Eur Biophys J (2009) 39:175–178
DOI 10.1007/s00249-009-0431-3

TRIBUTE

Biographical memoir: Alexander Beaumont Hope, Australian biophysicist, 1928–2008

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Received: 3 February 2009 / Accepted: 23 February 2009 / Published online: 25 March 2009
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Abstract This introductory article is the first of four short articles from the Tribute to Alex Hope Symposium held at the 2008 Australian Society for Biophysics meeting in Canberra, Australia, as a tribute to Professor Alex Hope, who died in July last year. As well as briefly introducing the other three articles by three former PhD students, it will also be a biographical memoir of Alex Hope.

Keywords Alex Hope · Algal cells · Action potentials · Plant biophysics · Photosynthesis

"Proteins, membranes and cells: the structure–function nexus". Contribution from a special symposium in honour of Professor Alex Hope of Flinders University, South Australia held during the annual scientific meeting of the Australian Society for Biophysics, Canberra, ACT, Australia, September 28–October 1, 2008.

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The introductory article is the first of four articles from a special symposium held at the meeting of the Australian Society for Biophysics in Canberra, Australia in 2008 as a tribute to Professor Alex Hope, who died in July last year. The three other articles are from former PhD students, Hans Coster, Peter Barry and Fred Chow, who subsequently reached professorial positions doing biophysics in physics, physiology and biological sciences. Hans Coster will discuss the discovery of a phenomenon known as "punch-through" or electrical breakdown in cell membranes discovered during his PhD work in Alex's laboratory and the impact that has resulted from it (Coster 2009). Peter Barry will discuss his PhD studies in Alex's laboratory and further studies that have resulted from them (Barry 2009). Fred Chow will outline the recent work done using Alex's equipment that had been relocated to Canberra (Fan et al. 2009). The rest of the article will be in the form of a biographical memoir (Fig. 1).

Professor Alex Hope made very substantial contributions to biophysics both in Australia and internationally, particularly in plant biophysics, but with repercussions that extended to biophysics in other systems. His work generally involved applying physics/physical chemistry and mathematics to the understanding of biological processes. He also played a pivotal foundational role in the Australian Society for Biophysics (ASB) and was President from 1978 to 1979. He was awarded the Bob Robertson Award and Medal [in honour of Sir Rutherford (Bob) Robertson FRS, FAA] in 2003 for his contributions to biophysics and to the ASB. In 2008, he gave a bequest to the ASB to establish the McAulay–Hope Prize for Original Biophysics to encourage and reward "true originality and innovation in the field of biophysics" (www.biophysics.org.au).

Alex was born in Launceston, Tasmania on 24 October 1928, to George Arthur and Evlyn Beaumont Hope, with

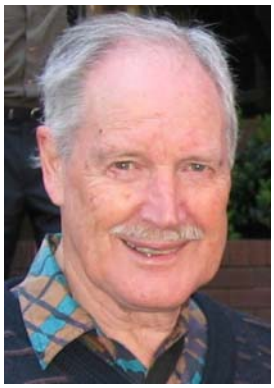

Fig. 1 Alex Hope 2003

one older sister and two older brothers. His first marriage in May 1952 was to Margaret Sidebottom, with whom he had two children: Ian, born in 1956 in Cambridge, and Evelyn, born in 1959 in Sydney. In 1975, he had parted from Margaret, and in 1977 he married Vivien Suit-Cheng Chin, daughter of K. C. Chin, with whom he remained till his death in Adelaide on 26 July 2008. Alex was an accomplished flute player and was a member of various chamber groups. He enjoyed mild bushwalking, tennis, wood turning and wine.

He was educated at Launceston State High School, before going on to the University of Tasmania, where he graduated in 1950 with a first class honours degree in physics, with a project in plant biophysics with Professor Alexander Leicester McAulay. He then enrolled in a PhD in biophysics under Professor McAulay, studying the means by which nutrient mineral ions entered plant roots, and graduated in 1953. During this time, he met Rutherford (R. N.) Robertson (later to become Sir Rutherford Robertson, often referred to by colleagues as "Bob") in the Division of Food Preservation and Transport of the Commonwealth Scientific and Industrial Research Organisation (CSIRO) and he arranged for Alex "to be appointed as a Temporary Research Officer in the CSIRO, on the understanding that he would be available for future employment in the Division", thus providing him with financial support for the last 2 years of his PhD. Alex's research involved measuring plant potentials and the influence on them of the ionic composition of the solution bathing the cells. In this early research, he also rediscovered, in giant *Nitella* algal cells, the "action potential" in which cells depolarise and recover in response to various stimuli. In 1953, he went with his wife, Margaret, to Sydney, where he took up a position as Research Scientist in the Plant Physiology Unit (PPU) located in Sydney University's Botany School and run jointly by the CSIRO Division of Food Research and Sydney University, under the joint headship of Bob Robertson and Professor Frank Mercer (Hope 2002). From 1955 to 1957, Alex and Margaret went to the UK, where they took up a CSIRO Overseas Studentship in the Botany Department of Cambridge University. During this period especially, he forged important research links with UK scientists, already distinguished or to be so later, such as Alan Hodgkin, Richard Keynes, George Edward Briggs, Robin Hill, Jack Dainty and Enid MacRobbie, together with overseas Australians, such as Doug Graham, Mike Pitman, Andrew Smith and John Cram, before returning to the PPU. In 1958, Alex became a Senior Research Scientist, and in the following year attended a conference at the University of Minnesota in 1959 in place of Bob Robertson and took the opportunity to visit distinguished researchers such as Sterling Hendricks and Laurence Blinks, who had worked with Osterhout on giant algal cells. In 1961, the size of the PPU Biophysics Laboratory doubled with the addition of Dr Geoff Findlay, also from the University of Tasmania. They set up a system to "voltage-clamp" giant *Chara* algal cells and to investigate the ionic basis of the action potential in these cells (e.g. Hope 1961; Findlay and Hope 1964). Shortly after this, two PhD students also joined the laboratory, Hans Coster in 1962 and Peter Barry in 1963.

In 1963–1964, Alex, by this time a Principal Research Scientist, went with his family to the UK to spend his study leave working with Jack Dainty, the Foundation Professor of Biophysics, at the new University of East Anglia on a Nuffield Foundation Overseas Fellowship. During that time. Alan Walker, a former research collaborator, also arrived from Australia to work with Jack Dainty. Furthermore, Alex met one of Jack Dainty's students, with whom he later collaborated in photosynthesis research at the Imperial College: Jim Barber FRS. Alex and his family returned to Australia via the USA, where he attended a conference in New York on the properties of water and visited various researchers including Lorin Mullins in Baltimore …[and] to Urbana, Illinois, to meet Rabinowitch and Govindjee, pioneers in the study of the biophysical aspects of photosynthesis. No doubt the latter visit was significant in the light of Alex's subsequent move into that area of research himself. In 1965, he with Mike Pitman organised a highly successful international conference on "The Physiology of Giant Algal Cells" sponsored by the Australian Academy of Science and held in the Academy, Canberra. It included international leaders in the field such as Richard Adrian, Richard Keynes, Enid MacRobbie and Jack Dainty from the UK; Lorin Mullins from the USA; Uichiro Kishimoto from Japan, and Alex Hope, Mike Pitman, Bob Robertson, Bruce Scott, Alan Walker and Geoff Findlay from Australia, together with PhD students, Hans Coster and Peter Barry.

In early 1966, Alex moved to Adelaide to take up the Foundation Chair as Professor of Biology at the new Flinders University of South Australia. Geoff Findlay moved with him to take up an academic position there. Peter Barry also moved with Alex to complete his PhD there, before

taking post-doctoral positions with Jared Diamond in collaboration with Ernest Wright at UCLA and with Richard Adrian in Cambridge, while Hans Coster, having finished his thesis, moved to an academic position at the University of New South Wales. Alex also had a number of other PhD students, who made their mark internationally, but one special one was Fred (Wah Soon) Chow, who continued to collaborate closely with Alex throughout Alex's retirement, as mentioned earlier (Fan et al. 2009). Alex continued his academic career at Flinders University as Professor of Biology, being Vice-Chairman of the School of Biological Sciences in 1966–1967 and 1972–1973 and Chairman in 1974–1975, retiring in 1993, but continuing on as an Emeritus Professor there from 1994, and Adjunct Professor (1992–1998) and Visiting Fellow (1998–2008) at the Research school of Biological Sciences, the Australian National University, till his death in 2008. He also held a Humboldt Fellowship at the Friedrich–Wilhelms Universität, Munster in Germany in 1986.

During his research career, Alex produced over 115 major publications, including at least 100 peer-reviewed journal papers, with many of these being in high profile international journals such as *Nature*, *Science* and the *Biophysical Journal*. These papers have been cited more than 2,400 times. He made a special point of also publishing in Australian journals to raise their international profile. In addition to numerous invited chapters in other monographs, he published three research monographs (Briggs et al. 1961; Hope 1971; Hope and Walker 1975) and three biographical memoirs (Hope 2002, 2004, 2006). Some examples of his research contributions follow.

With respect to plant cell membranes, Alex made the first electrical impedance measurements on isolated plant mitochondria and chloroplasts, which indicated that they were bounded by a resistant surface, not merely a phase boundary, and electron microscopy and osmotic studies of chloroplasts showed a lamellar structure and demonstrated the semi-permeable nature of the outer membrane (Mercer et al. 1955).

With respect to the ionic relations of plant cells, he did pioneering work with Geoff Findlay on the action potential of giant algal cells and the role of Ca^{2+} ions, together with experiments with Hans Coster on the efflux of Cl^- ions during the action potential. He was an early user, or pioneer, in the use of radioactive isotopes in Australian research in plant cell ionic relations and was also influential in steering Australian research into the area of ionic relations of giant algal cells, along with Geoff Findlay, Alan Walker, Mike Pitman and Andrew Smith. He independently discovered and correctly described the hyperpolarisation of the resting potential in Characean cells as due to active ion transport across the plasmalemma, though he had wrongly attributed it to a bicarbonate ion influx rather than to a proton efflux (personal communication). He made a preliminary study of the state of water in cytoplasm using nuclear magnetic resonance, which indicated that water was not ice-like, but less ordered near membrane surfaces (Walter and Hope 1971).

With respect to photosynthesis, Alex demonstrated the two-proton uptake at photosystem II (periodicity of two during single-turnover flashes), indicating that protonation of Quinone B occurred only after a two-electron reduction. He correctly predicted the magnitudes of the redistribution of ions (Mg^{2+}, K^+ and Cl^-) across the thylakoid membrane in response to proton deposition in the thylakoid lumen, in agreement with subsequent measurements (Chow and Hope 1976).

His extensive work on the "electrochromic shift" (ECS), indicating the trans-thylakoid electric potential difference, particularly the "slow" rise of the ECS, together with the concomitant reduction of cytochrome (cyt) *b*, has established, with others the working of a "Q-cycle", as originally proposed under most conditions for mitochondria by Peter Mitchell (Hope 1993). Alex's extensive measurements, with the equipment he designed that had a superior signal-to-noise ratio, of the kinetics of electron transfers around the cyt *bf* complex, using both isolated chloroplasts and isolated macromolecular complexes from thylakoids, laid the groundwork for a full mathematical description of these processes (Hope 2000). With collaborators, he made use of the Inverse Method to optimise the estimation of kinetic parameters in electron transfers around the cyt *bf* (Hope et al. 1992), altering the parameters through changes in pH or ionic strength or hydrostatic pressure. In intact leaves, through simulation of these electron-transfer events around the cyt *bf* complex by simultaneous solution of a package of linear differential equations representing the kinetics, Alex obtained close similarity of measurement and prediction for kinetic changes of cyt *b*, P700 and the ECS, though the matching was less satisfactory for cyt *f* (Chow and Hope 2004).

After retirement, Alex continued his push to probe photosynthetic events non-intrusively in leaves. Thus, till late 2006, he made numerous research visits to Canberra, where he worked on the quantification of cyclic and linear electron flow in leaf segments in various conditions, the putative variable proton pumping action of the cyt *bf* complex, the ratio of the two photosystems and rapid quantification of photosystem II, all assayed in leaves.

In addition, as an example of Alex's innovation and interest in new technology, in the early mid-1960s he designed, and with the help of Hans Coster and a research assistant (Pat Price, who subsequently, also went on to complete a PhD in physics) successfully built a very early analogue computer using operational amplifiers. This was used to perform compartmental analysis by solving the

differential equations governing flux data obtained from radioactive tracer studies.

Alex is fondly remembered for his sharp insight, remarkable technical know-how, hands-on approach, quick wit and, above all, his infectious passion for science, largely driven by a curiosity about electrical events in plant cells.

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