

Donald Ashley Bryant (1950–2024): An Extraordinary Cyano-Bacteriologist

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ABSTRACT

Donald (Don) A. Bryant was a leading microbial eco-physiologist in recent times. He focused on cyanobacteria by exploiting cutting-edge genetics, genomics and several aspects of molecular biology to understand their biochemistry and biophysics. In 2022, after almost five decades of outstanding university service, his generosity for education and the younger generation motivated him to donate two million US dollars to support a chair professorship in Microbial Physiology in the Department of Biochemistry and Molecular Biology at the Eberly College of Science, University Park, Pennsylvania, USA. After briefly discussing his personal and academic life, we present brief summaries of his research contributions, selected by the authors. This is followed by messages from Susan Golden, Lou Sherman, and Annick Wilmott. The Appendix lists some URL's on Don Bryant.

Keywords: Donald (Don) A. Bryant, Photosynthesis, Cyanobacteria, Phycobilisomes, Phycobiliproteins, Photoacclimation, Phylogeny, Genome sequencing, Chlorosomes

EARLY LIFE AND EDUCATION

Donald (Don) A. Bryant was born on 12 March 1950 to Wanda Partin Bryant and Roger Bryant Junior. Don is survived by his mother, his brother Larry Bryant, his sister-in-law Catherine, and nephews Seth and Jordan. He spent his early life in Henry County, Kentucky, USA, and completed his secondary education at Oldham County High School, also in Kentucky, with highest achievements in 1968. Don next attended MIT (Massachusetts Institute of Technology), in Cambridge,

Massachusetts, USA, where in 1972 he earned his BS degree in Chemistry and Biology with honours. Don then joined the graduate program in *Molecular Biology* at UCLA (University of California at Los Angeles), and in 1977 obtained his PhD on 'Comparative studies on cyanobacterial and rhodophyte biliproteins' under the mentorship of, among others, Alexander N. Glazer (1935–2021; https://en.wikipedia.org/wiki/Alexander_Glazer). This marked the beginning of Don's long-time study of cyanobacteria. From 1978 to 1980, he broadened his academic background and horizons with two one-year

***This Tribute to the Late Professor D.A. Bryant was written at the invitation of Professor Ashwani Kumar, Editor-in-Chief, of LS: International Journal of Life Sciences (India)

post-doctorate research experiences, first at the Institut Pasteur in Paris, France, with Roger Y. Stanier (1916–1982; https://en.wikipedia.org/wiki/Roger_Stanier) and Germaine Cohen-Bazire (Stanier) (1920–2001; <https://www-cyanosite.bio.purdue.edu/cyanonews/v16/Germaine.html>). Here he characterised the composition of the phycobiliproteins, as well as the mechanism of chromatic adaptation in hundreds of strains of cyanobacteria. After this, Don went to the Cornell University, Ithaca, NY, to work with Roderick (Rod) K. Clayton (1922–2011; see Wraight 2014) for a year (1980–1981). Here, with Rod's rigorous questioning style, Don excelled at bringing biophysics into his research. Don passed away on 28 August 2024 (<https://www.kochfuneralhome.com/obituaries/Dr-Donald-A-Bryant?obId=33287908>).

ACADEMIC POSITIONS AND FELLOWSHIPS

Donald A. Bryant was appointed as an Assistant Professor at the Pennsylvania (Penn) State University in 1981. By 1991, he was a full Professor of Biochemistry and Molecular Biology. Soon thereafter, in 1992, he was named the Pollard Professor of Biotechnology, Biochemistry and Molecular Biology. In addition, and concurrently, from 2009 through 2020 he had a research appointment at Montana State University, Bozeman, MT, USA, where he focused on microbial ecology. During this time Don joined an annual summer visit to the hot springs at Yellowstone National Park alongside Robert (Bob) Castenholz, Malcolm Walter and a host of later workers; many ground-breaking discoveries were made from their studies. During 2013–2018, Don also held a visiting professorship at the Nanyang Technological University, Singapore. In addition to the above, Don Bryant was a Fellow of the Board of Governors of the American Academy of Microbiology (AAM) and a Fellow of the American Association for the Advancement of Science (AAAS). In 2022, he received a special award from the AAM for basic research, recognising him as an outstanding scientist, whose work had been fundamental to advancing the understanding of the microbial world.

COLLABORATORS

Don Bryant worked with an enormous number of graduate students (more than 80), post-doctoral associates (more than 35), and many faculty members, publishing over 450 papers with, currently, 32,898 citations (Don's h-index was 101 at the beginning of February 2025). A former graduate student of Don's, Wendy Schluchter, has been a very special person in his professional life. She is co-author, along with several others, of another tribute to Don, in preparation, for *Photosynthesis Research*. Unfortunately, there were too many collaborators in Don's long and impactful scientific career for us to list them all. Instead, we mention just a few: Gaozhong Shen (University of Wisconsin-Madison), John H. Golbeck (Emeritus, The Pennsylvania State University), David Ward (Emeritus, Montana State University, MSU), Robert (Bob) E. Blankenship (Emeritus, Washington University in St. Louis and Arizona State University in Tempe; see Figure 1), Christopher (Chris) Gisriel (University of Wisconsin-Madison), and Nicole Tandeau de Marsac (1944–2020), in addition to Roger Y. Stanier & Germaine Cohen-Bazire, mentioned above.

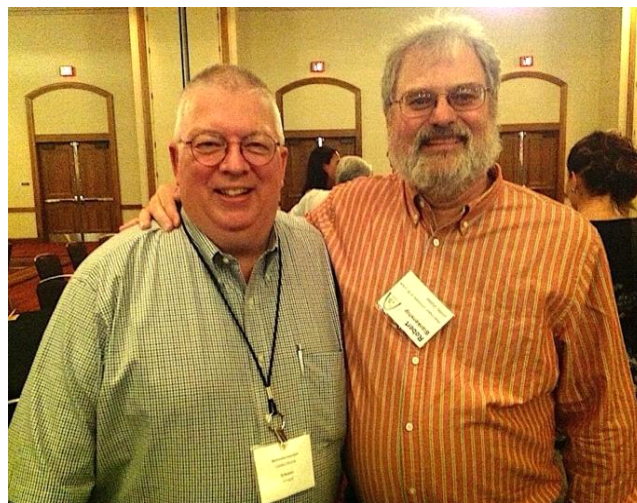


Figure 1: A 2013 photograph of Donald A. Bryant (left) and Robert E. Blankenship at the 16th International Photosynthesis Congress in St. Louis, Missouri, USA. For more information on this congress, see Blankenship et al. (2013).
Source: Robert Blankenship

DON BRYANT'S MAJOR RESEARCH THEMES

After an initial period exploring and elucidating the structure and light acclimation of phycobilisomes in remarkable detail, Don Bryant expanded his horizons to cover an exceptional number of topics in bacterial and plant biology (see the **Detailed Timeline** section). However, phycobilisomes and their component phycobiliproteins would remain a research focus throughout his scientific career.

When Don entered the field of microbial physiology and ecology in the 1970s, the field was at a nascent stage. It was recognised that bacteria were an early evolutionary development on the Earth, but many details had yet to be discovered. A major question was how photosynthetic organisms (cyanobacteria and their precursors), and, thus, photosynthesis, had evolved. There were two theories. Firstly, it had been proposed that the original photosynthetic (PS) organism arose at hydrothermal vents, deep in the oceans, where molten lava, accompanied by hydrogen gas (H₂) and hydrogen sulphide (H₂S), is expelled into the ambient seawater. Since there is no sunlight at such depths, it was inferred that the near infrared radiation (NIR) from the lava gave rise to the evolution of chlorophyll (Chl) or bacteriochlorophyll (BChl) in bacteria living in the surrounding water. Don wrote several papers on this subject (see below) leading up to a recent seminal paper on this proposal advocating not only that photosynthesis evolved here but also that it evolved to the oxygenic stage (Martin et al. 2018).

The other theory was that photosynthesis evolved on stromatolites, which possess a microbial film < 1cm thick. Modern stromatolites occur only in regions of hyper-salinity, where eukaryotic organisms, especially algae, are restricted. But in those Archaean times before 3 billion years ago (BYA) evidence indicates the universal presence of stromatolites in shallow marine waters, and even in freshwater lakes. Thus, these are good sites for the evolution of cyanobacteria or their precursors. Today, these regions contain a great variety of bacteria and Archaea, and cyanobacteria are also common. Of special interest has been the discovery of cyanobacteria with

far-red light (FRL; 700–800 nm) absorbing chlorophylls, Chl *d* and Chl *f*, found deep in the bacterial film. While Don Bryant did not directly study cyanobacteria from stromatolites, he did study both Chl *d* and Chl *f* in related organisms developing a theory about Chl *d* synthesis (Bryant et al. 2020a), and discovering the enzyme responsible for Chl *f* synthesis (Ho et al. 2016). Crucially, Don showed that the presence of Chl *f*, Chl *d*, and far-red absorbing phycobiliproteins was inducible under FRL by FaRLiP (Far-Red Light Photoacclimation) in some cyanobacteria. This FRL-induced system was the subject of numerous studies by Bryant and co-workers from the time of its discovery (Gan et al. 2014a) until the end of Don's career, and beyond.

Modern genomics has failed to indicate that cyanobacteria were formed by the association of Type I and Type II photosynthetic bacteria; rather, it has been suggested that the reverse occurred. Photosystem I is inferred as the most ancient Photosystem, possibly dating back to 3.7–3.8 BYA, with Photosystem II not far behind it (Cardona et al. 2019). Whatever the relationship between anoxygenic photosynthetic bacteria and cyanobacteria, the former has shown remarkable evolutionary development since they diversified. Don Bryant thoroughly explored the chlorosome, which is an outstanding example of this. In 2006, he wrote a seminal review on chlorosomes (Frigaard and Bryant 2006), and continued to publish papers on them until his final year (Dsouza et al. 2024). However, this was just a fraction of Don's amazing career. Don utilised the latest innovations in biochemistry, molecular biology, ecology, and biophysics to unravel many major secrets of cyanobacteria, anoxygenic photosynthetic bacteria, algae, and plants. The breadth of these discoveries is partially described in the detailed timeline below.

DETAILED TIMELINE OF THE RESEARCH CONTRIBUTIONS OF DON BRYANT: A PARTIAL LIST

Here, we provide a very brief overview of selected contributions of Don Bryant over the years, taken from his extensive research from the 1970s until 2024.

The 1970s

During this period, Don Bryant focused on the overall structure and function of the phycobilisomes – light harvesting protein megacomplexes found in cyanobacteria, red algae, and cryptophytes. Phycobilisomes are embedded in the stromal side of thylakoid membranes, and were initially thought to harvest light from ~500 nm–650 nm, a region in which chlorophylls and carotenoids absorb poorly, and funnel excitation energy to the reaction centres of the two Photosystems. One of Don Bryant's earliest discoveries was of allophycocyanin-B, a terminal emitter in phycobilisome energy transfer (Glazer and Bryant 1975). In addition, Bryant et al. (1978) provided a detailed comparison of bilin chromophore quantity, identity, and binding peptide sequence in different phycobiliproteins. Figure 2, reproduced from Bryant et al. (1979), shows their proposed structure of a hemi-discoidal phycobilisome, based on numerous electron micrographs.

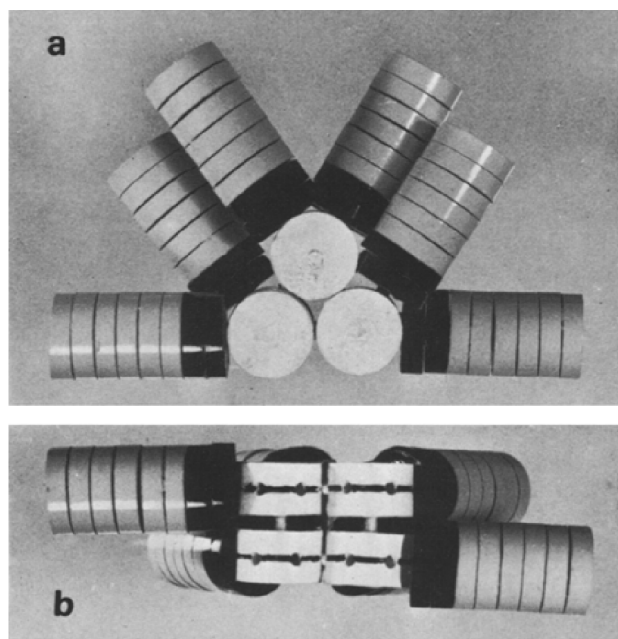


Figure 2: Don Bryant's Tinkertoy model for the hemi-discoidal phycobilisome. Grey, black, and white discs represent phycocyanin, phycoerythrin, and allophycocyanin, respectively. Individual discs correspond to phycobiliprotein trimers with a diameter of 12 nm and a thickness of 3 nm. (a) is the face view, and (b) is the bottom view. This figure is reproduced from Figure 18 in Bryant et al. (1979).

The 1980s

In addition to phycobiliproteins and phycobilisomes, Don Bryant's research focus of the 1980s expanded to include photosystem regulation and composition, characterisation of the cyanobacterial recombinase RecA, and stress responses in cyanobacteria. Several publications during this time featured the marine cyanobacterium *Synechococcus* sp. PCC 7002 (hereafter *Synechococcus* 7002), which would become the primary model organism of the Bryant Lab at Penn State.

The first half of the decade was almost exclusively dedicated to phycobiliprotein/phycobilisome research. Chromatic acclimation was discussed in Bryant and Cohen-Bazire (1981), which showed how growing *Pseudanabaena* in red light affects phycocyanin induction, and in Kipe-Nolt et al. (1982), which described the light-controlled synthesis of phycoerythrin in *Nostoc* species. Guglielmi et al. (1981) defined the structure of phycobilisomes in the unusual, primitive cyanobacterium *Gloeobacter violaceus*, which lacks thylakoid membranes and instead embeds phycobilisomes in the cytoplasmic membrane. In addition, Don's work during this time also provided a full description of the genes for both the alpha and the beta subunits of phycocyanin (de Lorimier et al. 1984).

Don Bryant's research output in the second half of the 1980s was such that we must limit our discussion to one publication per year, from 1985 to 1989. Bryant et al. (1985) managed to heterologously express phycocyanin subunit genes in *Escherichia coli* (*E. coli*) and identify the promoter region for those genes from *Synechococcus* 7002; Mazel et al. (1986) established that green light induces transcription of the phycoerythrin operon in the cyanobacterium, *Calothrix* sp. PCC 7601; Cantrell and Bryant (1988) cloned and identified the nucleotide sequences of Photosystem I subunit genes *psaA* and *psaB* from *Synechococcus* 7002, an early step in Don Bryant's lifelong study of cyanobacterial photosystems; Gingrich et al. (1988) reported the complete genetic analysis of two new mutations that resulted in herbicide resistance in *Synechococcus* 7002;

and finally, Bruce et al. (1989) examined state transitions, the preferential funnelling of excitations from the phycobilisomes to one photosystem or the other, in the wild-type and a phycobilisome-less mutant of *Synechococcus* 7002. Don Bryant also contributed to the book edited by Govindjee et al. (1989). Don's contributions to the book added major educational value for its readers.

The 1990s

The 1990s were a highly active research period in Don Bryant's life. Together with his co-authors, he published 50 papers and maintained the theme of going deeper into the molecular biology, biochemistry, and biophysics of photosynthesis. We mention just a few below.

***1990:** Bryant et al. (1990) provided a thorough structural and compositional analysis of phycobilisomes in *Synechococcus* 7002, as well as growth studies with a mutant strain lacking the genes for phycocyanin. Zhao et al. (1990) reconstituted Photosystem I electron transport in *E. coli* via heterologous expression of two subunits, PsuC and PsuD. The latter has additional significance as Don's first publication with his long-time friend and collaborator, John H. Golbeck.

***1991:** Don Bryant and John Golbeck continued their exploration of Photosystem I by showing that PsuD is required for the association of PsuC to the core of the complex in *Synechococcus* sp. PCC 6301 (Li et al. 1991).

***1992:** This was a highly productive year, with 17 articles, of which we will mention just two. Bryant (1992) wrote a beautiful essay on chloroplast ancestry, in which he grappled with lingering mysteries of the chloroplast-cyanobacteria relationship. Schluchter and Bryant (1992) continued to focus on Photosystem I electron transport in cyanobacteria by cloning and characterising the ferredoxin-NADP⁺ oxidoreductase of *Synechococcus* 7002.

***1993:** During this year, Don Bryant's work included the role of the Photosystem I subunit PsuE, first suggested to be essential for cyclic electron transport by characterisation of an inactivation mutant (Zhao et

al. 1993), then established as such by Yu et al. (1993). Don's work on phycobiliproteins also continued with spectroscopy defining the roles of the individual chromophores in energy transfer within monomeric phycocyanin (Debreczeny et al. 1993).

***1994:** From the perspective of researchers around the world, the book edited by Bryant (1994), titled '*Molecular Biology of Cyanobacteria*', has been highly educational, and its figures and discussion continue to be very relevant to the field of photosynthesis. We note that this book was Volume 1 in the series 'Advances in Photosynthesis and Respiration', which was launched by one of us (Govindjee).

***1995:** Stirewalt et al. (1995) sequenced and described the genome of the *Cyanophora paradoxa* cyanelle, providing a greater understanding of the plastids and their endosymbiotic origin. Don's work on phycobiliproteins also continued with a comparison of experimental and theoretical rate constants for excitation energy transfer in the monomers (Debreczeny et al. 1995a) and trimers (Debreczeny et al. 1995b) of C-phycocyanin, providing evidence for Förster transfer of excitation energy in this system. We note that Don had collaborated with the late Kenneth (Ken) Sauer (1931—2022) for these studies. Don also described a *Synechococcus* 7002 mutant lacking Photosystem I in his first publication with his long-time collaborator, friend, and lab manager Gaozhong Shen (Shen and Bryant 1995).

***In 1996,** Schluchter et al. (1996) characterised interposon mutants of the Photosystem I subunit genes *psaI* and *psaL* in *Synechococcus* 7002, allowing them to propose a new model for state transitions in cyanobacteria, a topic of ongoing debate to this day.

***1997:** Stress responses in cyanobacteria were discussed in several of Don Bryant's research articles that year, including Sakamoto and Bryant (1998) where the growth of *Synechococcus* 7002, at lower temperatures, was shown to be limited by nitrogen as opposed to damage to, or inactivity of, the photosynthetic apparatus.

***1998:** Photosystem I was a major focus of Don Bryant's research articles published that year. Yang et al. (1998) described unidirectional electron transfer in a strain of *Synechococcus* 7002 lacking Photosystem I subunit Psf, and Xia et al. (1998) detailed the structure and physico-chemical properties of Psd, an extrinsic Photosystem I polypeptide.

***In 1999,** Don Bryant again identified that nitrogen limitation, not photoinhibition, is the limiting factor for growth at lower temperatures, this time in the freshwater cyanobacterium *Synechococcus* sp. PCC 6301, showing that this is a feature of both marine and freshwater cyanobacteria (Sakamoto and Bryant 1999). Sakamoto et al. (1999) also characterised a new nitrate/nitrite permease in *Synechococcus* 7002.

The 2000s

In the 2000s (2000–2009), Don Bryant's research focus expanded to include anoxygenic photosynthetic bacteria. Don and co-workers published over a hundred papers during this time. Among these accomplishments were further studies on phycobiliproteins, foundational insights into anoxygenic photosynthesis and light-harvesting chlorosomes, and the discovery of the first chlorophototroph in the bacterial phylum *Acidobacteria*. A selection of these findings are highlighted below.

***In 2000,** Bhaya et al. (2000) described the biogenesis of the Type IV pilus machine and its role in motility in model cyanobacterium *Synechocystis* sp. PCC 6803.

***In 2001,** Frigaard and Bryant (2001) established chromosomal gene inactivation in *Chlorobaculum tepidum* (previously *Chlorobium tepidum*), establishing this green sulphur bacterium as a model for studying anoxygenic photosynthesis in the Bryant Lab and elsewhere.

***In 2002,** a pair of papers (Shen et al. 2002a, 2002b) detailed the role of a membrane-associated rubredoxin in the biosynthesis of Photosystem I in *Synechococcus* 7002. Additionally, Eisen et al. (2002) reported the full genome sequence of *Chlorobaculum tepidum*, and Bryant et al. (2002) suggested that CsmA forms the 'baseplate'

of the chlorosome complex and binds bacteriochlorophyll *a* (Bchl *a*).

***Don Bryant's output in 2003** included a detailed description by Frigaard et al. (2003) of structural, physiological, and metabolic information gleaned from the *Chlorobaculum tepidum* genome. That same year, Cheng et al. (2003) compared the divergent tocopherol synthesis methyltransferases of photosynthetic eukaryotes and cyanobacteria, identifying functional counterparts, differences, and speculating on their evolutionary origin.

***Among several new results for 2004,** Van Der Est et al. (2004) defined the role of the Psf protein in the forward electron transfer of Photosystem I in *Synechococcus* 7002. Furthermore, a pair of studies centred on gene inactivation in *Chlorobaculum tepidum* illuminated the roles of nine chlorosome proteins (Frigaard et al. 2004a) and nine carotenoid biosynthesis enzymes (Frigaard et al. 2004b) in green sulphur bacteria.

***2005** showcased Don's growing interest in genetically manipulating bacterial photosynthetic complexes, first with a study on electron transfer after incorporating a foreign Quinone into the A₁ site of photosystem I devoid of iron-sulphur clusters F_x, F_B, and F_A (Sakuragi et al. 2005), followed by characterisation of the 'carotenosomes' resulting from elimination of the most abundant pigment, bacteriochlorophyll *c* (Bchl *c*), from the chlorosomes (Frigaard et al. 2005).

***2006** was a particularly productive year, including the publication of reviews on all aspects of prokaryotic photosynthesis (Bryant and Frigaard 2006), and on the chlorosomes of photosynthetic green bacteria (Frigaard and Bryant 2006), a publication on the discovery of a new class of bilin lyase in cyanobacteria (Shen et al. 2006), and a thorough description of the Guerrero Negro hypersaline microbial mat (Ley et al. 2006), the latter distinguished as Bryant's most-cited primary research article at the time of its writing.

***2007** was a milestone in Don's career with the discovery of the first chlorophototrophic organism in

the phylum *Acidobacteria*, *Chloroacidobacterium thermophilum* (Bryant et al. 2007). This study was the first of four that Don would publish in the journal *Science* over the years. Also this year, Chew and Bryant (2007) published a thorough review on BChl biosynthesis in bacteria, which focused on its evolutionary origin and structural and functional diversity.

*A pair of papers published in **2008** featured phycobiliproteins once again, describing the roles of the CpcS-I and CpcU bilin lyases in chromophorylation of phycocyanin and allophycocyanin in *Synechococcus* 7002 (Shen et al. 2008; Saunée et al. 2008). The first in a series of publications on the production of solar hydrogen in collaboration with the Golbeck lab was also published this year (Grimme et al. 2008).

*Two of Don's publications in **2009** addressed transfer of excitation energy in light-harvesting complexes. Dong et al. (2009) showed that phycobiliprotein ApcD is not only essential for efficient energy transfer from the phycobilisomes to PS I but also helps prevent photoinhibition in *Synechococcus* 7002. Ganapathy et al. (2009) described how the geometry of BChl in chlorosomes enables efficient transfer of excitation energy.

The 2010s

Don Bryant's research output peaked in the 2010s (2010–2019), with over 160 publications. The following selection reflects his growing interest in applying cyanobacterial photosynthesis to generate useful products, and his continued commitment to foundational studies in bacterial photosystems, chlorosomes, and phycobiliproteins. Of particular importance were the studies on photoacclimation of non-model cyanobacteria to specialised light conditions, which became the basis for many publications from his lab and elsewhere.

*In **2010**, collaboration between Don Bryant and John Golbeck showed how solar hydrogen can be produced by attaching cyanobacterial Photosystem I to a hydrogenase (Lubner et al. 2010). Additionally, McNeely

et al. (2010) provided a way to metabolically engineer a cyanobacterium to redirect reductants to produce hydrogen, and Biswas et al. (2010) described heterologous production and chromophorylation of cyanobacterial phycobiliproteins in *E. coli*.

***2011** was an extremely productive publication year for Don. Xu et al. (2011) adapted endogenous plasmids for overexpression of genes in *Synechococcus* 7002, providing a set of tools used by many. Klatt et al. (2011) explored the communal ecology of cyanobacterial mats that form near hot springs, prefacing several further studies of microbial mats in collaboration with David M. Ward at Montana State University. On the other hand, Ludwig and Bryant (2011) profiled the transcriptome of *Synechococcus* 7002 using next-generation sequencing. Of great interest to microbiologists in general, Zhang and Bryant (2011) completely described the tricarboxylic acid (TCA) cycle of cyanobacteria in the journal *Science*.

***2012** featured several papers on the unique aerobic chlorotroph *Chloroacidobacterium thermophilum*, with its complete genome provided by Garcia Costas et al. (2012a), followed by the isolation and characterisation of its homodimeric Type I reaction centre complex by Tsukatani et al. (2012), as well as the identification of its pigments and other molecules by Garcia Costas et al. (2012b). On the topic of anoxygenic photosynthesis, Vogl et al. (2012) analysed the properties of chlorosomes incorporating artificial BChl *f*, considered the '*forbidden*' chlorophyll due to its absence from nature.

*Don Bryant's **2013** publications included a detailed characterisation of a phycocyanobilin lyase, CpcS, in *Thermosynechococcus elongatus* by Kronfel et al. (2013); a comparison of the chlorosomes from three phyla of green photosynthetic bacteria by Adams et al. (2013); genome analysis identifying key aspects of symbiosis within the unusual photosynthetic consortium *Chlorochromatium aggregatum* by Liu et al. (2013); and identification of temporal metatranscriptomic patterning in phototrophic *Chloroflexi* inhabiting a hot spring microbial mat by Klatt et al. (2013).

*Two publications in **2014** heavily influenced Don's later output. Gan et al. (2014a) reported in the journal *Science* a unique photoacclimation response to far-red light by non-model cyanobacterium *Leptolyngbya* sp. JSC-1. Briefly, prolonged exposure to light primarily in the far-red region (700 nm–800 nm) of the electromagnetic spectrum caused extensive remodelling of the cores of both the Photosystems (I and II) and the phycobilisomes in this organism, enabling photosynthesis at longer wavelengths than previously thought possible. A follow-up publication in *Life* demonstrated the presence of the genes enabling this Far-Red Light Photoacclimation (FaRLiP) response in diverse cyanobacteria (Gan et al. 2014b). Strains with the so-named 'FaRLiP Gene Cluster' are expected to be the subject of many future studies.

*In **2015**, Don and collaborators in the Ward lab at Montana State University published a series of three papers describing *Synechococcus* occupying various gradients (e.g., light, nutrient, temperature, pH) within the microbial mat, present at Mushroom Spring, Yellowstone National Park, focusing on the distribution

of *Synechococcus* ecotypes in the mat (Becraft et al. 2015), their behaviour under various conditions (Nowack et al. 2015), and comparative genomics and transcription patterns (Olsen et al. 2015). Another paper on FaRLiP described the elements controlling this photoacclimation response at the genetic level (Zhao et al. 2015).

Figure 3 shows a photograph of Don's research group in 2015.

*In **2016**, Günther et al. (2016) provided details on the structures of the light-harvesting complexes in individual chlorosomes, and Pérez et al. (2016) described cobalamin dependence and genetic control over expression in *Synechococcus* 7002 via cobalamin riboswitch. Returning to the topic of FaRLiP, Ho et al. (2016) identified the gene encoding chlorophyll *f* synthase, published in *Science*.

*In **2017**, Thweatt et al. (2017) provided the final missing piece of the bacteriochlorophyll synthesis pathway of green bacteria in the radical SAM enzyme BciD. A pair of papers (Ho et al. 2017a, 2017b) further described the regulation of the FaRLiP gene cluster and

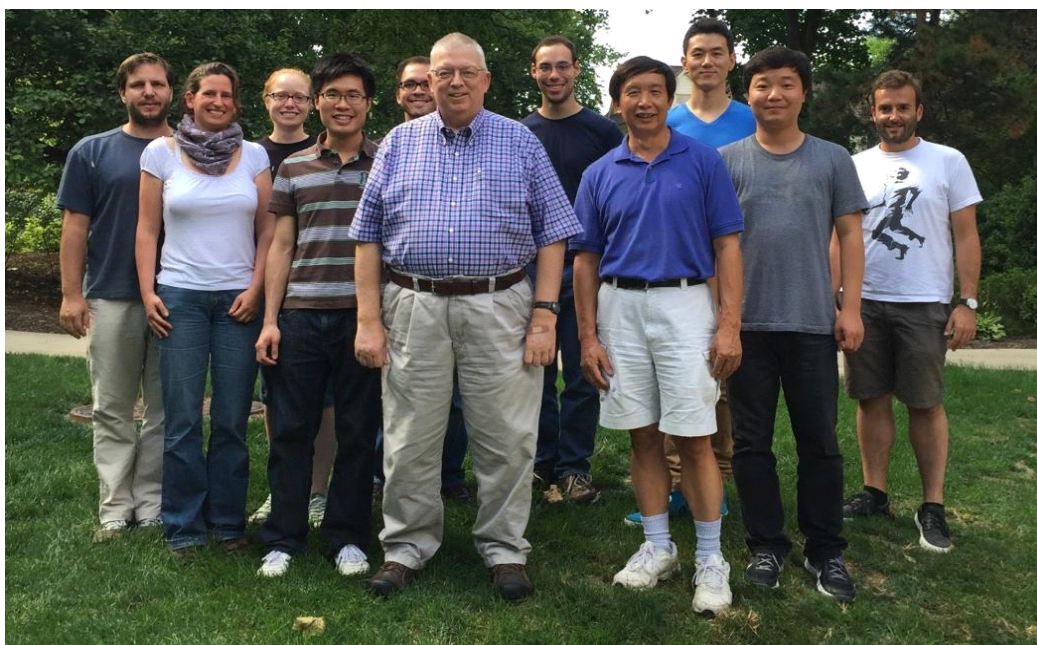


Figure 3: A 2015 photograph of Don Bryant and his research group outside his lab at Penn State. Left-to-right: Marcus Tank, Vera Thiel, Jennifer Thweatt, Ming-Yang Ho, Adam Perez, Don Bryant, Nathan Thomas Soulier, Gaozhong Shen, Chi Zhao, Shuyi Zhang, and Dan Canniffe. Photo courtesy of Dan Canniffe.

the unusual far-red absorbing phycobiliproteins encoded there. Ho et al. (2017c) reviewed the current understanding of both pigment and photosystem biosynthesis in cyanobacteria, including discussions on FaRLiP and low-light photoacclimation (LoLiP).

Figure 4 shows Don Bryant at a lab gathering that took place in 2017.



Figure 4: A Lab gathering on the back porch of Gaozhong Shen's house on 12 August 2017 in State College, Pennsylvania. Left-to-right: Ming-Yang Ho, Nathan Thomas Soulier, Jennifer Thweatt, Gaozhong Shen, Don Bryant, Tristan Cofer, Mattie Cofer, and Dan Canniffe. Photo courtesy of Gaozhong Shen.

*In addition to new discoveries in **2018**, Don contributed to three reviews of great interest to the photosynthetic community: Bryant and Canniffe (2018) described the natural design of light-harvesting antenna in chlorophototrophic prokaryotes; Martin et al. (2018) provided an ecophysiological perspective on the evolution of photosynthesis around deep-sea hydrothermal vents; and Thiel et al. (2018) delved into the taxonomy and phylogeny of chlorophototrophic bacteria, synthesising the knowledge of this group from the modern 'omics' approaches. As for research publications, we mention three united by the theme of artificial pigment production: Chen et al. (2018) engineered chlorophyll biosynthesis in *E. coli*; Ortega-Ramos et al. (2018) engineered biosynthesis of bacteriochlorophyll g_F in *Rhodobacter sphaeroides*; and Mancini et al. (2018) reported on the design and assembly of a *de novo* synthetic biliprotein, in which the mechanism of excitation energy transfer could be easily studied.

*In **2019** Don and co-workers continued to explore FaRLiP and artificial photosynthesis. Ho and Bryant (2019) provided insight into the regulation of Chl *d* synthesis in the FaRLiP organism *Chlorogloeopsis fritschii* PCC 9212, while Kurashov et al. (2019) examined energy transfer from Chl *f* to the trapping centre in natural and engineered Photosystem I. In the realm of artificial photosynthesis, Shen et al. (2019) characterised the heterologous production of Chl *f* in the non-FaRLiP organism *Synechococcus* 7002, Kumaraswamy et al. (2019) altered the metabolism of cyanobacteria to maximise fermentative hydrogen production, and Swainsbury et al. (2019) discussed incorporating alternate pigments to achieve rapid energy transfer in the antenna of *Rhodobacter sphaeroides*.

Figure 5 shows Don Bryant with former graduate student Wendy Schluchter and former postdoc Jindong Zhao at the 13th Workshop on Cyanobacteria in 2019. Also from 2019, Figure 6 shows Don Bryant and his former graduate student Ming-Yang Ho.

The 2020s

Don Bryant was extremely productive during the last five years of his life (2020–2024), and the impact of his research in this period is widely recognised. After his



Figure 5: Left-to-right: Wendy Schluchter, Don Bryant, and Jindong Zhao, relaxing during a break at the 13th Workshop on Cyanobacteria, held in June 2019, in Boulder, Colorado, USA. Photo courtesy of Gaozhong Shen.



Figure 6: Don Bryant and Ming-Yang Ho in Don's office at Penn State (July 2019). Photo courtesy of Ming-Yang Ho.

retirement from Penn State in 2022, Don continued to collaborate and write to answer lingering questions about the structures of FaRLiP complexes and other topics.

*Publications in **2020** were mainly on the topic of FaRLiP. Cherepanov et al. (2020) published evidence that Chl *f* functions exclusively as an antenna pigment in the FRL-acclimated Photosystem I of *Fischerella thermalis*. Ho et al. (2020) showed that FaRLiP cyanobacteria incur significant changes in energy transfer among their remodelled pigment complexes after growth in far-red light. Soulier et al. (2020) characterised FRL-absorbing allophycocyanins, individually, by heterologous expression, while Bryant et al. (2020a) suggested, from their new experiments, that those allophycocyanins play an important role in the FRL-driven Chl *d* accumulation. Bryant et al. (2020b) reviewed all that was known about the biosynthesis of modified tetrapyrroles in cyanobacteria, '*the pigments of life*'. In the first of several collaborations in structural biology, Gisriel et al.

(2020) described changes that occur in the structure and pigments of Photosystem I during growth of FaRLiP cyanobacteria in far-red light.

*Don's **2021** publications provided a bevy of structural information about far-red adapted proteins and complexes: Soulier and Bryant (2021) published their findings on the structural basis of FRL absorbance by some allophycocyanins as indicated by extensive mutagenesis of their chromophore binding sites; Gisriel et al. (2021) identified some of the binding sites for Chl *f* in FRL-acclimated Photosystem I from cryo-EM maps; and Tros et al. (2021) described, in detail, the efficient trapping of FRL by Chl *f*-containing Photosystem I.

*In **2022**, further structural insights into the photosynthetic machinery of FRL-acclimated cyanobacteria were provided, first on the structure of a far-red Photosystem I-ferredoxin complex (Gisriel et al. 2022a), followed by the structure of a monomeric, far-red Photosystem II core complex showing the functions of long-wavelength Chls *d* and *f* (Gisriel et al. 2022b). MacGregor-Chatwin et al. (2022) presented detailed information on the changes in the organisation of thylakoid membrane complexes in response to acclimation to far-red light. Additionally, a new type of photoacclimation response, termed LoLiP for 'Low-Light Photoacclimation', was described by Soulier et al. (2022) in mat-dwelling cyanobacteria isolated from a hot spring.

*In **2023**, Don Bryant and Chris Gisriel continued their fruitful collaboration with publications on the structure of dimeric Photosystem II complexes from FRL-acclimated cyanobacteria (Gisriel et al. 2023a), as well as the structure of the unique allophycocyanin associated with LoLiP, which forms helical nanotubes in solution rather than the typical discs (Gisriel et al. 2023b). To better understand the evolution of cyanobacterial light-harvesting, Jiang et al. (2023) described the molecular background of a relict phycobilisome from the thylakoid-less cyanobacterium *Anthocerotibacter panamensis*.

*Don Bryant continued to make remarkable contributions to science in his last year, **2024**. Cherepanov et al.

(2024) reported on the primary reactions of FRL Photosystem II using femtosecond spectroscopy. Dsouza et al. (2024) published an integrated approach to obtain information about the structure of chlorosomes from a mutant of *Chlorobaculum tepidum*. Gisriel et al. (2024) obtained a detailed structure of the antenna complex isolated from a FaRLiP *Synechococcus* strain after acclimation to far-red light. As a fitting capstone to a career investigating all manner of microbial light harvesting complexes, Bryant and Gisriel (2024) reviewed the progress in structural determination of light-harvesting components (both phycobiliprotein- and Chl-based) in cyanobacteria, red-algae, and cryptophytes.

MESSAGES

All in all, many of us will remember Don Bryant's personal insight and approach to integrating many different areas of science, as well as his passion to understand it through cooperation with others. We present below just a few of the messages we received on his behalf.

Susan Golden (sgolden@ucsd.edu)

Don Bryant has taken on a major role in my professional life from the time I was a graduate student. Because of his mastery of metabolism and ecophysiology in diverse cyanobacteria, he often was able to provide the answers to questions that arose at cyanobacterial workshops when the speaker to whom the question was directed was not able to provide any insight. I have known many scientists who are intense about their work, but few whose intensity is fuelled with such joy as Don's. He simply loved revealing the scientific secrets held by photosynthetic bacteria. Among his diverse contributions, he elucidated the pathways of the biosynthesis of chlorophyll, carotenoids, and phycobiliprotein as well as the structure-function relationships of the light-harvesting antennae and the reaction centres in diverse organisms.

After he retired, he still had stacks and stacks of data awaiting his attention to publish, and he continued to

produce quality work that moved the field forward. Beyond his contributions to the field, Don was a great friend to many of us. In recent years, as his health challenges and the need to sequester from the pandemic kept him at home, he became especially open in our correspondence about how deeply he cherished his friends in science. It was a pleasure and privilege to virtually share his house-bound celebration, in 2020, of the Charles F. Kettering Award in Photosynthesis from the American Society of Plant Biologists. I will miss him, and we will all miss his prolific contributions to our field, some of it mentioned above.

Louis Sherman (ls Sherman@purdue.edu)

Don Bryant and I were friends and colleagues for some 45 years. He first contacted me as he was finishing up his first postdoc with Roger Stanier and Germaine Cohen-Bazire at the Pasteur Institute in Paris. I encouraged him to seek a second postdoc with Rod Clayton at Cornell (my postdoc lab), and we each benefited from this experience. From that time forward, we discussed future research plans, grants, sabbaticals and the wonders of cyanobacteria and photosynthesis. When he took a position at Penn State, he and Ed Stephens developed an excellent genetic system in cyanobacteria and that gave us still another common area of interest.

I always considered Don to be one of the smartest guys on the block, and he did well from the start. When we first established the Workshop on the Molecular Biology of Cyanobacteria, I raised money to provide travel grants to this meeting in St. Louis. Don received the largest grant and brought about a dozen young scientists along with him! This level of success continued throughout his career and was truly highlighted by all the work that he did at Yellowstone National Park, via his time at Montana State University. We talked about that a lot, since I had wanted to do such research for many years but got distracted by such things as administration! I always felt that he was a leader within the group of cyanobacterial researchers, and I sponsored

him for some major awards, some of which were successful—and well deserved.

In later years, we also talked about Don's newest hobby—his interest in raptors. His world travels were not complete if he couldn't take a trip or side trip to view and photograph raptors. Yes, he was rapturous in his description of the birds, and it was fun to see his excitement (see Figure 7). We both retired at about the same time in 2022, even though I told him he was far too young to retire. But, not surprisingly, he left a legacy by establishing a professorship in his name at Penn State. I knew that he had health issues, but I was still shocked to hear of his death. He was a good friend and a great scientist; we all miss him. I attach a photo (Figure 8) that was taken in 2000 in Atami, Japan at the beginning of the US-Japan meeting on cyanobacterial



Figure 7: Don Bryant giving a presentation at the 2018 Photosynthetic Antenna Research Conference (PARC) at Washington University in St. Louis, Missouri, USA. On the screen is a photograph of an adult peregrine falcon, one of Don's favourite raptors. Source: Gaozhong Shen.



Figure 8: Left-to right: Don Bryant, Rob Burnap, Devaki Bhaya, Susan Golden and Lou Sherman during a break at the January 2000 meeting of the US-Japan group on Cyanobacteria & Photosynthesis. Source: Louis Sherman.

photosynthesis. Don shows his usual good humour on the left, while Rob Burnap, Devaki Bhaya, Susan Golden and I indicate our sleepiness after the long trip to Japan. A good photo of Don's smile.

Annick Wilmotte (awilmotte@uliege.be)

Dear Dr Govindjee, Thank you very much for your email. I must confess that I was not aware of the passing away of Don! It was in 1992 / 1993 that he had contacted me to write a chapter about the 'Evolution of Cyanobacteria' for the book he was editing, '*The Molecular Biology of Cyanobacteria*' (Bryant 1994). I was a young post-doc at that time and quite worried at the idea that I would not deliver a text of sufficient quality. But, when receiving it, Don wrote that it was what he had expected, and I was very relieved. I feel very thankful for his offer to participate to this major book and for his encouragements. As we were working in different fields, I have followed his superb work on photosynthesis mainly from his publications. I admire his energy and deep knowledge that has enabled him to make significant discoveries, such as on the new chlorophylls and on the mechanisms of adaptation in far-red light in cyanobacteria. I am just reviewing a PhD thesis on these topics from a colleague's laboratory, so his legacy is here to stay. Best regards- Annick Wilmotte

CONCLUDING REMARKS

Donald (Don) Ashley Bryant has been one of the world's foremost authorities on the molecular biology of cyanobacteria, and this work has been recognised on a broader level for its insights into microbial physiology and ecology. During the last quarter-century, Don Bryant's contributions have been enormously impactful and varied. During this time, he applied the latest developments in biochemistry, molecular biology, and physical chemistry to study a dizzying number of aspects of photosynthesis, physiology, and ecology in cyanobacteria, algae, and non-oxygenic photosynthetic bacteria. His contributions in the fields of microbial ecology, photoacclimation, and the structures and functions of photosynthetic complexes (including Photosystem I, phycobiliprotein complexes, and chlorosomes) will be remembered among his finest achievements. Don Bryant will also be remembered for

his numerous, in-depth presentations and interactions over the years at a large number conferences and universities. Figure 9 provides an overview of Don Bryant's research areas, as visualised by Dima Shevela.

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AUTHOR CONTRIBUTIONS

G.G., A.W.D.L. and N.S. wrote and edited this article. N.S. provided several photographs.

APPENDIX: URL'S FOR DONALD A. BRYANT

https://en.wikipedia.org/wiki/Donald_A._Bryant

https://scholar.google.com/citations?hl=en&user=2tT-FokAAAAJ&view_op=list

<https://www.legacy.com/us/obituaries/centredaily/name/donald-bryant-obituary?id=56459402>

<https://www.legacy.com/us/obituaries/name/dr-donald-a-bryant-obituary?id=56459288>

<https://www.legacy.com/us/obituaries/oldhamera/name/donald-bryant-obituary?id=56469711>

<https://www.peoplebehindthescience.com/dr-don-bryant/>

<https://science.psu.edu/bmb/people/dab14>

<https://www.huck.psu.edu/people/donald-bryant>

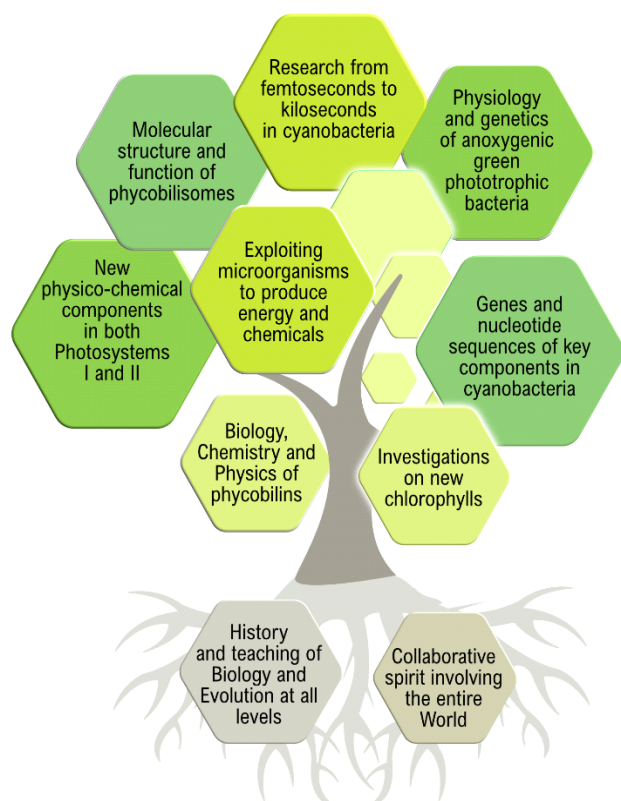


Figure 9: An overview of the major contributions of Donald A. Bryant. *Source:* Dmitry Shevela of SciGrafik, Umeå, Sweden

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