to the time line as Appendix B.

Alternative names of some anoxyphototrophs

'Traditional' name	Alternative names
Chlorobium thiosulfatophilum	*Chlorobium limicola*
Chromatium vinosum	*Allochromatium vinosum*
Chromatium gracile	*Marichromatium gracile*
Rhodopseudomonas viridis	*Blastochloris viridis*
Rhodopseudomonas capsulata	*Rhodobacter capsulatus*
Rhodopseudomonas sulfidophila	*Rhodobacter sulfidophilus* *Rhodovulvum sulfidophilum*
Rhodopseudomonas sphaeroides	*Rhodobacter sphaeroides*
Rhodopseudomonas gelatinosa	*Rhodocyclus gelatinosus* *Rubrivivax gelatinosus*
Rhodospirillum centenum	*Rhodocista centenaria*
Rhodospirillum molischianum	*Phaeospirillum molischianum*

Appendix B. General references

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