## Obituary

## **Robert M. Macnab**



Robert M. Macnab, Professor in and former chair of the Department of Molecular Biophysics and Biochemistry at Yale University, died unexpectedly on 7 September, 2003, as a result of a fall at his home. Bob Macnab's outstanding scientific contribution has been in the understanding of the bacterial flagellum, the organelle of motility for many prokaryotes. He was also a distinguished teacher of bio-

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chemistry and helped both his department and Yale in many key decisions about policies and their implementation. Bob matched his love for science with his enjoyment of fine foods, wines, single malt whiskies and the poetry of Robert Burns from his native Scotland. His friends and colleagues remember with gladness and sadness the times spent sipping scotch, munching on salted Japanese snacks and struggling to understand the workings of the amazing flagellar organelle that enables bacteria to swim.

Over the last 30 years, Macnab, with his wife and colleague May Kihara, pursued the assembly, structure and function of the bacterial flagellum. Bob began as a petroleum chemist with British Petroleum after receipt of his undergraduate degree in chemistry from the University of St Andrews in Scotland. Following his leave to get a PhD in physical chemistry at the University of California at Berkeley, which he received in 1969, Bob did not return to BP but instead took a postdoctoral position with Dan Koshland (UC Berkeley), with whom he began his work on chemotaxis and motility. Bob's first paper with Koshland in 1972 was a landmark work showing that bacteria detect spatial gradients by converting them to temporal gradients. If a cell is swimming up a gradient, the concentration is increasing in time. They put forward a simple, insightful model in which cells had a 'memory device' for detecting changes in time. In their model, the memory device used opposing fast and slow biochemical reactions to generate and remove a molecule that regulates the flagellar behaviour. The general features of the model are correct.

In 1973, he began his distinguished career at Yale University. In his early work there, Bob watched cells swim or tumble using a microscope he had developed while still in the Koshland laboratory. Using a high-intensity xenon arc lamp, he could see individual bacterial filaments on living swimming cells. Bob was the first to document how individual flagellar filaments move as cells of *Salmonella* run and tumble, and this was seminal and important work. It was about this time that he began the long task of enumerating, sequencing and determining the functions of the approximately 40 genes responsible for the assembly, structure and function of the bacterial flagellum. Although other laboratories were studying this organelle, Bob and his collaborators were the major contributors to the structure and organization of the components in the flagellum.

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More recently, he had turned his attention to the assembly pathway of the flagellum and, as he had done for the assembled flagellar structure, was well on the way to determining the main features of the flagellar export apparatus, which share similarities with the type III export apparatus.

In his 30 years as a citizen of Yale, Macnab was often called upon to provide insights and guidance. He played a major role in recreating the Microbiology Department, which had been closed in an earlier period. He was a member of many key committees and was particularly concerned with undergraduate life and education. Involvement with Yale College led him to be an active fellow of one of its residential colleges, Calhoun. Within his home department of Molecular Biophysics and Biochemistry, he served in several administrative positions, including terms as Director of Undergraduate Studies and as chair. His colleagues could always count on his clarity of thinking, his balanced judgment and his highly developed sense of principle.

Macnab's leadership in flagellar research is acknowledged by his election to the American Academy of Microbiology and the Japan Society for the Promotion of Science, by his chairmanship of the Gordon Conference on Sensory Transduction in Microorganisms, by his many presentations at and chairings of sessions on the flagellum, by his many invited reviews, by his contribution of the chapter on the flagellum to the two-volume Escherichia coli and Salmonella: Cellular and Molecular Biology and by his service on the editorial boards of the Journal of Bacteriology, the Biophysical Journal, the Microbiology Review and, most recently, Molecular Microbiology. With his keen mind, broad background and willingness to listen and help out, he was the perfect person with whom to discuss one's manuscripts, results or scientific difficulties. He was a superb writer who could express with precision his results and interpretations and did so in the over 110 papers he wrote over the course of 31 years.

His colleagues and collaborators will miss his sense of humour, his scrupulous sense of fair play in all matters, his insights and the contributions he surely would have continued to make. A memorial symposium is being planned for the spring.

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