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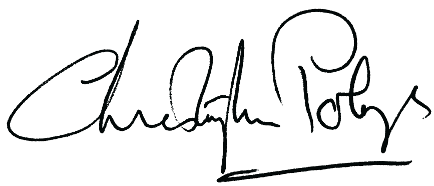

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Christopher Polge achieved distinction at a remarkably early stage of his career in biological research. He made key discoveries when he was in his twenties, and his work was internationally acclaimed when only just into his thirties. His name will always be associated with the deep-freeze preservation of mammalian spermatozoa and the massive boost that this gave to a fledgling artificial insemination industry, especially for the breeding of dairy cattle. Even so, his research contributions were wide-ranging, and their long-term influence on agriculture, medicine and biotechnology cannot be overestimated. Recognition came from many directions, perhaps most significantly as the recipient of the Japan Prize for Science and Technology for Biological Production in 1992.

Family background

As the name suggests, the Polge family had French roots on the paternal side. Christopher's great-grandfather, Henri Polge, left France for Germany as a young man and taught French at the University of Hamburg. As one consequence he met and married the English daughter of a ship's captain who plied the busy trading route between Hull and Hamburg. The only son from the marriage, Henry Polge, was born in Germany and started school there but, when he was 10 years old, the family moved to England at the time of the 1870 Franco-Prussian war. In due course, Henry went into banking in Leeds and married Ella Fenning, a young widow with two children. Five offspring came of this marriage, four sons and a daughter. The fourth son, Ernest Polge (1894–1980), was the father of E. J. C. Polge.

The family settled in South Croydon, comfortably within reach of the City of London although still quite rural in those days, and Ernest Polge was educated locally. On leaving school, he trained to work in banking in the City, but joined the army at the outbreak of World War I to become a Second Lieutenant in the Yorkshire Light Infantry. As a result of a

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severe head wound in 1915, he was invalided home and remained in hospital until 1920 and then retired from the army on a total disability pension. Because of his fragile health, he was advised to find a non-stressful outdoor occupation in the countryside and decided to take up poultry farming near Beaconsfield in Buckinghamshire. During the protracted recovery from his head wound, he had gradually come to reject war as a means of solving world problems and had developed an interest in Quakerism and their Peace Testimony. In 1920, while visiting Woodbrooke College, a Quaker establishment in Birmingham, he met Joan Gillett Thorne and they married in the Quaker Meeting House at Jordans, Buckinghamshire, in 1923.

On the maternal side, Christopher Polge was descended from a long line of Quakers and, with some poetic licence, could trace such ancestry to the Saxon earls of Mercia. The grandfather, Alfred Bleckly Thorne (1870–1922), married Mary Ellen Doeg at Evesham Meeting House in 1895; they had met at Sidcot School. Her father owned a chemist's shop at Evesham and was a keen naturalist with a specific interest in diatoms. Alfred Thorne was a printer who became extremely active in the Society of Friends and a staunch upholder of its principles. He was inspired to 'support movements which sought to place within the reach of all the opportunity to develop their personality and increase their capacity to take an intelligent share in the life and well-being of the community'. In essence, he was a Christian Socialist. Alfred Thorne was excited by the developments in early wireless communication and was a close friend of Marconi. Together they listened to some of the first broadcasts.

Polge's mother, Joan Gillett Thorne (1901–83), was one of the five children of Alfred and Mary Thorne, who had set a sound education for their children as an overriding priority. She trained in social science at the National Health Society and Woodbrooke College in Birmingham, studying towards a degree from that university. Before she married Ernest Polge she had been a health visitor in Bermondsey, London, from 1921 to 1923.

There were four children from the union of Joan and Ernest Polge, three girls and a boy. Christopher Polge, hereafter referred to as Chris, was the second child and was born at Jordans in 1926. There he grew up in perfect rural circumstances, becoming a keen naturalist at an early age and a willing young assistant on the poultry farm. By 1928 his father was able to purchase extra land on the Chalfont St Giles side of Jordans and there build a new house and gradually diversify. Because of his wartime head wound, Ernest Polge had to take life gently and, from the age of nine years, Chris was more and more involved in the activities of the small farm, especially at weekends and during school holidays. He was able to milk the goats and, as the farm expanded further because of the requirements for home food production during World War II, dealt with cows, the farm horse, and many of the essential tasks in crop production. Guidance and assistance were provided by the War Agricultural Committee, and there was an experienced old farmhand to teach many of the specific skills. One of Chris's occasional lapses into immodesty in his vintage years was to claim to be the only living Fellow of the Royal Society who could build a corn rick, do the necessary thatching and even lay a hedge in the traditional manner! As a result of selection criteria imposed by the War Agricultural Committee, he had also become proficient in handling poultry and selecting them for type and body conformation.

School and university

Despite this emphasis on assisting his father, Chris was able to enjoy a solid middle-class (as it was then) schooling—preparatory school and then on to independent school. Initially he went to a somewhat unorthodox preparatory school in Jordans village, with lessons held outdoor in the summer, lots of sport and colourful rural expeditions. However, at the age of nine years he moved on to a more traditional preparatory school, Gayhurst at Gerrard's Cross, some five miles away, travelling there in a friend's car or going by train but soon commuting independently on his bicycle. Chris records that the teaching was of a high standard, not least in Latin, and that chemistry, physics and biology were all part of the curriculum, even though there was no science laboratory. Daily sporting activities took place before afternoon schooling and included football, rugby, hockey and cricket. Chris enjoyed all of these but soon began to demonstrate special skills at hockey. As the clouds of war loomed in 1938, school activities expanded into the construction of road blocks, learning to handle barbed wire, fire-watching duty, and plane spotting from the top of a nearby tower. War broke out in his last year at Gayhurst. Having taken the Common Entrance examination, he obtained a scholarship to Bootham School in York, a small Quaker boarding establishment for 150 boys.

It is worth noting that the Quaker influence pervaded the Polge household throughout his early years, with grace being said before meals and a non-biblical inspirational reading after breakfast, for example from an anthology of poems. The whole family attended Jordans Meeting House for worship on Sunday, Chris's first participation being at its Sunday School. The subsequent immersion in a Quaker boarding establishment must have contained elements of familiarity, but there was no specific Quaker influence at Bootham and in fact fewer than half of the boys came from Quaker families. In later life, Chris ceased to attend Quaker meetings but he retained many of the Quaker beliefs such as that God was within each individual and not a figure outside.

The wartime train journeys up to York were sometimes stressful, with endless diversions, as were the rites of initiation at an English boarding school. However, Chris very much enjoyed Bootham from his second year onwards and became an active participant in the debating society and in dramatics and choir with the sister Quaker school in York, the Mount. Bootham had its own swimming bath and enviable games facilities, and there was sport every afternoon. Chris was in the school teams for both football and cricket, but hockey remained his best sport and he became captain. In addition to all this enjoyment, there was an active natural history club with expeditions onto the North Yorkshire moors. Back in school, members would give enthusiastic talks on topics associated with such adventures.

Bootham School had been evacuated to Ampleforth during the first year of the war but returned to York when it was considered that the city would not be bombed. In reality, the war did not impinge greatly on school life at all, apart of course from its influence on food rationing. Teaching was good at Bootham, one result being that Chris obtained a surprise distinction in Latin in the School Certificate Examination. Chemistry, physics and biology were his sixth-form subjects, and the excellence of biology teaching was long remembered. Chris was a Prefect during his two years in the sixth form, becoming Head Boy in his last year with a beautiful study looking out over York Minster.

Having passed his School Certificate in 1944, it was time to take decisions about university. Farming and rural activities were clearly in his blood so, on his headmaster's advice, Chris applied to Reading University, at that time considered the best for a degree in agriculture. Although conscription was in force and all young men were expected to do National Service, entry into the Armed Forces was deferred for those attending university and studying subjects considered to be of national importance. He had already registered as a conscientious objector because of his Quaker principles but, under the circumstances of wartime Britain, this had no detectable effect on his conscription status. Nevertheless, on leaving school in 1944 he was able to go straight to Reading to read for a pass degree, which was then a two-year course under an accelerated programme of wartime teaching, with four academic terms per year.

The curriculum was broad and, in addition to the traditional subjects of botany, chemistry and agricultural nutrition, it included economics, surveying and even building construction. Although at no stage of the degree course was there any attempt at depth or specialization, it is noteworthy that three of Chris's fellow students in the small wartime intake went on to become academics. Chris formed a close relationship with one particular lecturer, Dr D. J. G. Black, who was responsible for the university poultry enterprise and who taught poultry husbandry. As Chris was already well trained in the world of poultry farming, it came as no surprise when Black asked him to take charge of the university poultry unit during the summer vacation. Not only did this involve working specifically with the birds, but he was also responsible for harnessing up the horse and cart for moving foodstuffs around the substantial enterprise. He much enjoyed this vacation activity, and Black noted the skills of his protégé, with subsequent developments that will be seen.

Much of the practical instruction at Reading was on the University farm at Sonning, but there were also visits to the Artificial Insemination Unit, soon to become the Reading Cattle Breeding Centre at Shinfield. Semen collection was demonstrated and spermatozoa were examined under fairly simple microscopes. There was of course no notion then that any of these activities might be reflected in Chris's future career. The Royal Veterinary College had been evacuated from London to Streatley, near Reading, and because of joint social activities this paved the way for close relationships with individual vets and the veterinary profession throughout his career.

Reading had developed as a collegiate university with attractive residential buildings modelled around grassy quads; they were termed Halls. Chris was in St Patrick's Hall and records the strict discipline of those days, the main gates being closed promptly at 10.00 p.m. The Warden of St Patrick's, one Major Pearson, was not popular because he believed that all healthy young males should be in the Armed Forces rather than getting up to high jinks on academic premises. He had no qualms in reporting individuals to the Vice-Chancellor at the slightest whiff of misbehaviour. Revenge was exacted on VE night when the splendid gates of the Warden's official lodge found their way on to the enormous bonfire prepared on the green outside. In addition to such mischievous escapades and to whetting his tastebuds in a nearby hostelry, Chris played hockey for the university, being awarded his colours (termed a 'Shell' at Reading), and also represented the counties of Bedfordshire and Middlesex at this sport on various occasions.

Postgraduate opportunities; marriage

After graduation with a pass degree in agriculture, Chris was uncertain as to career direction so he returned home to work on the family farm for the next six months (1946). He was still subject to the regulations concerning National Service unless he could demonstrate employment in the national interest. Living at home and working on the family farm did not satisfy bureaucrats at the Ministry of Employment, and he was instructed to go for a series of interviews for various jobs. He managed to perform badly and demonstrate potential incompetence at each such interview until one caught his attention. This was a post in the Agricultural

Economics Department of Bristol University. Apparently, economics had become one of his favourite subjects at Reading.

After a successful interview, he took up an idyllic posting based at Newton Abbot in Devon, from which office Bristol University conducted its agricultural surveys in the southwest of England. The job entailed working out the cost of milk and beef production on farms throughout Devon and Cornwall and a portion of Dorset. Assisted by a generous postwar allocation of petrol coupons, Chris and a colleague motored along empty lanes to visit endless farms and then to try to assess the cost of inputs to the enterprises, for example labour, rent and fertilizers. These were set against the sales of milk and beef and, based only on the farmer's rough estimate, costings were prepared to the nearest halfpenny! Chris took such calculations with a healthy pinch of salt, but he hugely enjoyed the countryside, the farmers and their families, and some social life along the Dart estuary. He was particularly taken by the Lizard Peninsula and his first drive down the winding lane to Coverack to find its little houses clustered around the perfect small harbour set against a glittering blue sea. Being of a romantic disposition, he decided that if and when he got married, this would be the location for his honeymoon. And so it was, and for many subsequent family holidays too.

His salary from Bristol University was the modest sum of £350 per year, and yet he found that he was surprisingly well off. After a year of this employment as an agricultural economist, his horizons changed dramatically as a result of a letter from Dr D. J. G. Black, who had latterly been his tutor at Reading University. While sitting on an Agricultural Research Council (ARC) Poultry Committee, Black had met Dr A. S. Parkes FRS, Head of the Division of Experimental Biology at the National Institute for Medical Research (NIMR) in London, and Parkes was looking for someone interested in and able to develop artificial insemination in poultry, and perhaps to work on the storage of semen, too. Chris understood immediately that this might be an opportunity to do something new and, thanks to his thoughtful tutor, came to meet Parkes at the Institute's laboratories in Hampstead, followed by a visit to the NIMR farm laboratories at Mill Hill. The interview went well and then progressed to more relaxed discussions with Parkes in the neighbouring Three Hammers. By way of conclusion, and with no postgraduate credentials, he was offered a permanent post on the staff of the Medical Research Council. He commenced his new activities in the summer of 1948.

As one happy consequence of his move to the NIMR, he met a vivacious young blonde and soon discovered that he and his girlfriend were very much on the same wavelength. She was Olive Kitson, daughter of Mr and Mrs Robert Kitson of Hendon, northwest London. Olive Sylvia Kitson had been born in November 1928. When her family became established in Hendon, she entered the progressive co-educational grammar school there, much favoured by her parents and doubtless a useful counterbalance to the monastic schooling of her future husband. Subsequently she underwent specialized secretarial training and, after employment experience with W. H. Smith, moved to the NIMR. There she became secretary to the Department of Biophysics and Optics. It was in this role that she first met Chris. They were married on 3 April 1954, and enjoyed long years of wonderful happiness and fun together.

The marriage was blessed with four gifted children, two girls and two boys. The two elder children, Jane and Mark, qualified at Bristol University in dentistry and medicine, respectively. The third, Nicholas, trained in Agricultural and Forest Sciences at Oxford followed by a PhD at Bath University. The youngest, Katharine, graduated at Sheffield University in physiotherapy. All four have had successful careers and hold senior posts in their professions.

First research: freezing poultry semen

Because of Chris's background in poultry farming, no apprenticeship was required for the tasks of poultry husbandry, but he did need to learn the technique of semen collection and also to develop a means of artificial insemination. Having mastered the essentials during a brief visit to his old tutor at Reading University, he started his first studies on the cold storage of poultry spermatozoa. It is not clear from the written records whether Parkes saw this as a valuable project in its own right, thereby fulfilling agreements with the ARC Poultry Committee, or whether he believed that a successful outcome might pave the way for mammalian studies. It is undeniable that Parkes consistently thought well into the future, and he had certainly been intrigued by brief reports on the freeze-preservation of both fowl and human spermatozoa.

Under the guidance of colleagues at the NIMR, a 22-year-old Chris was introduced to the disciplined life of the laboratory and to techniques that might be applicable to the cooling and warming of suspensions of sperm cells. The medically qualified Dr Audrey Smith was his principal tutor. Chris initially found her somewhat formidable, both noisy and bossy, but he soon acclimatized and gradually developed a strong affection for her. One can well imagine that the transition from a world of farms and farm walks to that of white-coated laboratory procedures conducted in a postwar medical atmosphere took some weeks, and Chris's bubbling sense of humour needed to be controlled during the hours of daylight.

Freshly ejaculated semen contains a high concentration of sperm cells, and one of the first challenges was to select a diluent that would enable short-term storage at room temperature; antibiotics were included in the various media tested. Progressive cooling of sperm suspensions without obvious cell damage was the next step and, after numerous trials, Chris and Audrey Smith opted for solutions of the sugar laevulose. This had been noted to protect fowl spermatozoa during freezing at −79 °C. Systematic studies using different concentrations of laevulose resulted in limited success on insemination of the chilled sperm suspensions. However, freezing and thawing always resulted in cell damage and there were many frustrations. Motility was preserved, but no fertile eggs resulted from artificial insemination. Clearly, what was needed was a protective agent to render the sperm cell membranes less susceptible to the insults of freezing and thawing and to prevent the formation of intracellular ice. The manner in which glycerol was found to be a suitable agent has led to many colourful anecdotes, but Chris left a written record of the precise circumstances and they are quite straightforward.

In brief, after repeated trials with various stock solutions of laevulose and no fertility whatsoever on insemination of frozen–thawed spermatozoa, the work was suspended for some months and the remaining sugar solution was left in the fridge at the NIMR Hampstead laboratories. When studies were resumed in the Institute's farm laboratory at Mill Hill, a bottle of the old stock solution was brought out from Hampstead and, when used with freshly collected fowl spermatozoa, there was a surprising improvement in sperm survival. Indeed, not only was the post-thaw motility good but some chicks resulted from insemination. The initial presumption was that working with spermatozoa immediately on collection explained the different result, because semen had previously been transported from the Mill Hill farm to Hampstead. However, many subsequent experiments using freshly prepared solutions of laevulose and freshly collected semen were always unsuccessful. Hence, Parkes insisted on a chemical analysis of the original stock solution (only 10 ml remained), and a significant concentration of glycerol was detected. The eventual explanation was that labels had inadvertently become detached and swapped on bottles in the Hampstead fridge, and that the first success had, in fact, been with a solution of Mayer's egg albumen. This is a mixture of glycerol and egg white commonly used for sticking histological sections onto microscope slides.

Chris and Audrey Smith then examined the influence of various concentrations of glycerol in the medium. When fowl spermatozoa were suspended in a 15% solution (by volume), almost all cells were found to survive freezing and thawing. The steps of equilibration of the sperm suspension with the glycerol-containing diluent before freezing, and later removal of the glycerol by dialysis after thawing, were critical. When the optimized procedures were used, large numbers of chicks were obtained after artificial insemination. At this stage it is worth noting that Parkes had appointed Dr J. E. Lovelock (FRS 1974) to work on the biophysical effects of freezing and thawing and, in detailed collaborative studies with Chris, he was to clarify the means of the protective action of glycerol.

As to the chronology of the above events, one wonders whether bells might have been ringing at the back of Parkes's well-stocked mind. It is a little-known fact that a somewhat eccentric Parisian professor, one Jean Rostand, had already discovered the protective effect of glycerol when cooling frog spermatozoa to temperatures below 0 °C. Moreover, he had published two short papers in key French scientific journals (Rostand 1946, 1949).

Parkes had certainly attended biological conferences in Paris soon after the end of World War II and was in correspondence with Professor R. Courrier (ForMemRS 1953), later to become Secrétaire Perpétuel of the French Academy. It would seem unusual if the remarkable studies of Rostand had not been brought to his attention.

Freezing of mammalian spermatozoa

The success with freezing and thawing of fowl spermatozoa in Parkes's laboratories was published as a landmark paper in *Nature* in 1949, with Chris quite deservedly as the senior author (1)*; he had worked long hours and meticulously to take the studies to this stage. They formed the basis of his PhD dissertation. Next, he and Audrey Smith worked on freezing the spermatozoa of several mammals kept at the NIMR, notably rabbits and goats, but larger horizons loomed. The first artificial insemination centre in the UK at which selected pedigree bulls were kept for semen collection had been opened on the Huntingdon Road in Cambridge in 1942, with a veterinary surgeon, Mr L. E. A. ('Tim') Rowson (FRS 1973) as its Director. This was a shrewd geographical location, for Dr John Hammond FRS and Arthur Walton were actively engaged in sperm cell research and fertility studies at the nearby Animal Research Station. Both Parkes and Chris realized that the way forward would be to adapt the poultry techniques to enable the freeze-preservation of bull spermatozoa and, after struggles with both the Medical Research Council and the ARC, funds were eventually found to enable Chris to use a caravan as a mobile laboratory based at the Cambridge artificial insemination centre.

By 1952 extensive results were available from frozen–thawed bull spermatozoa, Chris having conducted the laboratory work and Tim Rowson the insemination and pregnancy diagnosis on farms throughout Cambridgeshire. Although nearly all the results came from Cambridge, it is a fact that the first calf born from artificial insemination of frozen–thawed semen in the UK was at Reading. While the two research councils were sitting on the fence over the financing

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

of cattle work, Parkes had contacted a friend at the National Institute for Research in Dairying at Shinfield, Dr S. J. Folley (FRS 1951). Chris travelled there and performed the laboratory work, and a small number of preliminary trials with frozen–thawed bull spermatozoa were made at the adjoining Reading Artificial Insemination centre. All the findings were presented by Chris at the Second International Congress on Animal Reproduction in Copenhagen in the summer of 1952 (2), and this was the start of a massive international interest. So important were the results to the cattle breeding industry and for genetic improvement of livestock that Chris embarked on a six-month world tour that took him to Asia, the USA and much of South America. On returning home, he concentrated on the fundamental work with Lovelock (3) and, together with Audrey Smith and Dr J. Smiles, he examined the steps of freezing and warming under the microscope in a specially constructed slide chamber. (This was referred to by Parkes as the first cryomicroscope.) There were also some studies on the freezing and thawing of red blood cells, paving the way for the establishment of tissue banks. However, with excitement over the potential of freeze-preservation of bull spermatozoa mounting in the agricultural world, it seemed progressively less appropriate to continue under the umbrella of the Medical Research Council. Accordingly, Chris left his employment at the NIMR in 1954 and moved full time to the Animal Research Station in Cambridge. There he joined Hammond's Unit of Animal Reproduction and was thereafter employed by the ARC until retirement.

During the two years preceding the definitive move to Cambridge, Chris and Parkes had been working on a patent application to be lodged in the USA on behalf of the Medical Research Council. Techniques for the deep-freeze preservation of bull spermatozoa had attracted widespread attention, and the Council was anxious that the fruits of British research should not be exploited by an American patent, as had happened earlier with penicillin. In the event, and as recorded in Chris's notes, the patent application was rejected on the grounds of Rostand's prior discovery of the protective effect of glycerol. Chris was subsequently able to purchase the failed patent application for the sum of one shilling.

First activities in Cambridge; collaboration with the Milk Marketing Board

Once established in Cambridge, Chris continued to refine the techniques of freezing bull spermatozoa and gave considerable assistance to various British cattle breeding centres (artificial insemination stations). He also collaborated actively with the Milk Marketing Board to help them set up laboratories in Northampton for work on freezing the semen of selected dairy bulls, and he continued weekly visits for this purpose well into the 1960s. The early studies with frozen semen involved storage in glass ampoules under solid carbon dioxide (−79 °C), but this was soon to change. The advent of convenient supplies of liquid nitrogen, together with suitable containers for holding this material, meant that storage of sperm suspensions in straws immersed in the liquid nitrogen or in its vapour (−196 °C) became common practice in developed countries. There was then a huge expansion in the use of artificial insemination.

Some of Chris's first work at the Animal Research Station involved studies with Tim Rowson on embryo transfer in cattle. Hammond had long believed that non-surgical egg transfer would be a step further than artificial insemination, giving full control over the genome of future offspring. He had termed the procedure 'inovulation'. However, these non-surgical studies met with little success, seemingly because broaching the cervix in the early luteal phase and irritation of the myometrium with the transfer pipette resulted in ejection of the embryo back into the vagina. Pyometritis was an associated problem during the luteal phase. Accordingly, Chris transferred his attention to pigs, using the herd already available at the Animal Research Station, previously used by Hammond and Dr R. W. Pomeroy. Studies on the freeze-preservation of boar semen were notably unsuccessful at this stage, but Chris did have a key role in the development of artificial insemination techniques in this species and its on-farm application (4). Semen was used freshly diluted or after 1–2 days of storage at 5 °C, and it was introduced into the uterus with various designs of catheter to enter the muscular folds of the cervix. By the late 1950s his attention was more fully focused on female pigs, and he became involved in pioneer embryo transplantation studies in sows, again collaborating with Tim Rowson.

Dr M. C. Chang of the Worcester Foundation for Experimental Biology, Shrewsbury, Massachusetts, USA, was a regular visitor to the Animal Research Station, having undertaken his PhD studies there in the early 1940s with Arthur Walton. In the late 1950s he taught Chris straightforward procedures for the microscopical examination of mammalian eggs. These involved the preparation of whole-mounts between glass slide and coverslip, fixation in acetic acid–alcohol, staining with a suitable dye (lacmoid or orcein), and examination under a phase-contrast microscope. Although such procedures are routine these days, they were novel in the 1950s, and Chris and Chang made detailed studies of fertilization and early embryonic development in pigs after artificial insemination. Alas, these studies were never published, although the findings were made freely available to all who worked at the Animal Research Station. More or less at the same time as these studies with Chang, the Meat and Livestock Commission awarded Chris substantial funding to develop a means of using artificial insemination more effectively in pigs. This coincided with the travel plans of a North American visitor.

Control of the oestrous cycle and related projects

During his extended tour of North and South America in 1953, Chris had met Philip Dziuk, a PhD student at the University of Minnesota. A strong friendship soon developed. They were both farmer's sons, they had a similar sense of humour, and they maintained contact. By 1961 Philip Dziuk was an associate professor at the University of Illinois and eligible for sabbatical leave; he arranged to spend this with Chris at the Animal Research Station, where he was made warmly welcome for a full 12 months between 1961 and 1962.

The visit was especially timely. Chris had mastered the intra-cervical technique of artificial insemination in pigs, but understood that there were limitations in using freshly diluted or short-term-stored boar semen in animals with a 21-day oestrous cycle and random distribution of mating times. Clearly, what was needed was some form of synchronization of oestrus so that groups of animals could be inseminated at the same time. Dziuk had started to explore potential compounds for this purpose in Illinois—a state with very large pig enterprises—and he already knew that solutions of progesterone administered by injection were unsatisfactory; they prompted the development of cystic ovarian follicles and, after treatment, animals frequently failed to show oestrus at all. By 1960, however, the American pharmaceutical industry was producing synthetic progestins that were active orally. Dziuk had begun to work with these and brought such compounds to Cambridge for his sabbatical. There were two in particular that he wished to examine with Chris, namely medroxyprogesterone acetate (Provera) and melengestrol acetate, the latter being 100-fold more active when administered orally.

In brief, they found that when pigs were fed with Provera for 18–20 days, most animals returned to oestrus 5–7 days later. Even so, there were two problems: individual feeding to ensure the correct dosage was not convenient and, more importantly, fertility was frequently depressed at the synchronized oestrus. On the grounds that the latter might be associated with a protracted period of ovulation, a preparation of placental gonadotrophin (hCG, human chorionic gonadotrophin) was injected shortly before the expected onset of oestrus. This induced a closely synchronous ovulation of most mature follicles 39–40 hours after the injection, but fertility was still not as high as expected. With the use of the techniques of egg preparation and examination learnt from Chang, a surprisingly large number of primary (immature) oocytes was recovered from the Fallopian tubes at autopsy. Meiotic maturation of pig oocytes was a topic that would be returned to in Chris's laboratory but, in the present instance, it led to the proposal that as a mammalian egg matures meiotically, so it develops its block to polyspermy. This remains essentially true, an underlying reason involving the location of the so-called cortical granules that release their enzymatic contents at the time of sperm–egg fusion.

Also undertaken with Dziuk during 1961–62 was a quite distinct form of experiment involving egg (embryo) transplantation, the surgery being performed by Tim Rowson. It had been known since 1787, when it was described in a famous publication of the Scottish surgeon and medical scientist, John Hunter FRS, that removing one ovary from a sow did not reduce fertility in the subsequent litters, because of compensatory hypertrophy in the remaining ovary, nor were foetuses limited to just one horn of the uterus. What was not known was the extent of intra-uterine redistribution of embryos in an intact sow nor the degree of mixing of embryos entering the uterus from each Fallopian tube. Accordingly, 'colour-marked' embryos were used in an egg transfer experiment to clarify the extent of intra-uterine migration and mixing, and Dziuk—who taught animal genetics at the University of Illinois—realized that the transferred four-cell embryos needed to be homozygous for the trait in question. They selected skin pigment and transferred known numbers of 'white eggs' to one Fallopian tube of an unmated recipient and known numbers of 'black eggs' to the contralateral tube. Autopsy was performed during the third month of gestation (about day 75), by which time foetal skin pigment was apparent, and the findings in this large study revealed that so-called intra-uterine migration of embryos between the two horns had occurred in every animal. Moreover, the eventual distribution and attachment of the colour-marked embryos was seemingly at random (5).

Also observed in transfer studies performed with Rowson was the fact that if recovery of embryos from the donor animal was incomplete, pregnancy might be established. It was clear that the number of viable embryos remaining in the donor was important, and it was concluded that a pig uterus normally needs four or five embryos at days 14–16 after breeding if pregnancy is to be established.

Shortly after Dziuk returned home to the States in 1962, Chris took on his first PhD student, who joined him from the School of Agriculture in Cambridge, where lectures in mammalian reproductive physiology were given by Dr T. R. R. Mann FRS (soon to become the Mary Marshall Professor) and Dr Brian (later Sir Brian) Heap (FRS 1989). Work in Chris's laboratory during the years 1962–65 then followed essentially two directions: (i) studies on the ovarian responses of mature pigs to injections of different placental gonadotrophins, and (ii) examination of normal and abnormal fertilization at various stages of the oestrous cycle. The viable lifespan of mammalian eggs after ovulation was of particular concern. In addition to the time and experimental animals committed to these projects, a new chemical compound for the synchronization of oestrous cycles was also being tested. The studies with gonadotrophins established a clear timetable of the meiotic response of ovarian oocytes to systemically injected human chorionic gonadotrophin, as well as the time of ovulation of mature Graafian follicles. Ovulation in pigs was found not to be a consequence of increasing intrafollicular pressure but rather a softening process rendering the follicle walls flaccid as a result of the influence of proteolytic enzymes, especially collagenase. The time of ovulation could be predicted with accuracy after a pro-oestrous injection of chorionic gonadotrophin, and this feature was incorporated into a planned breeding strategy for synchronized animals (see below).

Studies with pregnant mare's serum gonadotrophin (PMSG) in mature pigs established a dose–ovarian response curve in which the mean number of eggs shed at the end of a spontaneous cycle could be increased from 15 to 38.5 about three or four days after a systemic injection of 500–1500 i.u. of PMSG, respectively. Once again, this straightforward approach to increasing the number of eggs ovulated was incorporated into a planned breeding strategy that Chris would promote in future work for veterinary practitioners and technically minded farmers. In fact, as noted below, sequential injection of PMSG and hCG became a favoured route to ovulation control.

In contrast to the above, ovulation induced during the luteal phase of the oestrous cycle had been reported to liberate infertile eggs. Work in Chris's laboratory revealed that such eggs became highly polyspermic if the animals were force-mated or inseminated before the induced ovulation, whereas the eggs underwent normal fertilization and development if transferred to the Fallopian tubes of inseminated oestrous animals. Studies on delayed insemination in which the eggs had begun post-ovulatory ageing (that is, in the very early luteal phase) also revealed an incidence of polyspermy that increased with age at sperm penetration. Apart from a reduced effectiveness of the block to polyspermy in ageing eggs, increasing secretion of progesterone from the developing corpora lutea reduced the ability of the Fallopian tubes to control the number of spermatozoa reaching the site of fertilization, thereby augmenting the risk of polyspermic penetration.

As to the synchronization of oestrus, a new compound had been selected during laboratory screening procedures at ICI's Pharmaceuticals Division in Alderley Edge, Cheshire, and Chris was invited by Dr Arthur Walpole and Mr Tom Groves MRCVS to conduct trials in pigs. The orally active non-steroidal compound, initially referred to as ICI 33828, was tested on groups of animals during 1963–64, and Chris was able to report his findings to a large and excited Fifth International Congress on Animal Reproduction and Artificial Insemination at Trento, Italy, in September 1964 (6). In brief, feeding the compound for 18–20 days to groups of 'randomly cycling' pigs resulted in a greater than 90% synchronization of oestrus some 5–7 days after the cessation of feeding, and fertility at this synchronized oestrus was found not to be depressed. By late 1964, this very same ICI compound was being called methallibure and it underwent a further name change in 1965. The latter was because Chris, together with a second American visitor on sabbatical (Professor B. N. Day, of the University of Missouri), had found that a single injection of 750 i.u. of PMSG at the time of drug withdrawal followed by 500 i.u. of hCG 3–4 days later enabled artificial insemination at a predetermined time. Indeed, the time could be prescribed three and a half weeks earlier. This programme of treatment was the Polge, Day and Groves approach to batch breeding and, because of its suitability for on-farm application, the compound finally became Aimax (artificial insemination maximum). Unfortunately, just as the compound was finding widespread commercial application in the late 1960s it had to be withdrawn from Western European and North American markets because of teratogenic effects if inadvertently fed to pregnant animals.

Further studies on embryo transplantation

Very much with the support of Tim Rowson, Chris had become one of the pioneers in egg or embryo transplantation in pigs; two examples of such studies have already been given. Both involved a surgical approach to the reproductive tract by means of a mid-ventral laparotomy. A third involved the development of a technique for the transplantation of blastocysts, in part as a prelude to analysing, with Dr R. M. Moor (FRS 1994), the influence of location of embryos on the maintenance of the corpora lutea. A non-surgical study of embryo transplantation was stimulated by the presence of Professor B. N. Day, who was soon to become one of Chris's most valued scientific colleagues and closest friends. They both realized that a surgical approach to the reproductive tract would never find a large-scale application and that an on-farm technique of embryo transplantation would be a step beyond artificial insemination. These considerations were not new, of course, because Hammond had been promoting them since the 1930s, although very much with cattle in mind. However, the cervical barrier protecting the uterus in cattle is relatively straightforward to traverse with a pipette or straw—as demonstrated by the widespread success of intra-uterine insemination—whereas the extensive and tortuous cervical folds in pigs present a major obstacle to most forms of catheterization. Nonetheless, Chris and Bill Day reasoned that because cervical tone was regulated by ovarian steroid hormones, it might be possible to overcome the barrier when systemic concentrations of progesterone began to increase during the early luteal phase of the oestrous cycle.

After much preliminary experimentation and the expected problems of damaging cervical tissues and/or puncturing the uterine wall, they developed a successful technique and achieved the first pregnancies in pigs after non-surgical embryo transplantation (7). There was a fruitful sequel to this work, for it stimulated the design of catheters that could traverse the cervical canal during oestrus. These, in turn, prompted the manufacture of catheters that could be guided along the extensive uterine horns to the vicinity of the utero-tubal junction. Thus was deep uterine insemination born in pigs. It has found commercial application for two purposes: the introduction of very small numbers of spermatozoa close to the utero-tubal junction, giving successful pregnancies, and the use of sex-sorted spermatozoa (spermatozoa bearing an X or Y chromosome), which are currently available in only limited numbers.

Return to freezing: boar spermatozoa and bovine embryos

This mention of spermatozoa takes us appropriately to a major focus of work during the late 1960s and early 1970s—the development of a technique for the successful freezing and thawing of boar spermatozoa. Whereas Chris was able to guide the studies on the basis of his previous experience, much of the practical work was undertaken by a PhD student, Ian Wilmut (FRS 2002), who was later to achieve distinction in quite another sphere. When the general approach used for freezing and thawing of bull spermatozoa was followed, the overall results with boar spermatozoa were exceptionally poor: intra-uterine insemination resulted in negligible fertility. By contrast, surgical insemination of a suitable number of frozen–thawed spermatozoa directly into the Fallopian tubes of pre-ovulatory animals gave a good incidence of fertilization (9). This observation led to the conclusion that the combined processes of freezing and thawing rendered the sperm cell surface in some manner vulnerable to the uterine environment, especially to phagocytosis by polymorphonuclear leucocytes. As a consequence of this interpretation, attempts were made to protect the sperm surface during and immediately after thawing, and these included the addition of seminal plasma or synthetic macromolecules to the sperm suspension. Even so, only low levels of fertility were obtained by following such approaches, even when spermatozoa were treated by the so-called pellet method in which small aliquots of the sperm suspension are frozen individually. Conclusions drawn from these studies were that the rates of both freezing and thawing are critical, and that there is considerable variation between individual boars in the response of their semen to the various protocols. As a consequence of these problems, short-term storage (from one to three days) of cooled, diluted semen remains the norm in countries in which the artificial insemination of pigs is used on a large scale.

With his extensive experience of semen preservation in farm animals and of cryobiology in general, it was natural that studies in Chris's laboratory should examine the possibility of the deep-freeze preservation of mammalian embryos. As suggested above, the transfer of embryos to a recipient animal should give full control over the genome of any resultant offspring. Once again, the bench work was undertaken by Ian Wilmut, now in his postdoctoral year, with Chris remaining at his shoulder and offering encouragement on a daily basis. After some modification of the procedures applied to sperm cells, especially with regard to slower rates of cooling and thawing, these studies bore fruit when applied to bovine embryos. The first calf produced after the transfer of a frozen–thawed embryo was born at the Animal Research Station in 1973; a second was born a little while later. Needless to say, Tim Rowson was the key surgeon involved in transplantation of the embryos.

Steroid hormones and pheromones

From the mid 1960s, various lines of research concerning gonadal steroid hormones were pursued in Chris's laboratory, always in conjunction with appropriately trained colleagues. Knowing of the novel work on pheromones in mice by Dr Hilda Bruce at Mill Hill, and feeling that pigs of all species might be sexually programmed to a considerable degree by odours, Chris began studies in 1965 with Dr W. D. Booth. Their initial focus was specifically on odours emanating from boars, because these were known to be involved in the behavioural response at oestrus and in prompting the onset of puberty in young females. Although such odours were found in the skin, preputial fluid and saliva, the work concentrated on androgenic stimulation of the submaxillary glands; these act as secondary sex tissues and produce potent pheromones in the salivary froth around the mouth of sexually excited boars. The key molecules were soon synthesized and used by the pig breeding industry to aid in the detection of oestrus and in artificial insemination. In practice, an aerosol containing synthetic steroids was sprayed on the snout of selected females.

A separate line of work was pursued by Chris and an American colleague, Dr H. D. Guthrie, from the US Department of Agriculture, Beltsville, Maryland. Concentrations of gonadal steroid hormones circulating in peripheral blood were deemed to be one key to a better understanding of many reproductive processes and, potentially, to their manipulation. Work with Guthrie examined the luteal secretion of progesterone in pigs under various breeding conditions, especially after the synchronization of oestrus. Such studies were complemented by subsequent work with Dr A. L. Garverick from the University of Missouri on circulating oestrogens and on steroid hormone and gonadotrophin receptors in target tissues. The background to these fundamental studies was always one of attempting to improve the breeding efficiency of domestic livestock.

Karyotyping, micromanipulation and *in vitro* fertilization

During the late 1960s and early 1970s, Chris's laboratory was pursuing two other lines of research involving eggs and embryos. Because of the relatively high mortality of pre-implantation embryos, cytogenetic studies were commenced after various breeding protocols and specifically after delayed insemination in pigs. In this situation, an oocyte would have started post-ovulatory ageing in the Fallopian tubes before sperm penetration. Bench work involved karyotyping and associated chromosomal techniques such as banding, and was undertaken by Dr R. W. McGaughey, who had been trained in Dr M. C. Chang's laboratory at the Worcester Foundation. As might be expected, increasing chromosomal anomalies were associated with increased post-ovulatory age of the egg at fertilization, such degenerative changes now being known to reflect in part the activation of apoptotic pathways.

Short-term storage of eggs and embryos had been a requirement of the transplantation studies in Chris's laboratory since the early 1960s, for there was always a period of delay between egg recovery from a donor animal and transfer to a recipient. Such storage was usually in a culture oven maintained in theory at 35–37 °C but, in reality, at rather variable temperatures as a result of frequent opening and closing of the oven door. Eggs and embryos were held in a simple culture medium: a modified Tyrode's solution was the favourite to which bovine serum albumin or inactivated foetal calf serum had been added. More elaborate culture media were produced at the Animal Research Station during the PhD studies of Robin Tervit with Tim Rowson, and Chris maintained a keen interest in this work. Thereafter, various short-term visitors to his laboratory refined the procedures for pig embryos.

Although a period of storage of 2 hours or less seemed not to be harmful, greater flexibility in the surgical transfer routines would be offered by a longer period. In this context, storage of pig embryos in a rabbit Fallopian tube was examined with Dr C. E. Adams and, as had previously been demonstrated with sheep embryos, rabbits were suitable 'incubators' for the long-distance transfer of embryos. A Fallopian tube would clearly offer a more controlled environment in terms of fluid composition, gas tension and stability of temperature than some form of artificial medium held within a modified test-tube or culture dish.

By the early 1970s, large numbers of embryos were being handled *in vitro* in Chris's laboratory, so it was logical that attention should turn to manipulation of the embryo itself. Excellent micromanipulation facilities had been installed at the Animal Research Station, largely at the instigation of Dr Adams, and an Australian colleague on sabbatical leave from the University of Sydney (Dr N. W. Moore) was the first to use the facilities systematically. Neil Moore was no stranger to Cambridge, having undertaken his PhD studies on sheep reproduction with Tim Rowson. However, now collaborating principally with Dr Adams, he investigated the potential for dividing ('splitting') early-cleavage-stage embryos into their individual blastomeres as one approach to generating an increased number of embryos for transplantation. This approach was successful at the two-celled and four-celled stage of development and, in the latter case, three of the four blastomeres frequently developed into foetuses on transplantation into recipient Fallopian tubes. The reason for a fourth blastomere's seldom developing was thought to be physical damage at the time of separation. Although these pilot studies were conducted with rabbit embryos, they were soon extended to large farm species, including successful work with pig embryos in Chris's laboratory (8). Over and above examining the number of cleavage stages for which the individual blastomeres retained their totipotency, there was the practical consideration that embryos of valuable genetic merit would be in short supply. Micromanipulation of 'early' embryos could offer one route to their proliferation.

Chris's scientific reputation and outgoing personality had always attracted talented individuals who wished to work in his laboratory, and many of these were remarkable characters in their own right. None was more colourful than a young Danish veterinary surgeon, Steen Willadsen, who came as a postdoctoral fellow from the Royal Veterinary and Agricultural University in Copenhagen. Willadsen's initial studies with Chris continued work on embryo culture and storage, and also on the deep-freeze preservation of embryos. However, Willadsen was very much an individualist of artistic bent and he had absolutely no wish to continue other people's work or remain within conventional lines of research. He was seeking new horizons, and the temptations offered by a micromanipulator proved irresistible. After perfecting techniques for the splitting of very young embryos and demonstrating their potential for generating twin and triplet sheep and calves, he began a novel approach to producing sheep × goat hybrids ('chimaeras') by assembling respective sets of blastomeres within a protective zona pellucida. Damage to the manipulated zona was overcome by either coating with agar gel or exposing the embryos to the glycoprotein secretion of rabbit Fallopian tubes. The offspring resulting from this transfer featured on the front cover of an issue of *Nature* and prompted widespread discussion. Chris's laboratory became the subject of considerable interest and acclaim from the media.

Variations on the theme of chimaeras held Willadsen's attention for a while, but soon he moved on to nuclear transplantation, being well aware of the pioneering work of John Gurdon FRS in frogs. After introducing embryonic cell nuclei into enucleated oocytes, the notion of cloning mammalian embryos was seldom far from his mind, and he received full support and encouragement from Chris. Such attempts at cloning were always in a setting of multiplying up valuable farm livestock, especially dairy cattle. When Willadsen's research fellowship in Cambridge expired, he took his techniques to an embryo transfer company in North America, having left the provocative notion in Cambridge that he might well have inadvertently achieved cloning with a somatic cell nucleus during his transfer studies. This would have been because the micropipette used for introducing a nucleus into an oocyte might have displaced one of the investing cells of the corona radiata into the ooplasm at the same time. In essence, such a technique was first shown to be feasible as a route to cloning some 20 years later, by Professor R. Yanagimachi at the University of Hawaii.

After the excitements of Willadsen, Chris's laboratory returned to work on embryo culture and also examined systems for the *in vitro* maturation and fertilization of pig oocytes. Much of the bench work was undertaken by a research student from Taiwan called Winston Cheng, and Cheng was one of the first people to achieve the *in vitro* fertilization of pig eggs, in conjunction with Chris and R. M. Moor. Although this was a notable step, there were the twin disappointments that the work was never published as a full paper and that the technique resulted in only a small proportion of viable embryos with the potential for foetal development. This may have been due principally to the high incidence of polyspermic penetration of the oocyte, a problem that continues to bedevil the *in vitro* fertilization of pig eggs to this day.

Retirement and the formation of a private company

On retirement from the ARC at the age of 60 years in 1986, Chris still had far too much energy, far too many ideas, and far too many contacts across the complete spectrum of animal biology simply to slow down in the conventional manner. Instead, with considerable courage and drive and aided by extensive financial backing from various banks and venture capital investors, he and a business partner set up a company with the attractive title of ABC Ltd (Animal Biotechnology Cambridge). The initial intention was the *in vitro* production and storage of bovine embryos suitable for transplantation in beef herds, and the first steps involved the *in vitro* maturation of oocytes taken from ovaries at slaughter. The activities of this company, in part based in Aberdeen—a traditional region for beef cattle farming—expanded with the purchase of an Irish enterprise called Ovamass. The leading scientist from this Irish company, one Dr Lu who had been trained by Professor Ian Gordon in Dublin, was brought to Cambridge, where facilities were created for him at the Animal Research Station. Large numbers of beef cattle embryos were produced and stored, and some transplantation work followed. Although the writer of this memoir does not have any specific details, there is a strong impression that commercial success did not come easily. Chris himself left a note referring somewhat cryptically to ABC's existence as a saga.

A variation on the theme of *in vitro* fertilization for embryo production was to exploit the newly developed techniques of sperm separation ('semen sexing'), sorting spermatozoa bearing an X or Y chromosome to generate embryos of known sex. This approach involved a close collaboration with Dr Larry Johnson of the United States Department of Agriculture (USDA), who had developed a technique of fluorescence-based identification and sex separation of stained spermatozoa with the use of flow cytometry. In due course, Chris's company employed Dr David Cran, formerly of the Animal Research Station, to develop this new technology in Britain. There is enormous potential for its application in artificial insemination and in the production of pre-sexed embryos for transplantation but, because the process of sperm separation is relatively slow and costly, a major impact of 'semen sexing' has yet to be seen.

A new line of company activity involved the production of transgenic animals. Growth-hormone gene constructs had been shown at the USDA and elsewhere to be incorporated into newly fertilized pig embryos and expressed during development. However, as observed in a considerable body of work at the USDA, larger animals with faster rates of growth were extremely susceptible to arthritis. Accordingly, work with growth-hormone constructs ceased on welfare grounds, both in North America and in Cambridge. Moving to a completely different field, Chris and colleagues developed techniques to produce transgenic cardiac tissues, enabling functional valves to be harvested for use in human surgery. These techniques certainly had a future and were a commercial success; they were sold to the British company Immutran.

An overall impression gained on a purely social basis was that, exciting though the biological aspects were, Chris found the commercial pressures of running a company exceedingly stressful. He also seemed to be surprised by the fact that interactions with businessmen differed enormously from those with fellow scientists. Even so, he put on a brave face, confronted and overcame many serious difficulties, and kept dabbling with one project or another until 1996, when he finally drew his commercial activities to a close.

Administration and committees

Although the attractions of laboratory life remained strong, Chris pulled his weight in the world of biological organizations and the associated paperwork. He was the secretary of the Society for the Study of Fertility (now called the Society for Reproduction and Fertility) in the days when the officers knew almost everyone personally and correspondence was done on an individual basis with carefully composed letters (1960–63). In due course, he became chairman of the society (1978–81) and led it skilfully through a series of changes, not least those concerning the *Journal of Reproduction and Fertility*. He was also chairman of the Society for Low Temperature Biology (1976–79) and on the editorial boards of numerous journals, including the novel *Research in Reproduction*, which listed papers published in mammalian reproductive biology on a monthly basis.

In the broader sphere, his contributions extended from the Rare Breeds Survival Trust and the Bourn Hall Ethics Committee to consultant work for both the Food and Agriculture Organization in Rome and the World Health Organization in Geneva. In addition, while on sabbatical leave in the USA during 1966–67, various official bodies in Washington made use of his expertise, not least the USDA and the National Institutes of Health. He was an organizing force behind diverse international conferences, especially the four-yearly International Conference on Animal Reproduction and, during his last 20 years, on various specialist conferences dealing with reproduction in pigs.

In one sense, however, his greatest organizational contribution remained in Cambridge. What has not been brought out fully in this memoir is that for the whole of Chris's professional life there, the Animal Research Station was effectively synonymous with an ARC Unit. When Chris moved to Cambridge full time in 1954, he joined Hammond's Unit of Animal Reproduction and, on Hammond's retirement in 1955 and the appointment of Dr T. R. R. Mann as Director, Chris automatically became a member of the newly named ARC Unit of Reproductive Physiology and Biochemistry. And so he remained, progressing through the ranks from Senior Scientific Officer to Senior Principal Scientific Officer (special merit promotion). After Mann's retirement in 1976 and Rowson's in 1979, he became the new Director, although with the formal title of Officer-in-Charge because the Unit was by then an outstation of the far larger ARC Institute of Animal Physiology at Babraham (on the other side of Cambridge).

He remained at the helm through eight difficult years, difficult because of the financial climate, and stressful too because of the ARC's wish to close the Animal Research Station site and transfer the staff and work to Babraham. This proposal was based on a rationalization of resources and the interactions of staff. However, Chris strongly resisted all overtures and pressures to move his 'Unit' to Babraham, believing that future successes of the Animal Research Station team rested in the intimacy and informal interactions, the imaginative leaps forward, and the excellent large-animal facilities available at Huntingdon Road. Even so, physical amalgamation eventually became inevitable, and by the time of his retirement in 1986 the staff of the 'Unit' had moved or were in the process of moving to Babraham. As a postscript to this saga, it may be instructive to note that large-animal reproductive research is scarcely visible in Cambridge these days and currently represents the most minor part of the activities of Babraham. A tradition extending from Hammond and Walton to Mann, Rowson and Polge has effectively been extinguished; the loss is immense.

University contributions, national and international prizes

During much of his time at the Animal Research Station, Chris had no formal links with the University of Cambridge. His background at Reading and his PhD from London secured no such connection. However, his reputation was well known to colleagues in the Veterinary School at Madingley Road, and both veterinary and agricultural science students paid regular visits to his laboratory to learn about techniques of semen collection and artificial insemination. Belatedly, the university woke up to its oversight and Chris was made a Fellow of Wolfson College in 1984 and an Honorary Professor of Animal Reproductive Biotechnology in the Veterinary School in 1989. He lectured to students at Madingley Road and to those taking natural sciences on the Downing site. He greatly valued these interactions with young people and, because he had the gift of informality, the question and discussion sessions so generated were enjoyable to all. Undergraduates relished his vast knowledge worn so lightly and also his impish sense of humour. No lecture was complete without repeated rounds of laughter.

In addition to teaching in Cambridge, Chris gave invited lectures at diverse British universities with an interest in agricultural science. These included the Blackman lecture in Oxford, the Cameron–Gifford lecture at Newcastle, the E. H. Wilmott lecture at Bristol and the Clive Behrens lectures at Leeds. Surprisingly, there is no record of any invitation to lecture at his *alma mater*. His overseas lectures are too numerous to list in detail, but special mention could be made of those in Paris, Copenhagen, Uppsala and Milan. He was always a valued speaker at institutes of the French agricultural research service (INRA; l'Institut national de la recherche agronomique), and retained close contacts with its centres at Jouy-en-Josas (Versailles) and Nouzilly (Tours).

Recognition of Chris's contributions in reproductive biology and cryobiology came from many directions. His Fellowship of the Royal Society gave him lasting pleasure. He received the Marshall Medal of the Society for the Study of Fertility (UK) and the Sir John Hammond Memorial Prize of the British Society for Animal Production. In Israel he was awarded the Wolf Foundation Prize in Agriculture, in the USA he became a Foreign Associate of the National Academy of Sciences and in Sweden he received the Bertebos Prize. A highlight was, of course, award of the prestigious Japan Prize. This, in turn, prompted the award of the CBE some years after his formal retirement from government service, a timing that afforded him wry amusement.

Although a distinguished athlete in his youth, Chris encountered circulatory problems in his sixties and thereafter suffered declining health together with restricted mobility in his later years. The physical constraints were born stoically, his mind and sense of humour remained as sharp as ever, and his large circle of friends kept constantly in touch. Above all, he was sustained by the affection and close relationships of his family, and by a keen appreciation of the gift of a privileged life. He died peacefully at home one day after his 80th birthday, surrounded by members of his family.

Distinctions and awards

1969 Awarded (conjointly) the John Scott Medal by the Board of Directors of City Trusts of the City of Philadelphia 'for the invention of a method of low temperature preservation of living cells and tissues'
1971 Awarded the Sir John Hammond Memorial Prize by the British Society of Animal Production 'in recognition of distinguished work in the field of reproductive physiology'
1974 Sir John Hammond Memorial Lecturer, Society for the Study of Fertility
1979 Presented the Blackman Lecture, University of Oxford
1983 Elected Fellow of the Royal Society
1984 Presented the Cameron–Gifford Lecture, University of Newcastle
Elected Fellow of Wolfson College, Cambridge
Elected Honorary Fellow of the Royal Agricultural Society of England
1986 Presented the E. H. W. Wilmott Lecture, University of Bristol
Elected Honorary Associate of the Royal College of Veterinary Surgeons
1987 Pioneer Award, International Embryo Transfer Society
1988 Clive Behrens Lectures, University of Leeds
The Wolf Foundation Prize in Agriculture
Marshall Medal, Society for the Study of Fertility
1989 Sir John Hammond Memorial Lecture, British Society of Animal Production
Hon. Professor of Animal Reproductive Biotechnology, University of Cambridge
1990 Awarded Hon. DSc, University of Illinois
1991 Elected Fellow of the Royal Agricultural Societies
1992 Awarded the 8th Japan Prize—'Science & Technology for Biological Production'
Honoured by Her Majesty The Queen with the CBE
1994 Awarded Hon. DSc, University of Guelph
1995 Awarded the first Lazzaro Spallanzani International Award on Animal Reproduction
1997 Bertebos Prize, Royal Swedish Academy of Agriculture and Forestry
Foreign Associate of te US National Academy of Sciences

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