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JOHN RAYMOND POSTGATE FIBiol

24 June 1922 — 22 October 2014

Elected FRS 1977

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John Postgate was one of the foremost microbiologists of his generation. He is most famous for his lifelong research on sulfate-reducing bacteria and nitrogen fixation and for his seminal contributions to understanding the survival and death of bacteria. John Postgate is also known for his specialist and non-specialist books on science, most notably Microbes and man, first published in 1986 and now in several editions and translated into several languages. He played an important role in the development and dissemination of microbiology and in the leadership of science in the UK. John will also be remembered warmly as the supervisor and mentor of aspiring young microbiologists, several of whom have gone on to distinguished careers in microbiology. His other great love was jazz: he was an amateur cornet player of note, the leader of several jazz groups and a highly knowledgeable writer, reviewer and author of two books on the subject.

THE EARLY DAYS

John Postgate was born in London on 24 June 1922, the son of Raymond and Daisy Postgate (née Lansbury). His father was a historian, classics scholar, socialist writer, journalist and broadcaster and a gourmet most famously remembered for founding and editing The good food guide. His mother was the daughter of George Lansbury, Labour MP for Bow and Bromley, the socialist reformer and leader of the Labour Party from 1932 to 1935. John’s younger brother was Oliver Postgate, who with Peter Firmin wrote, produced and performed...
in classic TV children’s programmes such as *Noggin the Nog*, *Bagpuss* and *Clangers*. John grew up in a relaxed family background in homes in Hendon and then Finchley in North London that were visited by left-wing politicians and luminaries but few scientists. John’s interest in science seemed self-engendered and founded on his menagerie of fish, rodents, lizards, felines and other pets, the building of radios, conducting alarming experiments with the household electricity and sometimes even riskier fun with his chemistry set performed in the garden shed.

John’s early schooling took place in Woodstock School in Golders Green with fellow pupils from many different countries. After passing the 11-plus exam he attended the forward-looking Kingsbury County School in London, where he studied chemistry, physics, biology and zoology for his Higher School Certificate. This period of his schooling coincided with the outbreak of war in 1939, and John and his brother were evacuated to Totnes, Devon, where he studied at Hele’s School in Exeter, which he credited with having good teachers who instilled the need for hard work and success in examinations. For family reasons he returned to Kingsbury County School to complete his schooling during the Blitz. Success in his ‘Highers’ won him a minor scholarship to Balliol College, Oxford, and with his scholarship supplemented by family, the county and a qualification in Latin, he set off for Oxford in October 1941.

It was during his early teenage years that John discovered his great love for jazz. He was not enthused by formal music lessons at school and indeed never learned to read sheet music. It was listening to the radio in his mid teens on his home-made radios that John first became excited by the big dance bands and swing music. Just before leaving for Oxford he exchanged a barely played accordion for a hard-to-play vintage cornet in a second-hand shop and this propelled him into his amateur jazz career.

It is evident that by the end of his teenage years there emerged in John lifelong attitudes and passions. These included his somewhat left-wing, mildly non-conformist and anti-establishment views, probably developed during his early family and home life. We can also see the genesis and love of science and scientific experimentation encouraged by ‘garden-shed’ hobbies, and his passion for listening to, studying and playing jazz.

**Oxford**

Much to his surprise, John found himself studying chemistry, not zoology, at Oxford. He attended some zoology lectures but soon abandoned these because of the exacting nature of the chemistry course. John was adept in the laboratory, and in friend and fellow-student Christopher Longuet-Higgins (FRS 1958) he found a complementary study ‘buddy’ who was an exceptional theorist and who later became Professor of Theoretical Chemistry at Cambridge. In his third year he took biochemistry tutorials in the Department of Physiology with the physical biochemist and analytical ultracentrifugation expert, Alexander ‘Sandy’ G. Ogston (FRS 1955).

John undertook his fourth-year Part II research project with the influential Professor (later Sir) Cyril Hinshelwood FRS, who with Nikolai Semenov (ForMemRS 1958) won the 1956 Nobel Prize in Chemistry for their research into the mechanism of chemical reactions. In the late 1940s Hinshelwood became interested in applying chemical kinetics principles to the multiplication and variation of bacteria (Thompson 1973). John became interested in the
project and this was his first experience of working with bacteria, in particular *Bacterium lactis*, *B. aerogenes* (now *Klebsiella aerogenes*) and *B. coli mutabile* (now *Escherichia coli*). The project set out to study how bacteria grown on glucose adapted to use other sugars. This involved tediously counting the number of bacteria in replicate cultures, using a calibrated microscope slide called a haemocytometer. In 1946 this work became John’s first publication in *Transactions of the Faraday Society* (1)*. John enjoyed working in Hinshelwood’s supportive and friendly research group. Finding the esteemed Professor Hinshelwood clearing up a flood in the lab taught John the lesson that performing menial tasks in the lab was not beneath anyone. Those who worked with John in his senior positions often observed him carrying out humble laboratory tasks, thus passing on the lesson to others. John was also to learn another valuable lesson from his early work: Hinshelwood’s aesthetically pleasing mathematical theory for bacterial adaptation was proved wrong when its genetic basis was discovered.

John’s interest in a career in academia rather than in industry or the scientific civil service was sparked by his experience in Hinshelwood’s lab, but he realized that this required a research degree. John was taken on as the first PhD student of Dr Donald D. Woods (FRS 1962), who had just moved to Oxford’s Biochemistry Department. As a chemist, John was allowed a year to broaden his knowledge of biology by attending lectures and tutorials in several Oxford departments, and one of his first tasks was to help Woods and other colleagues paint the ceilings and walls of their new lab. This would amuse today’s academics and PhD students and horrify university campus service managers.

John started his research on the resistance of the bacterium *Acetobacter suboxydans* to sulfonamides. Woods had discovered that *p*-aminobenzoic acid (pAB) at very low levels was an antagonist of the sulfonamide drugs used in the 1930s and 1940s to fight pneumonia, puerperal fever, gonorrhoea and other diseases (Gale & Fildes 1965). The hypothesis was that sulfonamides negatively affected some process that required pAB. *A. suboxydans* was chosen as an organism to study because it was not a pathogen, could be grown on a chemically defined medium, required pAB for growth and was sensitive to sulfonamides. John set out to train the organism to withstand sulfonamides by using the technique he had learned from Hinshelwood involving serial subculture with increasing levels of the drug.

The work in the lab fell into a routine, which enabled John to enjoy the general Oxford milieu, and especially the jazz scene. Here he formed and led an amateur traditional jazz group called the Dixieland Bandits. They played at college dances and when required had to play dance music for waltzes and even the Hokey-Cokey, the dance sensation of the time. At one time or another, the group included various amateur musicians who became notable public figures including, on saxophone, clarinet and piano, Mervyn Brown, later Sir Mervyn Brown of the Foreign Office and, on clarinet, Paul Vaughan, later to become a well-known BBC broadcaster and presenter. Contemporaries and followers of jazz at Oxford during those days who would have heard the Bandits included the novelist Kingsley Amis and the poet Philip Larkin.

John drafted a short paper on his work but it was never published. This was allegedly due to Woods’s perfectionism and indecision and to John’s becoming engrossed in his first job. John also drafted other manuscripts but felt these were not of a standard that he would have liked, so he chose not to submit them. He learned early on the importance and necessity of

* Numbers in this form refer to the bibliography at the end of the text.*
publishing good quality research, which he was keen to encourage in younger colleagues in whom procrastinating over publishing was not looked on kindly.

From this early time John moved among illustrious figures in British microbiology and found particularly useful participation in several microbiology summer schools focused on recent developments in chemical microbiology. They were organized by stars of the Cambridge school of microbiology including Marjory Stephenson FRS, Sidney Elsdon and Ernest Gale (FRS 1952) as well as Woods himself. This was also the era of the establishment of the Society for General Microbiology, whose founding members included Woods, Kenneth (‘Butch’) Butlin and B. C. J. G. (‘Gabe’) Knight. John attended a few of the early meetings of the Society but found he was terrified of speaking in public. This phobia took him 25 years to overcome fully and even determined his ultimate career, which lay in research establishments and not universities, with their requirement for lecturing.

By the end of three years, he started to work on his thesis. Woods found the science solid, though with some loose ends and the writing lacking in clarity and organization, which John felt ‘pernickety’ and chose to ignore. This would return to haunt him. Two events delayed completion of the thesis. In 1948 John married Mary Stewart, who had already graduated in English from St Hilda’s. He also found a job with ‘Butch’ Butlin’s small research group at the government’s Chemical Research Laboratory, Teddington, in southwest London, where the role of bacteria in metal corrosion was being studied.

Once established and enjoying his new job, John resumed work on his thesis, which he submitted in late 1949. After the viva voce in Oxford, Woods informed him that he had failed not because of the science but for the poor presentation. This came as a deep shock but a saviour was close at hand. Mary, his wife, was an English graduate and she pointed out several non-scientific problems in the writing, which was an education that John’s tutors and research supervisor had neglected. In due course he resubmitted and passed without further trouble. This experience strongly influenced his lucid writing style in scientific papers and books. Many of his students and colleagues benefited from his advice about writing. He also became an editor, then Editor-in-Chief, of Journal of General Microbiology, where his editorial skills were bestowed on colleagues worldwide to their benefit but sometimes their chagrin.

In the late 1940s and early 1950s the cost of sulfur, mostly imported from the USA to produce the sulfuric acid needed by British industry, was very high. At Teddington, Butlin revisited an earlier idea to manufacture sulfuric acid from hydrogen sulfide (H$_2$S) produced by sulfate-reducing bacteria (SRBs). SRBs are obligate anaerobes and not easy to grow. They require cultures to be established in media free of O$_2$ in closed culture tubes and vessels. In addition, H$_2$S smells unpleasant and is highly noxious. Initial experiments suggested that the biological process might be uneconomic, but John’s laboratory skills soon produced dense viable cultures that could be grown with H$_2$ as a source of reducing power in addition to sodium lactate. The consumption of H$_2$ was measured with Warburg manometers, which were once common in biochemistry labs but were eventually superseded by gas chromatography and polarographic techniques. He showed that fresh actively growing cultures of Desulfovibrio vulgaris Hildenborough could produce H$_2$S at rates potentially...
70 times higher than previously recorded. This suggested a feasible industrial process. The government’s Department of Scientific and Industrial Research (DSIR) was enthusiastic about the news, and the focus of Butlin’s group shifted somewhat away from its original focus of understanding the role of SRBs in metal corrosion. However, scale-up proved disappointing and the idea emerged of finding more active new species of SRBs from known sulfur pools in North Africa. John travelled with Butlin via Benghazi to sample three sulfur-spring-fed lakes near El Agheila in North Africa (figure 1). They collected many samples and also described other life forms, including small fish living in the noxious environment of the pools, which were of interest to ichthyologists. The trip received worldwide attention, being heralded by the DSIR, and John gave interviews to the BBC’s Radio Newsreel. Britain’s sulfur shortage seemed to be over just at a time when it was most severe. The samples proved rich in SRBs, but these were not more active than local strains. However, work on the process continued for another nine years as Butlin’s lab grew. A pilot plant based on sewage and calcium sulfate was built and operated by London County Council. However, the cost of sulfur imports dropped slowly and the biological process became uneconomic.

During this time John took the lead in providing a more fundamental understanding of SRBs. He showed that selenate was a competitive inhibitor of sulfate reduction (2) and contributed papers on the carbon metabolism of these organisms and the biochemistry of the sulfate-reduction process. One of the most fundamental advances in the understanding of biological sulfate reduction arose from his insight and skill in designing media in which to obtain good yields of the organisms not obscured by the black iron sulfide precipitate normally produced when H₂S reacted with iron salts in the medium (3). This produced cell pastes with a pink hue. The absorption spectra of these pink cell suspensions were examined by June Lascelles, an outstanding young Australian scientist then on a Fellowship in Woods’s lab and who later became an expert in photosynthetic bacteria and a professor at the University of California, Los Angeles. June used a Hartridge reversion spectroscope that was perfected in the early 1920s to measure the level of carbon monoxide in blood and which is still used nowadays to examine gem stones. This was an ideal instrument
with which to characterize the visible spectra of translucent cell suspensions. She observed two clear absorption bands in the green area of the spectrum, which were bleached on exposure to air. Such bands had previously been seen only in aerobic bacteria containing cytochromes, leading to the dogma that cytochromes were present only in aerobes and not obligate anaerobes. It was suggested that John’s cultures were contaminated with aerobic organisms. However, his findings were confirmed with suspensions of repurified bacteria. It was proposed that SRBs contained a cytochrome that was spectroscopically distinct from cytochrome \( c \) from yeast or muscle.

John took extracts of his cells to the world authorities on cytochromes, David Keilin FRS and E. F. Hartree at the Molteno Institute at Cambridge, who were strong proponents of the exclusivity of cytochromes to aerobes. They confirmed both the presence of a new type of cytochrome and the presence of another novel substance characterized by an absorption band at the red end of the spectrum.

John first reported finding the new cytochrome to an International Microbiological Congress in Rome in 1953 and a year later produced two short communications naming it cytochrome \( c_3 \) and the substance responsible for the red absorption ‘desulphoviridin’ (4, 5). Also in 1953 Dr M. Ishimoto in Japan reported finding a cytochrome in a different species of SRB, and Martin Kamen in California found cytochromes in anaerobic photosynthetic bacteria. The ‘cytochrome’ dogma had been truly rebuffed. That at time, Butlin’s group were growing SRBs in continuous culture, a technique learned from the Microbiology Research Department in the then Ministry of Supply’s biological warfare research unit, at Porton Down near Salisbury in Wiltshire. Continuous culture provided John with a good supply of SRBs from which to extract and purify both cytochrome \( c_3 \) and desulfoviridin (6).

Our understanding of the nature of cytochrome \( c_3 \) and its role in dissimilatory sulfate reduction expanded dramatically as others applied new techniques to study sulfate reduction by SRBs. Soon it was shown that John’s preparations were not fully active or pure and even contained two other cytochromes. This does not detract from the importance of his original discovery, and today the crucial roles of cytochrome \( c_3 \) and desulfoviridin in energy conservation in SRBs have been elucidated (figure 2).

The ground-breaking discovery of cytochrome \( c_3 \) and other work on SRBs led to greater exposure of the work in Butlin’s group and to visits to Teddington by many distinguished microbiologists and biochemists. These meetings enhanced John’s reputation and led to invitations to speak at international conferences. In 1957 he embarked on an extended scientific visit to the USA arranged around an invitation to talk on the relationship of SRBs to the secondary recovery of oil, at a small symposium at St Bonaventure University in upstate New York. The tour took in a fortnight’s working visit to C. B. van Neil’s lab in Hopkins Marine Station in Pacific Grove, Monterey. The aim was to examine SRBs that Van Neil had isolated from marine environments. The ‘sluggardly’ revival of the cultures allowed John time to explore the Californian coast and sample local wine, which he found better than its reputation at that time in Britain. He also gave an invited seminar at University of California, Berkeley, in San Francisco, home to several distinguished US microbiologists, notably Roger Stanier (FRS 1978) and H. L. Barker. At the end of the visit he met A. I. Krasna at New York’s Columbia University to learn more about the enzyme hydrogenase that SRBs can use to fuel sulfate reduction.

An ulterior motive for John to go to New York was to visit the fountainhead of jazz. He took time out in Manhattan to explore record shops and listen to a lot of live jazz from some
great artists of the day, including trumpeters Sidney de Paris, Bobby Hackett and Charlie Shavers and the tenor saxophonist Coleman Hawkins. John published an article about his Manhattan experience in *Jazz Monthly* magazine in May 1958.

In the mid to late 1950s, and despite the scientific successes of Butlin’s group, its economic *raison d’être* was being questioned by its masters at the DSIR. In the spring of 1959 and despite vigorous lobbying, the group was disbanded and Kenneth Butlin retired. A reason for the furore among the scientific community was that, as part of the early expansion of the group in 1951, it acquired from the Medical Research Council the custodianship of the National Collection of Type Cultures. This nationally important collection was then expanded to include microbes of economic importance and renamed the National Collection of Industrial Bacteria (NCIB). On the group’s closure the NCIB was moved to the Torrey Research Station in Aberdeen and amalgamated with the National Collection of Marine Bacteria, becoming the National Collection of Industrial and Marine Bacteria, which exists to this day.
Microbiological Research Establishment, Porton Down

Just at this time, a senior vacancy opened up at the Microbiological Research Establishment (MRE) in Porton Down, then headed by Donald Henderson. John accepted the post and the family moved to Salisbury in the spring of 1959. He joined a biochemically focused section under the microbiologist Dennis Herbert, famed for being the first person to crystallize a bacterial enzyme, catalase, and an expert in continuous culture.

The fundamental goal of the MRE towards biological weapons development and defence did not align with John’s political and generally pacifist views. However, the MRE was then possibly the UK’s foremost microbiology research group, from which emerged fundamental advances in continuous, single-cell culture, mass cell culture, preservation of bacteria, microbial genetics, bacterial sporulation, mechanisms of animal pathogenesis, and propagation of viruses in cell tissue culture. John rapidly appreciated the value of the MRE’s multidisciplinary approach and collegiality. It was to prove an important cornerstone of his belief of how science could be best advanced, a belief he was later to put into practice when eventually he had the chance to direct a scientific programme at the Unit of Nitrogen Fixation at the University of Sussex.

John could not directly continue his research on SRBs but was encouraged to look into bacterial survival and death, which was already being studied by Dick Strange at the MRE but by few others worldwide. John’s work on bacterial survival and death soon proved productive once a method had been found to distinguish between dead and viable organisms. Of the several methods for doing this he settled on microscopic observations of the ability of individual bacteria to grow and divide on slide cultures. This was already in use at the MRE by Owen Powell to study the kinetics of bacterial growth and division. For this work John returned to the bacterium *Klebsiella aerogenes*, which he had studied in Hinshelwood’s lab. In one strand of experiments he and his team of Janet Crumpton and John Hunter looked at the effects of starvation on the viability of cultures. To provide a consistent source of organisms, cultures were first grown in continuous culture. Samples were withdrawn and subjected to starvation; from these, further samples were taken at timed intervals. These were inoculated into a thin layer of a nutrient-rich agar in a cavity created between a microscope slide and a coverslip suspended slightly above the slide by a metal ring. Cells were observed microscopically for their ability to divide or not. There remained difficulties in determining whether a bacterium is actually dead as opposed to being incapable of growth and division. Nevertheless a number of novel observations were published by Postgate and Hunter in their very detailed 1962 paper (7). They showed that bacteria consumed their own constituents such as carbohydrate, protein and nucleic acids to preserve vital functions, but once approximately half of those had been consumed they were unable to recover and divide. In a series of papers in the early 1960s Postgate and Hunter explored the survival of frozen bacteria and described the phenomenon of ‘substrate-accelerated death’ of *K. aerogenes*, *E. coli* and *Serratia marcescens*, in which death was hastened by the resupply of growth substrates of which organisms had previously been starved (8). They also described the phenomenon of ‘cryptic growth’, particularly in dense bacterial populations, where the dead bacteria leak nutrients that can support the growth and division of viable organisms.

Early in 1962 John received an offer of a year-long Visiting Professorship at the Microbiology Department at the University of Illinois, Urbana, with Leon Campbell and Ralph Wolfe as co-hosts. The MRE was content with a shorter stay and agreed that John
could resume his work with SRBs, which interested Campbell. John and Mary and their three young daughters, Selina, Lucy and Joanna, set off for the USA in the early autumn of 1962. This was his first experience of working as a university ‘academic’ but he had few lecturing and examination commitments, for which he was rather glad. This allowed him time to clear up some loose ends from his earlier work at Teddington and to examine some bacteria that Campbell had isolated. In only a few months he and Campbell had done sufficient work to publish six papers from their research over the period 1963–66. These included the description of novel SRBs and studies of the taxonomy of both spore-forming and non-spore-forming desulfovibrios.

Before John had left for the USA, the MRE had been looking to ‘civilianize’ its work by studying more of the microbiology of economic processes. John returned to the UK at the height of the Cold War and the international nuclear stalemate, and there was concern in the government that the UK needed its research on weapons and defences for biological warfare. He saw his future being constrained by this prospect and did not agree that the impressive facilities of the MRE should be devoted to defence purposes. He therefore decided to look for another job.

**THE UNIT OF NITROGEN FIXATION**

At the end of this sojourn John was tempted to take up a firm offer of an academic position in the USA, but he heard from Donald Woods that the Agricultural Research Council (ARC) was looking for an experienced microbiologist to join a new research group to work on nitrogen fixation. Indeed, this was one of the microbial processes that attracted the attention of the reports arguing for the civilianization of the MRE. John was told that he could meet the Director Designate en passant in New York.

\[ \text{N}_2 \text{ fixation} \]

N\(_2\) fixation is the process, restricted to a few prokaryotic organisms (bacteria and archaea), that converts atmospheric N\(_2\) to NH\(_4^+\). This ‘fixed’ N is used by all organisms such as plants as a starting point for the biosynthesis of protein, RNA and DNA and other cell components. The provision of fixed N either through biological N\(_2\) fixation or the industrial Haber Process is essential to agriculture. On a global scale, N\(_2\) fixation is an essential limb of the global nitrogen cycle sustaining all life on Earth.

An earlier report, commissioned by Shell and conducted by the now retired Kenneth Butlin, surveyed the study of this process since its discovery in 1886 and the research currently being undertaken in the UK and in particular in the USA. It noted an important breakthrough made in 1960 by the Dupont de Nemours Chemical Corporation at Wilmington, Delaware. Their research team of J. E. Carnahan, L. E. Mortenson, H. F. Mower and J. E. Castle had shown that the enzyme system responsible for this process could be made to work in vitro (Carnahan et al. 1960). This made tractable the study of the biochemistry and chemistry of N\(_2\) fixation and rapidly led to several papers on the essential characteristics and requirements of the enzyme system, called nitrogenase.

Although Shell decided not to set up a research team in this area, the ARC realized that it fell squarely in their remit and decided to set up a Unit to study the fundamentals of the biochemistry and chemistry of the process. It would leave the broader aspects to several other established university research groups around the UK. These included the diversity of nitrogen-fixing organisms and N\(_2\)-fixing symbioses especially with leguminous crops, such
as peas and beans, which through their *Rhizobium*-containing root nodules are self-sufficient in fixed N.

John’s meeting in New York in 1963 was with the Unit’s Director Designate, Professor Joseph Chatt FRS, a distinguished inorganic chemist. The plan was to develop the Unit along interdisciplinary lines. It would be the largest ARC Unit, with 10 senior scientists, 15 support staff and research students. John was appointed as Assistant Director.

The Unit started life divided between two sites in London, the chemistry side at Queen Mary College and the biology at the Royal Veterinary College in Camden Town. The first two additional senior research staff (Dr Ray Richards and Dr Michael Kelly) were appointed and PhD students were taken on. Eventually the Unit became known as the Unit of Nitrogen Fixation (UNF) and was consolidated in 1965 at the newly established University of Sussex in Brighton. In 1968 it moved into a custom-designed building.

An important strategic decision was the initial focus of the biological research, including the selection of organisms to study. It should complement but not directly compete with work elsewhere in the world. The strategy that emerged was influenced by John’s attendance at a symposium of world experts at Butternut Lake, Wisconsin, in 1964 sponsored by the C. F. Kettering Research Foundation. While in the USA he also visited several labs, especially at the University of Wisconsin, a historically important centre of academic research in N₂ fixation, where important figures in the field, including Perry Wilson, Bob Burris and Winston Brill, were located.

It was known that nitrogenase from the obligate anaerobe *Clostridium pasteurianum* studied by Carnahan and his group was destroyed by exposure to O₂. However, in the mid 1960s, W. A. Bulen, R. C. Burns and J. R. LeComte, working at the C. F. Kettering Research Laboratory in Ohio, described a much more O₂-resistant nitrogenase system from *Azotobacter vinelandii*, a bacterium capable of fixing N₂ in air (Bulen et al. 1964). *A. vinelandii* was then a workhorse in biochemistry, for example in seminal work on the enzymology of RNA synthesis and studies of enzyme kinetics (Lineweaver & Burk 1934).

In the mid to late 1960s John and his colleague Mike Kelly, the first senior scientific appointee on the biochemical side, studied the biochemistry of N₂ fixation in *Azotobacter chroococcum*, an O₂-tolerant N₂ fixer. They demonstrated that nitrogenase could reduce cyanide and isothiocyanate, an early example of the Unit’s interdisciplinary approach (9). They also confirmed that nitrogenase could reduce acetylene to ethylene, which could be measured by gas chromatography. This remains a standard assay for nitrogenase in both whole organisms and cell extracts.

An important biological problem, addressed early in the Unit’s programme, was to determine which microorganisms are capable of fixing nitrogen. Together with Susan Hill, a member of staff, John examined both continuous and batch cultures of seven microbial strains from collections, plus three local isolates, using isotopes of N₂ and acetylene and isocyanide as nitrogenase substrates. Of these only two strains were able to fix N₂, although some simulated fixation impressively in cultural tests but eventually proved simply to be very efficient scavengers of fixed nitrogen (11).

In the early 1960s Russian workers reported the isolation of nitrogen-fixing strains of *Mycobacterium* from acidic soils. It was thought that these strains might be important nitrogen fixers in soils since they are more acid-tolerant than the azotobacters. Therefore John, with a student, David Biggins, conducted a detailed physiological and biochemical examination of nitrogen fixation by *Mycobacterium flavum* 301. They concluded that the nitrogenase
from this organism catalysed the same reactions as enzymes from other organisms but was more similar to that of the azotobacters in being particulate, whereas that from clostridia was soluble. However, nitrogenase in the crude extracts form *Mycobacterium* was more sensitive to O\(_2\) than the enzyme in *A. chroococcum* extracts. This suggested that the protective mechanism was more primitive. The enzyme was purified from *M. flavum* 301, and immunological cross reactions were observed with nitrogenases isolated from some other organisms but not from the strict anaerobe *C. pasteurianum* (13). The nitrogenases from azotobacters were recognized as being particulate, suggesting that the enzyme might be protected from oxygen damage in the particles. It was later shown that the particles contained, in addition to the two component proteins in nitrogenase, a third protein (later to become known as the Shethna II protein) that was oxidized by oxygen and then formed a protected particle with nitrogenase (Haaker & Veeger 1977; Robson 1979).

In the mid to late 1960s John and research student, Howard Dalton (the late Sir Howard Dalton FRS; see Anthony & Murrell 2016), studied N\(_2\) fixation in *A. chroococcum*, in batch and continuous cultures under a variety of conditions. They concluded that two mechanisms existed to protect the nitrogenase from damage by oxygen: first, enhanced respiration to scavenge excess oxygen, and second, a conformational state of the enzyme that prevented damage by oxygen (10). In subsequent work with another student, Jan Drozd, John confirmed these proposals and was able to demonstrate the switching on and off of nitrogenase activity and the limits of the two mechanisms (12).

John was keen to encourage other scientists to take sabbaticals working in the Unit. An example was Howard Lees from the University of Manitoba, Canada, who worked with John on oxygen- and phosphate-limited cultures of *A. chroococcum*. Their findings supported the view that respiration provided, at least in part, a protective function for nitrogenase (22). They and Britton Chance (ForMemRS 1981) also published a theoretical *Nature* note clarifying the meaning of the terms ‘reversed electron flow’ and ‘high energy electron’ in biochemistry (15).

In another collaboration, with W. S. Silver, John considered the evolution of asymbiotic nitrogen fixation, which they noted was restricted to prokaryotic organisms, particularly those considered to have ‘primitive’ properties. They suggested that nitrogen fixation may have evolved before significant amounts of oxygen appeared in the atmosphere. They suggested that because there would have been adequate ammonia available for the growth of these organisms, the original role of nitrogenase might have been to detoxify the environment by removing chemicals such as cyanide and/or cyanogen (20). Later, with the emergence of an oxidizing atmosphere, facultative and aerobic nitrogen-fixing organisms could only retain nitrogenase if it was protected from inactivation in some way. In the Azotobacteraceae this is achieved by ‘conformational protection’ and in filamentous cyanobacteria by compartmentalization.

John combined his new enthusiasm for nitrogen fixation with his interest in SRBs and confirmed the presence of nitrogenase in *D. desulfuricans* and other *Desulfovibrio* strains. One strain exists in the sheep rumen, and with an assistant, David Ware, and in collaboration with colleagues from the Rowett Research Institute in Aberdeen, John attempted to assess whether the organism might contribute to the sheep’s nutrition. They concluded that although some activity was detected it was insufficient to make a significant contribution (21).

In 1969 the biochemical effort at the Unit was boosted by the addition of two new senior scientists: Bob Eady, a biochemist, and Barry Smith, a physical chemist interested in applying spectroscopic techniques to biological problems. Under John’s guidance, the new Unit members and a student, Keith Cook, studied in detail nitrogenase from the facultative
anaerobe, *K. pneumoniae* M5a1 (now renamed *K. oxytoca*) (16). The outcome was the most comprehensive description of a nitrogenase available in one place. This publication had the effect of putting the Unit at the forefront of world nitrogenase biochemistry. Later John appointed two more important members to the biochemical team, David Lowe and Roger Thorneley, who developed a conceptual model for the mechanism of action of nitrogenase, which they then computerized. This model was able to describe and predict the enzyme’s activity in considerable detail.

Probably John’s most important contribution to the scientific output of the Unit was his decision in 1969 to initiate, with research student Ray Dixon (FRS 1999), the study of the genetics of nitrogen fixation. Dixon and Postgate chose to study *K. pneumoniae* M5a1, an enteric bacterium that was likely to be genetically tractable because it was related to the extremely well-studied model bacterium *E. coli*. They established a conjugation system in *K. pneumoniae* M5a1 that enabled the transfer of genes between strains and discovered that genes required for nitrogen fixation (*nif*) were located next to the genes for histidine biosynthesis (14). The conjugation system also proved to be useful for inter-specific transfer of genetic material. Initially they tested the potential for genetic transfer of genes for histidine biosynthesis from *K. pneumoniae* M5a1 to a histidine-requiring (His−) strain of *E. coli*. Remarkably, some of the His+ transconjugants of *E. coli* gained the ability to fix nitrogen, demonstrating that all the genes required for nitrogen fixation were located next to the histidine operon in *K. pneumoniae* M5a1 (17). The creation of the world’s first engineered diazotroph created a stir in the scientific community and sensational reporting in the media.

John became fascinated with the idea of transferring nitrogen fixation to ‘alien’ genetic backgrounds. Together with a visitor, Viji Krishnapillai, and his assistant Helen Kent, he studied the transfer of *nif* genes from *K. pneumoniae* M5a1 to various representatives of the γ-proteobacteria (25, 28). Although these studies were of limited practical value, because diazotrophy is already represented in related organisms that inhabit similar environmental niches, they did show the evolutionary advantages of *nif* gene clusters and their potential to mediate horizontal gene transfer.

The breakthrough in the transfer of the *nif* genes to *E. coli* and the adoption of the then new tools of recombinant DNA technology and DNA sequencing led to the steady expansion of the genetics group with the appointment of Christina Kennedy, Frank Cannon, Mike Merrick, Martin Drummond and Martin Buck (FRS 2009). The work led to significant advances in the identification and function of the large cluster of more than 20 *nif* genes in *K. pneumoniae* M5a1, in particular in the synthesis of the complex iron- and molybdenum-containing metal centres in the enzyme and the supply of reducing power. A strong focus was the complex regulation of expression of the *nif* genes in response to fixed nitrogen and O₂ and the way in which this regulatory system was subordinate to the global nitrogen and oxygen regulatory systems in the organism. Studies on the biochemistry and physiology of *Azotobacter* were expanded by the early appointment of Geoff Yates and later Rob Robson and Richard Pau. Advances were made in understanding the role of hydrogenase in recovering the energy lost by the hydrogen produced as a by-product of nitrogenase activity. Studies of the mechanisms of protection of nitrogenase from O₂ yielded novel findings, and the development of molecular genetic tools for *Azotobacter* led to the discovery of the vanadium nitrogenase system.

The year 1977 was important for John. First, he was elected to the Fellowship of the Royal Society on the basis of the many advances he had made in microbiology. Second, towards
the end of the year he undertook a sabbatical for a year in Harold Evans’s laboratory at Oregon State University, whom he met originally at the Butternut Lake conference. Together with Robert Maier he isolated hydrogenase-deficient mutants of the legume symbiont *Bradyrhizobium japonicum* (23). This was an important initial step in determining the role of the uptake hydrogenase in recovering the energy lost by nitrogenase as a consequence of its obligatory hydrogen-evolving activity.

When Joseph Chatt retired in 1980, the ARC appointed John as the new Director of the Unit. This was a golden age for the Unit, which was renowned as a world-leading group for nitrogen fixation research that at its peak had a staff complement of about 45.

During this time the Unit made great contributions to the understanding of nitrogen fixation, including the function and regulation of the *nif* genes, the role of hydrogen metabolism in nitrogen fixers, the properties of the complex Mo-, Fe- and S-containing metal centres in nitrogenase and its reaction mechanism and kinetics, and the discovery of a genetically distinct vanadium-requiring nitrogenase enzyme system in *A. chroococcum*, which was produced when Mo was not available (29).

John had a delightful ‘hands-off’ approach to staff management, both when leading the ‘biologists and biochemists’ and later when directing the whole Unit. This is clearly explained in John’s book *Microbes, music and me*, in which he likened his leadership style to that of a big band leader:

> I like to think that my leadership echoed in some ways Duke Ellington’s approach to his orchestra. He never managed his musicians: he had a collection of brilliant, disparate and individualistic soloists and he gave them their heads musically. His contribution was simply to co-ordinate them, which he did in such a masterly fashion that he created the greatest jazz orchestra of the century.

Despite the heavy administrative load associated with his interactions with the Agricultural and Food Research Council (AFRC) and his duties as Director, John still found time to do some bench work and could frequently be seen in his lab coat, streaking out strains in his small laboratory (figure 3). But other responsibilities restricted his research activities. He became President of the Institute of Biology (now the Royal Society of Biology) in 1982, and in 1984 he was made President of the Society for General Microbiology (now the Microbiology Society). He had previously served on the Society’s Council and had been Editor-in-Chief of its *Journal of General Microbiology*, for which he was renowned as being extremely fastidious in the maintenance of editorial standards, perhaps as a consequence of the difficulties he himself experienced in writing his PhD thesis.

**SCIENCE AND OTHER WRITING**

Quite apart from John’s scientific papers and reviews he was a relatively prolific author of books over 38 years. These covered three areas: specialized scientific monographs, contributions to the public understanding of science and jazz, and biographies. His scientific monographs comprise an important early review of the sulfate-reducing bacteria (24), two monographs on nitrogen fixation entitled *Nitrogen fixation*, first published in 1978 and now in its 3rd edition (33), and *The fundamentals of nitrogen fixation* (26). His biographies were of his grandfather John Postgate, an early pioneer of food safety, entitled *Lethal lozenges and tainted tea* (35), and of his father, Raymond Postgate, entitled *A stomach for dissent*, which
he co-authored with his wife, Mary (31). John co-authored with Bob Weir a biography and discography of the jazz trumpeter Frankie Newton (36). He also published a rather ill-fated guide aimed at increasing the public’s appreciation of jazz (19). Unfortunately the publisher experienced financial difficulties and the whole edition was seized by the Official Receiver with only a few copies sold as remainders. John’s last book was his 2013 memoir entitled *Music, microbes and me: a life in science*, which is self-revealing and also wryly amusing in many places (37).

In 1965, when the Unit of Nitrogen Fixation was still in its infancy, John was commissioned by Penguin publishers to write an introduction to microbiology, accessible to the general reader, that would focus on the impact of microbes on people’s daily lives. *Microbes and man* finally emerged as a paperback in 1969. It soon gained popular acclaim, serving as both a teaching aid and an easy-to-read introduction to the world of microbes, illuminating both the positive and negative aspects of the huge microbial community on our planet. *Microbes and man* has undergone four revisions, been translated into nine languages and is still in print today (34). John also published *The outer reaches of life* (32), in which with typical clarity he provided an entertaining description of microbial life in a wide range of environments, some seemingly hostile to life but in which microbes have evolved to inhabit and thrive.
John was also concerned about broader societal issues that could perhaps benefit from scientific intervention. Concerned by the increasing world population and consequent shortages of food and raw materials, he wrote a notorious article in 1973 for *New Scientist* entitled ‘Bat’s chance in hell’ in which he advocated the use of a ‘man child’ pill in developing countries as a means to control the population (18). This created a furore, particularly in the feminist community. Far less controversial was an article published in 1984, ‘Biology in the eighties—and beyond’, which again alluded to world population growth and the depletion of energy resources (27). Drawing on his expertise in both sulfur and N₂ reduction, John enthusiastically promoted biotechnology as a means to supplement energy-depleting chemical production with cleaner biological processes. He also argued that this new revolution in biology would help to counter the growing wave of anti-science sentiment that blames science and technology for exacerbating humanity’s problems rather than alleviating them (27).

It would be remiss to omit John’s contributions to jazz (figure 4). Not only did he continue to play in and lead semi-professional jazz groups until his early eighties, he was a renowned writer and reviewer on jazz for more than 45 years for *Jazz Monthly*, *Jazz Journal* and *Gramophone*. His reviewing activity may have been encouraged by Mary, who was renowned for publishing many reviews of spoken word recordings from the 1960s.
John’s retirement in 1987 was mandatory and he became an emeritus professor at the University of Sussex. He never lost his lively interest in scientific matters and their communication to the general public. This continued past the loss of Mary, who died in 2008. They had been married for 60 years. At the time of his death in 2014 he had contributed approximately 50 reviews, letters and opinion pieces, mostly published in *New Scientist* and *The Times Literary Supplement* but several in mainstream scientific journals, including a history of the first 50 years of the Society for Microbiology.

John was concerned about the public understanding of science and the growth of anti-science attitudes. He felt that this was at least partly the fault of scientists themselves, who responded to anti-science criticisms by emphasizing the benefits deriving from the applications of science instead of defending science itself as a cultural activity. Contrary to the assertion that science does not impose moral values, John insisted that science imposes a stern, austere morality on its adherents, constantly open to challenge and modification, with no dogmas, there being no absolute truth because science only approaches the truth asymptotically and never gets there.

Most of his writings reflected his academic interests in nitrogen fixation, microbial sulfur metabolism and microbial survival and death, but some also broke new ground. For example he proposed a system (based on army practice) whereby professional scientists would be appointed for a fixed term of, say, 25 years and then (mainly) promoted one grade and retired on half pay. A few, outstanding, individuals would be retained for, say, another 10 years, after which a further assessment of their capability would occur. This system would prevent senior scientists who had effectively ‘run out of steam’ from blocking the promotion prospects of their younger, more productive and innovative colleagues and would also release capable, middle-aged individuals into the workforce for other roles.

A recurrent theme was to emphasize the difficulty of distinguishing between real and apparent observations. A good example is nitrogen fixation, for which several ‘ghosts’ have been reported, such as: How do termites and woodworm obtain enough nitrogen to grow when their diets seemingly consist only of the carbohydrate from wood? Can these organisms fix nitrogen from the atmosphere to make ammonia? The upshot of careful investigations is that only certain bacteria can fix nitrogen. Other organisms that have been reported to do so are either associated with such bacteria, for example the symbiosis between legumes and *Rhizobium* species, or are extremely effective at scavenging ammonia or other nitrogen compounds from the environment.

Another area where it is difficult to ascertain the validity of claims is that of microbial longevity. In ‘The microbial way of death’ (30) John explained that it was difficult to determine whether bacteria are dead or senescent. In a comment on a 1995 article in *Microbiology*, John examined the authors’ claims concerning the possible age of spores of a strain of *Bacillus sphericus* isolated from the gut of bees entrapped in amber between 25 and 40 million years ago. John felt that its veracity must await determination of whether over this length of time the amber could have been permeable to nutrients in liquid or vapour, which could have sustained the organism. If the putative age of the organisms is correct, then current views on the ‘tenacity of life’, the stability of DNA, the resistance of spores to radiation damage and aspects of bacterial evolution will need to be radically revised. John also questioned claims of viable spores in 8000-year-old sediments and viable non-spore-forming microbes isolated from the interior of 2400-year-old Egyptian bricks. Clearly this issue remains to be settled.
**John Raymond Postgate**

**CONCLUDING REMARK**

Quite apart from all of John’s many important contributions to science and its public understanding and to the development of the careers of many younger scientists, and also his writing and performance of jazz, John was rightly proud of his own family and their background. A typically non-religious memorial service for John that took place in Brighton in 2014 highlighted some of the many caring and amusing sides of John as a husband and father, of which many of those who worked with him were unaware.

**HONOURS AND AWARDS**

1965  DSc, Oxford University
      Fellow of the Institute of Biology
1977  Fellow of the Royal Society
1978  Member, European Molecular Biology Organization (EMBO)
1981  Honorary Member, Society for Applied Bacteriology
1982–84 President, Institute of Biology
1984–87 President, Society of General Microbiology
1988  Honorary Member, Society of General Microbiology
1990  Honorary DSc, University of Bath
1992  Royal Society Leeuwenhoek Lecture: ‘Bacterial evolution and the nitrogen-fixing plant’
1997  Honorary LLD, University of Dundee

**ACKNOWLEDGEMENTS**

We thank members of the Postgate family (Lucy, Selina and Joanna) for their helpful comments on the manuscript and for providing us with photographs of John.

The frontispiece photograph was taken in 1985 by Godfrey Argent and is reproduced with permission.

**AUTHOR PROFILES**

*Rob Robson*

Rob Robson was recruited by John Postgate as a Scientific Officer at the Unit of Nitrogen Fixation, which he joined in 1977. He was attracted by the Unit’s scientific focus and multidisciplinarity and carried out research on the molecular biology of nitrogen fixation in *Azotobacter chroococcum*. Supported by John, his work led to insights into O₂ protection systems, the molecular genetics of N₂ fixation, including the important discovery of the vanadium nitrogenase system, and, with colleague Geoff Yates, the genetics and role of the uptake hydrogenase system. Rob left the Unit in 1987 and was a founding member of the multidisciplinary Centre for Metalloenzyme Studies at the University of Georgia at Athens.
in the USA. He returned to the UK in 1994 as Professor of Microbiology at the University of Reading. He retired in 2012, having been a Pro-Vice Chancellor during his last six years there. With some leftover research funds he started a project to sequence the genome of *A. chroococcum*, the organism that John had chosen for the Unit to work on in at its inception. The paper reporting the genome sequence of this organism was published in June 2015, sadly after John’s death but nevertheless a fitting tribute to the opportunity and support he had given Rob earlier in his career.

*Barry Smith*

Barry Smith’s first and second degrees and postdoctoral appointments were in chemistry. In 1969 he was appointed by Professor Chatt and Professor Postgate as a Senior Scientific Officer at the Unit of Nitrogen Fixation. His initial role was to apply spectroscopic and biochemical methods to analyse the structure and function of the enzyme nitrogenase, which is responsible for biological nitrogen fixation. This approach, which involved collaborations both within the Unit and with academic groups expert in various techniques, was timely and successful. When John Postgate retired in 1987 the Unit was combined with some other AFRC establishments, and Smith was appointed as Head of the Laboratory, which then became part of the John Innes Centre in Norwich.

*Ray Dixon FRS*

Ray Dixon joined the Unit of Nitrogen Fixation in 1969 as a DPhil student under John’s supervision. With John’s support and guidance he developed genetic techniques to identify nitrogen fixation genes in *K. pneumoniae* (now renamed *K. oxytoca*). In 1972 they successfully transferred the complete cluster of nitrogen fixation (*nif*) genes from *K. pneumoniae* to *E. coli*, thus creating the first engineered diazotroph. Ray was appointed as a Scientific Officer at the Unit in 1975 and continued to perform research on the genetics and regulation of nitrogen fixation until the Nitrogen Fixation Laboratory at Sussex was disbanded in 1995. He then moved to the John Innes Centre (JIC), where he has pioneered studies on signal transduction and transcriptional regulation of nitrogen fixation. He is currently the director of a joint research centre established by the Chinese Academy of Sciences and the JIC, known as the Centre of Excellence for Plant and Microbial Science, located across campuses in Norwich, Beijing and Shanghai.

**REFERENCES TO OTHER AUTHORS**


**BIBLIOGRAPHY**

The following publications are those referred to directly in the text. A full bibliography is available as electronic supplementary material at http://dx.doi.org/10.1098/rsbm.2016.0006 or via http://rsbm.royalsocietypublishing.org.


(18) Bat’s chance in hell. *New Scient.* 58, 12–16.


