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TRIBUTE

Recollections of Thomas John Wydrzynski

Govindjee

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Abstract In appreciation of his contribution to the Photosystsem II research and commemoration of the book Photosystem II: The Light-Driven Water-Plastoquinone Oxido-Reductase, co-edited with Kimiyuki Satoh, I present here some of my recollections of Thomas John Wydrzynski and by several others with whom he has associated over the years at Urbana (Illinois), Berkeley (California), Standard Oil Company-Indiana (Illinois), Berlin (Germany), Gothenburg (Sweden), and Canberra (Australia). We not only recognize him for his unique career path in Photosystem II research, but also for his qualities as a collaborative scientist working on the only system on Earth that has the ability to oxidize water to molecular oxygen using the energy of sunlight.

Keywords Contributions of Thomas Wydrzynski · First application of NMR to photosynthesis · Artificial photosynthesis · Mechanism of water oxidation · Bicarbonate in Photosystem II

Thomas John Wydrzynski was born on July 8, 1947, in St. Louis, Missouri. He received his BA degree (cum-laude) in Biology & Chemistry from the University of Missouri at St. Louis (UMSL) in 1969 and then studied Plant Physiology for 1 year at Queens University in Kingston, Ontario, Canada. He returned to Missouri and worked for the Metropolitan St. Louis Sewer District as a laboratory technician in industrial waste-water analysis before he entered graduate school.

From here on, his life has been in research, particularly on the mechanism of Photosystem II (PS II), the unique enzyme that oxidizes water to molecular oxygen. He has exploited the use of many biophysical techniques: nuclear magnetic resonance (NMR), electron spin resonance (ESR), Fourier-Transform Infra-Red (FTIR) spectroscopy, and mass spectroscopy, among others, to probe this system. One of his major achievements has been the use of ^{18}O isotope exchange measurements to probe the binding of the substrate water in the Oxygen Evolving Complex (OEC) (see Hillier and Wydrzynski 2007).[1] Tom's current interest is in artificial photosynthesis, an area important for developing clean fuels (see Wydrzynski et al. 2007). I shall now present, in an approximate chronological order, Tom's journey from Urbana (Illinois) to Canberra (Australia) with photographs and testimonials.

Tom entered graduate school in 1972 at the University of Illinois at Urbana-Champaign and received his PhD in 1977

In the fall of 1972, Tom entered the graduate school at the University of Illinois at Urbana-Champaign (UIUC) and came to work with me in the Department of Botany. He was already a mature and experienced student, and this combination had attracted me to his application. What was

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[1] For a full account of various biophysical techniques in use today, see Aartsma and Matysik (2008) and for a summary of Photosystem II, see Wydrzynski and Satoh (2005).

exciting to me is that he wrote: "My interests in the Plant Sciences lie in the areas of Physiology and Photosynthesis. My ultimate goals would be to work towards a PhD degree and enter a research oriented career in the field." He added "Although I am not completely decided, among the problems which I have considered for advanced study are the effects of environmental pollutants on the physiological responses in higher plants, particularly on photosynthesis." Well, I was impressed. In his letter of reference, Dr. R. G. S. Bidwell (of Queens University) wrote: "*He has certainly guts to go after what he wants* …." Marilyn J. Holtzer, who taught Tom Physical Chemistry at UMSL, wrote: "He is an intelligent person, a good student, and a conscientious worker. His written work was always well thought out and completed on time"; Monroe W. Strickberger, who taught Tom genetics and evolution at UMSL, wrote: "His academic performance in the course was excellent (Grade A) and he was one of the most industrious and conscientious students I have come across." Thirty-six years ago, after a visit with me in July, 1972, Tom wrote to me "I am, of course, very interested in your research in *Photosynthesis* and I am looking forward to the opportunity to work in your group this fall."

On May 25, 1972, I had written to Tom welcoming him to UIUC and informing him of three research areas that interested me: (1) excitation energy transfer, chlorophyll *a* fluorescence; and primary photochemistry in PS II; (2) mechanism of oxygen evolution; and (3) effects of pollutants (lead, mercury, and cadmium) on photosynthesis. I had thought that Tom would opt for #3 (because of what he had stated in his application), but after playing a bit on #1, Tom finally chose #2, but only after introducing a brand new angle to the field: the use of nuclear magnetic resonance relaxation measurements. Tom had entered UIUC as an MS student in Botany, but on November 16, 1972, he requested to transfer to a PhD degree in Biology (Plant Physiology).

Tom's appointments and research areas at the University of Illinois

For the interest of today's young scientists, I present here what I think shows how Tom supported himself while being a graduate student. Tom started his PhD in the Fall of 1972 working as a half-time Teaching Assistant in Botany for 9 months on a salary of $340 per month. I hired him as a half-time Research Assistant for the summer of 1973 from my National Science Foundation (NSF) Grant. During this summer, Tom began working on the effect of bicarbonate on the light reactions in photosynthesis that later led to the discovery of the role of bicarbonate on the electron acceptor side of PS II (Wydrzynski and Govindjee 1975; Khanna et al. 1977; see reviews by van Rensen et al. 1999; van Rensen 2005). While Tom was on his second teaching assistantship, he studied salt-induced changes in green alga Chlorella (Mohanty et al. 1974). This phenomenon was extended by him to higher plant thylakoids (Wydrzynski et al. 1975a) and during this study, he learned how to exploit chlorophyll *a* fluorescence[2] as a powerful tool to monitor photosynthetic reactions; this came in handy in his discovery that bicarbonate may function in plastoquinone reduction. However, this was not exciting enough to Tom for further research. *He had to have a problem that was his own—one that he had thought of himself; and this was the unique, first application of nuclear magnetic resonance relaxation measurements to the study of photosynthetic oxygen evolution* (Wydrzynski 1977). This idea came out of a biophysics techniques course taught by Paul Schmidt in the Chemistry Department at UIUC.

In the summer of 1974, Tom was hired again on my NSF grant, but now at $380 per month salary. Being impressed with Tom's achievements and hard work, I offered him a research assistantship for the Academic Year 1974–1975 as well. As I did with all other graduate students, I made the future research assistantships conditional on not only doing research, but on writing it up for publication in a refereed journal. The new salary was then $400 per month. During 1975–1976, Tom received a United States Public Health Service (USPHS) traineeship in Biology. This was assured for 12 months, but it had a lower monthly salary ($325 per month); however, he was free to do research in any area of his choice. He started this position on July 21, 1975. Fortunately, I was able to add to this stipend by hiring him at 10% time on my research grant, thus raising his monthly stipend to $403.83 per month.

Tom made enormous strides in his research on PS II. On April 1, 1975, I recommended him for acceptance at the forthcoming Gordon Research Conference on Photosynthesis to be held at Tilton School in New Hampshire (July 21–25, 1975) for presenting his discovery of the role of bicarbonate on the plastoquinone (also called "reduction" or "electron acceptor") side of PS II. Clearly, this research problem was not the one Tom had originally initiated. As mentioned above, he had invented his own PhD thesis problem and moved on to work on the use of nuclear magnetic resonance (NMR) methods to probe the role of Mn in oxygen evolution. I was delighted with Tom's independence and innovative approach. Although the Wydrzynski and Govindjee (1975) paper was the precursor to the discovery of the unique role of bicarbonate in PS II,

[2] For a full account of Chlorophyll Fluorescence, see Papageorgiou and Govindjee (2004).

it was initiated by an earlier, equally independent PhD student, Alan James Stemler (PhD, 1974), and studied thoroughly in my laboratory for almost 25 years. It was pursued with vigor and innovation by several other graduate students of mine (see Eaton-Rye 2007): Rita Khanna (PhD, 1980); Danny J. Blubaugh (PhD, 1987); Julian John Eaton-Rye (PhD, 1987); Jiancheng Cao (PhD, 1992); Chun-He Xu (PhD, 1992); and Jin Xiong (PhD, 1996); and research associates: Willem F. J. Vermaas; Jack J. S. van Rensen; and G. Sarojini.[3] All of us owe Tom thanks for his 1975 Biochimica et Biophysica paper!

As noted above, the first experimental evidence to indicate that Mn changes oxidation states during O_2 evolution was obtained in Tom's thesis and publications (Wydrzynski et al. 1975b, 1976, 1978). Tom had worked jointly with me and the NMR group at UIUC headed by world's leading NMR authority, the late Herbert S. Gutowsky, who took the very first NMR spectrum in 1952 (see Wydrzynski 2005). Those involved in the project were Paul G. Schmidt, Nick Zumbulyadis, and Steve Marks. On September 22, 1976, we had a full discussion on the topic of "NMR Investigations Relating to Photosynthetic Systems." Based on this extraordinary unique research, Tom was the first place winner in the Sigma Xi Student Paper Contest. It was a distinct honor recognized by the then Director of the School of Life Sciences at UIUC, Urbana, IL, Joseph R. Larsen, who wrote a congratulatory letter to Tom; it was dated August 22, 1977. Tom received his PhD in June, 1977.

Recollections by Prasanna Mohanty, Barbara Zilinskas, and Rita Khanna

Figure 1 shows Tom's photograph with some of his contemporaries in my laboratory. Prasanna Mohanty (PhD, 1972, shown in the bottom panel of Fig. 1), Barbara Zilinskas (PhD, 1975, shown in the top left panel of Fig. 1), and Rita Khanna (PhD, 1980, shown in the top right panel of Fig. 1) have provided their recollections, reproduced below. In addition, Paul Jursinic (PhD, 1977, shown in a later figure), and Julian Eaton-Rye (PhD, 1987, shown in the bottom panel of Fig. 1) have also provided their recollections in later sections of this paper.

Prasanna Mohanty (Regional Plant Resource Centre, Nayapalli, Bhbaneshwar, Orissa, India), who did not overlap with Tom, but met later, recalled:

"Just before returning to Jawaharlal Nehru University (JNU) from Yellow Springs, Ohio, where I was working with Bacon Ke, I stopped by at Govindjee's laboratory. I entered the Morrill Hall and went to look for Beloko, as I fondly addressed Alan Stemler. His "Joliot Electrode" room was locked. But the main lab, where I used to work, was open. A young handsome man was sitting at the desk where I used to sit. I went straight to him and introduced myself; he smiled and told me, "I am Tom Wydrzynski, a coauthor of your paper (Mohanty and Govindjee 1974), and this is my first paper from this laboratory." It was indeed a pleasant encounter. Beloko came and we went out for coffee.

The very next week, Tom took me to the Noyes lab to show the NMR equipment. I do recall that Rita Khanna, another student of Govindjee, was there. Tom asked me if I had read papers on Chloride-NMR; I did not hesitate to show my ignorance. But I did disclose that I had taken Physical Chemistry courses at the UIUC (University of Illinois at Urbana-Champaign). For two long hours, Tom elaborated his ideas and approaches to explore the OEC. During the same period, Beloko was at the "Franck-Condon state," i.e., in an excited state, with his bicarbonate and formate effects on Photosystem II (PS II). That was one of the many "discovery periods" of Govindjee's lab. My stay in my old lab was short, but very exciting in the midst of my friends and colleagues.

Tom and I met again in 1980 at the Photosynthesis Congress in Greece. George Akoyunoglou (the Chair of the Congress) was kind enough to include me as a participant in the "Herbicides and Heavy Metal Discussion Session." After the session, I was very hungry and searching for a way to cash a twenty dollar American Express check. Suddenly, Tom appeared on the scene and gallantly offered me as loan, a "Five US Dollar Bill." Indian television puts out a beautiful advertisement called "Happy to help and Happy to get help." Whenever I see that advertisement, I remember and realize the many helping hands that were there during my "Breaking In" years of my life in Govindjee's lab (see Eaton-Rye 2007). Subsequently, Tom and I have met many times and exchanged notes, and through these meeting and notes, I have felt not only the depth of his scholarship, but also his humanism. Each meeting with Tom had a beautiful feeling. Tom readily reveals the "inside-out" of his personality, and no wonder, he from the outside easily peeps into the interior of Photosystem II. I must also add here that I took the decision to send my daughter Meeta to study in Canberra, Australia, because I knew that Tom was nearby, and he would help her, if she needed any. Thank you, Tom."

Barbara Zilinskas (Department of Plant Biology and Pathology, Rutgers University, New Brunswick, NJ, USA) who was in the lab when Tom came, wrote:

[3] For references, see Govindjee and van Rensen (1978, 1993), Stemler (1982, 2005), Vermaas and Govindjee (1982), van Rensen et al. (1999), and Eaton-Rye (2007).

Fig. 1 (*Top left panel*) A group photograph of Govindjee's laboratory at the University of Illinois circa 1975. Front row: Govindjee (on the floor), Rudolph Slovacek (standing, visiting student from Rochester University), Barbara Zilinskas (PhD, 1975), Daniel Wong (PhD, 1979). Back row: Ralph Schooley (MS, 1976), David vanderMeulen (PhD, 1977), Tom Wydrzynski (PhD, 1977), and Alan Stemler (PhD, 1974). Source: Figure 3 in Eaton-Rye (2007). (*Top right panel*) A late 1970s photo taken on the waterfront in St. Louis, Mo. Left to right: Daniel Wong, Rita Khanna (PhD, 1980), and Tom. Source: Rita Khana. (*Bottom panel*) A photo of Govindjee and his past students taken in Nagoya, Japan, during the 9th International Congress on Photosynthesis. Front row: Julian Eaton-Rye (PhD, 1987), Govindjee, Tom, and Prasanna Mohanty (PhD, 1972). Back row: Danny Blubaugh (PhD, 1987) and George C. Papageorgiou (PhD, 1968). Source: Govindjee

"I had the good fortune to overlap with Tom Wydrzynski in the Govindjee laboratory when he was embarking on his PhD research and I was finishing mine. Tom struck me then as a serious and creative student who was bent on tackling an important problem with all the intensity that it deserved. He was quiet and shy, but Rita and I worked hard to loosen him up and involve him in the many shenanigans we would concoct. Over those 2 years in Urbana, I learned that Tom was not only talented and clever but he was also kind and compassionate.

Time passed and the closely-knit Govindjee lab group of the 1970s dispersed across the nation. I fondly remember the first reunion of a subset of the group at an annual meeting of the American Society of Photobiology, followed by a vacation to Virginia Beach and Chincoteague Island where Tom rose before dawn to see the sun rise over the bay. A week of carefree fun ended at Rita's new home in Bethesda where Tom and Rita coerced me into joining them in the midnight premier of Star Wars (Empire Strikes Back) at the local theater, where I enjoyed a deep sleep from the beginning to the end. Those were the days!

Tom Wydrzynski went on to do amazing things in science. Early in Tom's career, I recall admiring his conviction, while at the same time questioning his wisdom, when Tom chose to leave a secure, high paying position in industry for a temporary, postdoctoral fellowship in Berlin. It was simple he said—I want to continue to study Photosystem II, and Standard Oil will no longer let me do this. How smart Tom was in his decision! His passion to understand the mechanism of the water splitting reaction has provided him an unparalleled opportunity to use his ingenuity and sharp intellect to dissect a very important problem. His contributions toward satisfying this passion have been remarkable. Moreover, what more could any mentor want than to witness his students receive international acclaim?"

Rita Khanna (International Technology Transfer Management, Washington, DC, USA) wrote:

"I met Tom Wydrzynski in Professor Govindjee's laboratory in 1974 where I came to do my graduate studies in photosynthesis. I was fortunate to have overlapped with Tom and did experiments to decipher the precise site of

bicarbonate effect in the electron transfer reactions on the acceptor side of PS II using biochemical methods (Khanna et al. 1977). Tom was an inspiring colleague and a very helpful and a sincere friend. From the day I joined the laboratory, I was impressed with his dedication and commitment to photosynthesis research. He was a pioneer in the sense that he was the first to use the NMR technique for photosynthesis research. It was because of Tom that I learned the value of this technique and to use it in my own research. Over the years, Tom's passion and commitment to photosynthesis research remained exemplary, and he has made many significant contributions to the field.

I remember the great times we shared along with the others in Govindjee's lab. Tom was a special friend who was always there to provide help and support in and outside the lab, who always saw the best in life and in people, who loved classical music (Carmina Burana, especially), science fiction, and his sporty Camaro (which he could drive without using his hands). I still remember the weekend cooking sessions with Tom and Daniel Wong when each one of us had to cook something special and exotic. It is for all of these qualities and memories, that I remember Tom with enormous respect and affection."

Tom in Berkeley, California: November 1977–September 1979: Research Associate, Laboratory of Chemical Biodynamics, Lawrence Berkeley Laboratory, Berkeley, California

I will no longer discuss details of Tom's research life after 1977, but instead, present some selected personal remarks from some others with whom Tom worked with. Tom left with a PhD (in Biology, in 1977) from the University of Illinois, and went to France on a NSF Energy-Related Postdoctoral Fellowship (which he had won in 1976; it provided a stipend of $12,000 for one year) to work with the late Jean-Marie Briantais and Anne-Lise Etienne in Gif-sur-Yvette, France, for 3 months (as an aside, Jean-Marie had earlier been my post-doctoral associate). After this brief sojourn to France, Tom went to work with Kenneth Sauer at the University of California at Berkeley. Chuck Dismukes and Harry Frank were also postdocs with Ken at the time. When Tom reached Berkeley, he wrote me a long hand-written letter on October 26, 1977. In this letter, he described the experiments he was going to do there and that he was going to be using EPR to probe Mn and would be involved with Mn Extended X-ray Absorption Fine Structure (EXAFS) measurements that Mel Klein had begun. Together with others, Tom participated in one of the earliest papers on the state of the manganese in photosynthesis using X-ray absorption spectroscopy (XAS) (Kirby et al. 1981).

Kenneth Sauer (Department of Chemistry, University of California-Berkeley), Tom's post-doc advisor, remembered:

"Tom arrived in Berkeley in 1977 for a 2-year stay following a period of 4 months working with Jean-Marie Briantais and Ann-Lise Etienne in France. He proceeded to follow up on experiments that he had begun in France using a brief heat treatment to block Photosystem II (PS II) O_2 evolution and cause the release of Mn from broken spinach chloroplasts. Using EPR to detect the amount of aqueous Mn^{2+} released, he found that this amount was decreased relative to a dark-adapted sample if the chloroplasts were pre-illuminated prior to the heat treatment. He provided evidence that the EPR-undetectable Mn was produced as Mn(IV) O_2. He then carried out a series of flash-train studies using 0, 1, 2, 3, or more flashes, followed by heat treatment. Assuming that any Mn(III) present in the sample would disproportionate into Mn^{2+} and Mn(IV) O_2, he interpreted his results to signify that Mn oxidation occurs during the $S_0 \rightarrow S_1$ and $S_1 \rightarrow S_2$ transitions, but not during $S_2 \rightarrow S_3$. He proposed that during the latter transition, bound water became partially oxidized, rather than a further increase in Mn oxidation (Wydrzynski and Sauer 1980). This ingenious and highly original work was little noted at the time. It remained for Johannes Messenger, following a period in Tom's lab, to come to Berkeley and lead a project involving single-turnover flashes applied to PS II preparations to show, using X-ray absorption spectroscopy (XAS), that the pattern of Mn oxidation-state changes that Tom proposed is verified by Mn K-edge XAS (Messinger et al. 2001). *To my mind, this is an outstanding example of a creative imagination supported by sound chemical thinking at work*."

Back at the University of Illinois for 1 year, Research Associate, 1979–1980

Before Tom's tenure at Berkeley had ended, Herb Gutowsky and I wanted him to come back to Urbana for a year or two. Gutowsky, in his letter to Tom of March 5, 1979, made the suggestion that he could work with us on ESR or on EXAFS (at Argonne National Lab) and added "*And no doubt you have more ideas than any five people can carry out!*" On March 21, 1979, I offered Tom $1,000^{+}$ per month salary for a Research Associate's position in the general area of "Photosystem II" on my NSF grant. On April 4, 1979, he responded in the affirmative and suggested. "If necessary, however, I can begin as early as July 15, 1979." This was a time when Tom made many crucial and critical experiments and focused on understanding the entire problem of water oxidation to molecular oxygen. I presented a summary of the NMR and

EPR work at the 5th International Congress on Photosynthesis, Kalithea, Kassandra, Halkidiki, Greece (Govindjee and Wydrzynski 1981). In a review article (Wydrzynski 1982), Tom summarized the entire process of oxygen evolution, as it was known then.

Research Chemist, Biotechnology Division, Corporate Research, Standard Oil Company of Indiana (AMOCO Corporation), Naperville, Illinois, July 1980–November 1984

Tom decided to take up employment in the private sector after a year's stay with us in Urbana. In June, 1980, he joined Standard Oil Company (Indiana) in Naperville, Illinois, as a Research Chemist in its Corporate Research Division. He set up a lab with Larry Morrison to work on the applications of photobiological systems and artificial photosynthesis. During this time, he discovered a peculiar effect of lauryl choline chloride (LCC) on PS II: apparent period 4 oscillations in delayed light emission without observable oxygen evolution!

Brad Huggins (Analytical Department, Corporate Research, British Petroleum Company Ltd), a friend and former colleague of Tom while he was at Standard Oil wrote:

"Govindjee, Thanks for the opportunity to provide some feedback on Tom Wydrzynski, from his Standard Oil (Indiana) days. In 1981, I joined Tom as his assistant in the Photobiology Lab at Standard Oil (Indiana), Corporate Research Group, Biotechnology Division. Tom had great ambition and a vision then to advance the basic working knowledge of light harvesting, Photosystem II (PS II), and PS I in photosynthetic systems; and from this platform of understanding, *Tom wanted to develop artificial photosynthetic systems*. One of my early tasks was to begin the purchase of chemicals forming a library of components that had promise in this plan. Ruthenium metal complexes were among those.

Of course, we had many tangents to follow, and since it was really only the two of us working on the photosynthesis theme, we were hands-on involved with many different tools, techniques, and technologies. We poked-at, prodded, and perturbed spinach thylakoid membranes from every direction that Tom could imagine. We used solvents, detergents, and a variety of other agents to pull and separate the membrane components and found some interesting results. We reported some unique changes when we used methyl ethyl ketone (MEK) and lauroyl choline chloride (LCC) (see Wydrzynski and Huggins 1983). In those days, our Company was very supportive of this basic research effort and soon Tom had plenty of specialized tools to utilize—from basic oxygen electrodes and electrophoresis gear to advanced spectrophotometry and fluorometry, including electron microscopes and electron spin/paramagnetic resonance. Tom kept old and formed new alliances with colleagues at Universities and Governmental Labs, greatly extending our two person effort. Our Division Manager, Cavit Akin, supported and championed Tom's research and project ideas, and in a few short years, we felt that we had accomplished much. At least enough to pique Tom's interest to continue his research path on his own, as Standard Oil tightened budgets and began to slash Research & Development (R&D) efforts. By 1984, Tom was already off to Europe to go on his own, but not before he had made many friends and formed great bonds with the people around him. And, he did live in my basement for a few months! He is and will always remain a true friend. It is very satisfying and even fulfilling for me to see the products of success in Tom's career. I do want to tell a story: Once, we were on a crude off-road trail, a bit stuck in the mud, and partially lost in the wilderness of a Northern Minnesota National Forest. I was busy in proclaiming to know where we were and how to get back, while, Tom wanted to continue our journey down the trail. We did both and didn't get lost. We played a lot like we were working together in the Lab!

My hat is off to Tom and the others of you, his colleagues, who have kept the Vision of, and remained on the trail to understanding (and eventually to mimic) the chemistry of photosynthesis, as Tom is currently doing in his Lab."

Paul Jursinic (Medical Physics, West Michigan Cancer Center, Kalamazoo, MI, USA) recalled about this time as well as his earlier association with Tom:

"My friendship and scientific interaction with Tom began in 1974 when I returned to graduate school at the University of Illinois at Urbana-Champaign, after serving 3 years in the US Navy. We were both in Govindjee's laboratory studying the process of oxygen evolution in higher plants. Tom was applying magnetic resonance spectroscopy techniques in order to better understand the molecular mechanism of water splitting, energized by the Photosystem II reaction center. I remember Tom as a cheerful and insightful colleague. He always had a quick understanding of experiments carried out by others and was generous with his suggestions and positive criticisms. He mastered experimental details and strived to give unbiased and globally applicable interpretations of his results. He could move beyond his own point of view, which I later appreciated to be a unique trait. Tom helped me in my thesis work by assisting me in formulating a magnetic spectroscopy method for measuring phase transitions in thylakoid membranes. These experiments provided an independent technique for monitoring a physical change in

the membrane. This was a great help to me in my study of temperature effects, with Govindjee, on delayed fluorescence that emanated from the PS II reaction center (see Jursinic and Govindjee 1977).

Later, long after our PhDs, Tom and I published two papers together (Wydrzynski et al. 1984, 1985) that characterized the effects of lauroylcholine chloride, LCC, on the water-splitting mechanism. LCC is a choline/fatty acid that at low concentrations decoupled oxygen evolution from electron flow through PS II. Mechanism of the LCC still remains to be fully understood (Eckert et al. 1988). Tom's understanding of membrane biophysics coupled with measurements of chlorophyll *a* fluorescence, delayed fluorescence, and oxygen yields following microsecond-duration light flashes gave rise to experiments that depicted an unusual alteration of PS II photochemistry; no oxygen evolution but continued electron flow that even showed flash periodicity in microsecond range delayed fluorescence. Tom's enthusiasm for experiments was infectious and it really brought an element of fun and excitement to long hours of work.

As I think of Tom, the word that continues to come to my mind is "humility." *He is an ideal colleague: extremely intelligent, self-effacing, hard working, honest, and a genuinely nice person*. The years I spent doing research on photosynthesis were greatly enhanced by the friendship and scholarship shared with Tom. I congratulate him on his professorship and extend my wishes for a continued productive career."

Germany, Japan and Sweden: Research Scientist, Max Volmer Institute for Biophysical and Physical Chemistry, Technical University Berlin, Berlin, Germany, January 1985–August 1991

Tom started work with Gernot Renger, already in December, 1984 at the Max-Volmer Instituite, Technical University, in Berlin. He held, in Berlin, a Humboldt Fellowship in 1985 (8 months) and again later in 1988 (4 months). In the last 4 months of 1985, he held the Japanese Versailles Fellowship with Yorinao Inoue at RIKEN, Wako-Shi, Saitama, Japan. This was followed by a Wennergren Fellowship (for 1 year) and he worked with Tore Vänngård at Chalmers University in Gothenburg, Sweden for 2 years; he also collaborated with Lars-Erik Andréasson and Örjan Hansson. Then, he returned to Renger's laboratory in April, 1989, and stayed there for 2 years on a DFG (Deutsche Forschungs Gemeinschschaft) grant before moving to down-under Australia.

Figure 2 shows selected photos taken in Germany, Sweden, Russia, and Japan. I will refer to them later as well. Figure 2 (top left): a photograph of Tom with his dog Diets when he was in Berlin. Figure 2 (top right): a group photograph, taken on the Technical University (TU) campus, with Gernot Renger and others. Figure 2 (middle left): with Lars-Erik Andréasson and others, in Sweden. Figure 2 (middle right): Tom in the Lab in Pushchino, Russia, with Gennady Ananyev. Figure 2 (bottom left): with Yorinao Inoue, Gernot Renger and Hermann Gleiter in Berlin; and Fig. 2 (bottom right): A Japanese telephone card showing Photosystem II (slightly modified by me).

RIKEN, Japan

Tom worked with Yorinao Inoue at RIKEN, Wako-Shi, during late 1985, where he probed the binding of various quinones at the Q_B binding site using thermoluminescence techniques. These findings have been published (Wydrzynski and Inoue 1987). Figure 2 (bottom left) shows Inoue wearing a tie and a drink in his hand.

Tom with the Photosynthesis Group in Gothenburg, Sweden, 1986–1990

Tore Vänngård (Department of Chemistry, University of Gothenberg, Sweden) remembered:

"Tom worked with us from April 1986 until April 1988. Our department has a biochemical section, at that time headed by Dr. Malmström, and a biophysical section, then headed by myself. Much of our work is related to electron-transfer processes and the energetics in biology. One of the groups studies the primary processes in photosynthesis and it was for that reason that Tom spent 2 years in our laboratory. By the time Tom came to us, the mechanism of oxygen formation in PS II was largely unknown. Together with Jonas Ångström, Tom found that hydrogen peroxide was produced under conditions when the oxygen formation was hampered, which had some implications for the mechanism (Wydrzynski et al. 1989).

It was a great pleasure to work with Tom. He certainly became a good friend to all of us!"

Lars-Erik Andréasson (Department of Chemistry, University of Gothenberg, Sweden) wrote:

"Although acquainted with Tom's work from his publications, I first met him at the Gordon Conference on Photosynthesis, held in 1985. During his 2-year stay in Gothenburg we had plenty of time to exchange ideas about our main scientific interest, oxygen evolution, but also to see each other a lot under more relaxed circumstances. Tom celebrated a traditional Swedish midsummer at our place on the Swedish west coast (see Fig. 2, middle left) and our two

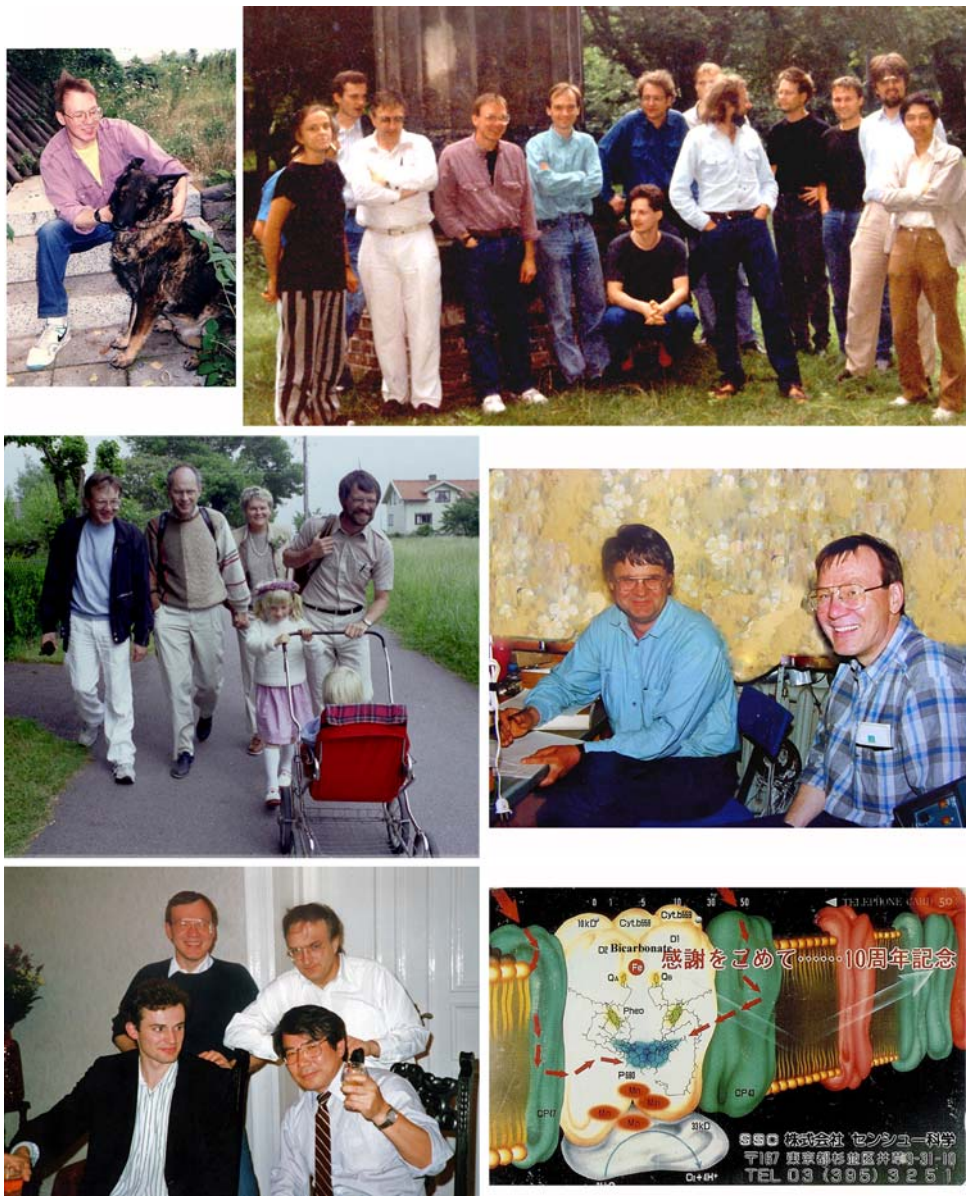

Fig. 2 (*Top left panel*): Photograph of Tom with his dog Dieter (Diets) taken in Blankenfelder, Berlin, 1991. Source: Tom Wydrzynski. (*Top right panel*): A group photograph of Gernot Renger's laboratory at the Max Volmer Institute, Technical University Berlin, circa 1988. From left to right: Bettina Geiken, Herrmann Gleiter, Gernot Renger, Tom, Johannes Messinger, Ullrich Wacker (black T-shirt), Bertram Hanssum (blue shirt), Hann-Jörg Eckert (in front), Klaus Dieter Irrgang (almost completely hidden by Hann-Jörg), Frank Reifarth, Artur Napiwotzki, Raimund Fromme, and Baining Liu. Source: Johannes Messinger. (*Middle left panel*): Midsummer celebrations in 1986 outside of Gothenburg, Sweden. Left to right: Tom, Karl-Erik Falk (Tom's backgammon partner and an associate of Mel Klein at UC-Berkeley), Catharina Falk, Lars-Erik Andréasson and his two daughters Anja and Åsa. Source: Lars-Erik Andréasson. (*Middle right panel*): In Vyacheslav Klimov's laboratory, Pushchino, Moscow Region, circa 1989: Tom and Gennady Ananyev. Source: Gennady Ananyev. (*Bottom left panel*): In Berlin, circa 1988. Standing: Tom and Gernot Renger. Sitting: Hermann Gleiter and Yorinao Inoue (of RIKEN, Wako-Shi, Japan). Source: Tom Wydrzynski. (*Bottom right panel*): A scan of a special Japanese telephone card showing Photosystem II (PS II) in full view. The author (G) has modified the card by adding "bicarbonate" on its electron acceptor side (Wydrzynski and Govindjee 1975)

little girls absolutely loved Tom and his big German shepherd Dieter (Fig. 2, top left), especially after he presented them with a very nice toy train (which we still keep).

Wydrzynski et al. (1990a) paper, done in Gernot Renger's Lab, really turned my attention to the role of chloride in PS II, an issue which I now could discuss directly with Tom and which came to occupy my co-workers and me for several years to come. I also had the privilege to collaborate with Tom on the work, which led to a joint publication on the use of radioactive chloride to track the binding to PS II (Lindberg et al. 1990; Wydrzynski et al. 1990b).

We have recently resumed our collaboration, now on the kinetics of water binding using the powerful isotope/mass spectrometer technique developed by Tom and his collaborators."

Örjan Hansson (Department of Chemistry, University of Gothenberg, Sweden) recalled:

"During most of Tom's time in Gothenburg, I was a postdoc with Paul Mathis at Saclay, France. But as I returned to Gothenburg, Tom asked if I was willing to co-author a review on PS II for Photosynthesis Research. Eager to learn more about PS II from Tom's vast knowledge, I accepted of course. There were plenty of PS II reviews around by then. But when it came to illustrating the article, Tom said that he didn't want to use his "fishy" model (see Fig. 3). So he spent quite some time with the artist, Lisa Fernold, to get it right. We had lots of fun when the end result looked like a crab! (Hansson and Wydrzynski 1990)."

Tom in Berlin (Germany) and Pushchino (Russia)

Tom worked in Berlin in the research group of Gernot Renger. He had a very productive research time there, some of which included additional collaboration with other

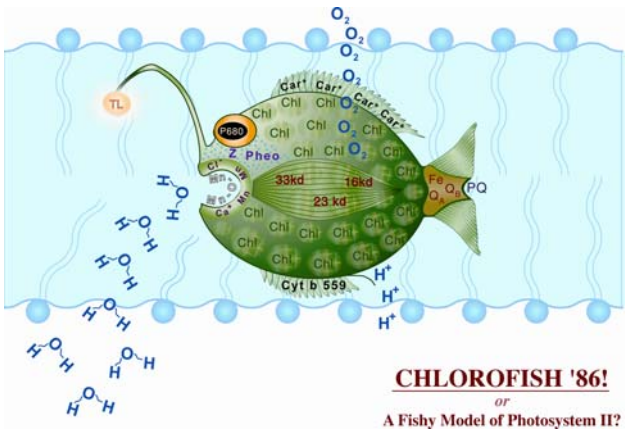

Fig. 3 A cartoon called Chlorofish 86 for Photosystem II (PS II), reproduced here for fun. Here, PS II is envisioned as green, chlorophyll-scaled complex swimming through a lipid stream gobbling up little water molecules. The manganese-containing teeth, which is activated by the P680 eye, breaks down the water molecules into bubbles of O_2 by a secret process hidden by the three extrinsic attachments and extrudes H^+s through the posterior port. The electrons are passed on through the tail to the next complex swimming in the stream, mediated by plastoquinone molecules, while the excess light absorbed by the chlorophyll-scales is somehow emitted through the anterior protrusion. TL stands for thermoluminescence; Car for carotenoids, and other labeled components have their usual meanings. This cartoon was evolved by Tom from an earlier bare-bone, much simpler, fun cartoon that was drawn by Rita Khanna and Tom Wydrzynski in Govindjee's lab when Tom and Rita were students there. Source: Tom Wydrzynski

research groups. This research concentrated on three related topics: (a) probing the oxygen evolving complex (OEC) through the use of EDTA (ethylene diamine tetraacetic acid), lauryl choline chloride and other chemicals (Wydrzynski and Renger 1986; Eckert et al. 1988); (b) understanding the role of chloride in OEC (Wydrzynski et al. 1990a, b); (c) understanding peroxide formation in OEC (Ananyev et al. 1992; Klimov et al. 1993).

Figure 2 (top right) shows a photograph of Tom together with Gernot and Johannes Messinger and many others in Berlin (see the figure legend for the names of everyone in the group); also see Tom's photo with Renger (Fig. 2, bottom left).

Hann-Jörg Eckert (Max-Volmer-Laboratorium, Institut für Chemie, Technische Universität Berlin, Germany) added his recollections:

"Tom was at the Max Volmer Institute of the Technical University in Berlin from the late 1980s until the end of 1991. In my experience, Tom is a person of high integrity and I, and my family, soon developed a close friendship with him. *Because of his positive outlook, his sensitive, perceptive nature and his ability to engage in constructive, stimulating discussions, it was always very pleasant to cooperate with him in scientific work* (see Eckert et al. 1988). After the fall of the Berlin Wall in 1989, Tom was quickly able to establish friendly contact with East Berlin scientists. His empathy and understanding was not just limited to the people he came in contact with but included the animal world, and most especially at this time his dog, Dieter, a German Shepherd that he had brought to Europe with him from the US (Fig. 2, top left panel). When Tom left Berlin to go to Australia, he was, unfortunately, not able to take Dieter with him as a result of the strict immigration regulations. Some months before his departure, he had secured a home for Dieter with friends who had a house and a big yard on the outskirts of Berlin and where he frequently visited Dieter. After Tom left for Australia, Dieter missed Tom so much that one day he just took off to find his master. After 2 days, Dieter was found near the Technical University where Tom had been working. Police had noticed him, were able to identify him by his markings, and informed his new owners. Looking for Tom, Dieter obviously had made it through 10 miles of city jungle in his search for Tom until he finally reached as close as he could to the place where Tom had been."

Johannes Messinger (Department of Chemistry, University of Umeå), a student of Gernot Renger, and former postdoctoral associate of Tom (after Tom had settled in Australia), recalled:

"I met Tom in 1989 in Berlin when I started my Diploma Thesis (later PhD) in the group of Prof. Gernot

Renger at the Max-Volmer Laboratorium of the Technical University (TU), Berlin. Tom worked in this lab as a postdoctoral research associate, first with a prestigious fellowship from the Humboldt foundation and later with a grant of the German Science Foundation (DFG). Tom loved his German shepherd and one of my first impressions about him is that he used to bring the dog into the lab until the cleaning personnel complained about all the hair. (Fig. 2 (top left) shows Tom with his dog Diets.) Over time, Tom and I became very good friends, especially through our common trip to Pushchino in 1991 (see a photograph of Tom, together with Gennady Ananyev; Fig. 2 (middle right)). In the laboratory of Slava Klimov, we performed experiments on peroxide formation in variously treated PS II preparations using Gennady's highly sensitive membrane covered oxygen electrode (Ananyev et al. 1992). Further, during our common time in Berlin, we had many very insightful and enjoyable discussions on water splitting in PS II.

In August 1991, Tom left Berlin to take up a position at the Research School of Biological Sciences (RSBS) at the Australian National University (ANU) in Canberra, Australia. Since I missed the discussions with Tom, I was more than happy to apply for an Australian Research Council (ARC) postdoctoral fellowship to follow him to Canberra, as soon as he mentioned this possibility. After our arrival in Australia in July 1993 (only a few days after my PhD defense), Tom took great care of my young family and we had several trips together to special places at the coast (see Fig. 4, middle right). Later I also drove together with him in his Jeep all the way from Canberra to the Ayers Rock. My family followed us by Airplane and we had a great time at the Red Centre! At work, we had a joint office, which I think was key for developing together the time resolved membrane-inlet mass spectrometry (MIMS) measurements (Messinger et al. 1995; Hillier et al. 1998). We also worked on oxygen flash yield measurements (Messinger et al. 1997).

I believe that Tom is often underestimated in the field because of his quiet and friendly nature. However, anyone who gets to know him on a personal level realizes quickly how immensely knowledgeable he is about PS II and water-splitting in photosynthesis. *I also value that he thinks freely and unconventionally, not bothered by current trends in the field. He is extremely open to new, challenging ideas, and is willing to follow them up, even against negative predictions by others*. I like to add that this strategy has been successful in many cases!

Tom introduced me to many colleagues in the field and thereby opened up several opportunities for me. He made sure that I was accepted to my first Photosynthesis Gordon Conference in 1994 (Fig. 4, middle left), so that I could present the water-exchange data on a poster, and in a short oral presentation. The 2 years and 2 months I spent in his lab and in Australia certainly belong to the best experiences my family and I had in our lives (Fig. 4, middle right). *I am very happy that Tom is being honored in this special issue of Photosynthesis Research*."

Vyacheslav Klimov (Institute of Basic Biological Problems, Russian Academy of Science) added:

"I know Tom as a true researcher, deeply penetrating into the essence of scientific problems, devoting all his life to solving the fascinating enigma of Photosystem II, and as a highly intellectual and friendly man, very pleasant in both scientific and social discussions."

Tom's collaboration with Klimov began when he had visited Klimov's lab and worked on the peroxide production (Ananyev et al. 1992; Klimov et al. 1993), and more recently on the carbonic anhydrase and the bicarbonate in PS II (Hillier et al. 2006).

Tom Moved to Australia in 1991, and has been there ever since

I begin this section by showing photographs, mainly from Australia; they show only some, not all, of the people Tom had been associated with in Canberra. Figure 4 (top left): Elmars Krausz and Ron Pace, two of his many collaborators there; Fig. 4 (top right): Tom's first PhD student Haoming Zhang; Fig. 4 (middle left): in addition to his postdoc Johannes Messinger, and his long time collaborator Warwick Hillier, it shows Mike Seibert and Ron Pace; Fig. 4 (middle right): with Johannes Messinger's young family (mentioned above); Fig. 4 (bottom left): with his postdoc Reza Razeghifard, and with Ron Pace; Fig. 4 (bottom right): with Christiane Funk and her husband Wolfgang P. Schröder. Figure 5 (top) shows a group photograph in Canberra that includes Tom, Jan Anderson, Fred Chow, Cornelia and Barry Osmond, among others; Fig. 5 (middle left) and (middle center) are photographs of Tom's students gathered for dinner at Tom's home; Fig. 5 (middle right) is a photograph with Chuck Dismukes. Figure 5 (bottom) is a group photograph of Photobioenergetics group at Canberra (see the figure legends).

Barry Osmond (Australian National University), who was responsible for Tom's appointment there, wrote:

"As Director-elect of the Research School of Biological Sciences in the Australian National University (ANU) in 1991, I had the opportunity to establish a small research team in photosynthesis research. The objective was to sustain a strong Australian presence in the biophysical and structural aspects of light reactions in photosynthesis, earlier established by Keith Boardman, Jan Anderson, and

Fig. 4 (*Top left panel*): A 1999 photograph in the Research School of Chemistry, ANU. Left to right: Ron Pace, Keith Jackman, Elmars Krausz, Gad Fischer, and Tom in front of the Magnetic Circular Dichroism (MCD) spectrometer. Source: Elmars Krausz. (*Top right panel*): In Canberra circa 1997. Tom and Haoming Zhang, the first PhD student of Tom. Source: Tom Wydrzynski. (*Middle left panel*): A photograph at the 1994 Photosynthesis Gordon Research Conference. Left to right: Johannes Messinger, Mike Seibert, Warwick Hillier, Ron Pace, and Tom. Source: Johannes Messinger. (*Middle right panel*): A beach near Bermagui, Australia in 1993: Tom with Felizitas and Franziska (1 year old) Messinger. Source: Johannes Messinger. (*Bottom left panel*): A 2000 photograph in the Research School of Biologial Sciences, ANU. Left to right: Tom, Reza Razeghifard, and Ron Pace. Source: Tom Wydrzynski. (*Bottom right panel*): In Canberra circa 2002. Left to right: Tom, Wolfgang Schröder and Christiane Funk. Source: Tom Wydrzynski

others that then were being phased out in the Commonwealth Scientific and Industrial Research Organisation (CSIRO). With limited personal experience in this area, after a worldwide search, I had an opportunity to interview a short-listed applicant before leaving Duke University to return to Australia. Tom Wydrzynski immediately impressed me by his distinctive approach to assessing Photosystem II (PS II) primary reactions and by his personal commitment to building a team. Tom accepted a senior non-tenured position, immediately demonstrated his leadership, and has since succeeded to a full professorship on the basis of his outstanding work in ANU. This was no small feat in the face of the labyrinth of ever changing appointment processes in the institution. Tom and I were delighted to secure an adjunct appointment for Jan Anderson and a succession of appointments for Fred Chow that has ensured a strong team. His wide network of collaborators in the US, Germany, and Japan has greatly strengthened Australian research in PS II photoreactions. Most significantly, Tom has mentored outstanding colleagues and students that have twice taken the Robin Hill Award of the International Society of Photosynthesis Research (postdoc Johannes Messinger and former PhD student Warwick Hillier) and now hold key appointments in Sweden and Australia."

Figure 5 (top) shows a photograph of Barry Osmond with Tom and many others at RSBS, Canberra, Australia (see the figure legend). Tom has made Canberra his home. He has risen from a Fellow (1991–1996), a Fellow/Senior Fellow (1996–2000), a Senior Fellow (2001–2007) to be a Professor. He has collaborated with many international scientists and laboratories.

Tom's long-time collaborator and good mate, **Warwick Hillier** (Photobioenergetics, Research School of Biological Sciences, the Australian National University) remembered their first meeting:

Fig. 5 (*Top panel*): A photograph taken at the farewell party for Barry and Cornelia Osmond before their departure for Biosphere II in Arizona in 2001. From left to right (in approximate sequence): Brett Wallace (PhD student); Karin Åhrling (ARC Postdoctoral Fellow); Tom, Luke Hendrickson (PhD student, just behind Tom), Barry Pogson (all the way in the back), Adele Hendrickson, Jan Anderson, Fred Chow, Garth Hendry (PhD student (behind Fred)), Paul Smith and his wife Linda Johnston directly in front, Sam Hay (PhD student), Cornelia Osmond, Pattie Hay, Barry Osmond, a gentleman in white shirt, Pui San Chow, Paul Kriedemann, Eldon Ball (half squatting), Jan Kriedemann, Shizue Matsubara (PhD student), and Marilyn Ball. The remaining person (not shown) was Reza Razeghifard, the newly-arrived Postdocal Fellow. Source: Tom Wydrzynski and Fred Chow. (*Middle left panel*): A photograph of the students taken at Tom's home in 2007. Left to right: Adele Williamson, Carly Smith (Brendon's fiancée) Brendon Conlan, Iain McConnell (standing), and Rhys Smith (Adele's husband), and Tom. Source: Tom Wydrzynski. (*Middle center panel*): A photograph of students taken in Tom Wydrzynski's home. Left to right: Adele Williamson, Iain McConnell, Brendon Conlan, and Rhys Smith (Adele's husband). Sitting (with beer bottle in hand) is Tom. (*Middle right panel*): In Canberra 2003. Left to right: Chuck Dismukes and Tom. The two were celebrating the funding success of their Human Frontier Science Progrm (HFSP) grant on "the innovation and evolution of the photosynthetic water-oxidizing complex." Source: Chuck Dismukes. (*Bottom panel*): A 2004 photograph of Photobioenergetics (PBE) Group in the Research School of Biological Sciences (RSBS) at the Australian National University (ANU). Sitting: Eun-Ha Kim (left) and Adele Williamson (right). Second row (from left to right): Jan Anderson, Fred Chow, Tom, Reza Razeghifard, and Iain McConnell. Back rows (in one sequence): Brett Wallace, Warwick Hillier, Joel Freeman, Karin Åhrling, Sam Hay, Javier Fernandez-Velasco, and Amanda Harms. Source: Fred Chow

"I first met Tom in the summer (January) 1992 in Canberra, Australia, shortly after his arrival in the country. I was a student involved in a research project with low-molecular-weight polypeptides in PS II and had stumbled across a recent review on "The Current Perceptions of Photosystem II" (Hansson and Wydrzynski

1990). At the time I wasn't sure if anybody in Canberra could pronounce "Wydrzynski" and from discussions with people I was somewhat unsure if this was the person who wrote the article, and less sure how to say the name in the paper. But one afternoon I remember seeing Tom and asking him if he was the one who wrote the review and he was indeed that person. We talked and I said something along the lines of "all those polypeptides, what were they all doing"? … So moving beyond that first encounter, which effectively began my science career, we have made a number of studies together on PS II to the present (Hillier and Wydrzynski 1993, 2000, 2001, 2004, 2007; Hillier et al. 1997, 1998, 2001, 2006; McConnell et al. 2007; Singh et al. 2008; Williamson et al. 2007; Wydrzynski and Hillier 2005; Wydrzynski et al. 1996, 2007). During this period we enjoyed the many discoveries made in PS II, from site directed mutants, the crystal structure analysis to spectroscopic measurements of kinetic intermediates. Our perceptions of PS II have changed and it has been an interesting journey with Tom. Since that time I have grown to share Tom's passion for understanding the mechanism of photosynthetic water oxidation, Nature's most elusive secret."

The above testimonial from Warwick reminds me of the time Tom was my PhD student. Someone telephoned me and said that he wanted to talk to someone whose name sounds like "*Why drink Whiskey*." It took me a while to figure out that he meant "Wydrzynski."

Reza Razeghifard (Department of Chemistry, Novo University), a former postdoc with Tom wrote:

"Tom is a scientist of high caliber who offers great opportunities for independent research to his students and postdocs. It was pleasure to work with him on research projects, which involved Photosystem II and protein engineering. His new idea was to mimic some aspects of photosystems by introducing photoactivity into small water-soluble proteins (Razeghifard and Wydrzynski 2003, 2005; Razeghifard et al. 1997, 2005, 2007). We often discussed our approach in his cozy office or during group gatherings in the balcony of his house while enjoying a beautiful view of Canberra. I have several papers published with him and many good memories. Tom has been a good friend and an excellent mentor."

Christiane Funk (Department of Biochemistry, University of Umeå), also a former posdoc with Tom, recalls:

"My husband (Wolfgang P. Schröder) and I spent a wonderful post-doctoral research year in Australia in Tom Wydrzynski's laboratory. We thank Tom for this opportunity as we had a great time with him (see Fig. 4, bottom right). In addition to great science, we had the pleasure of seeing first time kangaroos and hearing Australian magpies "singing" when Tom had invited us to his house at the border of Canberra. It felt like another world. In collaboration with Tom and Julian Eaton-Rye, we published a paper on Photosystem II (PS II) assembly (Clarke et al. 2002)."

Haoming Zhang (University of Michigan Medical School), Tom's first PhD student, wrote:

"From a personal perspective I cherished my PhD study with Tom. As his first PhD graduate, we did original research together. When I saw my first paper published in Photosynthesis Research (Zhang et al. 1997a), I was ecstatic. I enjoyed the afterglow for days (see Fig. 4, top right for our photo together). Tom was a patient mentor and gave me freedom to explore and find research topics that interested me. Our research led to the exploitation of Fourier-Transform Infra Red (FTIR) Spectroscopy to monitor both the acceptor and the donor side intermediates of PS II (Zhang et al. 1997b, 1998). Because of my excellent PhD experience with Tom, I was able to receive a very competitive fellowship from the National Science and Engineering Research Council of Canada to start a new career working on hemoproteins.

Over the past 17 years, Tom and I have developed friendship beyond our professions. I still remember clearly that Tom taught me how to drive a car and he rode in my car with me who had only a student driver's license. Tom has visited me twice in Ann Arbor, Michigan, since I left Canberra in 1997. I felt closer to him every time we met and had dinner at my house. I am pleased he is very active in photosynthesis research even though he endures some serious health problems. It is my ardent hope that he will continue to be active in photosynthesis research for many years to come."

Sam Hay (Manchester Interdisciplinary Biocentre, University of Manchester), also a graduate student of Tom and who worked on the protein engineering project (Hay and Wydrzynski 2005; Hay et al. 2004), wrote:

"I was Tom's fourth PhD student (2001–2004). For those of us in the Antipodes wishing to study photosynthetic processes, and particularly biophysics, the Photobioenergetics (PBE) group at the ANU was, and still is, an obvious first choice. Tom was the head of the PBE group while I was there and he was a wonderful supervisor. Never afraid to try new things, there was always a surprisingly varied range of projects on the go, and there are few places anywhere where I imagine I could have received a better education. Finally, Tom seems to have embraced the Aussie ethos, he's relaxed under pressure—e.g., when his students are off on a wild tangent—and he throws a good party."

Iain McConnell (Department of Chemistry, Yale University), another graduate student with Tom, recalled:

"I began my PhD in Tom's lab in 2004 coming straight from my BSc (Hons) at Otago, New Zealand. I worked initially on the role of bicarbonate on the donor side of PS II, and then moved on to substrate water interactions in the water oxidizing complex (McConnell et al. 2007). Tom was always ready to provide guidance and suggest new approaches. We got on well with overlapping interests in literature and film (generally what we deemed to be good science fiction). Tom was not only a good supervisor but became a good friend as well. My photograph is shown in Fig. 5 (middle left and central panels).

In 2005, Tom had just got a new Nissan X-Trail and was keen to take it on a road trip out of Canberra, Australia. He asked me if I'd like to go along and said I could drive. One aspect of this trip was that Tom wanted to try out the four-wheel drive capability of this vehicle. These turned out to be fateful decisions. We left Canberra early on a beautiful summer Saturday morning with the intention to do a little dirt road driving before getting onto a major highway. On this dirt road however I took a corner too fast and over-corrected, which left me driving the car up a steep bank that was directly adjacent to the road. The angle of the bank was such that the car tipped over and came to rest on its roof. There were Tom and I, stunned, hanging upside down in his brand new and newly written off X-Trail. I was mortified. Fortunately Tom and I were not hurt and some people living near by helped us out with getting the car towed and gave us a ride back into town. Furthermore, Tom's insurance produced a brand new X-Trail exactly like the old one. Much to my relief and I imagine Tom's as well. I could not believe what I had done, but Tom seemed to take it in his stride. It was not long before he suggested another road trip and asked me to drive again! (I accepted and we were fine). I think this tale reveals a lot about Tom's character. *He is very patient, calm, and generous.* Good qualities in a supervisor and friend."

Impressions of Tom by his current and past students Adele Williamson (Williamson et al. 2007), Garth Hendry (Hendry and Wydrzynski 2002, 2003), Brett Wallace (Hay et al. 2004; Razeghifard et al. 2007), and Kastoori Hingorani, are represented by the following write-up by **Brendon Conlan** (Photobioenergetics, Research School of Biological Sciences, the Australian National University), a graduate student currently working on the protein engineering project:

"Hello Govindjee, I have a few stories for your article on Tom. I joined the Photobioenergetics Group as a PhD student in 2005 under his guidance. I am still a student but through the help and guidance of Tom I have progressed significantly and should finish this year. I have been working on engineering a minimal protein mimic of PS II, which contains a light active pigment, an electron acceptor, and a manganese center as an electron donor (Conlan et al. 2008). Tom is a great supervisor, very supportive and always willing to help either in the lab or outside the lab. I recall an adventure outside the lab. [Note: The "car story" of Ian McConnell must have had a great impact on the group, as Brandon does repeat it, but with his own interesting twist to it—Govindjee] Due to his health, Tom often lets his students drive whenever we are going somewhere. On one occasion when he was going for a drive through the hills on the outskirts of Canberra with Iain McConnell, he allowed Iain to drive, who being a New Zealander, had never encountered Australian gravel roads. Unfortunately Iain lost control of the car on a curve and the two of them ended up crawling out the windows with the car on its roof. The car was a write off but Tom was not fazed by this at all. He soon got a new car under insurance and continued to let Iain drive, even though the rest of us were a little nervous to be in the car with Iain as driver after this incident.

Tom gives all of his students a lot of opportunities in both allowing them to visit other labs but also in allowing them to present our group's work. Tom does not like to give presentations these days and so he passes the honor on to his students. This enables us to get experience presenting our work, as well as facing an international audience. I accompanied Tom on a trip to Germany in 2006, and it was on this trip that I met you, Govindjee, for the first time when you gave a talk at the Max Planck Institute (MPI) in Mülheim. On this trip I also gave a talk at MPI and again later in Sweden when we visited Gothenburg University. Since then I have had the chance to talk at several international conferences on our group's work, which is a great opportunity for a PhD student.

Tom looks after his students well and is keen to associate with them outside of work hours. We often have video nights or beer and pizza nights at Tom's place for all of the students and Tom is renowned for putting on the best snacks menu around. So much so that rarely can anyone eat any of the pizzas ordered."

Figure 5 (middle left; middle center panel) shows photographs of Brendon Conlan and Iain McConnell, among other students of Tom.

Elmars Krausz (Research School of Chemistry, Australian National University), a faculty colleague at Australian National University, who also worked with Ron Pace (Department of Chemistry, Australian National University; see also Grace et al. 1995; Smith et al. 2002), wrote:

"Our research group started work on photosynthesis in 1998 with a small project with Tom to monitor

near-Infrared absorption changes in transforming from the S_1 to the S_2 state in Photosystem II (PS II) (Baxter et al. 1999). We were looking for an elusive Mn band that had been reported in EPR (action) spectra. This project was undertaken while we were re-building my main laboratory in the Research School of Chemistry at the Australian National University. In the following years Tom has always been very supporting and innovative in all the projects we have collaborated on. With his quiet ways he may not have always received the credit he deserves. In my opinion, his paper (Hughes et al. 2006) is one of his best papers and it indeed has attracted lot of interest in the field.

Fig. 6 (*Top panel*): A 1999 photograph of the retirement of the author (G) in front of the Alma Mater of the University of Illinois. Front row (left to right): Tom, Rajni Govindjee, and Barbara Zilinskas. Second row: Paul Jursinic, Professor Robert Blankenship (visiting from Washington University in St. Louis), Julian Eaton-Rye, Alan Stemler, Govindjee and Rita Khanna. (*Middle left panel*): A 1999 photograph of the retirement of the author (G) at his home. Standing (left to right): Tom, Paul Jursinic, Julian Eaton-Rye, Rita Khanna, Govindjee, and his grand-daughter Sunita. Sitting (Left to right): Alan Stemler and Maarib Bazzaz. (*Middle right panel*): A 1999 photograph of Tom sitting at the desk where he sat when he did his PhD in the 1970s (283 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL). (*Bottom panel*): A 2007 photograph of Tom walking with others at the 14th International Congress on Photosynthesis Research, in Glasgow, UK. Left to right: Vittal Yachandra (University of California (UC) at Berkeley), Kenneth Sauer (Tom's postdoc mentor, UC Berkeley), Robert Blankenship, Johannes Messinger, Julian Eaton-Rye, and Tom. In the back is Govindjee (red tie) and on the extreme right is Hari Sheth, a friend of Govindjee. Source: Zhen-Ling Sun of the University of Sheffield

Figure 4 (top left) shows my photograph with Tom and others in the instrument room at the Research School of Chemistry (Australian National University)."

Julian Eaton-Rye (Department of Biochemistry, University of Otago, Dunedin, New Zealand) has had many connections with Tom over the years. He wrote:

"Tom's lab has provided a good summer home for our undergraduate students at Otago University; they have been able to obtain a feel for photosynthesis research there. Several undergraduates who had carried out research projects in my lab have later joined Tom for their PhDs (Garth Hendry, Sam Hay and Iain McConnell). Currently, Kastori Hingorani is just embarking on a PhD this year. In a collaborative project with Tom and Christiane Funk, we have shown that specific amino acid deletions in CP47 (of PS II) slow the oxidation of Q_A^- and/or prevent PS II assembly (Clarke et al. 2002). I always enjoy visiting Canberra and discussing photosynthesis and PS II in particular with Tom and his research group. Tom has always been a great host—putting me up in his home and making sure no visit goes by without a chance to visit the surrounding countryside (Fig. 6, bottom is a photograph of the two of us talking at the International Photosynthesis Congress in Glasgow)."

Charles Dismukes (Department of Chemistry, Princeton University) wrote about "*Honoring Tom Wydrzynski for his contributions to photosynthesis research*"

"It is a special treat for me to offer my appreciation to Tom for his many contributions to photosynthesis, both in research and editorial work in organizing the first book dedicated entirely to PS II research (Wydrzynski and Satoh 2005). I have learned from and worked with Tom for a long time, since we were postdocs together in Ken Sauer's lab at the University of California Berkeley, where we overlapped (1977–1978). Tom had recently finished his PhD thesis with Govindjee on the subject of the role of manganese in photosynthetic O_2 evolution. In Berkeley he was attempting to determine the stoichiometry and oxidation states of the manganese ions using a method of heat shock to release them from thylakoid membranes and detection by Electron Paramagnetic Resonance (EPR) and other methods. No one else in Ken's lab was working on O_2 evolution during this time. I had no idea then that what I learned from Tom and Ken about Photosystem II (PS II) would prove to be so important to me later in Princeton, where I switched to PS II research within 2 years after arriving there. Tom's career has been a true global trek in pursuit of answers to one scientific puzzle: *How does PS II make O_2*? He was and is today so deeply committed to this goal that he gave up a secure position after 4 years in applied research at Standard Oil Company (Indiana) (AMOCO) to return to the PS II research bench in 1985. This began a string of fellowship opportunities which literally carried him around the world, from RIKEN (Wako-Shi), Berlin, Gothenburg, back to Berlin, and finally to Canberra where he has stayed permanently now. Throughout all this time he has remained dedicated to solving the mechanism of O_2 evolution and, more recently, in applying this knowledge to the construction of artificial water-splitting systems that use the principles of PS II. I know of no one else in the PS II research field who has made so many profound personal sacrifices to continue to remain engaged in solving this fascinating puzzle. Tom's rich contributions to our knowledge of PS II are published in top journals of the World. Tom, you have my deepest admiration not only for your important discoveries, but especially for leading an inspirational life of sacrifice chasing down Nature's secrets all over the globe.

Here, Gennady Ananyev (GA) and I(CD) have honored Tom by showing two of his photographs: Fig. 2 (middle right) is with GA, ~1989 in Pushchino, Russia and Fig. 5 (middle right) is with me at Tom's home in July, 2003."

A concluding remark

In this personal and informal essay, I now show Tom's photographs when he returned to his Academic home in Urbana-Champaign (Fig. 6) when I retired from active service there in 1999. Tom had a great Reunion with many of his contemporaries; he likes the photo (Fig. 6, top) in front of the Alma Mater, where the students of the past send greetings to the students of the future. However, I like Tom's photo relaxing at his old desk (in 283 Morrill Hall; Fig. 6, middle right), where he obtained his PhD. Figure 6 (middle left) shows Tom with other past PhDs from my lab (Paul Jursinic, Julian Eaton-Rye, Rita Khanna, Alan Stemler, and Marrib Bazzaz).

I end this Tribute to Tom by showing a photograph of Tom talking with Julian Eaton-Rye, at the 14th International Congress on Photosynthesis, held in Glasgow, UK; it also shows others of importance to Tom's academic life (Fig. 6, bottom).

Acknowledgments I thank Suleyman Allakhverdiev for inviting me to participate in celebrating Tom's academic travelog from Urbana (Illinois), USA, to Canberra, Australia. I thank each and everyone for sending their recollections of Tom. In alphabetical order: Lars-Erik Andréasson; Brandon Conlan; Charles Dismukes; Julian Eaton-Rye; Hans-Jörg Eckert; Christiane Funk; Örjan Hansson; Sam Hay; Warwick Hillier; Brad Huggins; Paul Jursinic; Rita Khanna; Vyacheslav Klimov; Elmars Krausz; Iain McConnell; Johannes Messinger; Prasanna Mohanty; Barry Osmond; Reza Razeghifard; Kenneth Sauer; Tore Vänngård; Haoming Zhang; and Barbara Zilinskas. Wherever available, credits for the photographs are given in their legends. I am highly thankful to Barry Osmond for all the support he has given to

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