EDWARD ARTHUR BOYSE
11 August 1923 — 14 July 2007
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Elected FRS 1977

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Edward Boyse was the consummate scientist. His interest was piqued by the unique, the undeveloped and the unthought of. When an area of study gained widespread attention, he moved on. The development of the field of cell surface immunogenetics, of which he was master, relied heavily on the use of Boyse’s congenic mouse strains, and on his improved methods for reliable serology. He founded the new discipline of odourtype genetics, revealing how immunohaplotypes were involved in assortative mating and related behaviours, thus promoting heterozygosity. He pioneered the now crowded field of cord-blood cryopreservation and transplantation, conducting the first laboratory studies in mice and assembling the clinical team that performed the first human cord-blood transplant. An educator and protector of graduate students, he instilled rigorous scientific discipline while broadening horizons. Boyse was a pilot in World War II, a physician, a biomedical innovator and a demon squash player. A lover of classical music (which love he transmitted to his children) and the Beatles (love of which they transmitted to him), he strenuously avoided both the intellectually self-absorbed and the ostentatiously populist. In leisure, he flew, hiked, ran, biked and, periodically, upholstered. Wit, generosity and loyalty were the most prominent features of his unique personality.

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Note: some of the material in this memoir previously appeared in Bard, J., Beauchamp, G. K. & Goldberg, E. H. 2007 Edward A. Boyse 1923–2007. Nat. Immunol. 8, 1011–1012. (doi:10.1038/ni1007-1011)

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http://dx.doi.org/10.1098/rsbm.2020.0035 Published by the Royal Society
Prelude

Edward Arthur Boyse (Ted) was born in Worthing, Sussex, on 11 August 1923. His parents, Arthur Boyse FRCO and Dorothy Vera Boyse (née Mellersh), married when Arthur was 65 years of age and his wife considerably younger. They produced four children, Edward being the third, and, it appeared at the time, the last. Father and son developed a close bond, beginning while Ted was still in the cradle, which was usually found under his father’s piano or at St Botolph’s Church, where Arthur was organist. This may explain Ted’s lifelong love of music—and ambivalence towards the Church.

Ted was an unusual child. From a young age, he was fiercely independent and enjoyed solitude, cycling over the Sussex countryside either with a friend or more commonly alone. He also exhibited early evidence of leadership and originality, directing a team of schoolmates in the creation of a miniature theatre, for which he wrote and produced plays. His interest in the theatre continued through his university years and beyond.

Ted was particularly fond of his maternal grandmother, Luci Charlotte Mellersh (née Sergeant), and spent many hours in the company of this Victorian lady, the epitome of English rectitude (figure 1).

World War II

In 1941, at age 17½, the youngest age of intake, young Boyse enlisted in the Royal Air Force and served as flight crew and then instructor-pilot. This led in due course to him being transferred to Canada, where he trained Royal Canadian Air Force pilots (figure 2).

During a brief leave, Ted travelled to Edson, Alberta, to visit his maternal uncle, who had migrated to Canada many years earlier. Oswald Mellersh was an adventurer, and was much admired by his nephew, not least because he had obtained a very early pilot’s licence, number 116. An ancient photograph of Uncle Oswald flying a vintage aeroplane remained one of Ted’s prized possessions for the rest of his life (figure 3).

Back in the UK, following his service in Canada, Ted was co-opted to represent a junior officer on trial for misappropriating a bicycle. The accused was exonerated, and charges dismissed, owing largely to the eloquence of counsel.

Ted served the remainder of World War II, demobilizing in 1946 with the rank of Flight Lieutenant. Flying remained his passion, and he often recalled a particular fondness for tunnelling in clouds: ‘First you have to make sure nobody else has borrowed that cloud.’ He returned to the air in later life in the form of skydiving and building ultralight aircraft with pilot friends.

Education and training

Upon demobilization, Boyse studied medicine at the University of London, St Bartholomew’s Hospital. He staunchly maintained that he chose medicine because there was nothing else he was suitable for, a fallacy that he clung to despite all evidence to the contrary (see, for example, advocacy, above).
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Figure 1. Luci Charlotte Mellersh (Granny) during the 1920s in Worthing.

Boyse received his MBBS in 1952 and his MD in 1957. His thesis research, on the spread of herpes virus through the cerebrospinal fluid of the rabbit (1)*, was conducted in the laboratory of George Payling-Wright at Guy’s Hospital. Boyse frequently recalled his old mentor with humour and affection. He delighted in quoting Payling-Wright’s unabashed excuse for non-appearance until ‘gentleman’s hours’: ‘Sorry I’m late, Boyse. A combination of sloth and loquacity.’

After the geniality of the Payling-Wright environment, Boyse completed his training with a brief rotation in patient care, and an equally unwelcome attachment to the Public Health Laboratory Service (where, he lamented, his most riveting assignment was the examination of ice cream for *E. coli*). These bothersome requirements accomplished, he was free to concentrate on the laboratory.

Boyse joined Peter Gorer’s lab at Gy’s at a time when the H-2 major histocompatibility complex (MHC) in mice was first being identified and refined (Gorer & O’Gorman 1956). Boyse credited many of his subsequent avenues of thought and exploration to his grounding in Gorer’s lab and its cordial rivalry with that of Peter (later Sir Peter) Medawar not too far distant. In particular, Boyse was intrigued by the number and quality of antigens (2), other than the MHC, that impacted skin transplantation, the focus of Medawar’s lab (see e.g. the Skn system in Sloan Kettering section below).

* Numbers in this form refer to the bibliography at the end of the text.
In 1960, Boyse was recruited by Chandler Stetson, then chairman of the Department of Pathology at New York University (NYU) Medical Center. This was a time of austerity in Britain, and many scientists succumbed to the relative wealth of research funding in the US—a period still known by British baby boomers as The Brain Drain. Among Boyse’s colleagues at NYU were Baruj Benacerraf (Nobel Laureate in Physiology or Medicine 1980) and Lloyd Old, both of whom played major roles in Boyse’s scientific career. Lewis Thomas, who graced the Department of Pathology until 1969, had a profound impact on Boyse’s subsequent
professional and personal life, particularly when, in 1973, Thomas accepted the presidency of
the Memorial Sloan Kettering Cancer Center.

SETTLING INTO SLOAN KETTERING

The move to the Sloan Kettering Institute (SKI), in 1964, made official an arrangement that had been de facto for some time. Among the attractions of SKI was a lack of formal teaching obligations, and a relatively unencumbering administration. Now agreeably situated, Boyse could concentrate on establishing his genetically defined congenic mouse colonies, in adequate and autonomous quarters. These mice, and the antisera that they produced (which Boyse shared freely with any investigator sufficiently hardy in requesting them), became the cornerstones of worldwide immunogenetic programmes, as did his improved materials and techniques for the conduct of reliable serology (3) (figure 4). Later, monoclonal antibodies were added to the serological arsenal, following their discovery by George Köhler and Cesar Milstein (FRS 1975), for which they received the Nobel Prize in 1984 (Köhler & Milstein 1975).

At SKI Boyse and Old resumed their collaboration, which would last many years and result in numerous publications (see Bibliography and electronic supplementary material). Old’s
interest in tumour-specific markers complemented Boyse’s concentration on the identification of cells by their surface markers. His cell system of choice was immunocytes, because of their ubiquity and accessibility. Together, Boyse and Old identified a series of antigens displayed on the surfaces of lymphocytes. The first of these was designated TL (for thymus leukaemia), and the genetic locus Tla (for thymus leukaemia antigen), which, interestingly, mapped to MHC (H-2) (4), in the same region as the Ir genes (McDevitt & Tyan 1968).

Most notable among the molecules thus defined was the Ly system of antigens (5). At the Dana Farber Cancer Institute, Harvey Cantor was similarly studying the immune system, specifically the varying, and often contradictory, functions of T lymphocytes. Together, Boyse and Cantor, in a long-running collaboration, determined that LyA (later Lyt-1) and LyB (Lyt-2/3) hallmarked functionally distinct subclasses of lymphocytes, the former denoted ‘helper’ and the latter ‘killer-suppressor’ (7). This turned out to hold true in all mammalian species. In humans these subsets are now known as CD4 and CD8, respectively; they have become universally familiar, not least because of their application in HIV/AIDS (figure 5).

Boyse was particularly intrigued by the definition of weak histocompatibility antigens. Years before, Medawar had conducted a famous series of experiments showing that neonatal mice injected with haematopoietic cells (using spleen or bone marrow) from an H-2-incompatible mouse strain would, as adults, accept skin grafts from the haematopoietic cell donor. In some cases, however, skin-graft rejection was observed at about 100 days, too
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Figure 5. With Harvey Cantor (left) and Judith Bard at ‘The history of immunogenetics: a symposium in honor of Edward Boyse’, held in Albuquerque, NM, in 1991 and hosted by Ellen Goldberg and Frank Lilly. (Online version in colour.)

long an interval to be attributable to the H-2 MHC. Because no weak antigens had then been recognized, Medawar proposed the term ‘split tolerance’ (Billingham et al. 1953), a nebulous term, and theory, which conflicted with Boyse’s biological sensibilities—rightly, as he would have known that Snell and Gorer’s genetic experiments with skin and tumour transplantation as read-outs (rather than serology) had revealed a number of non-H-2, minor histocompatibility antigens (see below).

The Skn system (6), originally identified serologically by Margrit Scheid—a research associate in Boyse’s lab and subsequently, with Boyse’s wholehearted approval, head of an independent lab—was the evidence. Graduate student Ellen Goldberg pursued this line of investigation. It was found that Skn was an alloantigenic system expressed selectively on epidermal cells of the skin and brain, and was responsible for late-stage skin-graft rejection by mice that had received bone marrow from a donor with an identical H-2 type.

How much of Boyse’s satisfaction with this finding was due to the earlier Gorer–Medawar cordial rivalry will remain a matter for conjecture. (Medawar was awarded the Nobel Prize with Sir Frank Macfarlane Burnet FRS in 1960; Gorer would undoubtedly have shared the Prize had he survived—his colleague George Snell shared the Prize with Baruj Benacerraf in 1980.)

Another cell-surface component, and weak histocompatibility antigen, described during this period was the H-Y system (Eichwald & Silmser 1955), expressed by male but not female cells of all mammalian species. In non-mammalian vertebrates, an equivalent molecule was
reported in the heterogametic sex. Always somewhat controversial, H-Y was at one time considered a candidate for the primary determinant of male sex (8), and some moderate success was achieved with H-Y in the serological sex-selection of embryos. This programme was conducted by Stephen Wachtel, whom Boyse had invited to join the lab upon discovering, among his other qualifications, that he had been a US Air Force pilot and was, by virtue of training, a third-generation skin-graftor from the Medawar–Billingham legitimacy. Wachtel recalls his introduction to the culture of the Boyse lab after his contretemps with a rat, which he tried to handle with heavy protective gloves. Boyse, hearing the commotion set up by a rat unused to such treatment, intervened. ‘We don’t handle rattos like that,’ he said, and cradled the rat in his hands. Rats were ‘rattos’; mice were ‘doodies’; and rabbits had their private runways. To be fair to Wachtel, however, it did indeed turn out that a vendetta was being waged against him, not by the rat in question, but by an entire breed of mice (C57BL/6Boy), who bit him exclusively. Serological definition of immunogenetic systems was the bread and butter of the lab, and in later years was effectively managed by Fung-Win Shen, an immensely talented young investigator, whose classic text accompanied all fulfilled requests for antibodies (9). Boyse was therefore somewhat freed to pursue interests that ranged far afield, into the serendipitous and into the esoteric.

INDIVIDUAL RECOGNITION AND MATE SELECTION

A chance observation in the Congenic Mouse Production Facility made by Jeanette Boyse (at the time Boyse’s wife, a former nurse and an expert in animal husbandry) and her colleague Zoilo Zayas led to a far-reaching programme. Boyse and Zayas noted, repeatedly, that male mice, given the opportunity to mate with a female of major histocompatibility type either identical to or different from the male, reliably selected the female of different haplotype (10). At about the same time, and independently, Lewis Thomas, president of the Memorial Sloan Kettering Cancer Center, noted in one of his essays (Thomas 1974) that dogs might be used to ‘sniff out our histocompatibility types’. Controlled mating trials established that the H-2 MHC was responsible for preferential mating in mice. Kunio Yamazaki, a visiting investigator from Japan, was given supervision of these labour-intensive trials. When it was suspected that the mode of recognition in this assortative mating phenomenon was mediated by olfaction (11), Boyse approached the Monell Chemical Senses Center, in Philadelphia, the largest institution in the world devoted to the study of taste and smell. Boyse engaged the enthusiastic interest of Gary Beauchamp, then a young investigator and subsequently president and director of Monell. Eventually the physical conduct of the programme, together with its staff, migrated to Monell, because of its experience in olfactory systems and expertise in the conduct of behavioural protocols. Boyse retained a special interest in this field, which has now become densely populated; and he developed a close personal friendship with Beauchamp, which encompassed, inter alia, rare books and investigation of derelict buildings (figure 6). That Boyse was willing to see the departure of a programme as far-reaching as odour-type genetics is just one example of his scientific altruism: what was best for the programme was what prevailed. He was equally generous in sharing his thoughts and hypotheses with others. He especially appreciated the series of Japanese visiting investigators who rotated through
his lab, each of whom took back to Japan, in addition to first-rate publications, something of the culture of the Boyse lab, which included open collaborations and avoidance of speaking engagements.

CORD-BLOOD TRANSPLANTATION

Cord-blood preservation and transplantation, now in worldwide practice, is another example of Boyse’s originality. It is a tribute to Boyse that colleagues and friends who expressed dismay that this programme no longer receives appropriate attribution were told that success has many fathers while failure is an orphan. Paternity in this case, however, is clear. It was Boyse who proposed that umbilical cord-blood could be used in place of bone marrow for haematopoietic reconstitution, and should therefore be preserved, particularly for use by the donor individual.

Boyse, together with his associate and partner, Judith Bard, later his wife, conducted the painstaking experiments in mice, which consisted in irradiating mice and then reconstituting them with the peripheral blood of newborns. As little as 0.2 ml of neonatal blood was sufficient to reconstitute a young adult. *In vitro* experiments with human cord-blood showed the applicability of this approach for haematopoietic stem cell replacement in the clinic (12). As was also noted later in humans, full repopulation took somewhat longer than was
customary with bone marrow, very likely because the donor cells came from an earlier stage of development. The latter may also account for the lower incidence of graft-versus-host disease, a perennial complication of conventional bone marrow transplantation.

The development of this programme required the collaboration of many scientists in many institutions, as well as independent sources of funding. Boyse and Bard together assembled the team that was responsible for the first successful clinical umbilical cord-blood transplant. The team’s *primus inter pares* was Hal Broxmeyer, whose *in vitro* studies were critical (14). Lewis Thomas provided the public face; Rodman Rockefeller supplied the initial funding; and Bo Dupont acted as advisor and ambassador. Also on the scientific advisory board of this group, subsequently incorporated as Biocyte Corporation, were Harvey Cantor, Pablo Rubinstein, director of the New York Blood Bank, and Gordon Douglas, chairman of OB-GYN at NYU Medical Center.

Joanne Kurtzberg and Henry Friedman, of Duke University Medical Center, recommended one of their patients, a five-year-old boy with Fanconi anaemia, as a candidate for this pioneer procedure. The boy’s mother was pregnant with a child whose MHC type matched the patient’s, and who was originally anticipated to be his bone marrow donor. When the child was born, blood from her umbilical cord was harvested and cryopreserved until the child was old enough to provide bone marrow as back-up in case of need.

For the transplantation surgery itself, Eliane Gluckman, at the Hôpital Saint-Louis in Paris, was the foremost expert in the management of the special ablation and reconstitution procedures required in Fanconi anaemia. She and her team embraced the challenge of performing the world’s first clinical cord-blood transplant with alacrity and complete success (13).

**MOVING TO ARIZONA**

‘Never grow old where you have once been great,’ said Niccolo to the Prince (Machiavelli 1513).

Whether this featured in Boyse’s decision to move to the University of Arizona in 1989 will never be known. Nonetheless, the Department of Microbiology & Immunology made the offer, and Boyse accepted. Thus, Boyse became Distinguished Professor in the School of Medicine in Tucson. When Lewis Thomas, long since retired, was informed of the impending move, he said: ‘Two things: Don’t go. And take me with you.’

Of the work conducted in Arizona, the engagement with the Navajo Nation brought attention to a rare disorder that is disproportionately prevalent in that population. Severe combined immunodeficiency disease is generally treated with bone marrow from an MHC-compatible donor. Clearly, Boyse concluded, the Navajo would benefit from the establishment of their own cord-blood bank, specializing in Navajo-specific MHC types. Many meetings with tribal councils finally elicited a positive response, which was somewhat more problematic than it would on the face of it appear because of the Navajo ritual of burying the baby’s umbilical cord to ‘keep the child tied to the land’. Upon reassurance that the cord itself was not involved in the procedure, merely the blood, the tribal councils were inclined to go forward. The grisly question of state funding then asserted itself. Applications were written and approved—and then the state research programme’s funding collapsed. It was a time of several ‘gates’ involving Arizona state and federal representatives.
Seeing that the time was approaching for retirement, Boyse decided that retirement was something not to be attempted all at once. A gradual ease into ease was required. Thus, one day a week was assigned to hiking in the desert and mountains, or to piloting gliders, or to skydiving. Eventually these activities ousted all others. The ease into ease was complete.

While in medical school, Ted met and married Jeanette Grimwood, who was at the time a nurse at Bart’s. They produced three children, Adrienne, Conrad and Dominic. All three were educated in England (US high school life being a thing of puzzlement to the parents). Adrienne toed the family line and, following training at Bart’s, specialized in anaesthesiology; she remains in England. Conrad graduated from the Wharton School in Philadelphia, and now runs his own business in California. Dominic, a photographic artist, predeceased his parents. Five assorted grandchildren are now, as Conrad has it, ‘off the payroll’; so far, one great-grandchild represents the next generation. Ted married Judith Bard in 1987. They remained together, both at work and beyond (figure 7).

Always a physically active man, Ted also espoused the dramatic and musical arts. In medical school he wrote and appeared in pantomimes. His greatest thespian triumph came in his role as an Ugly Stepsister, as recorded in newspaper clippings lovingly preserved.

Figure 7. Edward Boyse and Judith Bard in uncharacteristic costume. (Online version in colour.)
His appreciation of King Lear was summarized as follows: ‘Insanity is hereditary; you get it from your children.’ Music was never far from his consciousness. From Bach to the Beatles, it was all a wonderment. Alas, his dramatic career came to a close upon graduation, but music and sports remained an integral part of his life. Many a time he was seen returning from the squash courts atop Cornell Medical School, having pulverized some hapless opponent, often enough bearing an injury of his own. Ted never considered himself an intellectual or an academic. He was equally at home in the carpentry shop in the basement of Sloan Kettering, and on the thirteenth floor in executive committee (albeit the latter being less welcome).

The individuals with whom Ted, always a very private man, chose to share friendship were few and steadfast and had in common with him the traits of enthusiasm, joy and mischief. As former graduate student Ellen Goldberg recalls (Bard et al. 2007):

Ted was, by far, ahead of the curve when it came to developing new ideas and programs. Others would follow his lead. Not only were his scientific contributions and ideas brilliant but he openly shared these thoughts with students and colleagues. He was an extremely kind person with a wonderful sense of humour, so even as a student, I was comfortable discussing my thoughts with him. It was Ted who opened up the world for me, not just scientifically, but broadening my interests through literature and friendship. He was such a great man.

**HONOURS, AWARDS, ACADEMIES**

Recognition of Boyse’s research brought many invitations for lectures and meetings. Generally, these were viewed as distractions and politely refused. His receipt of the Isaac Adler Prize in 1976 proved an exception (Boyse was the sole recipient of the Prize awarded jointly by Harvard and Rockefeller Universities). One of the stipulations of the award was that the recipient deliver a lecture on his work at Harvard Medical School in Boston. He reluctantly agreed, mollified by his fondness for Cambridge book shops, which in those days housed remarkable collections of rare books and first editions. After the lecture, which was very well received, Boyse was heard to remark to his hosts: ‘Well, I have sung for my supper, now it’s off to Cambridge to visit old friends’ (H. Cantor, personal communication).

Other awards included the Cancer Research Institute Award in Tumour Immunology (1975) and the C. Chester Stock Award of the Memorial Sloan Kettering Cancer Center.

Boyse was elected Fellow of the Royal Society and Member of the American Academy of Arts and Sciences in 1977, and Member of the National Academy of Sciences USA in 1979. At that time, he was the only person to hold full membership in three national academies.

**ACKNOWLEDGEMENTS**

Thanks are due to Harvey Cantor for guidance on the text and for personal reminiscences. Much pleasure was taken in remembrance of things past. Similarly, warm thanks to Gary Beauchamp: colleague, friend and champion bookfinder. Hal Broxmeyer shared information and stories, most notably during a four-mile run down Sabino Canyon. In the lab family, I am, as always, grateful for Stephen Wachtel’s input and unique perspective; and for Ellen Goldberg’s profound knowledge and bizarre normality. My family, Conrad Boyse and wife Maria, and Adrienne Boyse Martin, provided fodder for the ages. My thanks without number to them, to their brother Dominic Boyse (1957–2006) and to Adrienne’s husband Richard Martin (1954–2010). Lastly, for critical reading of the manuscript (and uncritical
support), my thanks go to Benedict Bard and Joseph Bard. The photographs in the memoir, including the frontispiece portrait, are from the family’s personal collection.

**AUTHOR PROFILE**

After a period working in the international community in Geneva, Judith Bard began her career at the Sloan Kettering Institute (SKI) for Cancer Research in 1975. Initially her position was manager of the immunogenetics laboratory headed by Edward Boyse. It was soon apparent that Bard’s interest and inclination was research, rather than administration (an activity dubbed ‘the herding of cats’). Boyse, and some undaunted colleagues, undertook her intensive instruction in cell surface immunogenetics and related disciplines. As research associate at SKI, and then at the University of Arizona, Bard rejoiced in the sometimes unexpected mayhem of orderly research, and in the tumultuous interaction of a united nations of visiting investigators. Bard views her membership in the teams responsible for the notable advances described herein as an extraordinary and cherished privilege.

Bard retired to care for Boyse in his final years. She has now retired from retirement and is the founder and co-owner of a comprehensive music centre for the instruction and performance of the musical arts. She has her eye on developing a chequered future.

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