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TRIBUTE

Colin A. Wraight, 1945–2014

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Abstract Colin Allen Wraight, a central figure in photosynthetic electron transfer research since the 1970s, died in Urbana, Illinois, on July 10, 2014. Born in London, England, on November 27, 1945, he had only recently retired from his position as a Professor in Biochemistry, Biophysics & Quantitative Biology, and Plant Biology at the University of Illinois at Urbana-Champaign. Wraight was known especially for his pioneering studies on electron and proton transfer in the photochemical reaction center, and for his careful quantitation of the remarkable quantum efficiency of this device.

Keywords Chemiosmosis · Electron transfer · Proton motive force · Quantum yield of primary photochemistry · *Rhodobacter sphaeroides* · Two-electron gate

Colin Wraight completed both his undergraduate and graduate degrees at the University of Bristol (1964–1971), the latter in the laboratory of Antony (Tony) R. Crofts. Colin was the first (along with J. Baz Jackson) of Tony's graduate students. Those were heady days, at the height of the great Chemiosmotic Wars (Prebble 2002), and the Crofts lab was on the frontlines. Colin did some beautiful work including that determining the dependence of fluorescence quenching on the chloroplast ΔpH (Wraight and Crofts 1970), and building an intimidating phosphoroscope with which he established the dependence of delayed fluorescence on both components of the proton motive force, ΔpH and Δψ (Wraight and Crofts 1971). These results emphasized the vectorial nature of the initial photochemical reactions as Mitchell (1966) had proposed. Bristol was not far from Glynn House in Bodmin (Prebble and Weber

Mary Wraight: I would like to express my deep gratitude to all who contributed to this lovely piece. I know how hard it is to remember and yet it is also rewarding and life-affirming. Colin was a champion of living life to the fullest and taking 1 day at a time. In reading about the science I couldn't help but think that in all those years, when science was such a huge part of Colin's life, he always made us, his family, feel that we were front and center in his life. He was never too busy to help and guide with the smallest or the largest problem no matter what was happening in the lab. Colin was the kindest, gentlest, funniest, most generous and loving man. He always saw the best in people and he never judged. To have these thoughts shared by his friends, colleagues and students is a gift beyond words that will sustain us all down the years. Colin now has a grandson, Felix Colin Wraight, who will one day read this Tribute and have an insight into his grandfather that he would otherwise never have had. Indeed, since Colin never talked about himself, we all have an insight into him that we might never have had. So to everyone herein I offer deep, heartfelt thanks from us all.

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2003), and interactions with Peter Mitchell were a regular occurrence. Colin's PhD examiner was Robert (Robin) Hill (see Kamen 1992), and the 'examination' included Robin's demonstration of a "glow of light" from a chlorophyll solution in a darkened fume hood.

Figure 1 shows a photograph of Colin Wraight in Urbana, Illinois.

Colin spent a postdoctoral year in the Louis (Lou) N. M. Duysen's laboratory at the State University in Leiden (1971–1972), following up his work on delayed light emission (Wraight 1972; Wraight et al. 1972). He then moved to Roderick (Rod) K. Clayton's lab (see Wraight 2014) at Cornell University, in Ithaca, New York, for another stint as a postdoc (1972–1974). In Rod's lab he forswore chloroplasts to concentrate on photosynthetic bacteria, a decision he rarely revisited. In Ithaca he made one especially important (and well-cited) measurement (Wraight and Clayton 1974): that the absolute quantum efficiency of the photochemical reaction center of what is now known as *Rhodobacter sphaeroides* was 1.02 ± 0.04. As he and Rod pointed out then, this is 'in contrast to a value of about 0.7 predicted from the variations in fluorescence yield'! And what a number that is—as close to perfect as makes no difference! Furthermore, the quantum efficiency of the triplet state, generated when useful photochemistry is impossible because of the prior reduction of Q_A, was essentially identical (Wraight et al. 1974).

Colin had a brief sojourn on the faculty at the University of California at Santa Barbara, and in 1975 moved to the University of Illinois at Urbana-Champaign, IL. He joined the faculty as an Assistant Professor in the Departments of Plant Biology, and of Physiology & Biophysics. In 1999, he joined the Biochemistry department, where he finally put down his permanent roots. Perhaps not serendipitously, Tony Crofts moved to the University of Illinois in 1978, and the two resumed collegial (and occasionally experimental) interactions that led to a very important and highly cited review (Crofts and Wraight 1983), and several insightful papers (Shinkarev et al. 2001, 2006).

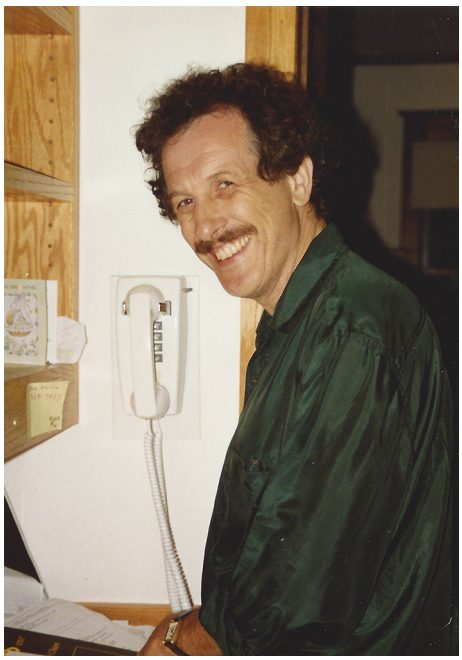

Fig. 1 Colin A. Wraight in the 1990s. Photo provided by Mary Wraight

In Rod Clayton's lab he had begun to get seriously interested in the quinones of the primary and secondary acceptors of the photochemical reaction center (Wraight et al. 1975), and these became a major focus of his research. Early work identified the two-electron gate of Q_B (Wraight 1977), and demonstrated once and for all that protonation was associated with electron transfer to this species (Wraight 1979a, b). This work continued throughout his career, probing the redox potential dependence of protonation (Maroti and Wraight 1988a, b, 1997), crucial amino acids in the binding domain (Takahashi and Wraight 1990, Shinkarev et al. 1993, Rinyu et al. 2004, Martin et al. 2010, Maroti et al. 2015a, b) and the effect of replacing the native ubiquinone with a variety of others (McComb et al. 1990, Wraight et al. 2008).

Most recently Colin and his group focused on the role of methoxy substituents on ubiquinone function (Taguchi et al. 2013a, b). It is one of nature's imponderable questions (at least with our present state of knowledge) as to why ubiquinone is so ubiquitous (hence its name), yet not present in the chloroplasts of cells that have ubiquinone in their mitochondria, but the 2,3-dimethoxy motif likely plays a role, and this work is the first clear experimental evidence addressing the question. Undoubtedly it will carry on, but it will be less fun in Colin's absence.

Colin was a gregarious companion, and an outstanding teacher, but his science often tended to be solitary and deep. He was renowned for his incisive analyses, which led to some well-cited reviews (Crofts and Wraight 1983; Wraight 1979b, 2006). More importantly, his penetrating intelligence made him the perfect companion at conferences, where his evident pleasure in learning made it a delight to join him in puzzling out what experiments might be most useful. He will be greatly missed.

Colin was widely admired beyond his science for his wit, engaging sense of humor and love of life. Some who knew Colin have contributed personal and scientific remembrances that are appended, as are many photographs featuring Colin at different times in his professional life.

A slightly modified version of the above text is being simultaneously published in Photosynthetica (Govindjee et al. 2015). Further, Mary, Colin's wife, has read our entire text; her comments on this Tribute as well as her personal memories are given upfront as a footnote on the previous page.

Remembrances of Colin Wraight

(This section was read and edited by *Govindjee* and *Antony R. Crofts*)

England

We begin by showing some photographs of Colin when he was very young (see Figs. 2, 3). Figure 2 shows him with his mother, and Fig. 3 shows him with his sister and his father.

Virginia Waterhouse, Colin's sister

My younger brother Colin Wraight

I do not think there was ever any doubt that my little brother, Colin, would become a scientist. From the earliest age he was obsessed with insects of all kinds and knew all the Latin names long before he read properly. In fact he did not really read until he was seven, after my mother refused to read him *The Life of the Leaf-Cutter Bee* ever again. Another early favorite was *The Insect Man*, the story of entomologist Jean-Henri Fabre and Colin longed to follow in his footsteps. After a visit to England's first butterfly farm he began to spend all his pocket money on butterfly and moth eggs. It was not unusual to find a newly hatched Atlas moth or a Swallowtail butterfly spreading its gorgeous wings on the fireplace in our nursery. On another occasion our bunk beds were smothered with tiny transparent stick insects, which had hatched and escaped through the air holes of the vivarium.

Fig. 2 Colin with his mother Annie Doris Gonggrypp (always known as Dolly; 1920–2003). Photo, ~1948; most likely in London. Dolly was a teacher and historian (publishing as A. D. Wraight during the 1960s and 1990s). Photo provided by Mary Wraight (it cannot be reproduced without her permission)

At primary school Colin was regularly late as his journey passed many houses with thick hedges—a happy hunting ground for [Privet] Hawk-Moth [*Sphinx ligustri*] caterpillars and Stag Beetles [members of the Lucanidae]. By the time I was eight and he was six I was regularly deputed to look after him in the school holidays. We would take sandwiches and lemonade and spend long days on Wimbledon Common while Colin went insect hunting, his trusty butterfly net in hand. In the winter we would pay our penny fares to travel on the bus to the Natural History Museum where we were regular members of the Children's Study Centre.

Colin was a happy and loving brother and we were close, but he was also rebellious which often led to scenes with our mother. His primary school espoused the very free educational philosophy of the time and he soon began to run wild. Not only late each morning, he sometimes truanted to hunt bugs alone on the common. My mother realized that he needed a much more structured and demanding environment, so at eight she coached him for the entrance exam to our local private (public) school: King's College, Wimbledon. In the long run this was certainly the making of him, but for the first six or seven years, he jogged along among the lower levels, often in trouble. A typical and memorable incident, when he was about 13, was the end of year RE (religious education) exam where one question about the creed simply began 'I believe ….". Colin's answer—'in fairies' caused a storm. Fortunately, from then on the science must have got interesting enough to engage his attention and at last he had a goal to work towards.

Colin was a child of the sixties in a way I never was, and many of his great passions, music and Dylan above all, and his attitude to life stem from that period in his late teens. We depended on each other and that closeness survived diverging paths and an adult life spent on opposite sides of the Atlantic. Though we spent so much of our lives apart I miss his big presence, his warmth and his empathy, that indissoluble bond which made him so special a brother.

I end my tribute by showing a photograph of young Colin outside his father's home in Cambridge, England (Fig. 4).

Before we present the tribute by Baz Jackson, from Colin's graduate student days, we show below two photographs, provided by Mary Wraight. The first one is of Colin with his father Robert Allen Wraight (Fig. 5); Robert Wraight (1913–2001) was a journalist and an art critic. The second one is a photograph of Mary with Colin right after their wedding in 1976 (Fig. 6).

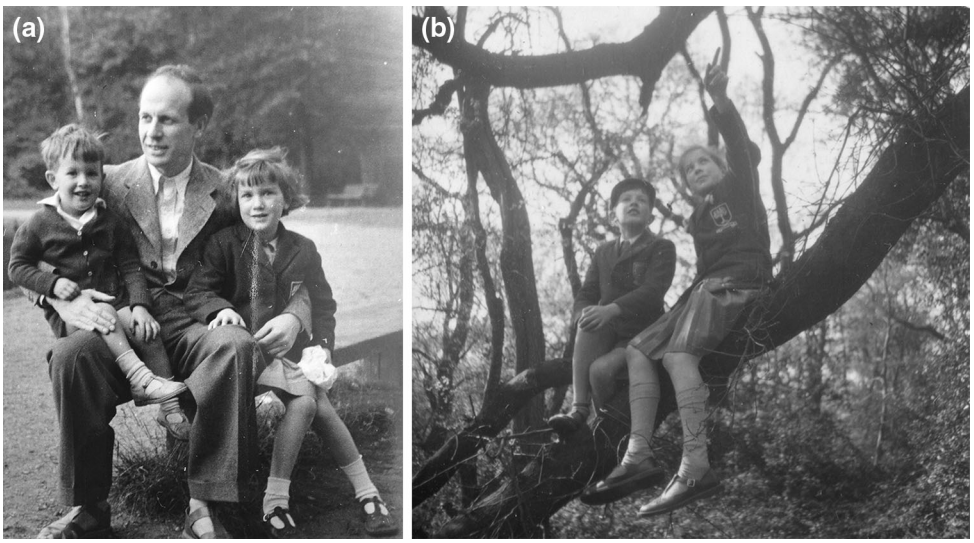

Fig. 3 **a**, *left* Colin and Virginia with their father, Robert Wraight, on Wimbledon Commons, UK, ~1948; photo provided by Virginia Waterhouse (**b**, *right*). Colin and Virginia playing among the trees; photo taken in London, England, ~1952. Photo was provided by Mary Wraight (these photos cannot be reproduced without permission)

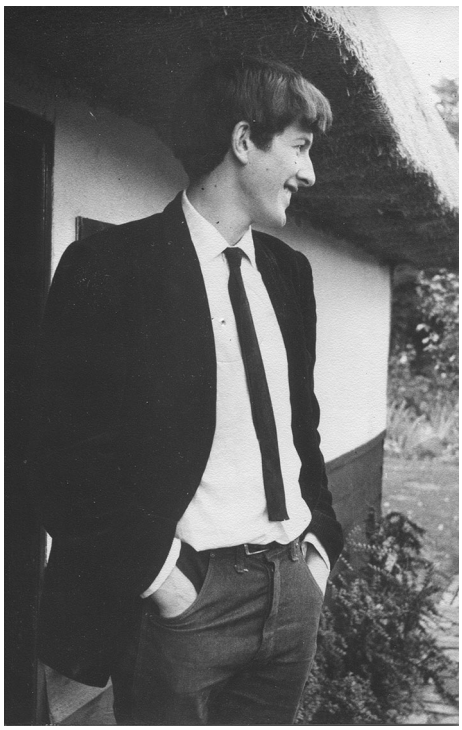

Fig. 4 Colin Wraight outside his father's home in Cambridge, UK, ~1962. Photo provided by Mary Wraight

Fig. 5 A photograph of Colin Wraight with his father Robert Wraight after graduation with a BSc degree from Bristol University. Photo provided by Mary Wraight

J. Baz Jackson, a fellow graduate student

Some recollections of the young Colin A. Wraight

I first met Colin in September 1964 as we started on our undergraduate biochemistry course together at Bristol University. In 1967 with kaftans and lengthening hair we both began our PhDs in Tony Crofts' lab—and cemented our lifelong friendship. Colin was in those days interested in exploring the relationship between delayed light emission from chloroplasts and the membrane high-energy state. In a corner of the lab he built a Becquerel phosphoroscope. Constructed from 1/4 inch aluminium plate, a cannibalised ultracentrifuge motor, a photomultiplier tube and homemade electronics, he called it the flipping-great wheel—I think that was the word; flipping. Anyway, the machine was a beast. People were known to flee from the Medical School when it was running, though Colin would brave the scary screech and juddering vibrations, and hang over it tweaking the sample or jamming pieces of cardboard under the base to stop it skidding across the bench. And the data were so complex that he was obliged (!) to

Fig. 6 *Left–right* Colin, Mary, Geraldine Gallagher (Mary's friend and Maid of Honor), and Baz Jackson (Colin's friend and Best Man) right after their wedding on October 2, 1976, at SS Peter and Paul Church, in Wirral, England. Photo provided by Mary Wraight

spend a few weeks in California talking to Norio Murata in an attempt to rationalize them—the trip was a great success, by the way; but dammit, I only got to visit Les Dutton (later to become Colin's brother in law) in Philadelphia. Although he might not have admitted it, I think Colin rather thrived on complex data—it required him to exercise both his brains at the same time. Naturally, as fellow students we spent a lot of time discussing one another's experiments. I think he was as expert on my stuff (chromatophore H^+ transport) as his own but I later liked to tease him that I provided all the groundwork and inspiration necessary for him to begin his brilliant work in the 1980s on proton binding to reaction centers.

Colin's thesis examiner was Robin Hill (he of the Reaction) who arrived for the viva as usual in his woad-dyed cardigan having lost his half-moon specs somewhere (on his forehead). From the beginning Robin decided the thesis was beyond criticism, and he spent the afternoon of the "examination" demonstrating light emission from extracted chlorophyll—something none of us had seen before. He had us all scurrying around the lab collecting spinach leaves, various solvents, wooden tongs and pieces of glassware, and then proceeded to show a dim glow from the prepared chlorophyll solution heated with a bunsen burner in the darkened fume cupboard. "Quite charming, wouldn't you say", said Robin. "Flipping far out", said Colin.

We went to our first scientific meetings together, including Freudenstadt in 1968 (the First International Congress in Photosynthesis, ICP), where we drank some beer and met the wonderful photosynthesis boys from Berlin. And Stresa in 1971 (the Second ICP)—after driving across the Alps with Tony and sleeping in tents at the local campsite to keep down the costs, and some more beer drinking, followed by the two of us spending a couple of cultural days in Florence (camping again; where can you camp in Florence?). I suspect that some of you went to one or both of those meetings and remember meeting Colin there for the first time. Always great fun and great science.

In the 1970s, with a 5-month pregnant Mary, Colin drove us across the US from Los Angeles to Philadelphia in his beat-up old red Ford. We did America—Yosemite, lakes in the High Sierras with the inch-long mosquitoes biting at our delicate English complexions, the Mohave Desert with a busted air-con (in August!). The public notice at the top of the Grand Canyon advised against going down and up on the same day, and to take at least a gallon of water per person. Colin explained that was just for the flipping Americans. Starting at dawn, and leaving Mary at the visitor center, we literally ran down the canyon secure in the knowledge we could keep refreshed with our bottle of coke, and then the same morning we crawled back up (on the longer route) in the heat of midday, skin burning, throats parched, desperately trying to catch slivers of shade from overhanging rocks. No more disparaging comments about Americans, at least for the next 2 days.

From our early years in Bristol a group of friends, John, Barry, Hilli, Tulip, Denise, Dave, Dan, Steve, all non-scientists, still regularly meet up. We have wonderful memories of Colin and really miss him. He was a great friend. We had a football team—see accompanying photo (Fig. 7, left) of the squad having their half-time ciggie on the Bristol Downs circa 1970. Perhaps not always the first name on the team sheet, gangly Colin was an early exponent of what in the modern game is called the false number 9; his style made him a kind of yesteryear Marouane Fellaini: if you are unfamiliar with the beautiful game, and you Google this guy, you will see that he has also adopted the hair style of the 1970s Colin Amazing Wraight.

For comparison, we show in Fig. 7 (right), a later photograph of Colin in a team that played football (soccer in USA).

C. Neil Hunter, a research colleague

Personal recollections

I will write just a brief, personal and largely non-scientific appreciation of Colin, since the sense of loss of Colin the person dominates my thoughts. I arrived at the Bristol Biochemistry Department in 1975, in the wake of Colin, Baz Jackson, Richard Cogdell, Roger Prince: tough acts to follow! And none tougher than Colin who was long gone by then, but people at Bristol still talked about how brilliant

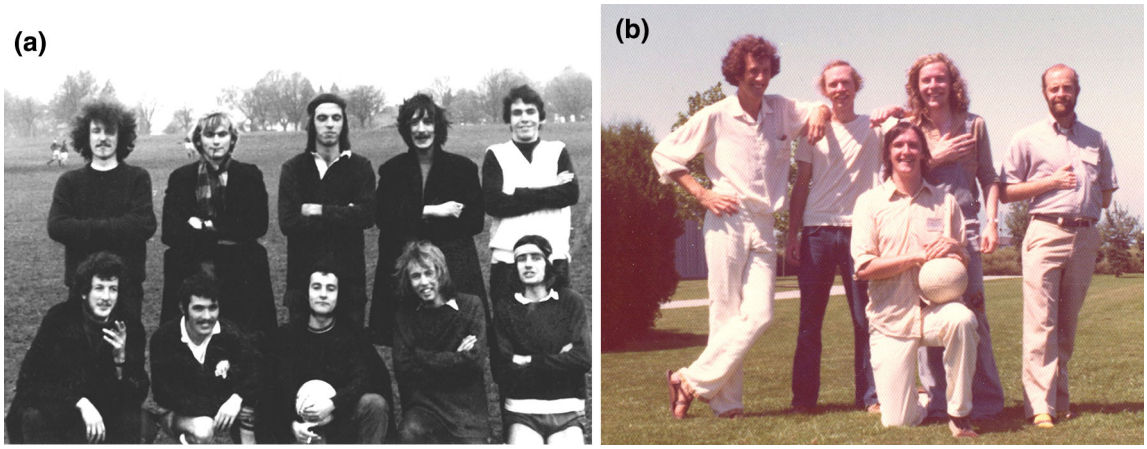

Fig. 7 **a**, *left* Footy team on the Bristol Downs, 1970. Colin, first on the left in the front row; Baz Jackson, second from the right in the first row. Photo provided by Baz Jackson. (**b**, *right*) Standing (*left–right*): Colin Wraight; William (Bill) Parson, Richard Cogdell; and Richard (Dick) Malkin; in front is Les Dutton (with the football); photograph taken at a Gordon Conference in the 1970s. Photo provided by Mary Wraight

a PhD student he had been. So I was already in awe of him before I met him, a feeling compounded by reading his paper with Rod Clayton (Wraight and Clayton 1974); Colin determined the absolute quantum efficiency of bacteriochlorophyll photooxidation in reaction centers, work that accurately reflected his immense scientific talents. Great scientific rigour and creativity were part of Colin's wonderful personality: a charmingly witty and imaginative temperament underpinned by a V12-powered brain. Many years passed since my first encounters with Colin, and it wasn't until 1989 that I spent a lot of time with him. Having returned to Bristol from a postdoctoral position with Bob Niederman, I had subsequently been appointed as assistant professor at Imperial College, London, in 1984, thanks to Jim Barber. In 1987 or 1988, I can't remember when, Colin had decided to enlist my newly acquired and thoroughly modest talents as a molecular geneticist to further his interests in bacterial reaction centers, and he thought the best way to do this was to come to the UK on a sabbatical to work in my laboratory. So, in 1988, Colin shipped his family over to the UK to start his sabbatical with me at Imperial. He must have been taken aback to learn that I wasn't actually in London, and that I had moved to Sheffield in the October of that year; looking back, I think I might have forgotten to tell him about my Sheffield job! So, after a hasty readjustment of his plans, Colin, Mary, Sebastian, Tristan and Lydia took up residence in Sheffield and Colin arrived in my laboratory in January 1989. My wife Jane and I loved Colin, Mary and their kids; they were such nice people to have around. See Fig. 8 for a photograph of the Wraight family.

Colin and I had a great time, messing about in the laboratory trying to create a deletion/complementation system so Colin could make site-directed alterations to the reaction center H-subunit. Colin learned some molecular biology and made a plasmid called pUBS1, which accurately reflected our real interests. We were successful in our endeavors, I recall, but typically we never published any of the work. It didn't matter; we played a lot of squash (he was an excellent player, as noted elsewhere by other contributors) and became very good friends. What more could anyone want than a friend like Colin? Subsequently I visited Colin and Mary several times over the years, met him at conferences, and looked forward to things continuing as they always had. I would have liked to collaborate with him again; he had reviewed some work from my laboratory that had used an atomic force microscopy tip derivatized with cytochrome c_2 to probe interactions with single photooxidized reaction center complexes. Colin's insight and level of understanding of this work were remarkable, just pure brainpower and scientific instinct; I would have liked so much to work with him on this project. I would have loved to have spent more social time with him, just hanging out; we once talked about taking a trip down Route 66 with Mary and Jane in a red Chevy convertible with white leather seats (it would have been the Bel Air, for sure). But now this will never happen and, like everyone else in this compilation tirelessly and affectionately compiled by Govindjee, I have had to write an appreciation of Colin; it isn't enough, but it's something nevertheless.

James (Jim) Barber

Personal recollections

Colin was special to me and I do not have enough words to express my feelings for him and also to Mary. Colin spent a

Fig. 8 **a**,*left* The Wraight family in 1987. *Left–right* Mary, Sebastian, Colin, and Catherine Lydia; sitting in front is: Tristan Alexander. (**b**, *right*) Colin relaxing in a garden in London, UK, ~1989. These photos were provided by Mary Wraight

year in my laboratory on sabbatical at Imperial College London in 1988/1989. One memorable event that happened at that time was my involvement in arranging a NATO (North Atlantic Treaty Organization) summer school at Anargyrios and Korgialenios School on the Island of Spetsai, Greece, called *Techniques and New Developments in Photosynthesis Research*. Colin and his family attended this very successful event and his father-in-law Maurice Dwyer acted as the unofficial photographer. Of course I had known Colin since he was a graduate student at Bristol University where we both shared an interest in the origin of delayed light emission from chloroplasts. In more recent years Colin visited Imperial College every year to participate in a small scientific discussion meeting, which has become to be known as the *Bunty Plot Meeting*. Colin attended these meetings together with a small core of distinguished scientists working on various topics of bioenergetics until his illness.

Colin always gave a lucid and thoughtful talk, which would generate considerable interest and discussion. There is no doubt that Colin was a first class scientist but he was also a wonderful human being. For me he was one of the nicest people that I have ever met and not surprisingly he had a most delightful wife and family. He will never be forgotten.

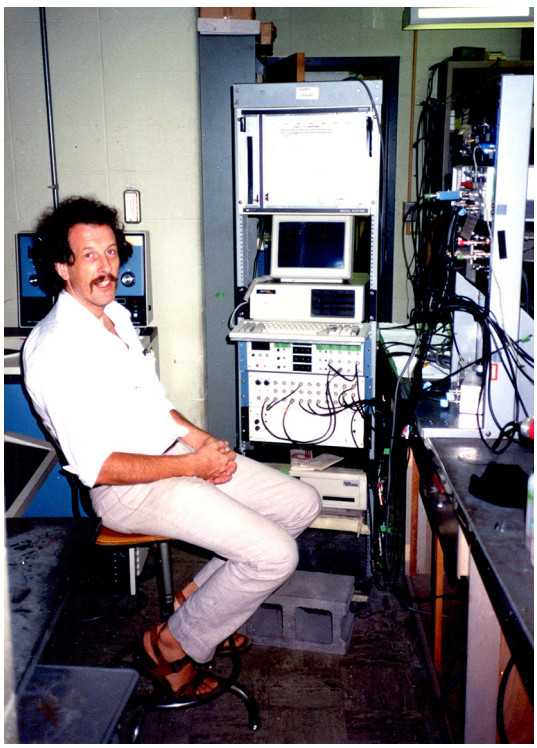

Fig. 9 Difference absorption spectrophotometer in the Wraight Lab (267–269 Morrill Hall), built by Wraight in late 1970s, and used by Wraight and his graduate students. Photo provided by Mary Wraight

Messages from those who worked with Colin in his lab at UIUC

We show here first a photograph of an early version of Colin's instrument in his Lab at the University of Illinois at Urbana- Champaign (Fig. 9).

Robert (Bob) Shopes

My recollections

Like a rolling stone, Colin Wraight has left his imprint on the world, with a body of exquisite science and good will

that has engendered the admiration, respect and love of his family, friends and colleagues. He will be missed, more than he likely knew. If you only knew of Colin through his scientific papers, you could not help but admire him. While that legacy is vital, it is just a fraction of what Colin meant to those of us who were lucky enough to spend time with him. For me, and I suspect many others, the news of Colin's death was a bitter blow cushioned by many happy memories of the bright, kind and wonderful man we knew him to be.

I met Colin at the Gordon Conference in Santa Barbara in 1980. I was interested in pursuing a PhD in biophysics and during a stroll on the beach, and I believe a Heineken or two were involved, Colin enticed me to move from Berkeley to Urbana. I jumped into research in Colin's lab straight away while simultaneously fulfilling my academic classes. As inexperienced students are wont to do I devised an overly complicated research plan. In my case, using EPR, lasers and a very finicky homemade high-pressure device, to manipulate protein motion and monitor subsequent electron tunneling transfer reactions. As a consequence, to be honest, those early years were not productive, but Colin, for some reason, stuck with me while I floundered.

In his usual casual style Colin dropped by the coffee machine to tell me that a German group had crystallized the first membrane protein and were on the way to getting good resolution structures. The good news was that the membrane protein happened to be our favorite protein, the bacterial photosynthetic reaction center (RC), but the bad news was that the RC was not from the species Colin and many others had been working on for years, *Rhodobacter* (Rb.) *sphaeroides* but from *Blastochloris* (known earlier as *Rhodopseudomonas) viridis*. Although less was known about how the *Blastochloris* (*Bc.*) *viridis* RC functioned, sufficient detail was available to lend meaning to the structural info that was likely to arrive. That tidbit of news gave me a direction for a nice PhD thesis project and kept me busy for the next 3 years. Piece-by-piece, we confirmed and added to knowledge of what was similar and what was different between the *Rb. sphaeroides* RC and the *Bc. viridis* RC.

That sort of careful, methodical, straightforward work was the hallmark of Colin's scientific legacy. One of his colleagues once complemented him as a "scientific ditch digger"; logical, consistent and not afraid to do long, hard, slow work. I like to think of him more as a master mason, laying bricks of facts kept together with logical mortar, and bit by bit, adding to the solid wall of knowledge. The combination of intelligence and diligence is what made Colin a masterful scientist.

As a graduate advisor Colin was as good as one could hope for. He did what every good advisor or mentor should do: point you in the right direction, give you the tools to do the job and lend support when needed. He allowed his charges independence while teaching us to do things the right way. As a mentor, Colin was tolerant of mistakes but an absolute stickler for scientific rigor. I once set the Beckman centrifuge to 51,000 rpm when the max was 50,000 rpm and, considering I nearly destroyed the most expensive piece of lab equipment that he owned, he was pretty calm. On the other hand, when I was going over some data with him that I was having trouble with, he asked how much of a chemical I had added at a particular step and I think I responded with "some, you know, just a bit". Colin lit into me for that scientific sloppiness, I think he used a term like "flippin' idiot", and I should not waste my time, or his, if I was not going to take things seriously. I was a bit taken aback. Not only was he right, of course, and I got exactly what I deserved, but in retrospect, I also got what I needed.

Colin was also generous in allowing me to work directly with his collaborators. I had the opportunity, I now realize rare for grad student, to travel to labs and carry out experiments with Marion Thurnauer at Argonne, Dewey Holton at Washington University and Les Dutton at Penn. Not all of these were productive, but great fun and a wonderful experience. And they were possible through Colin's generosity.

One of Colin's favorite sayings, at least to me, was "Best not to be too perfect". This did not extend to the written word however. Colin was well known for his ability to craft grants and scientific papers and was actively sought out for advice. Most people did not see the effort it took to get that level of excellence. Colin, in his grey "Knackered….Sod Jogging" sweatshirt with Kleenex up his nose to quell the nasal drip, would hunch for hours over a manuscript, even if not his own. Many faculty advisers who can write well, rip the data from the graduate students or even post-docs hand, and proceed to "write it up". Colin let his students take the lead. Even so, Colin was a tough editor. I remember proudly handing over a draft of the first paper I had written in his lab, thinking it was pretty good. That manuscript came back covered in red ink with whole sections crossed out and redone. I think it had fifteen original words remaining. That was still better than one of my fellow grad students whose manuscript came back with just the note "Please rewrite in crayon as that better suits your intellectual effort". Like I said, a tough editor. But Colin's version was always better, and the finished result, was clean and clear. It took me a couple of years, but eventually about 50 % of my words made it through Colin's hacking and into the final draft (see e.g., Shopes and Wraight 1987). Well, maybe 25 % is more like it, but the effort that Colin insisted upon, although painful at the time, gave me a skill, crucial in every step of my life.

As a graduate adviser Colin's generous spirit made me a real scientist and a better person. I'll be forever grateful for what Colin taught me.

Eiji Takahashi

Colin, my mentor

I had the great pleasure of working with Colin for over 25 years at the University of Illinois at Urbana-Champaign (UIUC), first as his graduate student, and then as a research scientist in his laboratory. While I was still trying to decide on my choice of graduate school, I was invited to visit UIUC, and it was Colin who met me at the airport and drove me to the campus. He made a great impression on me with his warm smile and laughter. When I started my graduate study in the fall of 1986, I had some background experience in bacterial photosynthesis from the time I spent with Darrell Fleishmann at the Charles F. Kettering Research Laboratory in Ohio, but my scientific interest leaned towards plant research. However, because of my previous encounter with Colin, and with urging from Darrell, I decided to do a rotation in Colin's laboratory, which was then located on the second floor of Morrill Hall.

Colin impressed me very much with his sharp mind and vast scientific knowledge, especially in the field of bioenergetics. He also enthusiastically discussed with me a new project he was just starting to undertake, involving site-directed mutagenesis of bacterial photosynthetic reaction centers. I joined his laboratory soon after the completion of my laboratory rotations. Since Colin and I did not have much experience with molecular biological techniques at that time, we were faced with a challenging task of creating a reaction-center deletion strain of *Rhodobacter sphaeroides*, as well as a suitable reaction-center expression vector as prerequisites for our planned site-directed mutagenesis work. However, we were very fortunate to receive invaluable assistance from the laboratory of Samuel Kaplan. We eventually worked out a mutagenesis system for the L- and M-subunits of the reaction centers from *Rhodobacter sphaeroides*, and, subsequently, the H-subunit as well. Colin and I employed this system in our research over the following decades and contributed to the understanding of the structure–function relationship of the ubiquinone-binding sites in the bacterial reaction center (Takahashi and Wraight 1990, 1992, 1994, 1996, 2006), often in friendly "competition" with Mark Paddock, Mel Okamura and George Feher at the University of California, San Diego.

Colin was very demanding scientifically, because he always held very high scientific standards. Thus, I spent numerous days and nights performing reaction center isolations and flash-spectroscopy experiments in a dark room. Nevertheless, Colin always kept science interesting with his endless ideas and lively discussions, and he encouraged the pursuit of basic scientific knowledge by creating a great laboratory environment. Outside the laboratory, Colin was a great squash player—one of the very best on the UIUC campus—and, yet, he very patiently taught me this game, even though I was just a beginner. Over the many years that I spent with Colin, I came to realize that he cared very deeply about everyone in his laboratory and looked out for our interests. Even after he became ill, he was still very much dedicated to science and his laboratory. Throughout his illness, Colin spent time in his office and laboratory in Davenport Hall, when he was able to do so, and communicated to us by emails, phone calls and video conferencing when he was unable to leave his house. I will always treasure the years that I spent with Colin, along with numerous colleagues that worked in his laboratory.

Péter Maróti

Colin, the renaissance man

Rather than simply having broad interests or superficial knowledge, Colin sought to develop his abilities in all areas of accomplishment: intellectual, artistic, social and physical. He was a talented biophysicist with very broad knowledge of supporting basic sciences of chemistry, physics, mathematics (computation) and biology (genetics). By finding unexpected connections of seemingly distinct phenomena, he enjoyed and could utilize the interdisciplinary character of biophysics. As a gifted scientist, Colin had profound knowledge, rich expertise and even proficiency in several fields of life sciences. His interest and expertise spanned a significant number of disciplines including social sciences and the arts. He had a great collection of English literature books at home, and had a fascinating knowledge of Shakespeare's poetry. In his writings as well as in his talks, Colin's English was unique and superb. The clear formulation, the elegant style, the accurate use of the language and (at least for me) unbelievable richness of vocabulary were unbeatable. Colin could easily talk with people of different backgrounds in a manner appropriate to them. His sensitivity to people made him particularly suited to be nominated to organizing and leading positions in the scientific and university hierarchy. He loved and played music. A Bob Dylan's concert even as far away as 200 miles from Urbana, Illinois, could not be imagined without his (and Mary's) participation. Colin enjoyed playing many sports. For decades, he was one of the best squash players at UIUC. At the beginning of the academic years, he was always very excited to play with the new (always younger and younger) challengers arriving on the campus. He had

excellent physical condition that helped him later in the long lasting bitter fight against leukemia.

Although Colin was not able to enter the more relaxed and peaceful old age, he lived a whole life. He developed his capacities as fully as possible both mentally and physically. As the Bible says, "For I am already being poured out as a drink offering, and the time of my departure has come. I have fought the good fight, I have finished the course, I have kept the faith;" [2 Timothy 4:6–7, New American Standard Bible (NASB), 1995 by The Lockman Foundation]. Colin kept the faith in science, family and friends. He was clearly an outstanding, versatile, and a well-rounded person, who did many things and did them well. That makes him a Renaissance man.

I became acquainted with Colin at the sixth International Congress on Photosynthesis that was held from August 1–6, in 1983 on the Campus of the Vrije Universiteit in Brussels, Belgium. After recommendations from both Laszlo Szalay and Govindjee, Colin accepted me in his lab for a long period (1983–1989). These years established a close relationship between us that became deeper and deeper in the following decades. I have considered him as an outstanding mentor who introduced me, with his fascinating personality, to the community of photosynthesis researchers. I was lucky to participate in many conferences, with his active contribution. He freely shared his splendid ideas with me, encouraged me to defeat all difficulties encountered during research, and paved the way for publication of our joint results in top journals in the field. Later, when my teaching duties at the University of Szeged, Hungary, did not allow longer stays in his lab, he frequently invited me to work during my summer vacations and offered me unforgettable hospitality in his house (earlier on Main Street, later on Broadway, in Urbana). I felt really at home in Urbana together with his lovely family (Mary and the kids: Lydia, Tristan and Sebastian). I have always felt dissatisfied that I have been unable to return his natural and wonderful hospitality. When he was already very ill, I flew to Urbana to visit him once more. However, I failed to see him and felt bad. I now know that life is not under our control. In my memory, I preserve his face, his smile and his right-minded personality—and it all is in a form as it was when I had first become acquainted with him, and has characterized him for decades.

The scientific cooperation between Colin and me can be described with three key words: protons, quinones and bacteriochlorophyll (BChl) fluorescence, all in the bacterial reaction centers (RCs). All these are Colin's favorite topics, rooted in either inspiration from H^+ transport in chromatophores studied by Baz Jackson or his successful previous work (co-discovery of semiquinone oscillation with Andre Vermeglio, and establishment of almost 99 % yield of photochemistry in isolated RCs obtained from the measurement of BChl fluorescence yield in Rod Clayton's Lab). We were able to detect the substoichiometric amount of H^+s bound/released to/from the isolated RCs of *Rhodobacter sphaeroides* upon single flash excitation that turned out to be dependent on both pH and the redox state of the RCs (Maróti and Wraight 1988a, b). A similar discovery was made by the San Diego group (led by George Feher) with different methods. The rate of the flash-induced proton uptake was limited to $\sim$100 μs, and determined by conformational changes of the protein (Maróti and Wraight 1997). This was an essential step in revealing the role of protonatable groups in the mechanism of light energy conversion by the RCs. We showed that the proton uptake was not evenly distributed among the many protonatable residues, and certain amino acids played a much more important role in the "quinone photocycle" than the others. Site directed mutagenesis work contributed in deciphering the stoichiometries, kinetics, energetics and pathways of the Bohr as well as the chemical protons. (Protons taken up in substoichiometric amount due to a pK shift of the residue, and protons bound to a residue upon chemical reaction in stoichiometric amount, are called Bohr protons and chemical protons, respectively.) Colin recognized, quite ahead of the others, the importance of "genetic surgery" in bacterial systems and was among the pioneers (Takahashi et al. 1990). Using a series of well-designed mutants of the acidic cluster in the Q_B pocket (Q_B, being the secondary quinone electron acceptor, whereas Q_A is the primary quinone electron acceptor), we were able to produce proton transfer mutants where the proton uptake was the rate-liming step of the second interquinone electron transfer. These mutants showed solvent isotope effect of the second electron transfer, and we were able to estimate the low proton affinity (p$K_a \approx$ 4–4.5) of the terminal proton acceptor Q_B (Maróti et al. 2015a, b, published posthumously).

The electron and proton transfer steps are indeed coupled in a sophisticated manner in the acceptor quinone complex, and they allow other remarkable observations. A striking example was the fact that the redox midpoint potential (E_m) of the primary quinone, Q_A^-/Q_A, was strongly pH-dependent in the chromatophores, but not in the isolated RCs (Rinyu et al. 2004). However, determination of the free energy gap between the excited reaction center BChl (P*) and $P^+Q_A^-$ by delayed fluorescence (delayed light emission) in the chromatophores revealed an identical (but mild) pH dependence to that seen in the isolated RCs and raised serious doubt on the potentiometric determinations of the E_m of Q_A^-/Q_A (Maróti and Wraight 2008).

These joint investigations and results have provided new information in Colin's wide field of research and his immense efforts in the understanding of different origins of the bioenergetics of proteins in different energy converting

membranes. A large number of graduate students and post docs have grown up under Colin's wings and have learned the elements of his intuitive way of thinking. I am sure that even in his absence, others will pursue the concepts and the methods of inquiry he has instilled in them.

Vladimir (Vlad) Shinkarev

The Wraight person in the right place at the right time: a tribute to Colin A. Wraight

I have divided my recollections in several sections.

Colin's international recognition Even before I had met Colin Wraight personally, I knew and had highest respect for many of his scientific achievements in characterizing reaction centers (RCs) from purple photosynthetic bacteria, including determination of the quantum yield of charge separation in purple bacteria (Wraight and Clayton 1974); the discovery of two-electron gate in RCs of purple bacteria (Wraight 1977; independently of André Verméglio); characterization of flash-induced proton uptake by RCs from purple bacteria (Wraight 1979a, b; Maróti and Wraight 1988a, b); and creation of the model for herbicide action via competitive replacement of quinone (Wraight 1981).

My first contact with Colin I wrote a letter to Colin asking him about the possibility of our collaboration. Colin replied very quickly, indicating that he will be delighted to see me in his lab. He sent me all his recent papers and preprints devoted to the (electron) acceptor side of the reaction center of purple bacteria, so I would be familiar with his current research.

I learned from Colin all information about the University, the twin cities of Urbana and Champaign, different shops and banks. He helped me to open an account at a bank and explained to me how to write checks. In Russia, we had no checks, so I didn't have even the slightest idea as how to do that. Later he took me, and my wife, to the supermarket and helped us to shop.

Building apparatus for direct electrometric measurements As our initial project, we decided to use the time-resolved electrometric method developed previously by Lel Drachev in Skulachev's lab (Skulachev 1988). The main advantage of the direct electrometric method is the absence of any "measuring beam", which is extremely important in the case of preparations from photosynthetic organisms. At that time Colin tried to understand the behavior of different RC mutants, recently made by his graduate student, Eiji Takahashi, including L212EQ mutant, in which glutamate at position 212 of the L-subunit was replaced by glutamine. He wanted to use the direct electrometric method to characterize different RC mutants.

Electrometric evidence that Q_BH_2 is not released from L212EQ mutant reaction centers The electrometric method was well suited for comparative studies of relative electrogenic activities in the RC and in the cytochrome bc_1 complex. We used the direct electrometric method to elucidate the nature of protonation reactions in L212EQ mutant RCs from the photosynthetic purple bacterium *Rhodobacter sphaeroides* (Shinkarev et al. 1993). The second flash-induced electrogenic phase of secondary acceptor quinone (Q_B) protonation in mutant RCs was 2-3-times smaller than that in the wild type reaction centers. Furthermore, the electrogenic reactions of the cytochrome bc_1 complex were absent in this mutant at pH 7.6, but appeared at lower pH, with normal sensitivity to antimycin and myxothiazol. Hence, in L212EQ chromatophores, ubiquinol, generated in the reaction center, fails to take up one of its two protons and remains bound to the protein at neutral pH. At acid pH, the second proton is taken up and ubiquinol is released from the reaction center.

On Colin's writing Colin was a talented writer, as clearly evidenced from Colin's papers, reviews, chapters and notes distributed in different classes he taught. He usually edited and rewrote the text of a paper many times over until he was completely satisfied (or exhausted) with the text. I noticed that many editors (including Govindjee) had tried to modify the text of his papers or chapters, but, in most cases he insisted on returning his wording back to the original form.

Colin often did experiments himself It seems to me that Colin missed the time when he was carrying out experiments in the laboratory by himself. I observed many times that Colin really enjoyed showing others how to isolate RCs. When the lab was short on students he often was doing experiments by himself, especially in the summer time when he had no teaching duties.

Working under pressure of a deadline Colin believed that "Nothing makes us more productive than the last minute". Due to large load of different duties, he constantly worked under pressure of a deadline and tended to wait until the last minute to do things. We even put this sentence on the blackboard in the lab with one small change, namely last minute was changed to "last second".

Humor and jokes Colin appreciated good jokes. His reaction to different things often exceeded the typical "scientific" approach and he laughed out loud at a good joke. He posted many cartoons on the board near his office, and I had good time reading them.

Colin welcomed new developments Colin told me many times that he is bored to do the same things and likes to begin a new challenging project. As a result, he welcomed most of my new developments that I did on the side, using new methods and approaches. This is how we moved ourselves to use near field scanning optical microscopy and atomic force microscopy to characterize different photosynthetic samples (Shinkarev et al. 1999a, b).

Colin never hesitated to ask questions Colin liked to ask questions at meetings and during public discussions. He believed in usefulness of public discussions. After watching the British Parliament on TV, I realized that this is part of the British tradition. He did not hesitate to ask questions to colleagues. On many occasions he asked my advice concerning different mathematical questions, originating from his *Introductory Biophysics* course that he was teaching at the UIUC.

Playing squash I believe that one of the secrets of Colin's high productivity was his love for squash. He played squash at a professional level and on a regular basis. I remember that at the beginning of my stay in the lab, we played both badminton (my favorite) and squash on the same day. For some reason he thought that he might switch to badminton instead of squash as his main game. Being the master of sport in badminton, I intentionally lost one point to Colin, so he will not be "upset" with his new collaborator. Funny part of this double match was the fact that when we played suash later, he did not give me a chance to take even 1 point and I lost with zero score. On the way back to the lab he bought ice cream for me and for himself, probably, to compensate for my lost game.

His teaching and work at the University Colin considered scientific research and teaching at the University as both an enjoyable and a rewarding job. On many occasions, Colin told me that he loves teaching students. He was a very responsible teacher. When he was teaching classes, he spent practically all the time in preparing lectures. He taught many different courses in the area of Photosynthesis, Bioenergetics, and Biophysics. Colin cared deeply about training students and he encouraged them to attend scientific meetings, where they had to present their results.

Colin's scientific productivity and efficiency To a significant extent, Colin's scientific productivity and efficiency was due to the fact that he was the right person in the right place at the right time to use his skills, knowledge, fundamental training, and personality to tackle problems he encountered. The majority of Colin's scientific achievements were devoted to the characterization of reaction centers from purple photosynthetic bacteria. Being one of the first people who had access to highly functional preparations of isolated reaction centers, he rigorously studied different aspects of the RC function using optical spectroscopy, potentiometry and other biophysical approaches and techniques. And for 40 years of systematic studies of bacterial reaction centers, he made many significant discoveries, which markedly resonated with scientific community, as indicated by high citation of his research papers. I was glad to have contributed to several exciting aspects of research in Colin's lab (see e.g., Shinkarev and Wraight (1993a,b,c; 1997; 2007).

We shall all miss this wonderful human being and a great scientist.

Alex Taguchi

My teacher Colin

The untimely death of Colin Wraight leaves me in a state of grief knowing that I will not be able to share any more experiences together with him. To say that Colin had a significant impact on my scientific career would be an understatement; he was the reason I've gotten to where I am today. My growth as a scientist under Colin's wing was an experience I think few could ever be exposed to. We made great strides together in understanding how interquinone electron transfer works in the bacterial photosynthetic reaction center. By employing high resolution pulsed EPR techniques, we found that differences in the methoxy orientation of ubiquinone in the Q_A and Q_B sites is responsible for establishing the functional redox potential difference necessary for electron transfer (Taguchi et al. 2013a, b; Almeida et al. 2014). This finding stimulated a follow-up computational investigation, which has appeared this year (Vermaas et al. 2015).

Colin, a wonderful person, and a great mentor, will always be immortalized through his scientific success, and forever remembered by his friends and family.

Chang (Charles) Sun

Colin Wraight, my advisor

What I want to share is not the sorrow of loss, but the joy of having known Colin. I feel deeply indebted to him. He had an incredible ability to understand and communicate with people; half of the reason for my joining his research group was that he was the only faculty member I could make myself understood in the department back then. As a Principal Investigator (PI) of research and training grants, he was faithful to basic science. He respected every experimental detail and quite often offered a unique perspective to approach the problem. He took every possible

chance to attend seminars on various subjects, sat in the second row, which was one row in front of me, and asked pertinent questions in an incisive manner. However, what struck me the most was his positive attitude towards life despite the leukemia and all the accompanying therapeutic pain. Whenever I felt that a graduate student's "PhD experience" was bitter and frustrating, replaying Colin's contagious laughter in my head would give me a lift and make a lot of my difficulties appear smaller. Besides, I really loved the beer time Colin arranged after lab meetings during the summers, and now my palate is accustomed to "Hoppy" beer, which was Colin's favorite! I worked with Colin on the LM dimer from bacterial photosynthetic reaction center from *Rhodobacter sphaeroides*; two papers are in preparation now regarding the electron transfer kinetics and quinone binding pocket structure of the LM dimer. Besides, H subunit (the third subunit of the bacterial reaction center) knockout strain of *Rb. sphaeroides* was incapable of photosynthetic growth, but using selection in the presence of a mutagen, strains displaying photosynthetic growth were found. Currently we believe that one critical mutation on the M subunit was responsible for this change in the phenotype, based on our preliminary sequencing analysis. Further biochemical and genomic analysis is ongoing under the supervision of Tony Crofts.

Graduate students trained by Colin

We could not reach all the students of Colin. Thus, Govindjee has prepared the following list. Colin has trained many graduate students, besides those who have sent their recollections. Most of those who had obtained their PhDs under his direction are, chronologically, listed here (next to each, we have selected one representative paper to give an example of research done): Robert (Bob) E. Overfield (1978; Electron transfer at the membraneinterface; Overfield and Wraight 1980); Randall (Randy) R. Stein (1985; Inhibitor-quinone interactions in reaction centers from *Rhodobacter sphaeroides*; Stein et al. 1984); David (Dave) R. Paterson (1986; The effects of chemical modification on herbicide binding in thylakoid membranes of *Spinacia oleracea* (spinach) and *Amaranthus hybridus* (pigweed), and the photochemical reaction center of *Rhodobacter sphaeroides;* Paterson and Wraight 1990); James (Jim) C. McComb (1987; Studies on the photoreduction of quinone analogues in bacterial photosynthetic reaction centers; McComb et al. 1990); Robert (Bob) J. Shopes (1986; Electron transfer in the reaction center from *Rhodopseudomonas viridis*; Shopes and Wraight 1987; see his recollections); Goran Neshich (1989) (co-advisor: Donald (Don) C. Devault; Biophysical investigations of electron transfer between high potential hemes and the special pair of reaction centers from *Rhodopseudomonas viridis*; see his current website http://www.cbi.cnptia.embrapa.br/~neshich/body.html); Jiliang Gao (1991; Structural and functional relationships of photosynthetic bacterial reaction centers; Gao et al. 1991); Eiji Takahashi (1992; Characterization of site-directed mutants of the Q_B binding site of the photosynthetic reaction center of *Rhodobacter sphaeroides;* see his recollections); Xutong Wang (1993; Protein engineering and molecular dynamics studies of electron transfer in photosynthetic bacterial reaction centers; see Wang et al. 1992); Cynthia J. Gibas (1996) (co-advisor: Shankar Subramaniam; Computer simulation of titration behavior in proteins); Jonathon W. Larson (2000; Cytochrome c oxidation by the bacterial photosynthetic reaction center from *Rhodobacter sphaeroides*; Larson and Wraight 2000); Ahmet S. Vakkasoglu (2008) (co-advisor: Robert (Bob) Gennis; Fourier-transform Infrared Spectroscopy of Cytochrome Oxidase; Wraight et al. 2008); Oleksandr Kokhan (2008; Ligand binding and structural dynamics in *c*-type cytochromes; Kokhan et al. 2010); Erik Martin (2010; The binding pockets of Q_A and Q_B in the photosynthetic reaction center of *Rb. sphaeroides* probed by pulsed EPR; Martin et al. 2013); Alexander (Alex) Taguchi (2014; see his write up; also see Taguchi et al. 2014).

Messages from Colin's colleagues

Marilyn Gunner

A personal recollection

I met Colin in the early 1980s when I was a graduate student in Les Dutton's lab. I remember coming back from a winter, west coast meeting and getting stopped in Chicago by snow on the east coast. Les bundled us all into a car and we ended up in Urbana at Colin and Mary's house. The ease of their home was wonderful, reflecting the special love and affection they had for each other, which spilled over to anyone lucky enough to come into their sphere. Years later at Telluride science conferences the whole Wraight clan would arrive and rent a large condominium. Each year Colin and Mary would demonstrate they could effortlessly recreate a haven of comfort and joy in any impromptu setting.

As a colleague, Colin always combined his warmth and gentleness with an acute and penetrating intelligence. You would always find him sitting relaxed at the back of the room at conferences lobbing disarming questions that would get us all to dig a bit deeper and understand a bit more.

He cared so much about knowing and had so much evident enjoyment that it was a pleasure to watch him and

then join him in puzzling something out. Colin and I shared a deep interest in quinone redox reactions in biology and this area retains stubborn questions that will be much harder (and not as much fun) to solve without him.

Govindjee

On my friend Colin

I have already written a brief tribute to Colin; it is at a web site of the Department of Plant Biology at the UIUC: http://www.life.illinois.edu/plantbio/Features/ColinWraight/ColinWraight.html.

Here, I show several photographs of Colin: Fig. 10 has three photographs in the 1970s; Fig. 11 shows a photograph with the 1997 Nobel-laureate John Walker and others; and Fig. 12 shows a collection of 4 group photographs taken with several colleagues of Colin at the University of Illinois at Urbana-Champaign.

I have taken the liberty of reproducing here some of my personal recollections on working with Colin, who was a dear friend, and a brilliant scientist. Colin had established (1) the dependence of quenching of chlorophyll (Chl) a fluorescence, associated with photosystem II (PSII; the water oxidizing system) on the pH gradient, leading to the important area of non-photochemical quenching (NPQ) of the excited state of Chl a, which is the basis for how plants protect themselves against excess light. This is an area that has interested me greatly and Volume 40 on NPQ in my series, Advances in Photosynthesis and Respiration, is now published (see reviews in Demmig-Adams et al. 2014); (2) the dependence of delayed fluorescence on the proton gradient (and membrane potential), studied through the kinetics of onset, again, an area very dear to my own research.

Fig. 11 A 2002 photograph at the University of Illinois at Urbana-Champaign. *Left–right* Deborah Leckband, Robert Switzer, John Walker, and Colin Wraight. Photograph provided by Govindjee (this photograph may not be used without his permission)

Colin was in the Department of Botany (Plant Biology) for 20 years before moving to Biochemistry. He was associated with Biophysics from day 1 (see Wraight 2014 for his story as to how I was involved in his coming to

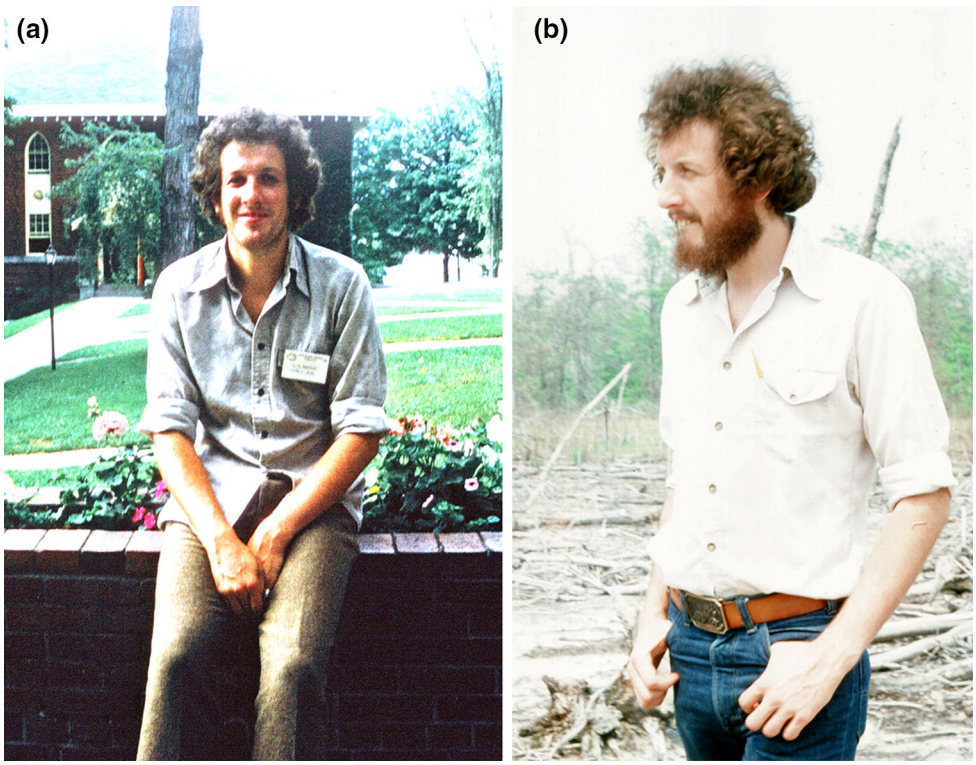

Fig. 10 **a**, *left* Colin Wraight at a Gordon Conference on Photosynthesis, 1973; (**b**, *right*) Colin at Brookhaven National Lab, at Long Island, NY. These photos were provided to Govindjee by the late Janet Brown

Fig. 12 Photographs of Colin Wraight at the University of Illinois at Urbana-Champaign. **a**, *top left* (*left–right*) Tony Crofts, Colin Wraight, Julian Eaton-Rye, Govindjee and C. John Whitmarsh. **b**, *top right* Thomas G. Ebrey and Colin Wraight. **c**, *bottom left* Rajni Govindjee, Tony Crofts, Christine Yerkes, Colin Wraight, Govindjee, and Robert Clegg (now deceased). **d,** *bottom right* Steven Sligar, Robert Gennis and Colin Wraight. Photographs provided by Rajni Govindjee

Urbana, Illinois). His laboratory was on the north side of the 2nd floor of Morrill Hall in space currently occupied by the Plant Biology office (see Fig. 9). I had the other half of that side of the 2nd floor. I had fun collaborating with Colin, discussing and writing papers together. He was not only brilliant and open in his thinking, but was a "hands on" person, and did experiments with us, turning and adjusting knobs, and sometimes even swearing. We collaborated on three topics, publishing four research papers: (1) With my PhD student Paul Jursinic, Colin and I showed, in 1978, a detailed and important relationship of membrane potential with microsecond delayed fluorescence from plants and algae, a topic he had earlier contributed to with Tony Crofts (see Jursinic et al. 1978); (2) With several of our PhD students, Colin and I showed, in 1989 and 1992, that bicarbonate, which my Lab had shown to be essential in the reduction and protonation of mobile quinone molecules in plants, algae and cyanobacteria (Shevela et al. 2012), was not needed at all in a similar reaction in anoxygenic photosynthetic bacteria (Shopes et al. 1989; Wang et al. 1992); (3) With Vladimir Shinkarev, Colin's long-time brilliant associate, Colin and I succeeded, in 1997, in obtaining new information on the kinetics of oxygen evolution via chlorophyll *a* fluorescence measurements (Shinkarev et al. 1997).

I remember many things about Colin, but some personal recollections come to mind. I am proud that I was, in some sense, responsible for Colin to come to Urbana. Wraight (2014) wrote:"*Luck would have it that at the Biophysical Society Annual Meeting in the spring of 1975, Govindjee came up to me and asked why I hadn't applied for a job opening at Illinois! ……...The search was actually closed, but Govindjee and Tom Ebrey (also a former postdoc with Rod, but a couple of years before me) arranged for me to go immediately to Urbana for a job interview. In spite of misjudging the length of my seminar, such that Gregorio Weber left before the end, I got the job and started there in the Fall. Harvard was not pleased*". I remember lot of details including the fact that Colin kept talking long after the allotted time had passed, but everyone was glued to his engaging presentation, rather unusual for the department. And to top it all, we were able to convince Plant Biology, which was very easy, even though the job description in Plant Biology did not quite fit the

area Colin was in. All of us were delighted that Colin came to us, and not to Harvard!

Another recollection is quite on the personal side: it was when he was going out to celebrate his first wedding anniversary. He was indeed wearing a tie (a rare thing), and Mary asked my wife Rajni to tie an Indian sari on her. The couple looked like Bollywood movie stars.

A last recollection has to do with my own life. This concerns the time when I transferred to Plant Biology since the "Biophysics Division" in "Physiology & Biophysics" was being closed in favor of a Center of Biophysics. A condition was placed on me that I would have to teach a large introductory biology course, which quite upset me until I found out that it was Colin who had suggested it, and then I accepted it right away. Later, I thanked him because I discovered that I really loved to teach those 700+ students. Further, I had great fun editing and interacting with Colin while I dealt with his excellent chapter in my book on Photosynthesis (Wraight 1982).

As I finish my recollection, I would like to mention that to honor Colin, I presented one volume each from the Series "Advances in Photosynthesis and Respiration" to four of the best young researchers "*In Memory of Colin Wraight*" (Fig. 13; see Rappaport et al. 2015). This was done after Les Dutton's brilliant talk, at the 2014 Gordon Conference on Photosynthesis, on Colin's life and enormously insightful and brilliant research contributions.

I know well that Mary and their children, Lydia, Tristan and Sebastian, remember Colin fondly as the most loved person on earth. Neither they, nor I, nor his many friends, can accept that he is no longer here with us. We miss him dearly.

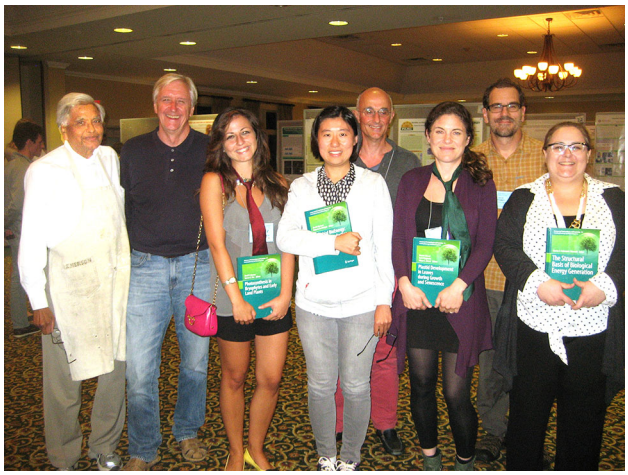

Fig. 13 2014 Colin Wraight awardees at the Gordon Research Conference on Photosynthesis; they are marked with* (and they have in their hand the book they received from Govindjee). *Left–right* Govindjee (wearing Robert Emerson's lab apron), Les Dutton (who gave the lecture honoring Colin Wraight and his research), Nicoletta Liguori*, Han Bau*, Fabrice Rappaport (Vice- Chair), Ute Ambruster*, David Kramer (Chair) and Anat Shperberg-Avni* (reproduced from Rappaport et al. 2015)

Thomas (Tom) Jacobs

From Plant Biology

Colin will be remembered for his exquisite combination of intellect, wit, modesty and generosity….Colin delighted in uncovering secrets of protein-mediated transfer of protons and electrons in energy conversion …in chloroplasts, mitochondria and bacteria using state-of-the-art technologies from genetic engineering to spectroscopy. Colin was treasured by all as a kind, creative and unerringly sensible colleague in the laboratory, in the classroom and in routine institutional matters. Characteristically sitting front and center in seminar audiences, Colin would invariably lead off the question period with an acutely incisive query for the speaker, never to call attention to himself, but simply to satisfy his urgent curiosity about biological mechanisms at all levels.

Antony (Tony) R. Crofts

From Biophysics and Biochemistry

I had the great good fortune in 1967, shortly after I started as a young Assistant Lecturer in the new Department of Biochemistry at Bristol, of having Colin Wraight and Baz Jackson join me as my first research students. I was blissfully unbothered by such problems as nowadays face those launching on their academic careers. The universities were expanding, the baby-boomers were upon us, and I had been launched on my own path by the happy circumstance of an introduction to the exciting area of bioenergetics by Brian Chappell, a rising star in that area, and my PhD supervisor at Cambridge, with whom I initially moved to Bristol in 1964. Colin and Baz were among the first flush of graduates from the Bristol Department. What extraordinary luck to get this pair! What good fortune that the low-hanging fruits of the chemiosmotic controversy offered themselves for the picking to launch their stellar careers! What fun to have been on the winning side! Baz has captured the joy of those years brilliantly, but I can offer a few supplementary asides to emphasize the importance of that early work.

As is obvious from Baz's account, the camaraderie between the two was close, and their research efforts interlocked. Around this time, we had constructed a dual-beam spectrophotometer for the lab, following Britton Chance, and ideas from an earlier prototype built with Brian. Baz used this to demonstrate reversed electron transfer to NAD in intact cells of *Rhodospirillum rubrum* as

his first project. Colin had decided that green plant photosynthesis would be more fun, and was particularly interested in using chlorophyll fluorescence as a probe of the machinery, and we built a fluorimeter to enable this. I forget just what the initial connection was,—Colin was always an independent spirit, and I think this was his own initiative,—but he headed off to Stanford and Stacey French's lab for a few months and met up there with Norio Murata, who had just discovered the energy-dependent fluorescence lowering effect (q_E-quenching). On his return, Colin started the work on characterizing the contributions of ΔpH and $\Delta\psi$ to fluorescence lowering, and demonstrated that ΔpH was the active component (Wraight and Crofts 1971). In order to characterize these contributions, we made use of ionophoric antibiotics, in particular valinomycin, gramicidin and nigericin. Brian Chappell had pointed out that, in addition to the monovalent cations, uncoupling by gramicidin likely reflected transport of H^+, and (as part of my PhD work) we suggested an ionophoric mechanism for both antibiotics (Chappell and Crofts 1965) which then had obvious implications for Peter Mitchell's chemiosmotic hypothesis. Baz had gone on, in collaboration with Lars-Victor von Stedingk (Jackson et al. 1968; also see Jackson and Crofts 1968), a graduate student visiting from Herrick Baltscheffsky's lab, to investigate the action of these ionophores on the proton gradient in chromatophores for *Rsp. rubrum*. From this, and the characterization of the electrochromic carotenoid absorbance changes, and from parallel work in Chappell's group, it was clear that valinomycin in the presence of K^+ collapsed $\Delta\psi$, while nigericin catalyzed a neutral exchange of K^+ for H^+ across the membrane so as to collapse ΔpH. This work introduced the use of these ionophores as reagents for dissection of the proton gradient. Colin's work had demonstrated a direct role of the pH gradient on q_E-quenching; unbeknown to us, the nice work on the xanthophyll cycle and its dependence on ΔpH, first noted by A. Hager (Hager 1969), and studied in detail by Harry Yamamoto (Yamamoto 1979), was underway at the same time, but it took many years before the connection between these two starting points was recognized. These beginnings spawned the non-photochemical quenching (NPQ) industry (c.f. Demmig-Adams et al. (2014)).

The fluorescence work led Colin to his next challenge,—delayed fluorescence and its relation to the proton gradient. With the behemoth phosphoroscope that Baz Jackson describes so graphically, we were able to tease out the different components of the kinetics of onset of delayed fluorescence during the first few seconds, and by exploiting the ionophores, to show how the kinetic phases were differentially affected by $\Delta\psi$ and ΔpH components. In collaboration with Darryl Fleischmann (Crofts et al. 1971), we were then in a position to develop the first thermodynamic model for the relation between the photochemical processes and the proton gradient, with an accounting of the energy conservation in terms of different contributions from redox and protonic work, all in the context of the heat-engine treatment of efficiency by Louis N. M. Duysens (Duysens 1958), as extended by Robert Ross and Melvin Calvin (Ross and Calvin 1967) and by Robert (Bob) Knox (Knox 1969). This early thermodynamic framework, which for the first time placed the photosynthetic machinery, the chemiosmotic model, and fluorescence/delayed fluorescence in a common molecular framework, provided the basis (not often recognized) for more comprehensive models later developed for thermoluminescence, electroluminescence, and related phenomena involving back reactions of photosystem II.

A major contribution from Colin's mature work,—starting with the post-doctoral work with Rod Clayton that established the reaction center as a model system, and demonstrated its high quantum efficiency,—has been to our understanding of the acceptor side of the photochemical reactions in what are now known as type 2 reaction centers. Although the two-electron gate was discovered in green plants, it was Colin's meticulous and detailed kinetic dissection of the bacterial system, the role and mechanism of H^+ uptake, and its structural basis, that pushed the field forward. The current model for the photosystem II reaction was heavily dependent on Colin's insights. Bob Shopes, Eiji Takahashi and Peter Maroti have nice accounts of the molecular engineering and kinetic studies that supported the ground-breaking work and of their years in Colin's group. Alex Taguchi has a nice summary of more recent developments, especially the collaboration with Sergei Dikanov on the use of pulsed EPR to pin down topological features in the semiquinone binding, and Charles Sun has added a heartfelt closing chapter. These contributions from students and collaborators are touching and inspiring,—Colin really looked after his guys.

Vlad Shinkarev outlines Colin's later career including his collaboration with Colin in the cytochrome bc_1 complex area, much of which was also in collaboration with my group. His account also provides a segue to the next overlap of our paths. I owe both Colin and Govindjee a debt of gratitude because they were the main driving forces in my move to Urbana in 1978 to head up the Biophysics program. After my first efforts to establishing the Center for Biophysics fizzled out amidst departmental jealousies in 1991, an interim committee took over, and Colin eventually took on the task of reviving that effort. It was under his leadership that the Center for Biophysics and Computational Biology evolved to eventual establishment; he had the steadfastness, intelligence and leadership to pull off the job. Recognition of these qualities has been a common theme in the tributes to Colin. He had the happy knack of

combining honest intervention with a finely tuned timing and sense of humor that disarmed resentment. His skills in leadership were to become a major factor in bringing the department together when he took on the headship of Biochemistry in later years,—that and the parties he and Mary threw that so warmed us all.

My admiration for Colin has deepened over the years, but perhaps most keenly during his fight with leukemia. The qualities that inspired his students and colleagues,—his high intelligence, the directness of his vision, the depth of his understanding of science, his sympathy for the human condition, his resolution in the worst days, his calmness, and above all his sense of humor, often at his own expense,—were all molded into the unique personality we remember with so much affection, and steeled him with fortitude to the end. Central to all has been the love and stability of his family,—in particular, Mary, who has sustained him through it all,—indeed, who has been his sustenance through the joys and sorrows of a long life together, and in a different sense, a sustenance through her hospitality to so many of us as well.

Goodbye Colin, dear friend, academic child, brother in battle, boss, colleague, collaborator, mentor,—what a fine man, what a tragic loss.

Stephen (Steve) G. Sligar

From Molecular & Cellular Biology (MCB) and Biochemistry

"Bloody Hell!" (as Colin would say). It seems surreal having to comment on his impact. How a few words can capture the multiple connections that meant so much! Friend, colleague, fellow administrator. The shared alcohol, most often to celebrate scientific and personal achievement, but perhaps too often to commiserate over the challenges of the academic bureaucracy. His contributions to science are well represented in this memoir. But his interest in the success of others in diverse fields, made Colin the go-to person to share new discoveries or advice on how to circumvent obstacles. Colin was a wonderful leader, Department Head for too short a period, but one noted for his ability to bring a diverse faculty together toward a common goal. No one could match his linguistic talents (the accent helped of course!), nor his ability to articulate a clear definition of a problem and a path to solution. His calm, logical approach was an inspiration to all. Colin is sorely missed by all at Illinois, and in the broad international arena in which he operated. Bloody Hell he is gone!

We end this section on Remembrances by reproducing what Robert (Bob) Gennis, a friend of Colin Wraight, and a faculty member of the Department of Biochemistry of the University of Illinois at Urbana-Champaign, said.

Robert (Bob) Gennis

Concluding remarks on Colin

I had the great pleasure to be a colleague of Colin's for almost 40 years. He was part of the environment, adding measurably to the pleasure of everyday life at the University. His presence was one important reason to be proud to be at the University of Illinois at Urbana-Champaign. In everything he did, he was a force and an active contributor. What wonderful scientific intuition and insight, combined with a curiosity about nearly everything, a dry sense of humor and a sharp intellect. And let's not forget a very sharp wit and occasional sharp elbows as well. I am sure Colin would wholeheartedly agree that he died much too young. He left us all better off for his presence. Rest in peace, my friend.

Acknowledgments We are highly thankful to all those who have participated in this Tribute including those who wrote their *remembrances*. In alphabetical order, they are: James (Jim) Barber, Antony (Tony) R. Crofts; Robert (Bob) Gennis; Marilyn Gunner; C. Neil Hunter; J. Baz Jackson; Thomas (Tom) Jacobs; Peter Maroti; Vladimir (Vlad) Shinkarev; Robert (Bob) Shopes; Steven (Steve) Sligar; Charles Sun; Alexander (Alex) Taguchi; Eiji Takahashi; and Virginia Waterhouse. We are grateful to Mary Wraight, Virginia Waterhouse and late Janet Brown for several photographs; others are from the collection of one of us (Govindjee). Govindjee thanks Rayme Dorsey (Plant Biology), Cindy Dodds (Biophysics), Marla Wilson (Biochemistry) and Jeff Haas (Information Technology, Life Sciences) for providing him departmental and UIUC academic files on Colin Wraight. We thank Les Dutton for his encouragement in this venture, and we thank several participants of this Tribute (especially Alex Taguchi and Tony Crofts), Mary Wraight and Rajni Govindjee for reading this entire text before submission for publication. We are thankful to Barbara Demmig-Adams for her approval of this manuscript for publication in *Photosynthesis Research*. She wrote to Govindjee: "I have read through this Tribute; it is a moving tribute to a great scientist, and a great man! It will be inspiring and informative for young scientists to read about the personal attributes that foster lasting contributions to science as well as to the lives of others." Govindjee is thankful to David Knaff, chief editor of Photosynthesis Research, for his continuous support for the *Historical Corner* of this journal. Finally, we refer the readers to a Historical Corner paper that presents one of Colin Wraight's last lectures and one of his last posters (see Maróti and Govindjee (2015). It gives a perspective of Colin's thought processes.

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