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OBITUARY

John Rodney Quayle (1926–2006), a brilliant scientist who was also a wise and innovative academic administrator

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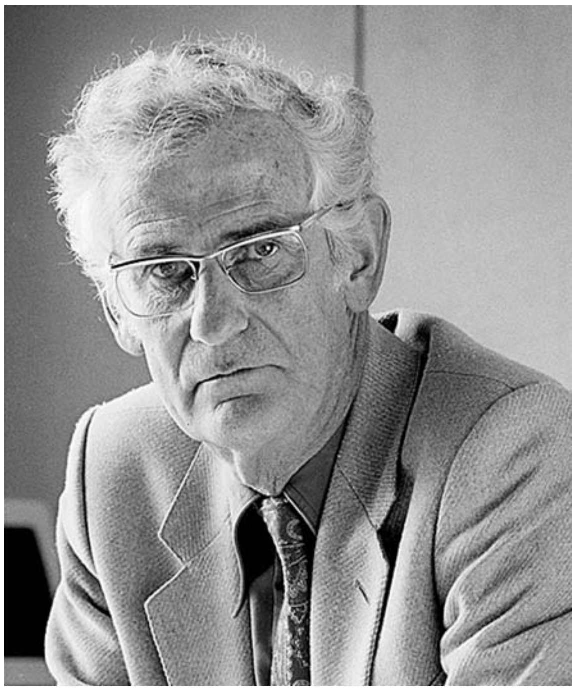
John Rodney Quayle, universally known as ''Rod'', died on February 26, 2006, in the picturesque Somersetshire village of Compton Dando, UK, to which he and his wife, Yvonne, had retired in 1992. His death, in his 80th year, brought to an end a career in which he had made outstanding contributions to at least three separate but related areas of science and in which he had also established himself as a brilliant teacher and an able and innovative academic administrator.

Rod was born on November 18, 1926, in the little Welsh country town of Mold, in the county of Flintshire. He attended the local Alun Grammar School and then entered the University College of North Wales, Bangor, located in a lovely old Cathedral City located between the Menai Strait and the Snowdonia National Park. It was this environment that fostered his love of the outdoors.

After graduating with B.Sc. (Honors) in Chemistry in 1946, Rod stayed on to take a Ph.D. in Physical Organic Chemistry. His thesis was adjudged to be of such excellence that he was awarded a University of Wales Fellowship and a Senior Research Award of the Department of Scientific and Industrial Research (DSIR); this, in turn, persuaded Professor Alexander (later Lord) Todd to accept him into his laboratory at the University of Cambridge. Here Rod chose to study the structure and chemical synthesis of the blood pigments of *Aphididae*; this not only resulted in a steady stream of publications in the *Journal of the Chemical Society* but also gained Rod a second Ph.D. degree. This happy event, in 1951, was paralleled by an even happier one—he married Yvonne Sanderson, who had been a fellow student in Bangor and who became and remained his inseparable companion throughout the subsequent nearly 55 years.



John Rodney Quayle (1926–2006)

In 1953, Rod was awarded a Fulbright Research Fellowship, to be held in the Department of Chemistry of the University of California at Berkeley, and Yvonne and he duly set off for 2 years in that new and

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initially strange environment. Rod had become excited by the work that Professor Melvin Calvin and his co-workers were doing to elucidate the chemical steps whereby plants, under the influence of light, effect the synthesis of carbohydrates from carbon dioxide and water. This research employed novel techniques for the identification and analysis of products formed, in only a few seconds, from radioactive carbon dioxide and various reactants; these techniques had been ingeniously developed largely by Andy Benson and Al Bassham (see Benson pp. 793–813, and Bassham pp. 815–832 in Govindjee et al. 2005; also see Fuller 1999). By their use, Rod became the senior author of a scientific publication (Quayle et al. 1954) that is still regarded as the key piece of evidence that conclusively established ''the Calvin–Benson Cycle'' as the path of carbon in photosynthesis.

A paper now rightly regarded as one of the great classics of plant physiology (Bassham et al. 1954) had indicated that plants fixed labeled carbon dioxide initially by cleaving ribulose 1,5-bisphosphate (RuBP) into 2 molecules of triose-phosphate, which were either 2 mol of 3-phosphoglycerate or, possibly, one each of 3-phosphoglycerate and one of glyceraldehyde 3-phosphate. From the data obtained with whole algae it was not possible unambiguously to decide between these options although the evidence strongly suggested the former to be more likely. This synthesis of $2 \times C_3$ compounds from CO_2 and a C_5 precursor would subsequently lead both to the net formation of carbohydrates and the re-formation of the initial CO_2 acceptor.

However, although the weight of evidence strongly supported this hypothesis, it was left to Rod and colleagues to show that cell-free extracts of the green alga *Chlorella*, exposed to labeled CO_2 for only 1 min, indeed formed labeled phosphoglycerate when RuBP was also added, and that labeled phosphoglycerate was not formed when ribulose 5-phosphate, or ribose 5-phosphate, or fructose 1,6-bisphosphate, were added instead. As the authors of this succinct one-page *Communication* to the Editor rightly concluded, ''It is clear that the extracts contain an enzyme (or enzymes) capable of catalyzing the carboxylation of ribulose diphosphate (*sic*), specifically, to form phosphoglyceric acid. No intermediates between these compounds have been detected.'' (Quayle et al. 1954)—another brick had been securely added to the edifice of knowledge about plant metabolism.

It was just after this paper had appeared that I appeared in Berkeley. By a laughable misreading of the letter in which I had asked to be permitted to spend a couple of months in his laboratory, Melvin Calvin assumed that it was the distinguished American biochemist *Arthur* Kornberg, and not the inexperienced British post-doc. *Hans*, who had thus applied. Rod was therefore immediately instructed to make space available at his bench and to place himself entirely at the disposal of the Great Man about to arrive. That Rod concealed the disappointment he must have felt when he realized who it was who was to work with him is an eloquent tribute to the tact, forbearance (and appreciation of the absurd) which characterized all his actions and which also laid the foundation of our friendship which was to endure over more than half a Century. As a result of our relatively brief collaboration, we were able to dispose of the possibility that the cleavage of RuBP by CO_2 was a reductive one: our evidence clearly ruled out glyceraldehyde 3-phosphate or dihydroxyacetone 3-phosphate as immediate products of the carboxylation reaction (Kornberg et al. 1955).

In 1955, Rod and Yvonne returned to England. Rod had accepted a post in the DSIR's Tropical Products Institute, to study the chemistry of the naturally occurring pyrethrin insecticides. Although the Quayles soon settled into London life, it also soon became clear to Rod that his interests had moved from the purely chemical to the biochemical. He mentioned this to me, when I had the pleasure of visiting them in their Kensington apartment, but, as so often happens, the matter passed out of mind. However, by an extraordinary coincidence, my future wife and I had been invited to a performance of Samuel Beckett's *Waiting for Godot* and found the Quayles sitting in the row behind us. In the intermission, Rod told me further of his present discontents and indicated his interest in joining me in Sir Hans Krebs' Unit for Research in Cell Metabolism, at the University of Oxford. Naturally, I was delighted at this possibility and swiftly sought, and obtained, Krebs' agreement to offering Rod a position there. And so, from 1956 on, Rod turned his attention from plant products to tracing metabolic pathways in microorganisms.

Initially, Rod and I collaborated on a problem arising from work that a Canadian post-doc, Neil Madsen, and I had been doing and which had resulted in our postulating a ''glyoxylate bypass'' of the tricarboxylic acid cycle (TAC), to explain how pseudomonads could grow upon acetate as sole source of carbon (Kornberg and Madsen 1957). We had shown that the key enzymes were present in cell-free extracts, but, as David Green once memorably remarked, a sufficiently ingenious mechanic could take a Rolls Royce apart and re-assemble the parts to make a washing machine: this was not evidence that the washing machine necessarily functioned as a component of the car. Clearly, it was essential to show that what had been demonstrated to occur *in vitro* indeed occurred *in vivo*. Using the chromatographic techniques that had proved so successful in Berkeley, Rod, and I therefore isolated, and he characterized by chemical degradation, intermediates formed from labeled acetate and unlabeled CO_2. The isotope distributions observed supported the simultaneous operation of the TAC and the glyoxylate bypass (Kornberg and Quayle 1958).

After our initial joint effort, Rod and I decided to study the metabolism of C_2-compounds more highly oxidized than acetate but to divide our forces. He was joined by an Australian visitor, Bruce Keech, to investigate the routes by which *Pseudomonas oxalaticus* grows on formate or oxalate: this revealed that formate behaved as if it were just CO_2 with hydrogens stuck on and that RuBisCO was active in these non-photosynthetic bacteria when grown on formate (Quayle and Keech 1959a, b) whereas, oxalate utilization did not involve RuBisCO. Instead, oxalate was activated to oxalyl-coenzyme A (Quayle and Keech 1960; Quayle 1962), which was reduced to glyoxylate and then followed a biosynthetic route that (another happy coincidence!) had, at just that time, been elucidated by my student Tony Gotto and me, on the other side of the laboratory bench that Rod and I shared. It gave us great pleasure that the work of our two groups was published side-by-side in *Nature* (Kornberg and Gotto 1959; Quayle and Keech 1959c).

Rod's experience with formate utilization stimulated his interest in the metabolism of a wide range of C_1 compounds by a variety of microorganisms. This soon revealed the occurrence of hitherto unknown biological processes, to demonstrate the participation of novel intermediates, and enabled him to isolate and characterize novel enzymes—a brilliant trail of imaginative insight coupled with meticulous attention to the validity of interpretations, which remained the hallmark of his work throughout his scientific career. In later years, Rod surveyed the vast field of C_1-metabolism in a number of lectures to congresses and meetings, and in two masterly reviews (Quayle 1961, 1972).

Our position in the mid-1950s as members of staff of a Research Unit which happened to be within the precincts of Oxford University but was not of Oxford University left us in a kind of academic limbo, unable to participate in what made that ancient university so highly prized—the life and activities of its constituent Colleges. It was thus particularly welcome to Rod when, in 1957, he was invited to accept a Lectureship in Biochemistry at Oriel College. This not only obliged him to offer tutorial instruction to undergraduates of that College, for a trifling fee, but also gave him membership of that collegiate society. It was in that capacity that Rod demonstrated his exceptional gifts as an inspiring and caring teacher whose tutorial sessions were greatly valued by all who were privileged to learn from him.

Although the Quayle family—by now increased to four, by the birth of Susan and Rupert—was happily living in Kidlington, a village only a few miles from Oxford, they realized that the future of Krebs' Unit was uncertain in view of his impending retirement from the Oxford Chair (mandatory at reaching the age of 67). Rod, therefore, in 1963 accepted a Senior Lectureship (equivalent to an Associate Professorship in an American University) in Biochemistry at the University of Sheffield. By that time, Rod had securely established his reputation as an outstanding microbiologist and it occasioned no surprise when, only 2 years later, he was appointed as the University's West Riding Professor of Microbiology, a post he held with outstanding distinction until 1983. It was also entirely fitting that he was elected Chair of the British National Committee for Microbiology from 1985 to 1990 and, some years later, President of the Society for General Microbiology.

Appointment to the Chair not only gave Rod the opportunity to guide the growth of a rapidly expanding and active Department but also brought with it wider administrative responsibilities. Thus, Rod served as Dean of his University's Faculty of Science from 1974 to 1976, was a member of numerous governmental and non-governmental official bodies and, after his widely welcomed election in 1978 as a Fellow of The Royal Society, as Chairman of one of its Sectional Committees. In all these activities, he proved to be unobtrusively but firmly effective, able to achieve his objectives without antagonizing others—an ideal preparation for his appointment as Vice-Chancellor of the University of Bath (a position corresponding roughly to the Presidency of an American University), a post he held with conspicuous success from 1983 to 1992. In his time there, he vigorously championed that relatively young university as a center for both pure and applied research, in the conviction that there is only one Science—"Science applied to useful ends" and "Science waiting to be so applied". Rod did so by example as well as by precept: in moving from Sheffield, he brought with him his research team and, despite the demands made on him by his administrative duties, spent every spare minute in his laboratory. It is impressive to record that, in his studies on methylotrophic yeasts, published a year after he assumed the Vice-Chancellorship, he identified formaldehyde as a central intermediate of methylotrophic metabolism

(Attwood and Quayle 1984); three further publications followed in later years (Egli and Quayle 1986; Quayle 1987; Hacking and Quayle 1990). The remarkable growth in size, scope, and influence of the University of Bath owes much to Rod's vision, leadership, and enthusiasm for science.

Rod's achievements were recognized by a variety of awards. In addition to his election as a Fellow of the Royal Society, he was awarded Honorary Doctorates from the universities of Göttingen, Bath, and Sheffield; elected to Corresponding Membership of the Academy of Sciences of Göttingen; and awarded the CIBA Medal and Prize of The Biochemical Society (Quayle 1980). But, perhaps, his greatest memorial is the affection in which he is held by his many students and colleagues—he was a warm, witty, and wise man, and he will be much missed.

Rod is survived by his widow, Yvonne, by his children Susan and Rupert, and by five grandchildren (David, Hannah, James, Joseph, and Rebecca).

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