

## David W. Krogmann, 1931–2016

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**Abstract** We provide here reflections on the life and career of David W. Krogmann (1931–2016), a great scientist, a mentor and an outstanding teacher, who had a remarkable impact on anyone who came in contact with him. Dave was a pillar of photosynthesis at Purdue University, and an international authority on electron transfer intermediates in oxygenic photosynthesis, particularly the soluble cytochromes. The photosynthetic system of his choice was cyanobacteria, and one of his major discoveries was the Orange Carotenoid Protein in these microorganisms.

**Keywords** Cytochromes · Cyanobacteria · Orange carotenoid protein · Electron transport · Phosphorylation · Plastocyanin

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This manuscript was read, edited and accepted by Thomas D. Sharkey with the following comment: This description of the life's work of Professor David Krogmann provides insight into his generous and kind nature, and the effect he had on so many people studying photosynthesis.

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### Introduction

David W. (Dave) Krogmann (October 21, 1931–January 22, 2016) did pioneering research in the area of biochemistry of photosynthesis throughout his career (see Fig. 1 for two portraits). He was an exemplar of a biologist immersed in the joy of his vocation; a dedicated bench scientist who made original observations in the laboratory throughout his academic career (see Fig. 2). He utilized cyanobacteria as the experimental organism of choice during his entire tenure as an academic scientist. In addition, he served and supported the photosynthesis research community in many ways, including active leadership in several US government agencies. He was an outstanding teacher, mentor and collaborator who has had a profound impact on the field (see *Remembrances* below; also see Appendix for a partial alphabetical list of coauthors of David W. Krogmann). Dave's contributions to the chronology of discoveries in photosynthesis were exemplary (see Govindjee and Krogmann

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**Fig. 1** Two portraits of David Krogmann. **A** 1998, when he became Emeritus Professor; **B** 2003, at the home of Carlos Gómez-Lojero (photo by Fernando López-Casillas)



**Fig. 2** A 1959 photo of David Krogmann at the bench in the laboratory of Birgit Vennesland at University of Chicago. Source: Krogmann family

2004). In 2000 he wrote a perspective on important contributions and contributors to the biochemistry of photosynthesis (Krogmann 2000). This highly personal account describes his excitement for scientific research and the accomplishments of many individuals who made key discoveries during the latter half of the twentieth century.

## Personal life and professional development

David W. Krogmann was born in Washington DC on October 21, 1931. His parents, Rudolph Francis Krogmann and Cecelia Mar O’Dea Krogmann, were American-born children of immigrants from Germany and Ireland. His mother, an accomplished pianist and voracious reader of non-fiction literature, greatly influenced his lifelong love of classical and chamber/concert music, and his inquisitive nature. A childhood interest in tropical fish and aquarium keeping led to his desire to study biology. While in junior high school, he was befriended by a neighbor who built models of historic ships in transparent wine bottles. That relationship, along with his own constructions, instilled a fascination with ships and the sea that he retained throughout life. He often spent time on seashores, observing ships during childhood, vacationing on beaches with family members as an adult, and collecting cyanobacteria in later years. He attended The Catholic University of America in Washington D.C., where he obtained a B.A. degree in biology, in 1953.

Dave enrolled as a graduate student at The Johns Hopkins University in 1953 under the supervision of André Jagendorf (see below for his *Remembrance*). There he met and married Loretta Kurek, his wife of 50 years, until her untimely death in 2009. Figure 3 shows a photograph of the couple holding orangutans in the Singapore zoological garden. Dave received a doctoral degree in 1957, and continued his research with André Jagendorf for another year, and then with Birgit Vennesland at the University of Chicago (Fig. 2). Dave’s studies at John Hopkins ignited a fascination with—and desire to elucidate—the components and function of electron transport and phosphorylation in oxygenic photosynthesis.



**Fig. 3** A 1994 photo of David and Loretta Krogmann’s “breakfast with the orangutans” taken in Singapore Zoological Gardens. Source: Krogmann family

In 1960, David accepted a faculty position in the Chemistry Department at Wayne State University where his research program focused on membrane-associated components of photosynthesis, especially in cyanobacteria. This became the primary focus of his research throughout his career. He developed a love of undergraduate teaching through the biochemistry course he taught at Wayne State.

In 1977, Dave moved, with his wife and three young children, to West Lafayette, Indiana as a Professor in the Biochemistry Department at Purdue University. Although adapted to life in large cities, he quickly embraced the spirit of the smaller community. He taught biochemistry courses and mentored graduate students at Purdue for 33 years. He retired as Professor Emeritus in 1998.

Krogmann died on January 22, 2016 in West Lafayette. He is survived by his two daughters Michele (of West Lafayette, Indiana) and Pat (of Aliso Viejo, California), and son Paul (and his wife Elizabeth), also of West Lafayette, along with two grandchildren, David and Kelleigh. His sister Cecilia Rounds preceded him in death. (See below for the *Remembrance* of Michele Krogmann.)

### Teaching and advising

David Krogmann was fully committed to teaching throughout his academic career. He was a remarkably dedicated instructor and mentor of both undergraduate and graduate students. His office door was always open for students. His preferred lecture course was *Introductory Biochemistry*, which enrolled mostly freshmen. He carefully prepared new lecture notes prior to each presentation even after he had taught the same subject many times over. At the beginning of every semester he obtained a photograph of all the students in his class, numbering more than 50. He then prominently placed the gallery of pictures and corresponding names in front of his desk, where he memorized every one before the second week of class.

Although Dave mentored up to nine graduate students at one time during his early years at Purdue, he generally preferred fewer students so he could devote time to each one, and to his own bench work. Regardless of the number of students, he was always available to discuss science with anyone who requested a conversation. He loved discussing individual research projects with graduate students, not only to learn of their latest results, but also to provide encouragement and to offer suggestions for further experiments. On numerous Saturday mornings, he could be found washing laboratory dishes that students had neglected, tidying workbenches and interacting with any graduate student who was in the laboratory. He was also interested in the activities of his students, other than that in science, and would frequently invite his entire group to his house for social conversation and Loretta's

Lasagna dinners. Even after completion of their degree, Dave encouraged his former students to return for visits so he could keep up with their activities and offer encouragement, regardless of the paths their lives had taken. He seldom sponsored post-graduate associates in his laboratory, preferring instead to develop collaborations with scientists elsewhere who offered complementary skills.

Dave's love of teaching and personal friendships led him to visit Mexico several times (during 1987–2007), where he taught courses in writing scientific papers to graduate students at the Mexican Society of Biochemistry (Sociedad Mexicana de Bioquímica), at the Cellular Physiology Institute, UNAM (National Autonomous University of Mexico), UAM-Iztapalapa (Metropolitan Autonomous University), and in San Luis Potosí State (Cuernavaca Morelos) at the Center of Genomic Sciences, UNAM. (See *Remembrance* by Diego González-Halphen.) Besides Mexico, Dave also taught and lectured at institutions in Singapore, Thailand, Japan and South Africa.

### Research

#### *1954–1960: Doctoral and post-doctoral research*

From the beginning of his doctoral training, David Krogmann was interested in biochemical processes associated with photosynthetic electron transport. Through his graduate-student research, he developed improved quantitative methods for probing photophosphorylation and photosynthetic electron transport in spinach chloroplast preparations. His first published manuscript describes a novel method to monitor the Hill reaction by spectral changes at 510 nm in a dye molecule (Krogmann and Jagendorf 1957). With his mentor (André Jagendorf) and a visiting scientist from Israel (Mordhay Avron), he provided some of the earliest details of the relation of phosphorylation to electron transport in chloroplasts (Avron et al. 1958; Krogmann et al. 1959).

In 1958, Dave accepted a postdoctoral appointment with Birgit Vennesland at the University of Chicago. There he provided further insight into photophosphorylation in the presence of oxygen, which was called “oxidative photophosphorylation” (Krogmann and Vennesland 1959; Krogmann 1960). His studies on photophosphorylation expanded into the characterization of soluble electron carriers and the decision to move from chloroplasts to cyanobacteria (then called blue-green algae). His comment on this decision was, “If you are going to escape from spinach chloroplasts, you might as well go all the way” (Krogmann 2000).

### 1960–1966: Research at Wayne State University

David Krogmann's graduate school and post-doctoral studies of the photosynthetic "light" reactions were expanded during his early independent career, in which he developed fruitful correspondence and collaboration with many scientists. He demonstrated a key role of plastoquinone in photosynthetic phosphorylation (Krogmann 1961; Krogmann and Olivero 1962; Lightbody and Krogmann 1966; also see a Tribute by R.A. Dilley (2016) to a faculty colleague of Dave, Fred Crane). Dave's very first PhD student was William Ogren (see below for his *Remembrance*). Dave soon recognized the advantages of cyanobacteria as experimental organisms, due to the relative ease of their laboratory culture and manipulation, the relative simplicity of their cell structure, their photosynthetic apparatus (which, in function, is almost identical to that of plants and eukaryotic algae), and the potential for their genetic modification.

Dave became increasingly adept at extracting and purifying soluble proteins from cyanobacteria. These biochemical studies, which became a major research theme throughout his scientific career, established his international reputation as a biochemist. *Anabaena variabilis* was the cyanobacterium of choice for many of his experiments. This research was initiated by Susor and Krogmann (1964, 1966) and by Duane et al. (1965); and, plastocyanin in this system was studied by Lightbody and Krogmann (1967). Soon thereafter, the Mehler reaction (i.e., reduction of oxygen) was examined by Honeycutt and Krogmann (1970, 1972).

### 1967–1998: Research at Purdue University

At Purdue, Dave's scientific interest remained centered on the soluble protein components attached to photosynthetic membranes of cyanobacteria. Much of his work concerned the molecular structure and function of these proteins. Often this research required copious amounts of material from a single species in order to extract, purify and characterize a substantial quantity of a specific protein. Dave's solution to the challenge of obtaining large quantities of cyanobacteria came to him during a vacation. As a houseguest of his sister in Washington, D.C., Dave read in *The Washington Post* of a bloom in the Potomac River and went to observe it with a microscope. He realized that this was a huge source of almost pure *Microcystis*, a cyanobacterium, which could be brought back to the laboratory for large-scale protein extraction and purification. For the rest of his career, Dave collected natural blooms of cyanobacteria from various lakes and rivers (Figs. 4, 5; see *Remembrance* of Toivo Kallas). Floating species were skimmed from the surface and deposited in five-gallon drums, typically about 10 per expedition, and transported back to his laboratory for drying and protein



**Fig. 4** A 1996 photograph of David Krogmann harvesting a cyanobacterial bloom from Candlish Harbor Creek, Oshkosh, Wisconsin. By this method, kilograms of biomass, predominantly *Microcystis*, could be collected for subsequent processing and purification of cytochromes and other interesting and unusual, sometimes rare, proteins for structure/function characterization. Photo by Toivo Kallas



**Fig. 5** Another 1996 photograph of David Krogmann near High Cliff State Park, Lake Winnebago, Wisconsin. Shown are David Krogmann (center), John Miller (left) and Alexander (Sasha) Tsapin (right) exploring a site on Lake Winnebago for possible cyanobacterial bloom collection. John Miller was a graduate student and Sasha Tsapin a senior research associate of Toivo Kallas at the University of Wisconsin Oshkosh. Photo by Toivo Kallas

purification. Mat-forming cyanobacteria were collected in buckets and sun-dried prior to transport back to his laboratory. He was probably one of the few people who greeted blooms of cyanobacteria (even toxic species) with pleasure. Dave realized that commercially cultivated *Spirulina* was also a useful source for large-scale protein extraction. Dave's observations of cyanobacteria in various natural environments, and the physical and chemical differences between cytochromes isolated from these diverse cyanobacteria (and from higher plants), led

to his interest over many years in evolutionary and environmental adaptations that might explain the observed differences.

William (Bill) Cramer, one of us, recalls that Dave Krogmann was a *pillar of photosynthesis at Purdue*. Bill noted that for something like 2 decades, Dave and his students contributed to the weekly Friday afternoon seminar, at which one could say “photosynthesis was significantly illuminated.” Dave made major contributions to the biochemical description of the soluble c-type cytochromes of the photosynthetic apparatus, mainly in cyanobacteria. Particularly notable contributions were (i) the description of the specificity of amino acid interactions of cytochrome *f* with plastocyanin and cytochrome *c*<sub>6</sub> (Ho and Krogmann 1980; Morand et al. 1989); (ii) the NMR studies of cytochrome *c*-553, in collaboration with John Markley and Eldon Ulrich (Ulrich et al. 1982); (iii) semiquinone electron donor reactions with cytochrome *c*-553 and plastocyanin, done in collaboration with T. Meyer, M. Cusanovich, and G. Tollin (Meyer et al. 1987); (iv) structure studies done with C. Kerfeld and T. Yeates (see below); and (v) some of the earliest primary structure analyses on the photosynthetic cytochrome system, with M. Hermodson and P. Chitnis (Cohn et al. 1989; Kang et al. 1994). Dave wrote (with C. Kerfeld) an important review on the topic of cytochromes (Kerfeld and Krogmann 1998), centrally important for photosynthetic energy transduction, of the electron transport function and position of c-type cytochromes in cyanobacteria, algae, and higher plants. (Also see *Remembrances* of Kwok (Phil) Ho, of Larry Morand and of John Whitmarsh.) Dave was always generous with his time and resources. On more than one occasion, his generosity of sharing resources of purified proteins, mainly plastocyanin, was noted by the students and postdocs in Bill Cramer’s laboratory; all of them respected not only his knowledge, but also his professional and generous sharing of precious resources.

As molecular tools became available, such as cloning of genes and, subsequently, whole genome sequencing, Dave readily adopted these approaches. In 1981 he published a paper describing a water-soluble carotenoid-binding protein that frequently co-purified with cyanobacterial cytochromes. He named the protein the orange carotenoid protein (OCP) (Holt and Krogmann 1981). Wu and Krogmann (1997) identified the OCP gene in the *Synechococcus* genome. The OCP is now known to govern photoprotection in cyanobacteria (Kirilovsky and Kerfeld 2016). Subsequently, the structure of the OCP was determined and shown to be a key response protein under stress conditions, particularly important in photoprotection and OCP-related research has become a field of its own.

Cheryl Kerfeld, one of the authors, was introduced to Dave by Sabeeha Merchant in the context of cytochrome research in the mid-1990s. Dave and Cheryl collaborated

on structural analyses of numerous cytochromes (Hervás et al. 2005; Ho et al. 2011; Kerfeld and Krogmann 1998; Kerfeld et al. 1997a, 2002; Sawaya et al. 2001); it was an ideal partnership, Dave providing pure protein and mentorship. The OCP was prepared by Dave and crystallized by Cheryl in the late 1990s. As was typical of the quality of Dave’s purified proteins, the OCP crystallized immediately (Kerfeld et al. 1997b), and its novel structure was reported (Kerfeld et al. 2003). Dave and Cheryl suggested that its ability to change color was a hint that it played a role in photoprotection in cyanobacteria, supported by the demonstration that the OCP quenched singlet oxygen species. Dave also isolated a proteolytic fragment of the OCP, red in color, that he called the Red Carotenoid Protein (RCP). A determination of its molecular structure revealed that the red color was the result of a substantial conformation change in the position of the carotenoid within the protein (Leverenz et al. 2015), a unique observation for carotenoid binding proteins. Dave’s support and encouragement was as essential to Cheryl’s career as much as the beautiful protein preparations he provided to her for study (see also Kerfeld 2016).

For research on plastocyanin and other intermediates, see *Remembrances* of Jerry Brand, Manuel Hervás and Don Ort.

#### 1999–2015: Research after retirement

Dave was provided a modest laboratory in the Biochemistry Department after his retirement in 1998. He could be found there virtually every weekday for nearly a decade, often preparing soluble extracts from cyanobacteria or performing chromatographic separation of proteins. For as long as his health permitted, he retained a keen interest in discussing with colleagues the roles of cytochromes and the OCP in cyanobacterial photosynthesis. Dave continued to do experiments and to support those he had mentored. He traveled to UC Berkeley (in California) in 2011 to show a member of the Kerfeld group, Ryan Leverenz, how to purify the OCP directly from cyanobacteria. Extraction tools included hammers and hair dryers, which resulted in high-quality protein suitable for crystallization. These “native source” preparation methods continue in the Kerfeld laboratory today, providing the material for new insights into structure and function of the OCP.

During his retirement years, Dave collaborated with one of us (G) on the historical aspects of photosynthesis (see *Remembrance* of Govindjee). Dave stayed in touch with professional friends and colleagues until his health failed. He remained immersed in studies of cytochromes, especially those from organisms living in cyanobacterial mats. Cheryl Kerfeld kept him informed of progress in OCP

research and frequently discussed over the phone Dave's findings about cytochromes.

### Service to the scientific community

Dave developed a keen respect for the instruments of government as a boy growing up in Washington DC. Accordingly, he readily accepted a position as Program Director of the Molecular Biology program of the National Science Foundation (NSF) during the last year of his tenure at Wayne State University (1966–1967). A decade later (in 1977) he returned to Washington as a Program Manager of the Photosynthesis Program in the US Department of Agriculture (USDA) Competitive Research Grants Office, followed by 2 years as head of that Grants Office, and then as a member of the USDA Policy Advisory Committee. He was instrumental in ensuring that for several years grants submitted to the USDA Competitive Research Grants Office were rigorously peer-reviewed for their scientific merit prior to making awards. He served on various panels of the NSF, USDA, US Department of Energy (DOE), National Institutes of Health (NIH) and the US National Academy of Sciences.

David was a meticulous scientific writer, which ensured that his published manuscripts were succinct and lucid. His critical thinking and editorial care made him an effective member of editorial boards on several international journals. He was always willing to critically examine the manuscripts of friends and colleagues prior to their submission for publication. These pre-reviews sometimes made the difference between journal acceptance and rejection.

David was an active member of his academic department, frequently serving on College and Departmental committees. He was especially interested in promoting effective undergraduate education and willingly taught the introductory course in his department. He served as acting Departmental Chairman in 1969–1970 while the Chairman and his best friend, Bernard Axelrod, was on sabbatical leave. This was the most turbulent year of the “1960s revolution” at Purdue, but Dave handled the ensuing confrontations in his department with unflinching grace and sensitivity.

David W. Krogmann developed many enduring friendships during his scientific career. These included not just his graduate students and collaborators, but technicians, departmental colleagues and scientific associates throughout the world. The admiration and friendship of some of these individuals is expressed in the following section.

### Remembrances

We provide below tributes first from the family (Michele Krogmann), and then from Dave's PhD advisor (André

Jagendorf) and his first PhD student (William L. Ogren). This is then followed by all others in alphabetical order.

**Michele Krogmann** (on her behalf, and that of Krogmann family; e-mail:shell301@yahoo.com)

When asked to write about our father and his scientific work, I decided to share some experiences that my sister (Patricia), brother (Paul) and I had while growing up. One fall, we all spent a Saturday on the Purdue University campus picking up and squeezing the seeds out of ginkgo fruits for an experiment Dad wanted to run. Our mother was at a home football game, so this was a perfect opportunity. Dad told us that sometimes you had to suffer for science—in this case the horrible smell of the ginkgos. When we got home, he had us change our clothes in the garage and Mom never knew.

At some point in our early teenage years we all worked at his lab in the summer to earn our bicycles and such. We washed “dishes”, cleaned the teaching lab and prepped spinach for experiments. We also proofread the galleys for his textbooks. I proofed a great many papers and dissertations for my father and his students and co-workers.

We all remember having the graduate students over to our house. We shared many holiday meals with students who were here over the school breaks. We also had parties featuring my Mother's famous lasagna and backyard cook-outs in the summer. I learned much about Chinese cooking from some of his students who would bring dishes or cook at our house. Many of his graduate students are still in touch.

My father helped all of us with our biology and chemistry homework while we were in high school. While in high school taking biology, we encountered student teachers, who had taken Dad's biochemistry class. This often made it hard for us to ask questions about photosynthesis in class.

There was always a bag of small plastic bottles in the trunk of our car. Whenever we were on a trip and Dad would see a pond with green growth on it, he would pull over to get a sample—whether it was on a busy interstate or quiet country road. I think we all still look in our travels for ponds that Dad might have found interesting.

Even near the end of his life he was still interested in the science that he had worked on for so long. My brother, Paul, and I often brought over news stories and magazine clippings about red tides, algal blooms occurring in drought-stricken areas and the like to him at the nursing home. He enjoyed hearing about these things.

While none of us have pursued careers in science, we all have very good memories of how our Father's work came into our lives.

**André Tridon (T.) Jagendorf** (Cornell University, Ithaca, NY, USA; e-mail: atj1@cornell.edu)

David Krogmann was my first graduate student. I was a fairly new Assistant Professor at The Johns Hopkins

University, and had no training as a teacher or supervisor. It was a learning period for both of us. *David turned out to be a wonderful learner; anxious to accomplish something, persevering in spite of initial difficulties. He helped other incoming students to find their way. I also found him to be a calm, kind, thoughtful, intelligent and upstanding person.* Although we did not keep up a close contact, I am sure his life has given meaning to a large number of people over the years.

**William L. Ogren** (Hilton Head Island, South Carolina, USA; e-mail: ogren@hargray.com)

David Krogmann was a major fork in the road my life has taken. After receiving my B.S. degree, I took an industrial chemist position at a company in Detroit. I entered graduate school at Wayne State University with the idea of taking some informational night classes and perhaps pursuing a graduate degree. My interests and expertise were inorganic and analytical chemistry. There were no offerings in these subjects at night but there was a class in biochemistry and, since the hours would count toward a degree, I decided to take it along with a course in chemical engineering. Dave was teaching the biochemistry course, made the subject interesting to me, and I did well on the exams. During the second semester, Dave asked me to have dinner with him one night before the class and made a strong pitch that I should give up my job and come work in his lab. My knowledge of photosynthesis was pretty slim as my biology background comprised only one survey course taken as an undergraduate, and the teaching assistant (TA)'s salary he mentioned was less than a third of what I was making as a chemist, so I expressed a lot of doubt about doing it. Dave persisted, explaining how important the subject of photosynthesis was and, for emphasis, brought up the fact that Melvin Calvin had recently won the Nobel Prize. This statement had zero impact on me and I actually asked, "So who is Melvin Calvin?" As always, Dave was unruffled by my obliviousness and continued to make his case. I told him I would think about it and, a couple of months later, I did wisely decide to quit my job and join his lab. Dave was at the beginning of his career (I was his first graduating Ph.D. student) and set a terrific example on how to work toward success, starting with asking important questions, designing incisive experiments, and just working hard. (See e.g., Ogren and Krogmann 1965.) He was the first one in the lab each morning but did have a young family and usually went home after the rush hour, while a couple of us unattached folks routinely pursued his work ethic well into the night and weekends. Dave was a kind and gentle soul, and never raised his voice. Our mistakes, and there were plenty of them, were met with soft-spoken encouragement on what we had done and suggestions on how we could maybe do it better. His patience with us inexperienced students was endless, and his quiet advice took firm hold. Most things I learned

about how to do science were from lessons Dave taught me, and for that I will be eternally grateful to him.

**Jerry Brand**, one of the authors of this Tribute, added:

I was a graduate student of Fred Crane (see Dilley 2016) in the Department of Biological Sciences at Purdue University when David Krogmann began his career in the Biochemistry Department. I was interested in Dave's work and visited him soon after his arrival. His laboratory was already full, since graduate students arrived from Wayne State University with him and he attracted others soon after arriving at Purdue. However, he and Fred Crane agreed that I could conduct most of my research in Dave's lab. Thus, I was mentored and encouraged by two outstanding scientists, and all of my publications from Purdue were co-authored by both. In Dave's laboratory, I explored photosynthetic electron transport in spinach chloroplasts while everyone else in the laboratory was using cyanobacteria. Utilizing resources in both the laboratories, we demonstrated that plastocyanin is essential for Photosystem I activity in highly enriched Photosystem I particles (Baszynski et al. 1971). This led to the discovery that polycations inhibit photosynthesis at a site between the two photosystems, at or near plastocyanin, facilitating full Photosystem II-mediated Hill activity to an indolephenol dye or ferricyanide with no interference from photosystem I (Brand et al. 1972). This served as a useful tool for biochemically isolating Photosystem II activity.

Dave served as a mentor well after I left Purdue and he remained a close friend through the remainder of his life. I visited him at Purdue almost every year and he visited me in Texas at least on 20 different occasions. During five of his visits, we collected massive quantities of the mat-forming cyanobacterium *Lyngbya wollei* from a nearby lake bottom. It was dried on my driveway and shipped to Purdue, where Dave utilized it for cytochrome extraction. Dave and I would talk by telephone almost every Sunday during the last 20 years of his life. He loved discussing science, scientific societies, funding agencies, and scientists. However, he was conversant in a broad range of topics, from science philosophy to politics. Dave's influence on my life is just one example of the profound effect he had on many individuals who crossed his path.

**Diego González-Halphen** (Instituto de Fisiología Celular, Universidad Nacional Autónoma de México, México D.F. Mexico; e-mail: dhalphen@ifc.unam.mx)

I met Dave many years ago when I was a Master's student in Carlos Gómez-Lojero's lab at CINVESTAV (Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional). Dave had come down to Mexico with several purified soluble *c*-type cytochromes from different cyanobacteria. His objective was to test their redox activity in *Spirulina maxima*, using a double-beam spectrophotometer. It was an exciting time for me, and I enjoyed

spending hours in front of the spectrophotometer. I also spent some time at Texcoco Lake collecting relatively large quantities of *Spirulina*. With time, and with every new visit, Dave discovered the way to navigate his way through the labyrinth of Mexican bureaucracy and managed to export several kilograms of frozen *Spirulina* back to his lab in order to study the endogenous cytochromes.

Dave taught “*How to Write a Scientific Paper*” at UNAM (Universidad Nacional Autónoma de México) a number of times (1998–2007). He spent two and a half weeks at my home while he was teaching this course. I remember that he especially liked February because it allowed him to escape from the last part of the long and harsh winter in Indiana. The writing workshop was offered by both the Biomedical Sciences Graduate Programs in Biomedical Sciences and Biochemistry, and was one of the official courses of these programs. This workshop became very popular, and the enrollment had to be closed a week after the course was announced. In order to remember the names and faces of all the students, Dave took their photographs in the first lecture. He worked intensely with the students in the class for two weeks, and then with every student individually. In the afternoons and weekends, he spent a considerable amount of time reviewing student’s papers. I usually took advantage of the situation to burden him with even more work, requesting him to correct the manuscript I was writing at the moment. I vividly remember that on two occasions, his voice started to fail at the end of the course, mainly because he had been talking continuously for several hours a day, every morning, for 2 weeks. On one occasion, we ended up visiting a doctor’s office to have his laryngitis treated, because his voice had completely gone. With time, he was able to identify some very common mistakes made by Mexican students when writing in English, and he developed an English-‘Spanglish’ glossary that helped students identify those grammatical errors. He called his glossary a “*Handout of things you will not find in the books*”, and this included some jewels like the following ones: “*relatedwith*” should be “*relatedto*”, and “*associatedto*” should be “*associatedwith*”; *English uses “the” and “a” or “an” more frequently than UNAM students do.*”

The last time he taught, Dr. Adolfo García-Sáinz, the Head of my Institute at UNAM, organized a special ceremony to thank Dave’s commitment and efforts in developing this course. Dave was presented a very nice silver plate with his name engraved. He also received on my behalf a fake diploma from Mexican Revolutionary times where he was depicted as a “bandido” with long moustache, bold enough to dare “invade” Mexico at many occasions.

When coming to Mexico, Dave never forgot to order “*enchiladas suizas*”, a dish of tortilla and chicken covered with mild tomato sauce and melted cheese, prepared at *Sanborns*, a popular chain restaurant in Mexico. When visiting

on one occasion, along with Jerry Brand, Dave was eager to have some enchiladas suizas, and we went directly from the airport to Sanborns in the downtown. During Jerry’s visit to Mexico, Dave was able to catalyze the start of a fruitful collaboration, which eventually crystallized in a paper coauthored by Jerry’s lab, Louise Lewis’s group from the Univ. of Connecticut and my own group (Rodríguez-Salinas et al. 2012). When visiting Mexico City, Dave would not forget to drink “*Negra Modelo*”, a popular dark beer that is served everywhere in Mexico. I usually bought a stash of *Negra Modelos* and kept them at home before Dave’s arrival. During one of his multiple visits, I remember the beer was out of stock for some time, and there was no way to find a single bottle of *Negra Modelo* in the Mexican republic for a week or two. During his visits, we used to take short trips around Mexico City, and some even longer ones—such as the ones through Chiapas with Carlos Gómez-Lojero and his wife Ember. A huge “*paella*” at Carlos’ place was also part of the protocol displayed every time Dave visited. In return, Dave visited my family during our sabbatical at the University of California at Riverside in 2000–2001.

I recall visiting Dave three times at Purdue. There I had the chance to meet his wife Loretta and their children Michelle, Pat and Paul. My first visit was in 1984. We then travelled along with Carlos from West Lafayette to Meriden, NH, to attend the Gordon Research Conference on Photosynthesis (Fig. 6). Dave made sure that each one of us did not drive for more than 3 h continuously; he watched out for the “Golden Arches” for a lunch break, and we stayed overnight not at an ordinary hotel but at a “place with character”. I visited him at two more occasions: The first occasion was a happy one when he celebrated his retirement, becoming Professor Emeritus at Purdue. The second occasion was a sad one as his beloved wife Loretta had passed away.



**Fig. 6** A photograph of a few of the participants at a Gordon Research Conference on “*Biochemical Aspects of Photosynthesis*”, held at Kimball Union Academy, Meriden, NH, USA, during August 20–24, 1984. From left to right, with arrows, Dave Krogmann, Carlos Gómez-Lojero, and Diego González-Halphen. Source: D. González-Halphen



I truly miss Dave's self-effacing and chivalrous attitude, his willingness to converse with all kinds of people, his determination to learn Spanish, his passion for Science, and his suggestions concerning research: “*when choosing your research interests don't follow the band wagon*”. Maybe someday we'll drink again a nice, cold Negra Modelo and talk some Science.

**Govindjee**, one of the authors of this tribute, added:

I remember Dave as a very kind and polite person. I was very happy that he came to attend my retirement symposium in August of 1999. An important aspect of his research life was his interest in *historical evolution of photosynthesis research*. After I coauthored a list of historical papers with him (Govindjee and Krogmann 2002), Howard Gest and Thom Beatty invited Dave to coauthor, with me a “Time-Line of Photosynthesis Research” from 1700s to 2000s, which he gladly accepted. It was published as Govindjee and Krogmann (2004); this article received much attention from many countries and two of us were invited in 2006 to republish an amended version by *Accademia Nazionale dei Lincei* in Italy, with enhanced photographs (see Govindjee and Krogmann 2006). I miss this wonderful gem of a person.

**Manuel Hervás** (Universidad de Sevilla, Spain; email: mhervas@us.es)

The death of Prof. David Krogmann has been really a great loss for all people working in photosynthesis. In the 1990s, our group started working on the iso-functionality of plastocyanin and cytochrome  $c_6$  admiring and recognizing the relevance of previous papers of Prof. Krogmann describing for the first time this heme protein. It was a great honor and a privilege to collaborate with him, although briefly, and at a “long distance”. We exchanged some extremely pleasant and helpful e-mails, and he showed to be always modest, not ever giving importance to his own great achievements. I have a profound admiration for him.

**Kwok Ho** (Biochemistry Department, Purdue University, West Lafayette, IN 47906, USA; e-mail: phokk@purdue.edu)

Dave was a teacher, mentor and dear friend to me. When I think of him, I remember how much he enjoyed teaching biochemistry to undergrads, mentoring graduate students on their research, and doing bench work. He also took his passion for biochemistry to places near and far to collect plant specimens. In fact, many of his summers were spent enthusiastically looking for cyanobacteria for protein purification. He once told me how he boarded a rickety old turboprop aircraft in Hawaii in search for his research specimens. Despite the bumpy rides and the nausea he experienced, he returned triumphantly with several kilograms of *Spirulina*. I think this particular example illustrates the passion he showed toward science and research.

Dave's humility and generosity are qualities for which I most admire him. On many occasions, he expressed to me how grateful he was to be born in the United States, with boundless opportunities to pursue his interest in science and to participate in the golden age of biochemical research in photosynthesis. I am sure his friends and students from Mexico can also attest to his passion for biochemistry as well as his generosity and willingness to share his knowledge and excitement for the subject. For many years, Dave committed a period of time each summer or fall tutoring Mexican students in writing English scientific papers. I recall the long hours he put in learning Spanish, organizing lectures, and revising students' research papers until they achieved an adequate level of understanding. I had the pleasure of witnessing this same generosity during his tenure as a Visiting Professor at the National University of Singapore while I was teaching there.

The last time my wife and I saw Dave was shortly before he passed away. Although he was too weak to carry on a conversation, I was still able to get a glimpse of his generous and compassionate nature. While we were interacting, I noticed he said something to the nurse who was taking care of him. I later found out that Dave had told the nurse he wanted to get us some ice cream. This small but meaningful gesture of friendship touched us deeply. One last thing you may not know is the work done on and off during his retirement. He left me with a paragraph that was intended to be the abstract of his last paper in photosynthesis, which I include below as an illustration of his enjoyment in his work on the cytochromes.

A Favorite Memory by D. W. Krogmann: “I have long been interested in the water cyanobacterial photosynthesis redox chain which is otherwise very similar to the chain in higher plants. Research on these chains is regularly done with axenic cultures grown in conditions optimal for photosynthesis. I happened on several small samples of an exotic cyanobacterium—*Lyngbya wollei*—and found that they release too many bands of cytochrome on ion exchange chromatography of extracts. K.K. Ho surveyed a large set of genomes of different strains of cyanobacteria and found that different strains had 1–3 additional cytochrome *c* genes that differed in isoelectric points. We collected cells from different lakes, in different seasons, with different light antennas, and different electron paths in photosynthesis. Some expressed different cytochromes that had never been seen before. It was lots of fun.”

**Toivo Kallas** (University of Wisconsin Oshkosh, WI, USA; e-mail: kallas@uwosh.edu)

David Krogmann was a great scholar, a wonderful human being, and a friend. I had the pleasure of getting

to know him over the years through photosynthesis and cyanobacterial meetings. He was an avid reader; he once gave me a book by Dava Sobel, *Longitude*, that describes the eighteenth century challenge of accurate longitude determination, the prize offered by the British Parliament, and the clockmaker who developed a reliable ship-board chronometer to solve the problem. David had a wealth of knowledge of history, photosynthesis, electron transfer, protein chemistry, and of course, cytochromes, and he was an excellent dinner companion and conversationalist. He visited us in Oshkosh, Wisconsin on several occasions and gave a great Microbiology Banquet seminar on “*Microcystis*, the oldest inhabitant of Oshkosh.” One of the photos (see Fig. 4), shown above in this Tribute, has David collecting cyanobacterial biomass from the creek behind our house and the other (Fig. 5, also shown above) shows him with a student and a colleague exploring another possible site on Lake Winnebago. Indeed, David took advantage of the massive, largely unialgal blooms of cyanobacteria on Chesapeake Bay and Lake Winnebago that enabled him to discover unusual cytochromes as well as the orange carotenoid protein (OCP), which has subsequently been shown to play a crucial role in excess excitation energy dissipation from photosystem II complexes of cyanobacteria. At the time of his 1996 visit, the first complete genome sequence of a cyanobacterium, that of *Synechocystis* sp. PCC 6803, had just emerged. True to his nature, David was excited by this new information, the insights it provided, and the possibilities that it raised. Further, he was equally excited by the metabolic behavior of cyanobacteria, in their microbial mats, and particularly the bubbles of hydrogen they produced! We had some great conversations. He will be greatly missed.”

**Larry Morand** (University of California, Davis, CA, USA; e-mail: lzmorand@ucdavis.edu)

I did my PhD in 1989, in Biochemistry, at Purdue University. Upon Dr. Krogmann’s passing, a peer of mine in graduate school, who is now the President of a private university, remarked, “He was the gentlest person I have ever known”. This reflected my experience as a graduate student in his lab from 1984 to 1989. This time-frame was late in his career, thus I was privy to his stories about previous graduate students. He shared joyful remembrances of everyone. My research interests were in photosynthesis and I had some fun delving into this favorite subject at the time. Sometime in my third year, I recall thinking, ‘If I never work in science again, I will be forever grateful to have worked for him’. He was a mentor in its truest meaning. My primary goal to earn a doctorate was to teach life sciences in college, which wasn’t respected by some other faculty or many of my peers, yet Dr. Krogmann fully supported my efforts. Today, I am fortunate to report that I have a successful and fulfilling career teaching upper

division biochemistry and molecular biology courses at a highly ranked R1 research university. My approach: *treat each student with respect and consideration; provide unsolicited encouragement when the opportunities present themselves; and regard all comments and inquiries as genuine. In the end, to offer what understanding, guidance, and, or support I am able to do. This is the legacy of Dr. Krogmann towards my students.*

**Donald R. Ort** (University of Illinois, Urbana, IL USA e-mail: d-ort@illinois.edu)

I was very fortunate to meet Dave Krogmann while still a PhD student with Norman Good and Sei Izawa at Michigan State University. In fact, Dave was a co-author on my very first publication (Ort et al. 1973). At the time, the number and location of “coupling sites” (i.e., electron transport reactions that are coupled to ATP formation) was still uncertain and dissecting these was reliant on the use of specific inhibitors along with artificial electron donors and acceptors to create electron transport partial reactions. While at that time there were an ample number of inhibitors that acted at or near PSII, only recently discovered KCN (Sei Izawa/Norman Good lab) and polylysine (Krogmann lab) treatments acted near PSI and were believed to be plastocyanin inhibitors. In this short paper, we showed that both of these inhibitors could be used to isolate PSI- from PSII-dependent ATP formation. After completing my degree at Michigan State University, and having moved to Purdue University to do a postdoc with Dick Dilley, I had many opportunities to interact with Dave that began a life-long friendship. While Dave always impressed me as a deep and insightful thinker he also had an amazing knack of capturing life lessons in memorable phrases. Two that I have passed along to countless students and postdocs are : “*It’s easy not to find something*” and “*You know that you are teaching just the right amount when you are looking forward to the start of semester and you are glad when it is over*”. Dave enriched the lives and careers of many people and I feel very fortunate to have been one of them.

**C. John Whitmarsh** (Board Member Association for Frontotemporal Degeneration, Sacramento, California, USA; e-mail: jwhitmarsh@me.com)

I first met Dave as a mentor and a friend when I was a postdoc in Bill Cramer’s lab. As I think on the times I spent with him, what stands out is his smile and his warmth. It was a delight to see him work with students, who he truly valued. As he shared his knowledge as a scholar and scientist you could see students opening up, sharing their own thoughts and ideas. He had the gift of presenting his science as a story, one that drew everyone in. I know that like me, there are many students, postdocs, and colleagues who look back and are grateful for the opportunity have known Dave. He made science fun.

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## Appendix

**Incomplete alphabetical list of coauthors of David Krogmann** (those deceased are indicated with an asterisk (\*)); prepared by Govindjee, Manuel Hervás and Rachel Weaver)

Jawed Alam; Bette Armstrong; Mordhay Avron\*; Rita Barr\*; Robert (Bob) C. Bartsch\*; Tadeusz Baszynski; Steven P. Berg; Andres Binder; Clanton C. Black\*; Vishnu Brahmandan; Jerry Brand; Ruth Butalla; Alfonso Cárabez-Trejo; Duilio Casico; Alicia Chagolla-López; Cheryl Chan; R. Holland Cheng; Parag Chitnis; Yoon Shin Cho; Dennis Cipolo; Cathleen L. Cohn; Kim K. Colvert; Fredrick L. Crane\*; Stephanie E. Curtis; M.A. Cusanovich; Danny J. Davis; Miguel A. De la Rosa; Antonio Díaz-Quintana; Richard A. Dilley; Maria Diverse-Pierluissi; S. Dodge; Warren C. Duane; William L. Ellefson; Paula Kay Evans; Melinda K. Frame; Martin Gibbs\*; Carlos Gómez-Lojero; Luis González de la Vara; Norman E. Good\*; Solon A. Gordon; Govindjee; Emma Berta Gutiérrez-Cirlos; Toshiharu Hase; Ruedi Hauser; Mark A. Hermodson; Manuel Hervás; Kwok Ki Ho; Mary C. Hohl; Thomas Kay Holt; Richard C. Honeycutt; Sei Izawa\*; André T. Jagendorf; Dale A. Johnson; Charmaine Kang; Cheryl A. Kerfeld; Joe Key; Shaw Shan Lee; James L. Lightbody; John L. Markley; Hiroshi Matsubara; Berger Mayne\*; Terry E. Meyer; Larry Zee Morand; Tokumasa Nakamoto; Seiichi Nakayama; José A. Navarro; William L. Ogren; Edwin Olivero; Donald R. Ort; Cathleen Lindsay Overholt; Mary P. Padgett; Antonio Peña-Díaz; Bertha Pérez-Gómez; Wendell H. Powers; Guadalupe Prado-Flores; Anthony San Pietro\*; Michael R. Sawaya; Richard Schneeman; Ahmen Serag; Stanley Smith; James Sprinkle; Mary L. Stiller; Walter A. Susor; Flora L. M. Tang; Gordon Tollin; Colleen C. Trevithick-Sutton; John F. Turner; Eldon L. Ulrich; Birgit Vennesland\*; Qingjun Wang; Richard A. Whitake; C John Whitmarsh; Yi Pyng Wu; Yasusi Yamamoto; Todd O. Yeates; and Michael Young.

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