JOHN HESLOP-HARRISON

10 February 1920 — 7 May 1998

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Elected F.R.S. 1970

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There could be no better words with which to open an account of John (Jack) Heslop-Harrison's life than his own advice to students: 'He who makes botany his life's work has many satisfactions before him; not least the sheer pleasure of investigating and handling entities so intrinsically beautiful and perfect at all levels of organization as plants' (1).*

Early influences and upbringing

In the year that Jack was born, his father changed profession from schoolteacher to university lecturer in zoology, at Armstrong College, University of Durham. The family moved to the mining village of Birtley, five miles from the college, where Jack's grandfather had worked and his father had been born and married.

In an unpublished account of his family history and schooldays, Jack wrote that his father played little part in his early life, beyond imposing rigorous discipline when he was at home. He kept primroses, willows and roses for experimental purposes in the back garden and used the kitchen mantelpiece as an incubator to hatch moth larvae, so Jack and his elder brother and sister were exposed to natural history and the spirit of enquiry from early on. All three became biologists. When Jack was old enough, his father took him on local field trips and through these he developed a lifelong enjoyment of entomology—he had a keen eye for Lepidoptera and could identify them with authority in his future home countryside of Herefordshire. He was also influenced by his great-uncle, Revd J.E. Hull, a classicist, local folklorist and arachnologist. Jack was encouraged to experiment and the result was that his first public lecture was on the subject of butterfly life history. He was seven, the occasion a

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meeting of the Wallace Club, a local naturalists' society. It was the first of many appearances for him in the Armstrong (later King's) College Botany Department lecture theatre, where he would both listen and perform in later years. His first published papers came a little later, when he had moved from the Infants' to the Elementary School: there one teacher edited a magazine for the National Association of Schoolmasters and Jack recalled that 'when he found I had something unusual to write about he printed one or two of my natural history essays'.

His father became Professor of Botany in 1927 and was concurrently Reader in Genetics. In 1928 he was elected a Fellow of the Royal Society. He imposed a rigid mental discipline and work ethic on himself and his children, for whom he had high academic ambitions. Jack, third in line, felt that he was under continuous pressure to achieve: 'anything less than first position in my class in any subject (especially in science) was regarded as tantamount to failure'. But although brusque, and inclined to tell Jack to 'find out for yourself' when he asked a question, his father did broaden his son's education, taking him on long field excursions in Britain and continental Europe. In 1933, detouring from visits to entomologists in Germany, he took him to Brno to see the monument to Mendel.

By then Jack was in his second year at Chester-le-Street Secondary School. He looked back on his seven years there as a time of hard work, discipline and an excellent education from first-rate teachers. In the lower school his strength was in English; indeed he won the school essay prize twice, so was not allowed to compete for it again. He wrote science fiction stories and a 40 000 word story about New Forest ponies. Entering the upper school, he was already six feet tall, on his way to six feet three inches. To his father's relief he ended up in the science side and at the Higher School Certificate examinations gained distinctions in chemistry and physics but did less well in mathematics—this was a disaster, for he just missed a university scholarship. He also just failed to win a scholarship to King's College, University of Durham in a subsequent examination, and recalled, 'My father's reaction to these various performances need not be documented'. The fates were kind, however. After he had spent a 'miserable period' in the summer of 1938 with a King's Botany Department field party on the Hebridean island of Rhum he returned to find a letter saying that because of a drop-out he had inherited a three-year scholarship of £60 per annum. He felt he had not earned it, but entered King's College to take an honours degree in botany, with ancillary zoology, chemistry and archaeology.

University of Durham, 1938–41; war service, 1941–45

Jack enjoyed biochemistry and physiology, taught by M. Thomas (F.R.S. 1949), in the Botany Department at King's. Another lecturer who influenced him was K. Blackburn, who had made pioneering discoveries on sex chromosomes in flowering plants and had a wonderful knowledge of plant cytology. She also lectured on the use of fossil pollen to study postglacial vegetation history—a subject considerably furthered by Jack when he became Professor of Botany in Belfast. His father lectured to him on evolution and genetics, and his brother-in-law, William Clark, on morphology of flowering plants, origins of the British flora, and photoperiodism.

Jack and some of his classmates had been registered for conscription for war service but after interview by a committee chaired by C.P. Snow were marked for deferment until their

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degree courses were complete. He was a competitive undergraduate, perhaps seeking to overcome his feeling that he had not really earned his scholarship, but also to keep pace with another brilliant student, Yolande Massey. Despite having their final examination interrupted by having to take shelter during an air raid on Newcastle, Jack and Yolande were both awarded first-class honours in botany in June 1941. They had been competitors as students, sharing most of the first places on the exam lists, but they maintained contact through the war and became friends afterwards when they were doing their respective PhDs, Jack in Belfast and Yolande in King's, and married in 1950.

Jack wrote a long account of his wartime experiences, part hilarious, part harrowing (unpublished). He said he gave little thought to the possibility that plant research would play any part in his future, although he carried some of Darwin's books with him and did some field studies in occasional moments of relaxation. He widened his horizons, gained technical knowledge on electrical installations, telecommunications and electronics, all useful later when he built phytotrons and laboratory equipment; and he acquired management skills when he was promoted to Captain and put in command of 400 men.

Like other biologists before him, he topped the examination list after introductory courses on electromagnetics and radiolocation for gun-laying. He was given some options on where he would be posted and selected the Orkney Islands. His first duty was at a remote gun emplacement, then he had a roving inspectorate of all radar establishments, having first been commissioned into the Royal Army Ordnance Corps. Finally he was transferred to the Royal Electrical and Mechanical Engineers and placed in charge of the large engineering workshop that serviced all units on the archipelago. When the strategic role of the Orkneys as a major naval base diminished after D-Day he was sent to London to a unit attempting to track incoming V-2 rockets, and then in March 1945 to Brussels. There his biological background was used in an assignment to collect a culture of the B-vitamin-producing fungus *Erymothecium ashbyii* from the Dutch National Mycological Collection, which had miraculously survived the occupation. On the way he detoured to Utrecht to see if any trace remained of the Wents' laboratory, where seminal work on the plant growth regulator auxin had been done before the war. He was back in Brussels for VE Day and was then attached to one of several units set up to inspect German technical establishments and return important research material to the Royal Aircraft Establishment at Farnborough or the Telecommunications Research Establishment in Malvern. His unit went to the Baltic coast, via Osnabrück, Hamburg and Lübeck, through detachments of the now quiescent German army, seeing terrible scenes of devastation on the way to a radar-research station at Pelzerhaken, still more or less intact except for buildings that had been occupied by displaced persons. Images of that experience haunted him for the rest of his life. He made (secretly and against orders!) a photographic record of this assignment, not printing the negatives until the last year of his life.

Lectureships and Readership, Belfast and London, 1945–54

He was released from the army in September 1945 to 'undertake work of national importance' at Glaxo laboratories. However, he had already decided that he would prefer an academic and research career, so instead he accepted a lower salary as a junior lecturer in the Agricultural Botany Department at King's College, University of Durham. Here, in addition

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to his teaching, he worked up his notes from prewar excursions to the Hebrides for a Masters thesis. Meanwhile he applied for and received a lectureship at The Queen's University, Belfast, and moved there in mid-1946.

His own wish for an academic career had coincided with some parental pressure to join the staff at King's, where there was such a strong family connection. At Queen's he was truly independent, and threw himself into the world of Irish botany. The physiology of flowering had interested him as an undergraduate and now he started experiments on the control of sex expression. This, with genecological work on dactylorchids and analyses of naturally occurring intersexes in willows, became the material of his PhD thesis, which was accepted in 1948. It is fascinating to discern in it the origins of so many of the trademarks of his writings in later years: command of language and vocabulary, exhaustive literature reviews, discussions structured as flowing arguments starting from fundamentals, extrapolations from his own data to other branches of the subject (as, for example, when he used the morphology of intersexual flowers in his willows to contribute to arguments about the origin of the angiosperms), and topics (including his first micrographs of pollen grains) that were to be his life's work. His first major paper appeared in 1948 and on average he wrote nearly five every year thereafter.

He travelled extensively throughout Ireland, lecturing to field clubs, particularly on the geographical origins of the Irish flora, making friends with botanists and geologists north and south of the border, taking over the editorship of the *Irish Naturalists' Journal* from 1947 to 1950 and extending his prewar knowledge of Hebridean orchids to Irish forms. Early in 1949, as he was building his own reputation as phytogeographer and orchid genecologist, a letter was published in *Nature* suggesting obliquely that his father had falsified phytogeographical evidence concerning Hebridean plants. Jack never subsequently discussed this matter with his wife or son. He had not referred to the disputed species in his own phytogeographical writings up to that time, nor did he afterwards. Later in that same year he was invited to serve as a local expert guide for an International Phytogeographic Association Excursion to Ireland. This was no ordinary field trip, but a gathering of world leaders in taxonomy, phytogeography, ecology, genecology and palynology. Jack evidently made a strong impression, for one of the participants, W.H. Pearsall, F.R.S., offered him there and then a lectureship in University College London, on condition that he would concentrate on taxonomy. It was a defining moment in his career in one other respect: he also met A.R. Clapham (F.R.S. 1959) and H. (later Sir Harry) Godwin, F.R.S., and fifteen years later they, with Pearsall, were among those who proposed Jack for election to Fellowship of The Royal Society.

Jack moved to University College London in late 1950. There he relished the almost daily opportunities to widen his horizons in discussions on a wide range of topics with many colleagues who were at the top of their respective fields and who set exceptionally high intellectual standards. He fulfilled the requirement to become a taxonomist and was soon promoted to a Readership. His book *New concepts in flowering plant taxonomy*, published in 1953 and translated later into several languages, was a marked departure from traditional approaches, dealing with micro-evolution, speciation, phenotypic plasticity, plant geography and reproductive isolation, the use of cytological methods and the taxonomic and evolutionary significance of cytological observations. All of his research publications from University College were on orchids, including a prescient paper on pollinia, in which he noted that the constituent pollen mother cells progress through meiosis synchronously, as if they are

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parts of a physiological unit. He wrote several articles on plant geography and statistical taxonomy, and a penetrating review of the significance of plant teratology which included a comment that should strike a chord among the present-day legions who exploit mutants and transformants: 'All developmental abnormalities are physiologically significant since through their study lies the hope of comprehending the normal'. He also had his first experience of developing an experimental garden and an associated laboratory. Here, in the grounds of Nuffield Lodge, he studied pollen development with the use of tissue culture techniques; pollen and botanical gardens would both become important in his future career. In 1953 he was elected a Fellow of the Royal Society of Edinburgh, the first of many national academies to give him such recognition.

Professor of Botany at The Queen's University, Belfast, 1955–60

In 1954 Jack returned to The Queen's University, Belfast, to meet a totally new challenge, that of modernizing a small and impoverished department. The Vice-Chancellor was the eminent botanist-turned-administrator Eric Ashby, later Baron Ashby (F.R.S. 1963). Jack had overlapped with him for one term before leaving for London in 1950 and came to know him well, eventually serving as his biographer for The Royal Society in 1995 (*Biogr. Mem. Fell. R. Soc. Lond.* **41**, 1–18). In that memoir he quotes Ashby's policy of appointing to chairs 'persons in their thirties who would be likely to be leaders themselves in ten or more years time'. Jack was one of his appointees, then aged 35. They were both interested in how the onset of flowering is regulated, so when Jack arrived and wrote him a long letter setting out a hypothesis on the photoperiodic control of sex expression, Ashby provided space in a glasshouse at his residence, there being no departmental facilities at that time.

Among those who received great stimulation from the new professor were J.S. Pate (F.R.S. 1985), who had just started a PhD on nitrogen fixation in leguminous root nodules, and Brian Gunning, a third-year student when Jack arrived. For John Pate he produced a list of the ten best areas of research on legume nodule biology (he says that he is still working on them). For myself he delivered a memorable series of one-on-one honours tutorials in 1955–56, on subjects ranging from the history of botany to the significance of a paper recently published in *Nature* by Watson and Crick. On these occasions, in what had been the drawing room of a Georgian terrace house but was then the professorial office in the Botany Department's main home, I took notes on one side of a huge desk with Jack holding forth on the other, seated on the velvet-upholstered 'Chair of Botany' bequeathed by his predecessor, James Small. At the time he seemed to me to have the ability to speak off-the-cuff with authority on every conceivable subject, but his wife Yolande has testified that in fact he prepared assiduously so that he could give his sole honours student full benefit from the weekly tutorial. That same painstaking preparation lay behind all of his performances, large or small, for the whole of his life, and just as for my own reaction as an honours student, most of his listeners would marvel at his eloquence and erudition without perceiving the industry that he put into his assembly of material, choice of words, crafting of sentences and structuring of his presentation.

He acquired a plot of land and designed experimental gardens and a small phytotron with eight chambers, each with temperature and lighting controls that he mostly installed himself using parts bought locally. He started his work on sex expression by manipulating the

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succession of male and female flowers found in *Cannabis* inflorescences, and went on to show that a range of monoecious, dioecious and hermaphroditic plants shares similar regulatory mechanisms and that auxin and photoperiodic treatments can induce male sterility and production of female flowers where males would otherwise occur—all in accord with a hypothesis that he had advanced in his PhD thesis. His 1957 review of sex expression contains a good example of his punctilious searching of the literature for ultimate source references: he unearthed and gave due credit to the first unequivocal demonstration of the photoperiodic control of flowering, published by Tournois in 1911, considerably pre-dating Garner and Allard's more widely recognized work.

In his four years at Queen's he designed a new Botany Department in a new science building; he built up the departmental staff by appointing first-rate lecturers in physiology and biochemistry, ecology and plant geography; and he established a Quaternary Research Unit, which developed a flourishing programme on Irish vegetation history through carbon dating and palynology. He published twelve experimental papers (more than half co-authored by Yolande) and twenty-five other articles, adding physiology to his repertoire of experimental taxonomy, biometrics and phytogeography. He was elected a Member of the Royal Irish Academy in 1956, as a 'recognised authority on certain aspects of the flora of Britain and Ireland, especially the orchid flora'. He started research on the reproductive biology of grasses and as part of this programme Robert Bruce Knox arrived from Edinburgh in 1959 to work with him for a PhD: it was the start of a collaborative research programme and friendship that was to last nearly four decades. He also subtly changed his surname in an effort to reduce confusion between his mail and that belonging to D.C. Harrison, the Professor of Biochemistry at Queen's: he began to use the hyphenated surname 'Heslop-Harrison' and retained this form thereafter.

Mason Professor of Botany, University of Birmingham, 1960–67

In 1960 Jack was invited to move to Birmingham to take a leading role in establishing the first (at least among the 'older' British universities) unified School of Biological Sciences. He became its Chair in 1963, having helped, as in Belfast, to plan a new building, which was opened in 1964. The planning processes, both architectural and for the integration of teaching activities, brought out his organizational skills and incisive administration. He also enhanced the facilities at yet another experimental garden—his third, at Winterbourne—and wrote monumental review articles on genecology and plant growth substances, and published papers on taxonomy, flowering, sex expression and apomictic reproduction in grasses (the latter with Bruce Knox, by then continuing his PhD in Birmingham).

Electron microscopy made the 1960s a decade of exciting developments for all biologists. Jack had used a commercial electron microscopy service while in Belfast, and now he was able to borrow facilities in Birmingham to make his own observations. Later he set up his own Electron Microscopy Unit, among the earliest in the UK to specialize in plant ultrastructure. Progress was rapid, so much so that in 1967 the Linnean Society awarded him its Trail–Crisp Medal 'in recognition of outstanding contributions to biological microscopy'.

With his honours student from Belfast, P. Jagoe, who had come to Birmingham to start her PhD, Jack had used the unnatural pyrimidine 2-thiouracil to disrupt developmental processes that are mediated by RNA metabolism. It interfered with flower differentiation in

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Cannabis and also caused chloroplasts to develop abnormally. He reported on ultrastructural aspects in several papers, but it was the untreated controls that led to the major advance. He derived a satisfactory model of the complex architecture of grana—the photosynthetic membranes of chloroplasts—after spending many hours making reconstructions in modelling clay ('helped' by his four-year-old son Pat). Its essential features have survived the test of time and remain basic to our understanding of the light-harvesting reactions of photosynthesis. This was a short-lived project with a long-lived outcome; he never again worked on chloroplasts.

In each of his earlier posts he had touched on aspects of pollen biology. Now he started ultrastructural observations that were to fascinate him for the rest of his career. He began with *Silene* and *Cannabis*, plants in which he had induced male sterility in experiments in his Belfast phytotron. A paper in *Nature*—the first of many with carefully crafted alliterative titles, in this case 'Origin of exine'—marks the real onset of his pollen period. He followed it with accounts of events in the tapetum (nurse tissue for pollen), pollen mother cells (especially cytoplasmic continuities between them, which helped to explain the synchronous development of microspores) and all stages of pollen development. In this work Hugh Dickinson, who had come to Birmingham as an undergraduate and now started his MSc, became another long-term collaborator and friend. He concluded his two decades of publications on orchids, which had begun with field observations in the Hebrides and continued through genecology and microevolution, with excellent electron micrographs of microtubule disposition in asymmetrical pollen mitosis.

Jack attracted many visitors to his department at Birmingham, among them Professor Folke Skoog from the Botany Department at the University of Wisconsin, Madison. Upon his return to Madison, Skoog and his colleague R.A. Brink campaigned for a Brittingham Visiting Professorship on Jack's behalf, writing in June 1963, '…it would be difficult to find a person who could contribute to research and could catalyze activity in all areas of basic and applied botanical sciences on this campus to the same extent as he', and 'Heslop-Harrison combines an extraordinary breadth of knowledge about plants with unusual ability to communicate his ideas, both from the public platform and in private conversation, with clarity, enthusiasm and grace'. At the same time his case for election to The Royal Society was mounted, on the basis of his accomplishments in taxonomy, cytogenetics, biometrics, flowering and sex expression; his work on pollen was too new to be included.

University of Wisconsin, Madison, 1965 and 1967–70

The Heslop-Harrisons spent the first nine months of 1965 on sabbatical in Madison. Jack had designed his own electrophoresis assemblies in Birmingham and now, always dextrous and always delighted to try a new technique, used the ultramicrochemical electrophoretic methods of Edström to analyse RNA fractions from individual pollen mother cells, isolated by the use of a de Fonbrune micromanipulator. The objective was to follow up electron microscope observations made by Hugh Dickinson, showing a sharp decrease in the population of ribosomes during meiotic prophase. His confirmation of the observation led to several more papers on the phenomenon, in which pollen mother cells clear out most of their 'parental' RNA, and then the haploid gametophyte generation that arises during meiosis subsequently resynthesizes its own new complement.

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His sabbatical was also a reconnaissance. It was put to Jack that he should become the first Chair of a proposed Institute of Plant Development in Madison—a continuing appointment. He was attracted, returned to Birmingham, and replied in August 1966 that he would take up the offer in the following year. In three years, starting in August 1967, he wrote 35 papers. Some were with his wife, including a methodological one on the use of fluorescein diacetate to assess pollen viability, which has become the most heavily cited of all Heslop-Harrison papers. Others were with Hugh Dickinson, who joined him as a PhD student to continue his work on ribosome dynamics and pollen wall morphogenesis. A very important set of papers came from collaborations with Bruce Knox, who visited on leave from his lectureship in Canberra. Jack directly supervised rather few PhD students in his career: the last, E. Williams, worked in Madison on the 'nucleoloids' that repopulate young microspores with ribosomes after meiosis.

If there was one principle that guided his work more than any other it was that form and function are interrelated at all levels of organization. Having described the micro-morphology and morphogenesis of the sculptured walls of pollen grains—including pioneering applications of scanning electron microscopy with the first Cambridge Stereoscan to arrive in the USA—it was natural that he should think about possible functions of their elegant lacunae and layered organization. He had already related the ribosomal cycle to the occurrence of two-celled and three-celled pollen and the existence of two self-incompatibility mechanisms that promote outbreeding in flowering plants: one determined by the parent, or sporophyte generation, and the other by the haploid pollen, or gametophyte generation. He envisaged links between incompatibility genes and cell-wall cavities and their contents, which he surmised might include 'incompatibility proteins'. He went on to devote many years of work to flesh out these ideas.

Jack and Bruce Knox began to use enzyme cytochemical and immunocytological methods to study diffusible proteins, already known to be carried by and released from pollen grains. They identified various hydrolytic enzymes and a major hayfever antigen, localizing some to the outer, exine layer of the wall, which were released within seconds of hydrating pollen grains, and others to the inner, intine layer, which were released within minutes. Those in the exine are deposited there by secretory activity of the tapetal nurse tissue while the pollen is developing in the anther locule; those in the intine are placed there by synthetic and secretory activity of the pollen grain's own cytoplasm. The next logical step—proof that incompatibility substances were indeed present—came soon afterwards.

In 1969–70 the Madison campus was a focus of student demonstrations against certain defence department research contracts. Although the Botany Department and its Institute of Plant Development were not directly involved, they too suffered disruption. Jack had to destroy all of his stocks of *Cannabis* (even though it was a fibre strain). All this was very unsettling, so when Sir George Taylor, F.R.S., wrote in early 1970 to suggest that Jack should consider succeeding him as Director of the Royal Botanic Gardens at Kew, it was not only a wonderful opportunity but an opportune moment. This was an eventful period for him. News arrived of his election as Fellow of The Royal Society; he was interviewed for the Directorship and by 18 May he had received a formal offer. In his letter of resignation he wrote to the Departmental Chair in Madison: 'I don't have to tell you that in many respects I feel very sad indeed about going. In spite of the various difficulties we have all experienced, both Yolande and I have felt that the last three years have been among the happiest in our lives, and certainly among the most productive'.

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Director, Royal Botanic Gardens, Kew, 1971–76

Jack was 'Director-Designate' until 1 June 1971 because Sir George Taylor postponed his departure from Kew. He thus had nearly a year (unsalaried), part of which he spent writing a superb book-length account of sexual reproduction in flowering plants and a landmark paper with Bruce Knox tracing the fate of protein diffusing from pollen grains on to stigmatic papillae, notable for their introduction of the term 'recognition substances'.

The prospect ahead

One of his first tasks as Director was to reappraise the role of the Royal Botanic Gardens (RBG), as required by the Rothschild Report and subsequent Green Paper on Government Research and Development. Kew was administered by the Ministry of Agriculture, Fisheries and Food (MAFF), which, Jack was to find, rather liked it as a public park and was not very receptive to his view that Kew should have major scientific and policy roles. A forward-looking article entitled 'The prospect ahead' in *Journal of the Kew Guild* (2) included his list of the functions of the RBG: public amenity and education; curation of the largest existing collection of living plant species, exceeding 20 000 taxa, and the compilation of floras and monographs; operation of a seed distribution system and a seed bank; horticultural training through a diploma course; identification, advisory, quarantine and forensic services for various clients worldwide; research in plant taxonomy, geography, anatomy, physiology, cytology, biochemistry, ecology, genetics; plant introduction and many aspects of horticulture and associated technology. Government often added the duty of entertaining visiting dignitaries. The RBG also had its own detachment of police. As he said: 'Few institutions can lay claim to so many roles'. He could well have added '…and such a burden of administration for the Director'.

Jack's period as 'Director-Designate' had given him an opportunity to visit Kew and formulate plans that he hoped to implement quickly upon his actual arrival; his wide experience of research and administration enabled him to see where modernization and reorganization were necessary. All sections of the RBG came under scrutiny. An article in *Journal of the Kew Guild* for 1972 (written by a member of Kew staff, probably before the end of 1971) marvels that 'so much is happening at Kew … that it is difficult to keep pace with events'. He reinstated the RBG Annual Reports (last published in 1958) as soon as possible and the first of these (in *Kew Bulletin* for 1973) documents many of the initial changes to the Gardens and far-reaching administrative reorganizations of the Divisions.

He had ambitious plans for some of Kew's landmark buildings, but was not there to see all come to fruition. In 1971 the Orangery had been restored but, as Jack pointed out, it apparently had no function because its original design was incompatible with growing the genus *Citrus*! His decision to use it as a gallery to display Kew's art, history and scientific work, and to sell publications, started industries that flourish still. By 1974 the Temperate House, the largest of Kew's glasshouses, designed by Decimus Burton and built between 1860 and 1899, had to be declared unsafe, closed to the public, stripped of all movable plants and made a 'hard-hat' area for researchers. Jack sought the advice of architects and historians in planning a restoration, and the Treasury finally approved expenditure towards remedial work, initially planned for late 1975 but only completed much later. He also planned a new Alpine House, which again was long-delayed. One of his dreams was to construct at Kew a twentieth-century counterpart of one of the great glasshouses of the last century. He wrote in

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'The prospect ahead': 'With modern materials, new constructional techniques and state of the art environmental engineering they could be surpassed in function and perhaps even matched in majesty … the prospect for increasing the range of contrived environments is exciting indeed: arctic houses, true desert houses, photoperiodic houses modifying—even reversing—the march of the seasons are all within practicality.' His proposal was shelved by the MAFF because of financial constraints at the time. Nevertheless he held to his dream and his plans were later refined, leading to a feasibility study in 1977 and the eventual realization of his concept in 1987 with the opening of the superb Princess of Wales Conservatory, with its ten climatic zones from arid to moist tropical.

Jack's first priority was to enhance the RBG's scientific roles and to introduce state-of-the-art technology into several new and existing units and laboratories. Above all the newly titled Living Collections Division was integrated and strengthened under a newly appointed and enthusiastic curator, J. Simmons, to carry the onerous responsibility of being the most important focus in the world for holding plants of wide diversity in taxonomy and habitat. The establishment of a technical (mainly micro-propagation) unit for cell, tissue and meristem propagation was one of the star achievements of the period, drawing on Jack's previous experiences of tissue culture and planned with the help of F.C. Steward, F.R.S., one of the pioneers of the field. He set up an Enquiries Unit, a Palynology Unit in the Herbarium, promoted electronic data processing, inaugurated a seminar programme and reorganized the three-year Kew Diploma course in horticulture. His other innovations, the Cell Physiology Laboratory, the Seed Bank and the Conservation Unit, merit treatment in more detail below. In promoting the cause of science at Kew, Jack increasingly felt the need for a high level of academic support, and the MAFF acquiesced with his suggestion in 1973 of convening a Science Advisory Panel 'To advise the Director on the scientific functions of the Royal Botanic Gardens, with particular reference to the long-term development of new and existing lines of research'. In itself this was a coup, because it had become clear to him that the MAFF had little interest in science at Kew. From the first meeting in May 1974 Jack was able to count on backing from this group, chaired by G.E. Fogg, F.R.S.

Cell physiology

One of the miracles of his time at Kew was that as well as raising the research profile of the Gardens as a whole, he was able to make a personal contribution through his 'Cell Physiology Laboratory'. This was a labyrinth of rooms, originally part of the old Servants' Hall of the Director's residence on Kew Green. He assembled good facilities for cytochemistry, microscopy and associated photography. There were no full-time staff, but Yolande, a collaborator in much of the work, became an Honorary Research Fellow. Here he was able to escape sometimes from the burden of administering the Gardens, regarding out-of-hours work in 'Cell Physiology' as a form of relaxation.

At Belfast Jack's main research focus had been on flowering and male sterility, leading on to his studies of pollen development in Birmingham and Madison. Now, at Kew, pollen–stigma interactions were the next logical topic. Once again it was a time of exciting progress. Jack and Bruce Knox added five important papers to those already produced in their previous collaborations, submitting them over a twenty-one-month period in 1972–74, aided by a visit from Bruce on a Royal Society Commonwealth Bursary and work by his graduate student in Canberra, B. Howlett. They exploited the differing kinetics of release to distinguish between exine-held and intine-held proteins from pollen grains and proved that these emissions include

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recognition substances (their own new terminology) by monitoring rejection responses in stigmatic papillae of plants with dry stigmas. Agar blocks containing diffusates of tapetal substances from incompatible pollen caused the deposition of callose rejection plaques in papillae, similar to those seen in genuine incompatible pollinations. Moreover, they found that if they bathed stigmas in protein from compatible pollen, incompatibility barriers opened to the extent that incompatible pollen could then germinate and the resultant pollen tubes could penetrate and effect fertilization. Evidently, once pollen tubes are permitted entry they can proceed. Biologically active fractions showed partial immunological cross-reactions with sera to authentic hayfever antigen E obtained from the National Institute of Allergy and Infectious Diseases in Bethesda. This classic series of papers thus documents the properties of pollen wall proteins, including recognition substances, allergens and a range of hydrolytic enzymes, the latter hypothesized to aid in penetration of the walls of dry stigmatic cells by the emerging pollen tubes in situations in which appropriate recognition has been achieved.

O. Mattsson (Copenhagen) joined the Heslop-Harrisons for the next step. Seeking the receptor side of the recognition system, they detected a hydrophilic, proteinaceous 'pellicle' overlying the cuticle of dry stigmatic papillae. That it has a part in the cross-talk between pollen grain and stigma was proved by the observation that enzymic erosion of its protein stops penetration (though not germination). Clearly, stigmatic surfaces required further investigation, and here the resources of Kew were used to the full. Yolande and K.R. Shivanna (visiting from Delhi) surveyed almost 1000 species: they established functional and phylogenetical correlations between wet and dry stigmas, gametophytic and sporophytic compatibility controls, and bicellular and tricellular pollen. The distinctive chambered wall of *Crocus* stigmatic papillae yielded wonderful images of cytoplasmic membranes involved in secreting the (glyco)proteins.

Jack received the honour of being asked to deliver The Royal Society's Croonian Lecture in 1974, just four years after his election. He focused on pollen–stigma interactions, giving special acknowledgement to his collaboration with Bruce Knox (an audio-visual recording of this lecture is held by The Royal Society). He and Bruce felt that they had reached a watershed in knowledge of the recognition system by then, to the extent that when Jack visited Melbourne, the home of the immunologist Nobel laureate Sir Macfarlane Burnet, F.R.S., to give a talk in a symposium, they presented it in immunological terms under the title: 'Self and not-self in plants'. Other honours from the first decade of his long period of pollen studies included the Erdtman Medal and the Cooke Award of the American Academy of Allergy for his work relating to hayfever (shared with C. Reed, Head of the Allergy Clinic at the University of Wisconsin).

The Seed Bank

Jack enunciated his vision for the Kew Seed Bank (formed in 1968 to service an exchange scheme operated through the Index Seminum) in 'The prospect ahead':

> It is impossible to believe that we will reach the end of the century without the national recognition of the need to hold our own substantial stock of important genera, and contribute thus to conserving their worldwide variability as human pressure on the plant kingdom increases. … It is equally improbable that a new national gene bank should be set up without major participation by Kew, all the more so since the Seed Bank would be a vital complementary adjunct for any such operation.

He drew attention to a proposal from the Food and Agriculture Organization of the UN to establish a network of stations for conserving genetic resources, and expected that Kew

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would have special responsibility for wild species. Refurbishment of the mansion at Wakehurst Place (Kew's satellite garden in Sussex) gave him an opportunity to make a start. He decided to move the Physiology Section, including P. Thompson's programme on germination, to Wakehurst Place, thus providing it with much extra space. The germination work and the previously separate Seed Bank were amalgamated in new laboratories there and extra staff were appointed for a major expansion of seed collection, storage and germination operations. For these initiatives and the associated lobbying and fund-raising Jack deserves full recognition for giving the first effective political and practical momentum to the long-term cause that has culminated in the construction of the 'Millennium Seed Bank' on the Wakehurst site, due for completion in 2000.

Conservation

A role for Kew in conservation was to be one of Jack's great campaigns. He saw that Kew could be a base for both national and international policy in relation to conservation, and moved quickly in 1971 to liaise with the World Wildlife Fund, the UN Food and Agriculture Organization, the Eco-Sciences Panel of NATO and the International Union for Conservation of Nature (IUCN). Foreseeing the need for a much more active national policy in the near future, he initiated and obtained funds for a NATO conference at Kew on the role of botanic gardens in conservation. He emphasized 'the need to hold well-documented and properly identified material … for nothing else is really worth the time of a botanic garden claiming scientific status'. He initiated efforts to coordinate the conservation activities of botanic gardens in Britain and overseas, giving a new sense of scientific purpose and leading to the creation of national collections of certain genera. It was as a result of his arguments in favour of a 'total biome' approach—as distinct from policies aimed at conserving particular threatened animals such as the panda—that he was asked by the IUCN to set up a new organization, its Threatened Plants Committee. As its inaugural chairman he provided a secretariat at Kew. He persuaded the Council of Europe to support the production at Kew of a list of rare and threatened European plants—a blueprint for comparable efforts elsewhere. By his second Annual Report, Conservation Activities needed a special heading, and he was able to record that the MAFF had agreed that he should set up a Conservation Unit at Kew (it was enthusiastically headed by G. Lucas when it was formed) 'to devote its energies to the growing conservation interests of the institute and also to provide technical information for other parts of the Ministry in plant conservation matters'. With Jack's encouragement, Kew staff found themselves engaged in more and more international conservation initiatives.

Jack was a master at presenting arguments succinctly and convincingly, and among the dozens of public lectures that he gave while Director many were devoted to conservation themes, such as 'Plants for the future', 'The plant kingdom, an exhaustible resource', 'Conservation and the activities of the IUCN', 'Genetic resource conservation, the end and the means', and 'Resource and conservation: whom must one convince?'. A quotation from 'Man and the endangered plant' epitomizes his strength of feeling for conservation: 'How sad that we should still think of the task of preserving some residues of the richness of the biome that nurtures us and within which we evolved as some kind of charity'. He was not reticent about government policy (or, as he saw it, the lack thereof) on some of these occasions, and in a letter to his local Member of Parliament long afterwards stated that in response to his public stance on conservation 'I was actually given to understand [by his Civil Service masters at the MAFF] that it was not my part to involve myself in such matters of high policy'.

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On a more parochial scale a 'wild' area illustrating conservation of the local flora was created around Queen Charlotte's Cottage in the Kew grounds, and Wakehurst Place became, thanks to dedicated labours by J. Simmons and T. Schilling, a conservation area quite different in soil type, topography and habitats from Kew, and outstandingly successful for preserving and displaying elements of British, Himalayan and other floras.

Administrative and lecturing commitments

Jack felt the call of public duty keenly, and responded to it perhaps too conscientiously for his own good. In the period of his directorship he served on the following bodies:

> Board of Governors of the Plant Breeding Institute, Cambridge 1972–82; Governing Body of the John Innes Institute, Norwich 1973–78; University of Reading, Honorary Visiting Professor and Member of Plant Sciences Joint Committee 1971–76; Academic Advisory Council for the New University of Ulster 1973–75; Member of Board of Studies, University College London 1971–76; Biology Sub-Committee of the NATO Science Committee 1973–77; Commission of the European Communities, Consultant on Community Programme on Biotechnology (later the Biomolecular Engineering Programme) 1974–76; Chair, Threatened Plants Committee of IUCN 1973–76; Advisory Board of the UK Research Councils 1974–76; Biology Sub-Committee of the University Grants Commission 1974–76; Committees of the Science Research Council and the Agricultural Research Council 1975; British Council Scientific Advisory Panel 1974–75; British Library Advisory Council 1974–75; Council of Scientific and Technical Institutes 1974–75; Institute of Biology, Vice-President 1973, President 1974 and 1975; British Association for the Advancement of Science, President Section K 1974, Vice-President 1975, Council 1972–76, sometime Joint Secretary; Botanical Society of the British Isles, Vice-President 1973–74; Linnean Society, Vice-President 1973–75; Council of The Royal Society 1975–76; Member of Royal Society Agricultural delegation to China, 1975; Council of the Royal Horticultural Society 1971–76; Sports Turf Research Institute, Honorary Scientific Advisor 1972–75; Chelsea Physic Garden, Committee of Management 1973–76; Annals of Botany Company, Chair 1974–76 (he served the Company in various capacities for 37 years from 1961); Board of The Company of Biologists 1975.

Often being an office-bearer of these councils or boards carried the duty of public presentations, for example presidential addresses. Between these occasions and his efforts to keep the scientific output of Kew (and his own research) to the fore, he had a staggering schedule of travel and speaking engagements. As an example, here is a compilation of his major engagements (outside Kew) for 1973:

> 29 January to 18 March in Israel and India, lecturing in the Universities of Jerusalem, Tel Aviv, Jaipur, Panjab (Chandigarh), Lucknow, Varanasi and Calcutta; Ghosh Memorial Lecture in the Bose Institute, Calcutta; address to the Indian Academy of Sciences; course of fifteen lectures on the physiology and biochemistry of reproduction in angiosperms in the University of Delhi; discussions with the Indian University Grants Commission, the Indian Council of Agricultural Research, and the staffs of the Indian Agricultural Research Institute and the National Botanic Gardens at Lucknow and Howrah for critical assessment of a new 'Flora of India' project and aspects of the Botanical Survey of India. At Jaipur he received the Gunnar Erdtman International Medal for Palynology and delivered the Fifth Erdtman Lecture. Banquet Address at retirement of Professor F.C. Steward, Cornell University, New York (1 May); Royal Society Conversazione on 'Incompatibility and pollen-borne proteins' (May); Meeting of the Eco-Sciences Panel of NATO in Brussels (18–20 June); exhibit on 'Insectivorous plants' in the Scientific Section, Chelsea Flower Show; Evening Address at opening of the Botanical Research Institute, Pretoria, South Africa, and participation in the Symposium of the South African Association for the Advancement of Science (25 June to 10 July); two presentations on pollen wall proteins at Linnean Society Symposium on 'The biology of the male gamete' (September); meeting of the Survival Service Commission of IUCN, Switzerland (7–9 October); four lectures for

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students from all London University colleges, starting 16 October; meeting of Eco-Sciences Panel of NATO in Istanbul, Turkey, and lecture at the Hydrobiological Research Station (18–22 November); lecture to Linnean Society on 'The cell since Brown', in Robert Brown Centenary Symposium (6 December).

Some of these engagements clearly went with the directorship, but many, perhaps most, were above and beyond the call of any reasonably defined duty. Jack took them on because he was a passionate advocate, a passionate researcher and a passionate communicator, and he felt that his job carried with it some obligation to be generous with his knowledge, eloquence and advice. Meetings often involved travel and time-consuming preparation. He never went to them lightly, and if he was in the chair himself he would invariably have a game plan ready to achieve a desired outcome. He felt strongly about many causes and key meetings often represented opportunities to put his case.

Resignation from Kew

At Kew, Jack suffered again from a duodenal ulcer that had required him to have massive blood transfusions when he was in Birmingham, as well as from bouts of crippling migraine. In 1974 he developed pains in his leg and heart. His doctor fortunately associated the symptoms and called in a specialist, who diagnosed a thrombosis. On another occasion he had a less severe attack in his lunch break. In neither case did he tell anyone at the RBG what had occurred.

The strenuous efforts involved in realizing his vision of transforming Kew into a major scientific institution added to the administrative burden of the directorship. With the already prodigious routine tasks of running the RBG, where every day brought meetings, discussions, decisions, events in-house and, often enough, crises, it became a remorseless treadmill. As already noted, the Royal Botanic Gardens was then under the purview of the MAFF, and it was their officials, not the Director of the Gardens, who determined the hours of opening, entry fee, industrial awards, salary scales, conditions of appointment and staffing, even in the Director's office. Their approval had to be sought for all policy changes, proposed developments and overseas travel. At one stage Jack was reported as being 'incandescent with rage' when the MAFF tried to downgrade the post of Curator of the RBG to the status of Head Gardener, to bring Kew into line with other Royal Parks. They held nearly all of the purse-strings—one exception being the Bentham–Moxon Trust, a fund administered by an external Board of Trustees on behalf of the Gardens and the staff. G.E. Fogg told Yolande in 1998 that Jack had quietly lodged proceeds he gained from lecturing appearances into this Trust, thus augmenting funds for general use.

Towards the end of 1975 Jack found himself coming to an agonizing decision. His wife expressed his dilemma thus: 'he was becoming more and more aware that unless he could spend more time for personal research in reading about current work, through personal contacts and in working himself in the laboratory he would never be able to get to the forefront of his chosen subject again, and would have to settle down to becoming an administrator entirely until his retirement as Director—a matter of another four or five years'. By Christmas he had made up his mind. Down all the long years since Sir Joseph Banks became the first unofficial Director in 1772, and Sir William Hooker the first official Director in 1841, no Director of Kew had ever resigned. He would be the first to do so. He would step back from the prestige and the prominence and the prospects so that he could make better use of his talent for personal research.

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Many tributes arrived when the news broke. One of his replies (to a member of the Board of Trustees of Wakehurst Place) is quite blunt about his reasons for resigning:

> The truth is, as things are at present the job is uncontainable for someone who wishes also to retain a credible foothold in science. I think we now have very little sympathy or understanding in the higher echelons of MAFF and the Civil Service Department, to whom Kew must now seem an unmitigated nuisance, and regrettably we have been served very badly over the years on the administrative side. … Our own decision has been a terribly difficult one for Yolande and myself, since we both love Kew and Wakehurst so much, and have so much respect for all aspects of the work, both in the UK and overseas. … But we have to be honest with ourselves in the end and recognize that we could not really be happy giving up botany and soldiering on with the organizational and administrative side for our remaining four years.

When he tendered his resignation he had no plans, except that he could take up a long-standing invitation to visit the University of Massachusetts. However, on 17 June 1976 he was able to write to Sir Harry Godwin, F.R.S.:

> A considerable time ago you said in a letter to me that one should think about a Royal Society Research Professorship, and since that day I have always looked upon that possibility as an ideal. Yesterday it was realised, when I was invited to accept one; we do indeed feel that this is what we have been working towards—or as you said in your last letter—what one was made for! We plan to link up with the Welsh Plant Breeding Station and the University of Wales, Aberystwyth and of course to develop the reproductive physiology work, in the first instance mostly with grasses. I feel the opportunities are tremendous—and I hope we have the energy left to exploit them all. Certainly there will now be no excuse.

Royal Society Research Professor, 1977–85; honorary research worker (Welsh Plant Breeding Station) 1985–93; research worker, Bargates, 1993–98

From this time on, at age 56, he published 102 further papers, so his energy was not in doubt. Indeed, he enjoyed the most concentrated research of his career as Royal Society Research Professor from late 1977 to late 1985 and thereafter as Honorary Visiting Research Worker. First, however, came a period of regeneration. Within a few days of leaving Kew at the end of August they were in Amherst, Massachusetts, leaving their hastily moved belongings in a newly purchased house in Leominster. He wrote to me: '[I felt] as though I had inherited a new lease of life'. As a Visiting Professor, Jack gave a course of thirty-five lectures on 'Gametophytic development, pollination and compatibility control in flowering plants', enjoyed by staff and students alike, and so popular that he was asked to return two years later to present an updated version.

The day-to-day routine at the Welsh Plant Breeding Station (WPBS, now the Institute of Grassland and Environmental Research) could scarcely have been more different from that at Kew. Jack was given the choice of a new laboratory or the top floor of the original mansion, isolated from the rest of the institute, with panoramic views of fields and hills, and often no contacts other than the twice-a-day mail deliveries. He chose the peace of the top floor. He still felt it his duty to retain responsibilities on numerous councils, boards and committees in the causes of conservation, renewable resources, agricultural policy and information technology, and felt pangs of guilt when he worked in the laboratory, so ingrained had the

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habits of community service become. ‘Sometimes I am appalled by the obligations I let myself in for’, he wrote, ‘but somehow most things seem eventually to get done’. He continued to give many keynote addresses and to travel a great deal. Battles to forestall the privatization of the Plant Breeding Institute at Cambridge and the closure of the Long Ashton Research Station occupied much time and effort on his part. He archived his part in these affairs as a record of what he described as ‘grotesque bungling by the government departments concerned’. But at last he could concentrate happily for long periods at a time on what he liked best: the joys of discovery, ended not by any lack of energy or ideas or hospitality on the part of the institute, but by a leaky roof and dry rot in their attic premises. He worked entirely without secretarial help, conducting research with his wife and just a few colleagues (E. Lord, O. Mattson, D. Mulcahy, K. Shivanna, V. Vithanage) who came for brief periods, and, by way of visits, with a US Department of Agriculture team in Athens, Georgia, working on remote hybridization in tropical grasses.

Jack’s work on grasses started in 1959 in Belfast. In WPBS and shortly thereafter he covered many aspects of grass reproductive biology in more than twenty papers: the diversity of breeding systems in the family, anatomical adaptations of the florets, the effects of environmental variables (especially humidity), and the features underlying the fantastic speed with which pollen–stigma interactions are accomplished. The desiccation and rehydration of pollen were researched in unprecedented detail, covering membrane permeability and the adaptations that permit germination within a couple of minutes when a grain is deposited by the wind on a stigmatic papilla—the germination aperture and its specialized pad of underlying wall material, the stockpile of a million or so vesicles containing pollen tube wall precursor within each grain and the esterase enzymes that etch an entry path through the stigmatic cuticle. If the incompatibility tests are passed, the tube embarks on an intensely competitive journey, growing at several micrometres per second along an intercellular route down the stigma, inducing as it moves a most unusual hypersensitive cell death reaction in the surrounding cells, thereby destroying the path for any pollen that may arrive subsequently (only in *compatible* pollinations). The route to the ovular micropyle was characterized anatomically and cytochemically, leading to ideas (which turned out to be fruitful—literally) about how to bypass some of the incompatibility barriers to produce novel hybrids. This series of papers is without counterpart as an analysis of structure–function relationships in a breeding system.

Jack wrote another book, *Cellular recognition systems in plants*, and sets of papers on glands of carnivorous plants and pollen–stigma reactions in the legumes *Trifolium*, *Vicia* and *Phaseolus* (with their distinctive stigma morphology), primroses and hazel. The primroses were obtained from local hedgerows, just as Darwin had done when he first described the intricacies of the two ‘morphs’, with their different pollen and stigmas—work that Darwin said had brought him the greatest satisfaction. This was only one of several parallels between the interests of Darwin and the Heslop-Harrisons, others being orchids, insectivorous plants, plant growth substances and of course cross-fertilization and self-fertilization. It was therefore most fitting that Jack and Yolande were awarded jointly the Darwin Medal of The Royal Society in 1982, the centenary of Darwin’s death. In the same year Jack was elected a Fellow of the US National Academy of Arts and Sciences, and a year later to Foreign Associateship of the US National Academy of Sciences, then to the Academie Royale de Belgique (1985), adding to his earlier election to the German Academy of Science (Leopoldina) (1975).

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In 1983 he was awarded the Lemberg Travelling Fellowship of the Australian Academy of Science, enabling him to visit myself, Bruce Knox and John Pate, among others. In Canberra he and Yolande spent a week at the bench running staining protocols to reveal the cytoskeletal elements of pollen tubes. His youthful exuberance on seeing the results of his first preparations stemmed from his burgeoning interest in the cell biology of pollen germination and pollen tube growth. Back in Aberystwyth he refined the procedures and embarked on observations and experiments on motility within pollen and pollen tubes, amassing twenty-five papers on the subject. One of them was given pride of place as the first submitted paper in the first issue of *Sexual Plant Reproduction*, a journal created to meet the demands of the field that his leadership had done so much to expand. Other workers had published the first micrographs of actin, myosin and microtubules in pollen tubes, but he made many new contributions, relating his observations to classical papers on cytoplasmic streaming and the stately coordinated movements of the vegetative nucleus and the generative cell or sperm cells. Some of his illustrations of actin arrays in pollen grains during hydration and germination or experimental re-desiccation are elegant: it is no wonder that the system is now seen as a good model for examining the molecular basis of assembly and disassembly of this component of the plant cytoskeleton.

The scientific work of the Heslop-Harrisons' WPBS era thus included many novel contributions to knowledge. More than that, however, the range of the experimental approaches that they brought to bear—genetical, cytological, anatomical, physiological, biochemical and physicochemical—and the variety of arenas they influenced, from molecular biology to agronomy, led to a new appreciation of the scope and significance of the field of plant reproductive physiology, and provided it with a solid basis for future growth. This broad nurturing of a growing field was one of their greatest achievements.

Retirement from the WPBS to Bargates, the home that Jack and Yolande had bought in Leominster when they left Kew, was gradual, but it did not stop their research, for they built a basement laboratory with a full range of optical microscopes including video recording, and a photographic darkroom. They were at Bargates to celebrate further honours: the Linnean Medal for Botany from the Linnean Society and the Royal Medal of The Royal Society. Here they enjoyed 'Bargates Symposia' with Hugh Dickinson, now Sherardian Professor of Plant Science at Oxford University, and their son Pat, now a third-generation Heslop-Harrison professor of biology. It gave Jack particular pleasure to have a laboratory named in his honour in Hugh's department. At Bargates, too, they experienced some of their happiest moments of discovery. Their penultimate research paper, in 1997, is an outstanding example of their ability to see what few others would look for or think about. It deals with a mysterious ballet performed by the vegetative nucleus and generative cell within developing wheat pollen. The discussion mirrors the great span of Jack's own career, for it runs the gamut from genecology to cell biology, placing the subcellular events they observed into the contexts of adaptations for evolutionary success of opportunistic grass species in ephemeral habitats on the one hand, and on the other the molecular biology of actin gene expression. And even in his final paper he took yet another portentous step on the road that had led him from flowering physiology to pollen to interactions with the stigma and onward to pollen tubes, for in it he drew together many threads from his long experience to give new insights on the properties and protection of the embryo sac, which is the target of the growing pollen tube: the paper was published posthumously in 1999, very appropriately with Yolande and Pat as co-authors.

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The many facets of Jack Heslop-Harrison

By any standards Jack Heslop-Harrison was one of the greatest botanists of the second half of the twentieth century, with a host of scientific discoveries, the transformation of the RBG to a premier scientific institution and the engendering, nurturing and leadership of a major field of plant science as outstanding achievements. Most knew him only from his writings or from listening to his eloquent lectures; far fewer had the privilege of knowing him as a person, although he had a gift for making lasting and warm friendships. His dedication to his science might give an impression of single-mindedness, but in fact he had many facets. His lectures were invariably products of careful preparation and rehearsal, but he was also a spellbinding raconteur who could fascinate audiences large or small with humorous anecdotes and knowledgeable insights, delivered extempore. Then there was Jack the music connoisseur—a lover of classical music ever since his sister gave him a record of *Peer Gynt* at age seven, humming Sibelius symphonies through the war years on Orkney, making his own music system (partly from components collected in abandoned German research stations at the end of the war), attending concerts in Belfast and Birmingham but thereafter with little time to do so, and resuming full enjoyment via a vast collection of CDs and musical evenings in retirement. There was Jack the chef (when Yolande was barred from the kitchen), Jack the accomplished artist in oils, seized at unpredictable intervals by some nostalgic mental image and impelled to capture it as quickly as possible on canvas—Hebridean landscapes remembered from prewar excursions (one annotated '…and we in dreams behold the Hebrides'), or catacombs in Italy, or spring blossom in the Great Smoky Mountains. There was Jack the supremely skilled photographer, not just in photomicrography, but also of landscapes, still life and archaeological sites, Jack the computer programmer, who collected and used so many generations of machines that the Bargates house became a veritable museum of personal computing, Jack the goldsmith and silversmith, as dextrous in making jewellery as he was in dissecting plants, mastering bezelling, planishing and enamelling brooches, rings, pendants and medallions for Yolande, and Jack the wordsmith, seldom far from a thesaurus and meticulous in his wording (to use one of his favourites, he would much prefer this memoir to be a *conspectus* of his life, not a summary). On sleepless nights he would devise plots for novels, even as far as setting out chapter contents, but without ever completing any. His phenomenal memory enabled him to reel off chapters in English and Irish history, recall poems, sing Wagner to the Hereford cattle across the fence behind their country cottage, and, of course, call up names and facts from his immense knowledge of biological matters. And he had a great sense of simple fun and enjoyment of life, expressed by composing puns and limericks, drawing cartoons, adding pen strokes to micrographs to create funny faces, and an infectious laugh. He took most pleasure from seeing natural marvels: I well remember his expression, rapt in wonderment, seeking a rationale for the 'host mimicry' in Australian mistletoes; John Pate recalls a later episode on that same visit to Australia, after a day exploring pollination mechanisms of Western Australian flowers, Jack blissfully happy at a camp fire, mesmerized by watching a flock of white-tailed black cockatoos flying in to their roost in a brilliant sunset.

No account of Jack's work could possibly be written without paying tribute to his wife Yolande. At a memorial conference organized by Hugh Dickinson in 1999, it was well said by H.-F. Linskens that '…from the highest rooftop in Aberystwyth to the lowest basement in Leominster Jack's greatest delight was to work with Yolande'. She co-authored seventy-seven

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papers with him, but even that impressive statistic does not adequately measure the true extent of her dedicated support in their homes and laboratories over forty-eight years. It goes without saying that this 'conspectus' of Jack's wonderful life could not possibly have been written without her constant help and kindness to the author.

Acknowledgement

The frontispiece photograph was provided by Dr Y. Heslop-Harrison; it was taken in 1974 or 1975, photographer unknown.

Bibliography

Quotations in the text are from the following publications. A full bibliography appears on the accompanying microfiche, numbered as in the second column. A photocopy is available from The Royal Society's Library at cost. Autobiographical papers on 'Origins and ancestry' and 'War service' can be read at Professor J.S. Heslop-Harrison's Web site, along with extended biographical material compiled by B. Gunning from documents and summaries provided by Y. Heslop-Harrison.

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