GORDON HENRY DIXON
25 March 1930 — 24 July 2016
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Elected FRS 1978

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Gordon H. Dixon was a highly influential scientist who excelled in all the stages of his career and in each laboratory of every institution at which he was a member. Gordon began his graduate career at the University of Cambridge and completed his studies at the University of Toronto on the subject of transeptidation reactions in biological systems. At an early stage of his career, he developed the technique of starch gel electrophoresis with Oliver Smithies and made important discoveries on the structure of human haptoglobins.

Subsequently, Gordon contributed to the determination of the structure and active sites and mechanisms of action of trypsin and chymotrypsin and made seminal discoveries related to understanding the structure of the protein hormone insulin. However, he is best known for his later studies on the regulation of protamine genes and chromatin transitions

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in spermatogenesis. He is often considered to be the father of the protamine molecular biology underlying this gene system and his research is continually cited to this day. Gordon contributed to the identification and sequencing of the protamine genes, the discovery that methionine was required for initiation of protamine synthesis, understanding the roles of histone hyperacetylation and protamine phosphorylation, and the generation of the highly compact nucleoprotamine structure present in sperm, primarily using trout as a model system. Gordon is fondly remembered as a brilliant and very generous scientist by all his mentees, representing all levels from undergraduates to PhD and postdoctoral fellows, who provided a scientifically stimulating atmosphere in which they could develop their careers. From a more personal perspective, he also had a fun side and was devoted to his family. Gordon was a person who, owing to his legacy of great science and his fundamental humanity, still lives in the memory of many people.

**His early years (1930–1951)**

Gordon was born in Durban, South Africa, on 25 March 1930, the son of Walter and Ruth Dixon (née Nightingale). He was one of five children (Walter, b. 1917; Vera, b. 1919; Stanley, b. 1920; and Shirley, b. 1936). Gordon’s grandfather, Phillip Brassington Dixon, was an engineer who had left London in the 1880s to help build the national railway system in South Africa. Gordon’s father, Walter J. Dixon (b. 1887), was born in Ladysmith, South Africa, and came to Europe in 1914 to fight in the First World War. He married Ruth Nightingale and they returned to South Africa, where Gordon was later born.

The Great Depression hit South Africa hard, and the family returned to the UK in 1932 and settled in Girton, Cambridgeshire, where Gordon spent his childhood and early adult years. Growing up in the small village of Girton in the 1930s and 1940s during the Second World War years could not have been easy, and Gordon must have been affected by the death of his brother, Walter, in Burma in 1943, as well as the constant worry about his other brother Stan, a celebrated RAF pilot. However, during these years the seeds were planted for Gordon’s lifelong scientific curiosity and love of learning.

He gained admission to Cambridgeshire High School for Boys, where he excelled in the sciences. The standard of instruction at the school was uniformly high under the direction of the headmaster, Mr Brinley Newton-John (father of the famous entertainer Olivia N.-J.). His chemistry teacher, in particular, A. B. (‘Doc’) Adamson was an Oxford DPhil in organic chemistry and was very influential in Gordon’s education. At the same time, with the patronage and support of Mrs Helen Pease (of the famous Wedgwood/Huxley/Pease families), who lived in Girton, Gordon undertook an ambitious ecological succession study of the flora and fauna of the Madingley Brick Ponds, essentially as a high school science project. The care and attention to detail exhibited in the report of that project and its associated hand-drawn maps and figures hinted at Gordon’s future scientific promise. His outstanding High School exam results led to an open scholarship to Trinity College, University of Cambridge, where he completed a Double First BA Hons (MA) in medical sciences and the Natural Sciences Tripos. The listing of his 1950–1951 Part II class (see figure 1) and instructors reads like a Who’s who in the relatively new discipline of biochemistry (including as it does nine Fellows of the Royal Society, one also a Nobel Laureate).
Figure 1. Gordon with classmates and instructors in the undergraduate Biochemistry Part II class of 1950–1951 at the University of Cambridge. From the archives of the Department of Biochemistry, University of Cambridge (with permission). Back row (left to right): D. J. Bell; K. P. Harrison; K. McQuillen; Malcolm Dixon FRS; G. D. Greville; E. C. Webb. Middle row (left to right): Joseph Needham FRS; A. J. Thomas; H. Higgins; F. S. Grylls; P. A. Plack; B. A. Newton; J. A. Grunau; P. Plackett; Samuel Perry (FRS 1974); A. M. Freeman; Kenneth Bailey (FRS 1953); Peter Mitchell (FRS 1974; Nobel Laureate 1978); Don Northcote (FRS 1968). Front row (left to right): C. M. Gould; D. H. Shrimpton; C. J. Rondle; H. J. Levell; M. W. Herbert; P. Hurlock; Frank Young FRS; H. J. Shelley; B. K. Whitehead; J. S. Griffith; J. B. Chapell; Gordon Dixon; A. Korner; Dorothy Needham FRS.

GRADUATE STUDIES AND EARLY POSTDOCTORAL YEARS (1951–1963)

Gordon began his graduate studies at the University of Cambridge under the direction of Professor Charles Hanes FRS and followed his mentor to the Department of Biochemistry of the University of Toronto, where he completed his PhD in 1956. The title of his doctoral thesis was ‘Transpeptidation reactions in biological systems, with special reference to the specificity and kinetics of the reaction catalyzed by the cabbage glycy1 transpeptidase’ (Packham 2008).

It was also at this time in Canada that Gordon met the ‘love of his life’, Sylvia Gillen, who had independently emigrated from the UK and was living and working in Toronto. They married at Trinity Church in Thornhill, Ontario, in 1954 and began a 62-year partnership together. At that early stage of his career Gordon, together with George Connell and Oliver Smithies (FRS 1998; Nobel Laureate 2007), developed the technique of starch gel electrophoresis, which at one time was used in protein research throughout the world (2)*. Gordon, Connell and Smithies also made important discoveries on the structure of the human haptoglobins (8, 10, 14, 15).

Gordon’s PhD thesis was followed by postdoctoral work (1954–1958) on the structure and active sites and mechanisms of action of trypsin and chymotrypsin, under the direction of Hans Neurath at the University of Washington, Seattle (CSBMCB 2007) (1, 3, 4). Family life

* Numbers in this form refer to the bibliography at the end of the text.
for Gordon and Sylvia began at this time with the arrival of their daughter, Frances (1955), and eldest son, Walter (1956).

This postdoctoral fellowship was followed by a staff position with Hans Krebs FRS (Nobel Laureate 1953) and Hans Kornberg (FRS 1965) at the MRC Laboratories for Research in Cell Metabolism at the University of Oxford (5). Gordon’s ability to seek out and collaborate productively with the very best scientists, mentors and colleagues around the world characterized his career and few other researchers can claim to have worked directly with four Nobel Laureates during their careers (Hans Krebs, Oliver Smithies, Michael Smith FRS and Fred Sanger FRS).

Returning to Canada in 1959, Gordon assumed a research associate position at the Connaught Medical Research Laboratories in Toronto (1959–1960). As an associate professor, he then joined the Department of Biochemistry at the University of Toronto (1960–1963) and was soon promoted to professor.

During this time, Gordon made seminal discoveries that were focused on understanding the structure of the protein hormone insulin that eventually contributed to the complete chemical synthesis of insulin (CSBMCB 2007). Gordon, in collaboration with A. C. Wardlaw and S. Wilson, achieved the first recombination of the separated A and B chains of insulin (6, 7, 11). Gordon’s first graduate student was the distinguished Canadian biochemist and glycobiologist, Harry Schachter (CSBMCB 2007) (9, 12).

Gordon and Sylvia completed their family with the arrival of Christopher (1960) and Robin (1961). After impressive research contributions to protein biochemistry in his early career, he then moved to Vancouver as professor in the Department of Biochemistry at the University of British Columbia.

**THE WORK IN VANCOUVER (1963–1972)**

Having moved to the Department of Biochemistry at the University of British Columbia in 1963, Gordon began his studies on the regulation of protamine gene expression, largely concentrating on the trout testis (CSBMCB 2007). During this period, he recruited Victor Ling, Donald T. Wigle, Choy Hew and Peter Candido to join his research group, who all became important collaborators (figure 2). It is curious to learn how in some cases serendipity took some of the collaborators to join Gordon’s laboratory. Victor was on his way to Berkeley after graduating from the University of Toronto in 1966 when he realized that he would be eligible for the draft supporting the Vietnam War effort if he accepted a state of California scholarship. Not wanting to take this risk, he applied and was accepted to work with Gordon at the University of British Columbia. This was fortunate, as Michael Smith (Nobel Laureate 1993) and Gordon were collaborating on understanding salmon spermatogenesis. On arriving in the Dixon laboratory, Gordon suggested that Victor work on the biosynthesis of protamine during spermatogenesis in rainbow trout. This was of interest because the histones in spermatogonia appeared completely replaced by protamines during sperm development. Protamine is unusual in that it is a small, highly basic protein composed of about two-thirds arginine residues packaging the DNA into the sperm head (13, 16).

Gordon’s team found it was possible to induce full sexual maturation of male rainbow trout in about six weeks after injecting an extract made from pituitary glands of spawning salmon twice weekly, a system developed by Michael Smith and his colleagues in the Fisheries
Figure 2. Gordon Dixon, together with some of his PhD students, postdoctoral fellows and other staff in the Department of Biochemistry at the University of British Columbia during the 1960s, celebrating a special occasion. From left to right: Joe Durgo (Hungarian engineer), Victor Ling (in a tie, unusual), Choy Leong Hew (in a tie, also unusual), Sanga Pootrakul (MD from Thailand), Barry Malchy (graduate student from the University of Manitoba who worked on haptoglobin), Ken Stevenson (postdoctoral fellow), Mrs Lasco (glassware washer peeking out from behind), Dorothy Kauffman (senior research associate in protein chemistry), Don Wigle in the front (MD completing his PhD with Gordon), Gordon Dixon and Keiji Marushige (postdoctoral fellow, plant biologist, from Japan). (Online version in colour.)

Research Board. This offered a convenient and relatively synchronized model system to study spermatogenesis and, in Victor’s case, the ‘turning-on’ of protamine biosynthesis. Testes from naturally maturing rainbow trout were also collected from a nearby trout farm at different times of the year to supplement the hormone-induced system. Victor and Gordon’s research yielded the discovery that protamine was made on dimeric ribosomes, initially phosphorylated in the cytoplasm and later dephosphorylated in the nucleus (22, 25). It was speculated that phosphorylation/dephosphorylation regulated the repackaging of DNA with protamine (18, 20, 21), a topic that even 50 years later is still the subject of intense research (Soler-Ventura et al. 2019).

Gordon had a knack for identifying important biological questions and experimental systems for enabling their investigation. His general research approach was to recruit talented people and give them the freedom to work with each other. He encouraged them to be fearless in trying out new ideas or techniques. The laboratory was a fun and intellectually stimulating place. Victor benefitted enormously from the one-on-one sessions with Gordon, and he was very fortunate to have collaborated with and learned from senior people in the laboratory, including postdoctoral fellows from Canada (John Trevithick), Japan (Keiji Marushige) and
Sweden (Bengt Jergil). When Gordon saw new experimental results, he would break into the huge smile that he was famous for and immediately begin to speculate on the significance of the data as well as suggesting new experiments to do. When it came to writing scientific papers, Gordon was precise and meticulous. He made his colleagues better scientists.

Another important collaborator in Gordon’s laboratory during this period was Donald T. Wigle, who joined in 1967 after finishing his MD in 1966 and a rotating internship in 1967. Donald arrived at Gordon’s laboratory in Vancouver in September with a pregnant wife, an infant daughter, $10 in cash and no credit cards. Construction of the married student condominium was three months behind schedule, so he had no place to live. As an example of Gordon’s character and the personal qualities of his family, Donald remembers that Gordon and Sylvia generously housed Donald and his wife for several days and loaned them money until they could access their own funds and settle in.

Gordon assigned Donald a project initially focused on identifying the types of histones in developing trout testis cells, which led to the discovery of a new histone unique to testis cells (26). Subsequent studies in Gordon’s laboratory uncovered a fundamental property of gene expression and epigenetics, regulation through the acetylation and methylation of histones during development (26). This work was interrupted by Gordon and Donald’s accidental discovery that methionine was required for initiation of protamine synthesis in a trout testis cell-free system. This was the first evidence that methionine was an initiator in a eukaryotic organism (23). Gordon returned to his sabbatical at the MRC Laboratory of Molecular Biology at Cambridge, UK, as Donald finished these studies. Richard Jackson and Tony Hunter independently reported that methionine initiates haemoglobin synthesis in a mouse ascites cell-free system with hemoglobin mRNA. Both papers were published in the same 1970 issue of *Nature* (23).

In 1966, Gordon received the Steacie Award for the successful *in vitro* recombination of the two insulin subunits. This was a breakthrough, laying the foundation for the subsequent organic synthesis of the active hormone. At that time, Gordon recruited Choy Hew as part of a PhD programme (1967–1970) in the Department of Biochemistry at the University of British Columbia. The PhD thesis work focused on the structural determination of the beta subunit of human haptoglobins (HPs) (19), a group of serum glycoproteins capable of binding haemoglobins. Gordon had previously shown with Connell and Smithies that HPs consisted of alpha and beta subunits in all three types (8, 14) using 8 M urea starch gel electrophoresis and the complete denaturation of the proteins. While the beta subunits were common to all, there were two distinct alpha subunits of different sizes. They had proposed a partial gene duplication to explain the evolution of the alpha subunits (10). This was subsequently verified by the complete amino acid sequencing of these alpha subunits (17). The primary structure of the large beta subunit was determined by the fractionation of enzymatic digests using column chromatography and manual sequencing of the purified peptides, which was a time-consuming and a labour-intensive task.

The development of the automatic protein sequencer by Edman & Begg (1967) was a gamechanger. A worldwide rush to build similar instruments in many laboratories soon followed, with Gordon, Joe Durgo and Choy Hew electing to build their own protein sequencer. Joe, being an engineer and innovator, decided together with Gordon to build the instrument using an old jukebox from a junk yard. The rationale was due to the repetitive nature of the Edman reactions (i.e. coupling with phenylisothiocyanate (PITC), washing, cleavage, and conversion to phenylthiohydantoin (PTH) amino acids), consistent with the
sequential playing of the individual songs by the machine. They managed to get the first three amino acids of the sequence determined. However, owing to reagent impurities, the background noise became too high. It was not possible to continue to build the amino acid chain and they moved on, although the team benefitted from the wisdom and innovative approaches of Gordon and Joe.

Toward the end of this period, Gordon recruited Peter Candido (PhD student 1968–1972) to work on sperm chromosomal proteins. He would later return to the University of British Columbia as an assistant professor. Their work on histones and protamines in developing trout testis required the preparation of a salmon pituitary extract. This was obtained by crossing the border to a fishery just south of Seattle, WA, after leaving Vancouver at 4.30 a.m. for the three-hour drive. Using discarded Chinook salmon heads, local people were hired and trained to recover pituitaries! Along with sorties to obtain trout testes from a trout farm near Vancouver, these activities underscore the effort that is sometimes required to develop a biological system that can answer basic questions in biochemistry (24, 27–29). In 1970, before moving to the University of Sussex (UK), Gordon was elected to the Royal Society of Canada in recognition of his many contributions to biochemistry.

**University of Sussex (1972–1974)**

Gordon was appointed head of department in the Biochemistry Group of the University of Sussex, succeeding the late Professor Asher Korner, one of his former classmates from the Biochemistry Part II class at Cambridge. During his relatively short time there (1972–1974), he focused the studies of his group on the defining biochemical and structural transitions of spermatogenesis, specifically the study of the protamine messenger RNA (30, 31) (CSBMCB 2007). New PhD students and postdoctoral fellows joined his research team, some of whom (including Lashitew Gedamu and Kostas Iatrou) followed him when he returned to Canada and the University of Calgary in 1974.

**The University of Calgary (1974–1994)**

Gordon was recruited back to Canada in 1974 as professor of medical biochemistry at the University of Calgary under the auspices of the Alberta Heritage Fund for Medical Research, where he remained for the duration of his career (1974–1994) and served as head of the department (1983–1988). As an active and prolific researcher, Gordon led the Growth and Development Group and made many important contributions to understanding how DNA is packaged within the nucleus of cells and the exquisite control of its expression during growth, development and reproductive processes. Several of his team members during that period share their experience and memories of Gordon below (figure 3).

Kostas Iatrou (from Athens, Greece), who began as a PhD graduate student in the Dixon laboratory, first at the University of Sussex (1972–1974) and subsequently at the University of Calgary, summarizes the activity directed by Gordon (Dr Dixon to most of the collaborators both inside and outside the laboratory) as ‘work, camaraderie, and fun’. Gordon was always very selective as to who would join the group as he believed that all newcomers, students and postdoctoral fellows alike, should be able to work independently with minimal input from him. All team members had to design and execute their own study within the wider context
of the group’s interests, with no spoon-feeding from Gordon, hence the term ‘sink or swim’ for his laboratory. Close interaction with Gordon and his heavy involvement in the next steps for the team’s research would occur after their initial lines of inquiry started bearing fruit. Most of the time the result was fully rewarding, with significant publications that moved the field forward (32, 33). The synthesis of full-length protamine cDNA was described, a great achievement at the time, and its use for the hybridization-based deduction of the distribution
of poly(A)$^-$ and poly(A)$^+$ protamine messenger RNA sequences in the developing trout testis. A summary was published in 1978 describing the life history of protamine messenger RNA during spermatogenesis in the rainbow trout (34).

A new group of graduate students and postdoctoral fellows began to flow in, and the new technology with the advent of nucleic acid sequencing changed everything. In the collaborative spirit of Gordon’s laboratory, postdoctoral fellow Jovita Mezquita travelled to Chapel Hill, North Carolina, to attend the shot-gun sequencing workshop, and demystified the art of Sanger/M13 sequencing to Gordon’s team members. It was the dideoxy-sequencing enzymatic method developed by a double Nobel Prize winner, Frederick Sanger, a real genius in the field. This method was to replace the tough and toxic, although very ingenious, sequencing method developed by Maxam and Gilbert, which led to the sequencing of the histone genes and discovery of new histone variants (37–39). When Jovita returned, everyone in the laboratory entered this new era.

Another of Gordon’s postdoctoral researchers in Calgary’s laboratory was Stephen Krawetz, who joined after hearing of the legendary work of the Dixon, Smithies and Connell consortium at the University of Toronto and with respect for their cutting-edge research programme. The first collaborative paper described the isolation of the first mammalian protamine messenger RNA (43).

In the true spirit of discovery, and being on the leading edge of team science, the Dixon laboratory’s new ideas and members were always welcome. Ahead of its time, laboratories from different departments were clustered into research groups. Collaborations flourished and the benefits of these and other interactions were promoted by Gordon. This led to Steve’s introduction into computer-assisted sequence analysis, having been handed a set of GenBank disks, the laboratory IBM computer and manuals and Gordon’s request to ‘see what you can do to help with the analysis of the paper this group is working on’. This led to the discovery that DNA sequences adjacent to protamine genes could exist in the Z-conformation; and the corresponding paper, a team effort from the Dixon and Van de Sande laboratories, was submitted shortly thereafter (40). This timely assurance in this critical foundation from Gordon served as an integral part of the research programme, leading to method development and the sequencing of the human and bovine protamine genes (42, 45, 46, 48, 49).

One of the later team members to join Gordon’s laboratory in Calgary was Rafael Oliva. Over the summer of 1985, during two intense months of hard work and under the direct training and very close supervision of Jovita and Gordon, a testis cDNA library from *Gallus domesticus* was constructed and Sanger-sequenced to study protamine expression in this model species (47). This collaboration with Gordon paved the road to Rafael’s subsequent postdoctoral training in Gordon’s laboratory during the period 1986 to 1989. As a result of this collaboration in Dixon’s lab there emerged a substantial contribution to the understanding of the mechanisms involved in the nucleohistone to nucleoprotamine transition during spermatogenesis *in vitro*, spanning the description of the role of histone hyperacetylation (44, 52) to cloning, sequencing and tracing the evolution of the protamine genes (50, 51). This work was summarized in an extensive review that also integrated new original data towards the understanding of the evolution, function and regulation of the protamine genes and protamines, which became among the most highly cited articles in the field and published by Gordon (53). Several collaborative projects were developed and published with Gordon in subsequent years after Rafael had completed his postdoctoral training and become established as an independent scientist at the University of Barcelona (54, 55). The appreciation for the
reproductive biology experimental model from Gordon, as a major mentor, determined the primary focus of Rafael’s subsequent scientific career, with a substantial imprint in the study of the protamines, chromatin structure and the ‘omic’ composition in spermatogenesis (de Yebra et al. 1993; Oliva 2006; Jodar et al. 2011; Castillo et al. 2014, 2018; Barrachina et al. 2018; Soler-Ventura et al. 2019).

Every large research group relies on the lab manager. Wayne Connor was Gordon’s long-standing and highly qualified technician and laboratory manager who was the key person in the laboratory for ordering of reagents, laboratory organization, expense control and highly valuable help in the transmission of methods to the different laboratory members. Because of his involvement in the experimental work in the different projects, he also authored or co-authored many of Gordon’s publications from 1979 to 1995 (35–39, 41, 56). Wayne would see graduate students and postdoctoral fellows come and go, but he provided the needed stability and continuity to the laboratory.

Gordon’s academic achievements are well documented, but people may not know his fun side. At least once a year there would be an official downhill ski day declared. His colleagues would all be taken to the mountains in a bus, but Gordon would show up in his 5.0-litre Ford Mustang and roar off across the parking lot to the mountains with the gravel spraying and the stereo blasting. He loved that car. Gordon’s laboratory members and the department in Calgary also provided social interaction through the TGIF (Thank God It’s Friday) evening meetings in the Health Science Centre Hall of the University of Calgary and in the annual Department of Medical Biochemistry scientific retreats in the Rocky Mountains. Also on the social side, mention should be made of the team’s gatherings in the context of in-house parties to celebrate birthdays, some weddings and the many arrivals of new babies—the laboratory was also known jokingly as ‘the fertility laboratory’. Centre stage at these occasions would be the serving of injected gonadotrophin-free rainbow trout lacking their testes and cooked in a variety of ways depending on the ethnic origin of the occasional cook. Distinguished among such gatherings were the famous traditional Christmas parties hosted by Gordon and Sylvia. Last, but by no means least, the team’s day-long excursions to the Kananaskis provincial park and the Rocky Mountain national parks of Banff and Jasper, all within a relatively short distance from Calgary, were another regular feature greatly enjoyed by all laboratory members.

As a low-key supervisor, Gordon would suggest a project to a student and then let them run with it and pursue their ideas. Many of his colleagues found this to be an effective strategy that they later emulated with their own groups. Gordon’s office was adjacent to the laboratory, and was always open, and he was always available for advice and guidance or to discuss ideas. His laboratories had a real buzz to them. Gordon brought a controlled passion to his work. He was intense but kind, creative, fun and inspiring. His colleagues remember him as a generous person with an infectious enthusiasm for research ideas. Gordon would discuss the potential projects and experiments and come periodically to the laboratory and ask how the experiments were being developed. Laboratory members also helped each other with the dissemination of methods and always plenty of advice. Collaborations were a standard part of the Dixon laboratory, with Paul Wiersma, Toni Garber, Robert Winkfein, Stephen Krawetz, Jacques Retief and Wayne Connor working together. Neighbouring laboratories also contributed, and principal investigators (PIs) such as Jim McGhee, Hans Van de Sande, David Bazett-Jones and Don McKay provided advice in some of the experiments.
Gordon’s personality and the environment that existed in his laboratory awakened his colleagues’ confidence, inquisitiveness and curiosity, gradually generating a capacity to ask questions and to contrast answers as well as to dig deeper in the discovery of the most intriguing facts that emerge at all levels in the biology and physiology of the organisms. A special issue of *Systems Biology in Reproduction Medicine* (Balhorn et al. 2018) was dedicated in honour of these qualities that he instilled.

**His family life, personal qualities, and years of retirement**

Despite the demands of his busy professional career, Gordon always carved out time for his family and time ‘to have a life’. He and Sylvia were a great (and very complementary) team and did everything together. It is certainly true that much of what Gordon achieved in his life would not have been possible without Sylvia. Gordon was a family man whose children and grandchildren were a source of great joy to them both (figure 4). He always returned from his many travels to scientific conferences around the world laden with gifts for his family. His daughter, Frances, particularly remembers a beautiful traditional doll that he brought back from Japan. It could not have been easy for him to transport such a fragile item along with all the other souvenirs he had brought for the rest of the family, but he knew how thrilled she would be to receive such an exotic treasure.

Gordon took his children to the public library at least once a week even before they were of school age and, in his own quite limited leisure time, he read voraciously. His taste in books was very eclectic and included the classics, prize-winning modern novels, mysteries, thrillers, history, biography and social commentary. His favourite work was J. R. R. Tolkien’s *The lord of the rings*, which he read for the first time when he was in his forties. He was deeply affected by the nobility of the characters portrayed by Tolkien and by the epic scope of his vision of Middle Earth. Gordon’s love of reading and his support of this wonderful pastime was one of the most important gifts he gave to his children.
During their twenty-plus years of retirement, Gordon and Sylvia travelled extensively and held many gatherings of family and friends at their home in Victoria. Gordon’s many passions included reading, gardening (his garden was spectacular), classical music, history and walking. He loved to follow cricket, Formula One racing and current affairs. After his retirement, he opted to focus on his family and personal hobbies and activities and did not continue his direct involvement in research. However, he did follow the career progress of his many trainees with great interest and always viewed their successes as his most enduring contribution to science.

In a newspaper quote on the occasion of being awarded an Izaak Walton Killam Fellowship late in his career, he said of his research on gene expression: ‘Every cell contains the same basic genetic information yet varies in function according to its location in the body. It’s like the same orchestra playing different tunes—we’re just beginning to understand how it works.’

When he became ill in early 2016 and was contemplating different possible treatment options, he commented on his life using a cricket analogy: ‘Well, I’ve had a pretty good innings!’ In closing, we think it can be agreed that this is an understatement and that Gordon Dixon had a remarkable life and career, left a wonderful legacy of research and training, and will be greatly missed.

In addition to the review of Gordon’s scientific work and personal qualities provided in the current memoir, the reader is also referred to excellent complementary information (CSBMCB 2007; University of Calgary 2016; Balhorn et al. 2018; Dignity Memorial 2019).

**AWARDS AND RECOGNITION**

1966 Ayerst Award, Ayerst/Pharmacia/Merck-Frosst Award, Canadian Biochemical Society (now Canadian Society of Biochemistry, Molecular & Cellular Biology)
1966 Steacie Prize for Natural Sciences, the E. W. R. Steacie Memorial Fund
1970 Fellow, Royal Society of Canada
1978 Fellow, Royal Society of London
1979 Josiah Macy Fellowship, Josiah Macy Jr Foundation
1980 Flavelle Medal, Royal Society of Chemistry
1982–1983 President, Canadian Biochemical Society
1987–1990 President, Pan-American Biochemical Society
1988–1994 Member of the Executive of the International Union of Biochemistry
1991 Izaak Walton Killam Memorial Prize, University of Alberta
1993 Officer of the Order of Canada

**ACKNOWLEDGEMENTS**

We wish to thank the archives of the Department of Biochemistry, University of Cambridge, for information and for permission to reproduce the picture of Gordon Dixon’s classmates and instructors in the undergraduate Biochemistry Part II class of 1950–1951 at the University of Cambridge.

The portrait photograph was given to the Royal Society by the subject. It is believed to have been taken by James H. Peacocke in 1993 (copyright unknown). Unless otherwise indicated, all other photos were provided by the authors of this memoir.
Rafael Oliva

Rafael Oliva is a professor of genetics in the Department of Biomedicine in the Faculty of Medicine and Health Sciences at the University of Barcelona, Spain. He is also the team leader of the Molecular Biology of Reproduction and Development research group at the Biomedical Research Institute August Pi i Sunyer (IDIBAPS) and senior consultant at the Hospital Clinic, Barcelona. He obtained his PhD in 1984 from the University of Barcelona, under the supervision of Professor Cristóbal Mezquita, from whom he inherited a lifelong interest in reproductive biology. Subsequently, he became a postdoctoral fellow (1986–1989) at the Department of Medical Biochemistry, University of Calgary, Canada, under the inspiring and enthusiastic supervision of Gordon H. Dixon, studying chromatin structural transitions in spermiogenesis and the evolution and function of protamines. After a stage at the Human Genome Center, Lawrence Berkeley Laboratories, Berkeley, USA, he returned to Barcelona, where he consolidated his career in reproductive biology—largely inspired by his former main mentors Cristóbal Mezquita and Gordon Dixon—and set up his research laboratory and team (ORCID 0000-0003-4876-2410). Much of Rafael’s work has been on the study of genetics, epigenetics, genomics and proteomics of the sperm cell and germinal cell line in normal development and in male infertility, with a main interest in the mechanisms involved in the chromatin structure–function and transitions.

Stephen A. Krawetz

Stephen Krawetz is the Charlotte B. Failing Professor of Fetal Therapy and Diagnosis and associate director of the C. S. Mott Center for Human Growth and Development in the Department of Obstetrics and Gynecology and Center for Molecular Medicine and Genetics, Wayne State University School of Medicine, Detroit, Michigan. He is also the founding editor-in-chief of Systems Biology in Reproductive Medicine. Dr Krawetz received his PhD in biochemistry from the University of Toronto and then trained as an AHFMR Postdoctoral fellow with Gordon Dixon within the Department of Medical Biochemistry at the University of Calgary from 1983 to 1989, which set the path for his independent career. He has published more than 200 manuscripts and edited several books detailing the regulation of gene expression by chromatin structure, emphasizing human spermatogenesis, bioinformatics and its application to personalized medicine. Over the last two decades, his group has established that the fitness of the paternal contribution reflects the relative diversity of sperm RNAs that continually respond to the environment. These RNAs may provide an essential component to early paternal genome reprogramming, acting as genetic and epigenetic impactors of the fetal onset of adult disease. They provide a personalized timestamp of the physical and reproductive
health of Dad, providing the opportunity to develop a personalized blueprint promoting the birth and healthy life of his children.

**GHD Consortium**

Walter T. Dixon PhD is associate vice president of Research and Priority Initiatives, Office of the Vice President (Research and Innovation), and professor of biochemistry and molecular biology at the University of Alberta, Canada.

Victor Ling QC OBC is president and scientific director of the Terry Fox Research Institute in Vancouver, Canada. He provides overall leadership of the Institute and oversees the development of translational research projects, relationships with stakeholders and communications.

Donald T. Wigle MD PhD MPH is now retired.

Choy Hew PhD is emeritus professor at the Department of Biological Sciences, National University of Singapore.

Peter Candido PhD is professor emeritus in biochemistry and molecular biology at the Faculty of Medicine, Life Sciences Centre, Vancouver, Canada.

Kostas Iatrou PhD was a professor in the Department of Medical Biochemistry (Biochemistry and Molecular Biology) of the Medical School in Calgary from 1981 until 2001. He is currently emeritus research director of the Institute of Biosciences & Applications at the National Centre for Scientific Research in Athens, Greece.

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