BIOGRAPHICAL MEMOIRS

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Elected FRS 1976

By R. Neil Jones

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Hubert Rees was born on 2 October 1923 in Llangennech, Carmarthenshire, in Wales, and died on 13 September 2009 in Aberystwyth. Hugh, as he was known to his wide circle of friends and colleagues, was educated at Llandovery and Llanelli grammar schools. After leaving school he joined the Royal Air Force (RAF) and in 1944 he became a Lancaster bomber pilot. On demobilization in 1946 he enrolled as a student at Aberystwyth University, graduating with first-class honours in agricultural botany in 1950. After a short secondment to the John Innes Horticultural Institution at Bayfordbury he took up an appointment as Lecturer in Cytology at the newly-formed Department of Genetics at Birmingham University. In 1958 he returned to Aberystwyth as Senior Lecturer in Agricultural Botany, being promoted to Reader in 1966 and ultimately Professor and Head of Department. He rapidly built up an internationally acclaimed school of study into the genetic control of chromosome behaviour in plants, and on evolutionary changes in chromosome organization. Hugh Rees had an impressive intellect and was an inspirational teacher who left his mark on all who came under his supervision. In 1983 he was appointed Vice Principal at Aberystwyth. He retired in 1991 and then pursued his many interests and hobbies. Together with his wife, Mavis, he was well known to many friends and colleagues for his generous hospitality, his love of good food and wine, and as a raconteur. Hugh is survived by his wife, a son and two daughters. Another son predeceased him.

Personal history

Hubert Rees, known affectionately as Hugh, was born on 2 October 1923 in Llangennech, Carmarthenshire, in Wales, the son of Owen Rees and Eveline Tugela Rees (*née* Bowen). His father spent most of his working life as a police constable in various Carmarthenshire villages, and subsequently as storesman in a Royal Naval Establishment. The family moved from

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village to village—as Hugh said, 'mostly in delightful rural settings'. His father's family, up to two generations previously, were farmers. His great-grandfather, John Rees, was a farmer and miller at Felin Trosserch, Llangennech, in Carmarthenshire. According to the minister of the Baptist chapel, John Rees was said to be 'argumentative', which according to Hugh 'seems to be a family trait', although those of us who knew Hugh well can confirm that we enjoyed a good argument with him, always over substantive issues, and we always remained the best of friends. Two of John Rees's sons, J. B. Rees and Thomas Rees, Hugh's grandfather, enjoyed considerable reputations as poets (in the Welsh language). The poems of J. B. Rees were published under his bardic name of Morleisfab. Hugh's maternal grandfather was a coal miner, considered to be a gentle man of amiable disposition, notwithstanding his hard life. Eiluned, Hugh's sister, and Hugh himself were the first family members to benefit from a university education. Eiluned graduated with first-class honours in history at Aberystwyth; she was subsequently assistant keeper at the British Museum, and later at the National Library of Wales in Aberystwyth. Eiluned is the scholarly author of *Libri Walliae*, a massive two-volume catalogue of Welsh books and books printed in Wales before 1820.

In terms of his family background Hugh had great respect for his parents and grandparents, as well as for his wife and children. Although neither of his parents could lay claim to scholarship, he lived in a house well endowed with books, and both his father and particularly Thomas Rees, his grandfather, were avid readers. His grandfather, although self-taught, 'had a library that would do credit to a university don'. Hugh kept all those books, and his own library was likewise impressive and covered a wide range of subjects, 'from anthropology to relativity, and above all poetry'. Like his ancestors Hugh was also an avid reader, and 'it was made clear to me that scholarship, in its own right, was not only respectable but precious, and for that I am immensely grateful'. His home life was to him generally modest and congenial. He loved the idyllic countryside, especially the Towy valley and its fishing. He became addicted to fishing at nine years of age, and remained so for the rest of his life. He was proud to lay claim to the possibility that he might be the only university teacher 'to have caught two salmon in my lunch hour!'

Hugh attended two grammar schools, at Llandovery and Llanelli. According to his reminiscences,

> I was not a diligent student. The one teacher who stands out in my memory is Bryn Jones, biology master at Llanelli Boys Grammar School. He had a razor-sharp mind. He was particularly interested in genetics, at a time when few schools paid much attention to the subject. He taught it well. My introduction and enthusiasm for the subject I owe to him.

In 1941, while still in the sixth form, Hugh volunteered for the RAF, and, as he recalled, 'this would be my excuse for doing less work than I should have done'.

Hugh was married to Mavis Rosalind Hill, at Cilycwm Parish Church on 26 December 1946, after his demobilization from the RAF. Mavis Hill had been born in Cilycwm on 29 July 1923, the daughter of Rowland and Jessie Hill. The Hills later kept a guest house at Llanwrtyd Wells in Breconshire, and were noted for their hospitality and their love of music. They were accomplished singers but, as Hugh wrote, 'they failed to make one of me'. Mavis and two of her brothers entered the teaching profession, and the third brother became a garage owner. Her younger sister trained as a nurse but suffered a nervous breakdown and developed a lifelong mental disability that precluded further work; another brother died at the age of 18 months during the 1918 influenza pandemic. Hugh has written of his wife, 'she inherited to the full the generous characteristics of her family, and has deservedly a reputation for generous and

unstinting hospitality'—as those of us who know her well can concur. Hugh and Mavis met at Cilycwm, where her parents lived before moving to Llanwrtyd Wells, and where Hugh's father was a policeman at the time. It is a fond recollection of Hugh's that they were nine years old at their first meeting.

The union produced two sons (Wynne, born in 1948, and Hubert, born in 1951) and two daughters (Gwyneth, born in 1952, and Judith, born in 1966), who all benefited from the expanded postwar higher education system, to the satisfaction of their parents. The eldest (Wynne) qualified for a research studentship in the politics department of Lancaster University, 'where to our dismay he developed schizophrenia'. He went home, managed to cope with a job in local government for some time and then died suddenly in 1978. 'He was a fine, handsome and intelligent youth, and his death was shattering.' The resilience of Hugh and Mavis in the aftermath of this tragedy was an inspiration to their surviving children and others touched by the event. In particular, as Hugh wrote, 'my children owe a great deal to my wife. She is unsparing on their behalf. They adore her, with good reason.'

The RAF

Hugh left school to volunteer for the RAF, and after training in the UK and Canada he joined 75 Squadron (RNZAF) in 1944 to pilot Lancaster bombers. In his personal notes drafted in the 1980s he wished to say only two things about his experiences of war. 'First, it was exhilarating but at the same time horrifying. Second, it effectively erased any trace of bumptiousness in my character, and for this at least I am grateful.'

At the end of his first tour of 30 operations he was awarded the Distinguished Flying Cross (DFC) (figure 1) and then volunteered for a second tour but, soon after commencing, his aircraft was critically damaged over Homberg, Germany. He was able to retain sufficient control to allow the crew to bail out and, unusually, all survived. After capture, Hugh and his fellow officers were sent to Stalag Luft 1 on the Baltic coast, where they remained until liberated by the Russian advance in May 1945. Posted as missing in November 1944, it was not until two months later that his family received notification of his survival and internment, together with a laconic personal message from Hugh that he was 'playing quite a lot of bridge', a pastime shared with his wife Mavis that continued until late in life. In transit to his prisoner-of-war camp Hugh was caught in a night-time RAF raid that he was again lucky to survive. In notes made at the time he described the experience as 'unpleasant', a clear understatement judging from the rare occasions when he later spoke of these events. He spoke very little of his wartime experiences. He was a modest man but some of these experiences undoubtedly influenced his outlook on life and left a lasting mark. Nevertheless, it was in character that after his return to the UK, at the age of 22 years, he pursued his peacetime ambitions with drive and energy.

Scientific career

The undergraduate

In October 1946 he enrolled as a student at Aberystwyth University, and after initially switching courses he graduated with first-class honours in agricultural botany in 1950. His earlier experiences while at grammar school had also left their mark, and within a few weeks of registering

Figure 1. Hugh Rees in the immediate postwar period (1945) after the formal award of a DFC and his promotion to Flight Lieutenant.

for his degree he was already bent on pursuing a career as an academic or research scientist. His tutor, P. T. Thomas (affectionately known to this day as PT) was a geneticist, and his honours course was heavily biased towards genetics, particularly plant genetics. Some of the teaching was provided by staff of the Welsh Plant Breeding Station (now part of Aberystwyth University's Institute of Biological, Environmental and Rural Sciences, IBERS). PT had a strong influence on Hugh, who described him as 'a remarkable man, the best kind of university teacher', imparting a degree of enthusiasm for his subject so that the students themselves acquired the same zeal for knowledge and hard work. Much of the teaching was informal but immensely informative, with students encouraged to express their own opinions and to question the views and conclusions of the 'authorities'. Hugh recalled that under the supervision of PT he acquired not only the firm conviction that chromosomes were more important than any other organelles, but also a sense of joy and delight in looking at them in well-stained, well-spread preparations, a delight that persisted throughout his working life. He often spoke about how he carried on his work with the greatest of pleasure, and 'that work in short has been a joy'. Student days were not all work, as Hugh recalls: 'I caught 534 trout in my first year, and a few sea trout as well.'

The beginning of research into chromosome genetics

Hugh left Aberystwyth immediately on graduation, and took up, following PT's suggestion, a six-month secondment at the John Innes Horticultural Institution (now the John Innes Centre), then at Bayfordbury, under the tutelage of C. D. Darlington FRS. At the John Innes he became friendly with L. F. La Cour (FRS 1970), who incidentally started his work in the potting shed and ended up with his FRS as his only formal qualification. Hugh shared with Len La Cour the pride and satisfaction in the preparation of good microscope slides and in the interpretation of chromosome configurations—which was later to become his forte. At the John Innes he also met the well-known and controversial C. D. Darlington, and was astonished by Darlington's breadth of interests, literary and historical as well as scientific. He learned from Darlington about the interrelations between otherwise seemingly unrelated pieces of information, which

is where his passion for dealing with data (later coming from his own research students), and finding some meaning in it, probably came from. Darlington had a huge influence in developing Hugh's world of chromosome genetics and his self-confidence, and Hugh told of how, when expressing his doubts to Darlington over the interpretation of some particular chromosome configurations, Darlington told him to 'use his imagination'. In the 1950s the only tool that a cytogeneticist had was the light microscope, and it was a truly challenging prospect to interpret chromosome behaviour working with squashed-out preparations of meiosis, and to draw and to photograph them in a meaningful way: it is a skill that very few people possess to this day, although in a totally different and technological world. It was at the John Innes that Hugh had his first experience of personal research. He found himself 'good at it' and did 'some useful work' that led to the publication of two papers in the journal *Heredity* (1, 2)*.

Teaching and research at Birmingham University

In 1950 Hugh was appointed assistant lecturer in the newly formed Genetics Department at the University of Birmingham, under Professor Kenneth (later Sir Kenneth) Mather FRS, and also in the company of John Jinks (FRS 1970) (some of us would say this was a tough call, considering the high international stature of Kenneth Mather and John Jinks). He valued the skills of colleagues at Birmingham, and came to appreciate the power and satisfaction of designing and analysing the results of well-constructed experiments. He was later to transmit this ethos of experimentation and rigorous analysis of data to his many research students. It was during his spell at Birmingham that Hugh had the good fortune to work for six months, in 1957, with the eminent cytogeneticist Professor Marcus Rhoades at the University of Illinois in Urbana. Here he received the American experience: the superlative quality of the scientists there, as well as their less stuffy attitudes than their UK counterparts. He recalls having lunch cooked for him by the famous Theodor Dobzhansky FRS: 'the food was mediocre, the company superb'. It was during his time with Rhoades that he was greatly impressed with the way things were done in the USA. A classic paper by Taylor, Woods and Hughes, on the semiconservative replication of chromosomes, based on [^{3}H]thymidine labelling of *Vicia faba* root tip cells, appeared in *Proceedings of the National Academy of Sciences, USA*. Hugh was fond of recalling that this caused great excitement in Rhoades's laboratory, and that Rhoades simply put on his coat and hat, summoned the laboratory staff and they all took the train to Chicago to consult Hewson Swift (an internationally known expert on chromosome structure and function) in person on the meaning and significance of this early example of molecular cytogenetics.

At Birmingham, with Mather's encouragement, Hugh embarked on his now classic series of experiments to investigate the genetic control of chromosome behaviour at meiosis, in the cereal species rye. Rye is an easily grown plant with a small number (seven pairs) of particularly large chromosomes, making it an ideal resource for the cytological analysis of chromosome behaviour at meiosis, using the metaphase I stage (figure 2), and working only with the light microscope. Little was known at that time about the genes controlling the behaviour of the vehicles that carry them, and Hugh's quest was to begin to find out. The rationale was to take this useful outbreeding plant, with its rich store of genetic variation, and, by inbreeding it over several generations, to segregate (separate) out several pure lines that would vary in their specific and fixed combinations of genes and alleles, thereby exposing the genes that controlled the pairing behaviour of the chromosomes. In addition to that, hybrids made between

* Numbers in this form refer to the bibliography at the end of the text.

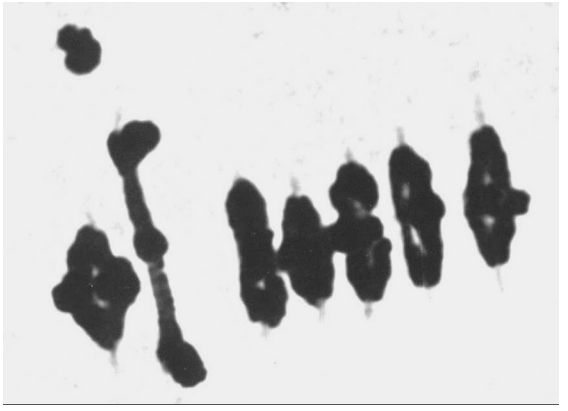

Figure 2. The beautiful chromosome of rye at metaphase I of meiosis.

different lines, and their descendent progenies, would also reveal aspects of hybrid vigour in chromosome dynamics. The thoughtful part for the start of the work was to obtain a series of ready-made inbreds from Professor Arne Müntzing in Sweden, thereby saving several years of preparative work. The questions to be answered were: to what extent is chromosome behaviour controlled by qualitative genes with major Mendelian effects (single genes), and to what extent by several polygenes acting together with minor quantitative effects? Polygenes were a big story in Birmingham at that time, and Hugh was in the ideal place for just this kind of work. It would also be in his mind that inbreeding could reveal homozygous combinations of recessive alleles affecting abnormal aspects of chromosome structure and function, which could uncover another rich harvest in the discovery of chromosome genetics.

The outcomes of this early phase of research led to a number of key discoveries, and to a set of early publications (4–8, 10–14) that became classics, and models of investigation, in the field of plant cytogenetics. He established that much of the variation in chromosome behaviour is controlled by polygenic systems, whereas previous work on genotypic control related only to genes of major effects. The characters investigated ranged from the frequency and distribution of chiasmata (sites of crossing-over) to chromosome disjunction (chromosome segregation) and breakage. Some of the interpretative drawings in the early publication covering this work are examples of superb craftsmanship in chromosome cytology, and the experimental system that was developed (inbred lines, hybrids and maintaining deleterious recessives as heterozygotes) is still followed to this day, for example in the Meiosis Group in Aberystwyth and by its collaborators in St Petersburg State University Department of Genetics, in which meiotic mutants in rye are a major field of study. The action and interaction of polygenes affecting chromosomes, such as those affecting continuous variation in other more familiar aspects of the phenotype, generated heterosis in hybrids between inbred lines and inbreeding depression, accompanied by recombination in the self-pollinated derivatives. The work on genotypic control embraced, among other forms, polyploids and structural chromosome mutants such as interchanges. The genotypic control of chromosomes at meiosis remained one of the chief themes of Hugh's work for the rest of his research career (15–17, 19, 21–24, 28, 29, 36–39, 43, 49, 51, 54, 55, 71, 72, 79, 85, 92, 94, 106) long after he left Birmingham, and was later taken on by one of his research students, Gareth Hudson-Jones, who also joined the staff at Birmingham and took on the mantle of one of the lead meiosis workers in the UK.

Returning to Aberystwyth

In 1959 Hugh was appointed as Senior Lecturer in Agricultural Botany at Aberystwyth University. He was later made Reader, in 1966, and became Professor and Head of Department in 1968 with the award of a personal chair. He was made Dean of the Faculty of Science in 1980 and 1981, and then became Vice Principal from 1983 to 1985.

At Aberystwyth Hugh rapidly built up an internationally acclaimed school of study on chromosome genetics, and on evolutionary changes in chromosome organization. His work, in addition to meiosis mentioned above, can be classified under several headings.

Chiasmata and selection

The significance of genetic variation affecting recombination at meiosis in terms of selection and adaptation within populations is a topic that always fascinated Hugh, and one that provoked much speculation based on a minimum of experimental data. My first task as a fledgling research student in September 1964 was to spend three weeks, before my PhD proper, looking at chiasma variation in several Irish populations of perennial ryegrass, using fixed meiotic material—a good grounding in understanding meiosis and in the level of application needed to tackle any serious research project. This first sojourn into serious meiosis work resulted in a short paper in *Nature* (26). A more detailed analysis came later with work on *Lolium* and *Festuca* with PhD student Phil Dale (66). Dale's results indicated that the response to selection for morphological and physiological characters is indeed achieved by, and dependent on, the redistribution of chiasmata to generate the associated recombinants. The work also showed how the potential variation present in the genomes is dissipated by the increase and redistribution of chiasmata. A point to note here, which runs through all of Hugh's research work, is the way in which ideas and the avenues of exploration needed to develop them, were always running as a 'batch' job in his mind. The time he spent fishing for salmon on the river was undoubtedly something he valued for these quiet reflective moments. When he announced that he was out fishing for the afternoon one could be quite sure that next morning he would be in early and would produce the first draft of a manuscript that day.

Variation in nuclear DNA

A large part of the later work of Hugh's research students concerned quantitative variation in nuclear DNA, and its association with the divergence and evolution of closely related species, made possible by the advent of microdensitometry. We finally had a research tool other than just a light microscope. Amounts of DNA were measured in arbitrary units in single root-meristem nuclei on the basis of staining with Feulgen's solution, which is a specific stain for DNA. There were several significant outcomes and publications. (i) Among species, even closely related species, of angiosperms there is an astonishing variation in nuclear DNA amount that is quite independent of change in chromosome number. (ii) The variation is attributable to the amplification of DNA sequences within the chromosomes. (iii) With an increase in DNA amount there is an increase in the amount of repetitive DNA, as would be expected. There is also an increase in the amount of non-repetitive DNA. What is particularly striking is the consistency in the increments of non-repetitive and repetitive DNA. In *Lathyrus*, for example, for each increment of 1 pg in non-repetitive DNA there is an increment of 3 pg in repetitive DNA. 'One concludes', he wrote, 'that there is a strict constraint upon the way in which the chromosomal DNA changes in conjunction with the evolution of the species.' (iv) The same kind of constraint is manifested with respect to the distribution of 'extra' DNA among chromosomes

within complements. Each chromosome, irrespective of its original size and DNA content, acquires the same amount of extra DNA. One of the consequences of this phenomenon is that as the genome size (nuclear DNA amount) increases, the chromosome complement becomes more symmetrical. The DNA variation work produced an impressive array of publications, at a time when 'genome obesity' had not even been heard of (18, 25, 27, 30, 32, 34, 40, 44, 46, 48, 52, 53, 56, 58–61, 64, 65, 68–70, 73, 78, 81, 82, 84, 86, 89–91, 95, 101). Later on he ventured into the molecular analysis of DNA variation, working with his colleague R. J. K. Narayan and others, and several key papers came from this time (50, 67, 75, 76, 82, 83, 96, 97).

Recombination and genome size

As the genome size increases, the capacity for recombination per unit of DNA decreases; and the regularity of the association between the DNA amount and the capacity for recombination is remarkable, over a wide range of organisms (94). Hugh applied himself, through his students, to determining the mechanical and molecular basis for such an association, and with the genetical significance with respect to the release of variability, one of his favourite themes, to gametes and progeny.

B chromosomes

The study of supernumerary B chromosomes was begun by me and later developed further by my colleagues G. M. Evans, Glyn Jenkins and John Forster. The early stages of the work were highly productive and demonstrated how B chromosomes could affect both the frequency and the distribution of chiasmata at meiosis (31, 39, 42, 47, 64, 65). The effects of B chromosomes on the organization of the nucleus, in terms of its physiology and replication patterns, also produced a rich set of papers (41, 45, 57, 62, 64, 65, 74, 77). Hugh believed passionately that all genetic and phenotypic variation ultimately had some adaptive significance, and he was not a strong advocate of selfish DNA. He devised several unique and clever experiments to demonstrate that B chromosomes fell into this category, with some success (63, 64, 80). The most ingenious of these experiments was to grow 200 seeds of ryegrass on tiny two-inch pots and to look for B chromosomes among the survivors. Perhaps the most significant aspect of the B chromosome story concerns the book that Hugh and I produced (87), based on a collection of the world literature on this topic from 1906 to 1980. This became known as the B-bible, and it is much quoted to this day.

Meiosis never left the scene

The genetics of meiosis was a constant theme running in Hugh's mind, and he never missed an opportunity to take it further. One significant event was the appointment of Glyn Jenkins to develop electron microscopy as a new tool with which to study chromosome pairing at meiosis in hybrids and polyploids, and this again produced a rich reward in terms of major contributions to this field of study, especially in the formation of the synaptonemal complex (88, 98–100, 102).

New directions and future foundations

Hugh's love of salmon fishing extended to his 'playing' with their chromosomes: counting the number and size (20, 33, 35), exercises that undoubtedly gave him great satisfaction.

From time to time he also worked on grasshoppers, cherished by all cytogeneticists for their large chromosomes (3, 9), and near the end of his research career he moved into plant tissue

culture with his students Julia White and Glynis Giddings, and again made some significant discoveries (93, 103–105).

The research that Hugh instigated and supervised extended beyond his own direct involvement and was progressed with much impact by other staff members (G. M. Evans, G. M. Jenkins, R. N. Jones and R. K. J. Narayan) to the extent that in the final Research Assessment Exercise before Hugh retired he had the satisfaction of attaining a grade four, no small achievement for a staff of only nine academics. He was elected a Fellow of the Royal Society in 1976, and thereby earned much respect from his colleagues and from his Alma Mater—Aberystwyth University. In the wider scientific community he kept several external contacts with whom he regularly communicated. Bernard John, who invited him to Canberra, was a close associate, as was Ralph Riley FRS at the Plant Breeding Institute in Cambridge, and Keith Jones, Keeper of the Jodrell Laboratory at Kew.

Administration

As Head of Department, Hugh directed the research and the teaching of the department in the disciplines of plant pathology, physiology, statistics, agronomy and plant breeding, as well as integrating closely with the Welsh Plant Breeding Station (WPBS) located nearby. One of his major projects with the former WPBS was to establish a jointly run two-year Master's course in plant breeding. Over a period of several years, students from 30 countries graduated from this course, and this had significant impact on several developing countries. Close links were also maintained with the Department of Genetics at Birmingham University under John Jinks—an arrangement that enhanced the international reputation of all three centres. The department was small by today's standards, with just nine academic staff, a small number of technicians and one secretary. Administration was therefore minimal, and any staff meeting that was required took place informally over morning coffee. Hugh had a rare capacity for quickly perceiving the crux of a problem in his own or related fields of research or, indeed, generally. He was a forceful presence in scientific meetings or in committee, and could be relied on to ask a critical question on the crucial issue early in the proceedings, initiating strong debate. Consequently, in parallel with his scientific research he was much in demand for advisory or administrative duties. Outside the university he served on the advisory committee of the WPBS, the governing body of the former Plant Breeding Institute at Cambridge and the Institute of Grassland and Animal Production; he greatly valued his work with these various bodies associated with the former Agricultural and Food Research Council (AFRC). Hugh also had a key role in the relationship between certain departments at Aberystwyth and Bunda College of the University of Malawi in southern Africa, in which many of his staff participated. The link was established in 1968 under the sponsorship of the British Council and the University of Malawi, and from 1977 to 1988 Hugh was correspondent and organizer of this collaboration. He visited Malawi on numerous occasions and drew his staff into a rewarding and satisfying educational experience. The main activity of Hugh's department was in the teaching of genetics, statistics and plant breeding.

Teacher, supervisor and personal character

Hugh was an excellent teacher with a powerful intellect, and he also had the talent to inspire his students and to evoke in students and staff a lasting feeling of respect, regard and loyalty. Many would go on to high achievement in research and university teaching, and all would remain his friends. His undergraduate teaching had a lasting impact on several students, including myself, who later went on to serve under Hugh in the Agricultural Botany Department. He set a high and uncompromising standard in his lectures, which did not suit all students, but those who stayed the course valued the structure and logic of his teaching, and those who went on in the academic world kept to the same standards and motivation with their own students.

His supervision of research students is still much talked about to this day. He would often suggest two different components to a PhD, one being rather mundane and certain to yield data, and the other more speculative and demanding; students had an opportunity to make something of their given project, and to develop it in their own way. In my own case, if another personal note may creep in, I was given the task of looking at DNA variation in the genus *Allium*, sure to give good data as well as a few surprises, and then another project in which he simply handed me a bag of rye seeds, saying 'there may be something interesting in there; have a look at it.' Indeed there was, but it was for me to find it. We were expected to work out our own experiments and find out for ourselves any new techniques that we might want to use, such as autoradiography. One did not ask how to do anything, not even statistical analysis (which was taught at the postgraduate level by Alan Durrant). Nonetheless the style of supervision was robust: it took the form of a visit to the laboratory on a daily basis, on his way home for lunch and often again at the end of the day, and this was the time for discussion and for learning from his wisdom and inspiration. He always opened his remarks with 'that is excellent, but…', or 'that is very good, but…', and then came the insight that we gradually learned to pick up and start to use for ourselves. To this day I believe that Hugh Rees taught me how to think, which I would not like to define, and how to write and how to extract the maximum from a set of data. We all were expected to complete our thesis within three years, and in the process to write the first drafts of manuscripts coming from our results. The student's name invariably appeared as first author on publications, and at times we were given the privilege, albeit a daunting one, of presenting our results at meetings of the Genetical Society. There was another aspect to his life that gave insights into his personality, and his thoughtfulness in dealing with his research students: he had steel tips and heels on his shoes, so we could always hear him coming along the corridor, and there was never any likelihood that he would catch us unawares, maybe doing something that might cause mutual embarrassment.

Hugh's leadership was much appreciated by the technical and other support staff as well as by academic colleagues. He treated everybody in the department with equal respect, regardless of their position. Morning coffee was an academic affair, taken with staff from other departments in the building, but afternoon tea was for Agricultural Botany, meaning all the staff. This human face made for a unified and harmonious working environment, and I can honestly say we all enjoyed our work, as he did, and we gave of our best. It was not unknown for a technician to come in on Christmas Day to make ready some fruitflies or some fungal cultures for the practical classes beginning early in the New Year—willingly working beyond the call of duty.

Figure 3. Rees fishing for trout in Rutland in the 1980s. (Online version in colour.)

An illustration of his involvement in departmental activities, and of his singular leadership style, was the initiation of each new intake of his undergraduate students to the joys of the countryside, especially through the climbing of Cader Idris. He used to tell them that if they remembered only one thing from their time at Aberystwyth, this should be it. He continued the activity even when, as he joked, the effort of reaching the summit left him too breathless to address his new charges. The departmental Christmas parties were famously festive occasions; Hugh's customary and colourful rendering of Lewis Carroll's 'Jabberwocky' will long be remembered by successive classes of students. His last big departmental event took place long after his retirement, and he still held his time in Agricultural Botany close to his heart. The event was held in a local hotel, organized as usual by his former technical and secretarial staff, to celebrate his 80th birthday. An impressive number of former students and colleagues turned up from far and wide, and for those in the know this represented a strong display of the loyalty and respect that he still commanded. His after-dinner speech was a masterpiece of story telling. Such activities also reflected his eclectic interests and voracious reading habit, extending beyond scientific matters in a wide range of English and Welsh literature.

There are many anecdotes surrounding the personal side of Hugh, especially in relation to his fishing (figure 3). He loved fishing for salmon and sea trout on the river, and when successful he would often come back to the department, on his way home, to display his latest catch and to get it photographed.

Hugh combined his heavy workload with a rich and varied social life. He liked nothing more than to entertain friends, associates and visitors to the department from the UK and abroad, to evenings at his home with the unstinting support of his wife, Mavis, and their family. As they were generous hosts, their parties rarely ended before the early hours. Hugh was an excellent raconteur, with an enviable eye for detail, and a talent for spotting the bizarre and quirky in any situation. Many of his memorable and humorous tales recalled prewar and

postwar life in the villages of south Wales, student life in the overcrowded 'digs' of postwar Aberystwyth, and incidents on riverbanks and lakes of mid-Wales, where he avidly pursued his hobby of fly fishing.

Retirement

After his retirement in 1991 Hugh pursued his favourite activities. As well as enjoying reading and fishing, he was a keen painter, bridge player and gardener. He also remained an enthusiastic member of the Thirty Club, a long-established group of individuals from Aberystwyth sharing a simple agenda of intellectual curiosity, and presented his last talk (appropriately, a reflection on universities) to a meeting in November 2006. In his early 70s he took to gentle cycling with a small group of friends through various regions of France, as a means of exploring the different wines and cuisine. Inevitably, because cycling in France is a cult, his distinctive patriarchal appearance and his decidedly unconventional garb often attracted the attention of photographers from the local press—while his charismatic presence at the lively evening festivities would lead to a gradually expanding entourage of other cyclists who would adapt their itineraries so as to join in.

Hugh thus remained physically active until late in life and he was still fishing his much-loved haunts on the River Dyfi up to his 80th year. Thereafter, respiratory problems increasingly limited his ability to pursue his outside interests, and failing eyesight due to macular degeneration was a source of particular sadness and frustration for him, given his lifelong love of reading. Expert medical attention, combined with the immense efforts of Mavis, sustained him in the face of increasing frailty in his final years. During this time Hugh lost none of his mental agility and, almost to the end, he promoted and relished any opportunity to engage socially with family or friends. He eventually died of heart failure on 13 September 2009.

Traits of resilience, determination and good humour, which Hugh shared with Mavis, along with his exceptional intellectual capabilities, help to explain why we are now able to fondly recall a long, energetic and productive life. It was a life that also greatly enriched many others along the way, both professionally and personally.

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The frontispiece photograph was taken in 1977 by Godfrey Argent and is reproduced with permission.

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