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Historical Records of Australian Science

John Foxton Ross Kerr (1934–2024)

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ABSTRACT

John Kerr (1934–2024) was internationally renowned for the discovery of apoptosis, the process of cell death to which he gave that name in 1972. He studied Medicine at the University of Queensland, completed a PhD at the University College Hospital, London, and qualified as an anatomical pathologist and a physician in both Australia and England. Most of his working life was spent at the University of Queensland, where he was Professor of Pathology for twenty years and also at the Royal Brisbane Hospital. As well as being a gifted and meticulous researcher, he was an inspirational lecturer. His life-long hobby was as a lepidopterist, and his impressive collection of butterflies and moths, one of the best in the country, was donated to the Australian National Insect Collection (ANIC), a major scientific resource managed by the Commonwealth Scientific and Industrial Research Organisation (CSIRO). He received numerous highly competitive awards for his ground-breaking research, including Officer in the General Division of the Order of Australia; the Fred W. Stewart Award, Memorial Sloan-Kettering Cancer Centre; the Paul Ehrlich and Ludwig Darmstaedter Prize; and the International Charles IV Prize, Charles University and the City of Prague. Kerr's early work on apoptosis fostered innumerable studies about the mechanisms of cell death in both normal physiological processes and in a wide variety of disease states, particularly degenerative diseases and carcinoma.

Keywords: apoptosis, carcinoma, cell death, degenerative disease, John Kerr, lepidopterist, medicine, pathology.

Early life and education

John Foxton Ross Kerr was born in Sydney, Australia on 24 January 1934, the elder child of John Ross and Mary Maud Kerr (née Hayley) (Fig. 1). Kerr's sister, Robyn was born in 1938. When he was a young child the family moved to northern Queensland, where Kerr's father worked for the Colonial Sugar Refinery Company Limited (CSR Limited) in the town of Innisfail, 90 km south of Cairns. For his primary education, Kerr attended a small government school at Goondi, near Innisfail. His father became manager of the Brisbane office of CSR Limited at about the time Kerr was due to commence his secondary education.

Both his parents had attended school in Sydney, and as the recipient of a boarding scholarship, Kerr attended Sydney Church of England Grammar (Shore) School in Sydney for his secondary schooling. There he was very positively influenced by the headmaster, Leonard Charles Robson (1894–1964), who had been awarded the Military Cross in World War 1, was a Rhodes Scholar who read mathematics at New College, Oxford, and was knighted for his services to education. Because Kerr's early education had been at a country school he was initially placed with the lower achievers in the class, but was soon moved to join the top students. Kerr did very well at school academically, and was awarded a number of prizes. He did acknowledge, though, that he was not successful at sport despite his best endeavours. In his final two years at school, he focused on mathematics, physics, chemistry and English, and in his last year was dux of his class. He was also editor of the Shore weekly newspaper. Kerr said that Robson used to send him mathematics problems to solve during the school holidays!

When applying for university entrance Kerr said that Science was his first thought, but it was pointed out to him by a school master that Medicine would likely present more

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Fig. 1. John Kerr with his father John Ross Kerr (courtesy of the Kerr family).

varied options of a scientific nature. Between 1951 and 1957 Kerr was enrolled in the MB BS course at the University of Queensland, with the course intermitted in 1955 during which he undertook a BSc in the University Pathology Department, and for which he received First Class Honours. In 1957, he graduated MB BS, also with First Class Honours, and he was the only student in his year to be awarded a university medal.

Kerr was an intern at the Royal Brisbane Hospital in 1958, and an acting medical registrar in 1959, and then for two years, 1960–1, he was a pathology registrar, also at the Royal Brisbane Hospital. In 1962 he went to London and there attended the Royal Postgraduate Medical School at the Hammersmith Hospital, where he completed their course in general medicine. Following this, he sat the examination for membership of the Royal College of Physicians of London, which he passed. In later years Kerr was awarded Fellowship of the Royal College of Pathologists of Australasia (1967), Fellowship of the Royal Australasian College of Physicians (1974), Fellowship of the Royal College of Pathologists (England) (1977), and Fellowship of the Royal College of Physicians of London (1992).

Postgraduate research in London

Between 1962 and 1964 Kerr undertook PhD studies in London under the supervision of Professor Sir Roy Cameron FRS (1899–1966) in the Department of Morbid Anatomy, University College Hospital Medical School. Born and educated in Australia, Cameron was always supportive of Australian researchers. Cameron's interest in experimental pathology was stimulated in part by his own work with Ludwig Aschoff (1866–1942) in Freiburg, Germany, where he concentrated on the pituitary.

Cameron suggested that Kerr should study the effects that would ensue in liver tissue after interrupting its portal venous supply, the hepatic artery supply remaining intact. This involved repeating the experiments undertaken by Peyton Rous (of Rous sarcoma virus fame) and Louise Larimore that were published in 1920.[1] Kerr ligated the portal vein branches supplying the left and median lobes of the rat liver. These lobes underwent both rapid and marked shrinkage, while the remaining two lobes, the right and the caudate, underwent compensatory enlargement. Within six hours of the procedure, confluent foci of necrosis were seen to develop around terminal hepatic venules, while nearby cells located closer to the portal tract remain essentially viable, being sustained by hepatic artery blood flow. The necrotic hepatocytes were quickly removed by mononuclear phagocytic cells, which had proceeded from circulating monocytes, as part of the inflammatory response. However, in the periportal parenchyma of these shrinking lobes, Kerr observed that scattered individual hepatocytes were also being progressively removed and this was by a process that was morphologically distinct by light microscopy to that of necrosis. The affected cells were transformed into small, round or ovoid masses composed of cytoplasm, some of which contained highly condensed fragments of nuclear chromatin. These structures were removed by Kupffer cells, resident mononuclear phagocytic cells of the liver or sometimes by epithelial hepatocytes. In the livers of healthy rats, occasional small

[1] Rous and Larimore (1920).

numbers of these structures could also be observed. That two different processes were occurring became indisputable and thus Kerr's early interest in cell death began.

At the time that these experiments were being performed, there was interest in the possible role that the rupture of lysosomes could play in causing cell death in response to a variety of injuries. Cameron's deputy, Professor Joe Smith, introduced Kerr to the histochemical demonstration of lysosomal acid phosphatase and esterase. Using frozen sections of the experimental rat tissue he had been investigating, Kerr was able to observe different patterns of distribution of lysosomal rupture. In normal liver, lines of discretely stained lysosomes were identified in the paracanalicular cytoplasm of hepatocytes, while there was diffuse paracanalicular staining in the areas of confluent necrosis consistent with the release of lysosomal enzymes. This lysosomal enzyme release was thought to reflect the general cell breakdown that is characteristic of necrosis rather than being an initiating event. However, the especially interesting observation was that the lysosomes stained discretely in the small, rounded cytoplasmic masses, indicating that they remained intact. Similarly, staining patterns with other histochemical techniques appeared to signify that ribosomes and mitochondria were also preserved in the rounded cytoplasmic masses. For this different type of cell death that was observed, Kerr suggested the term shrinkage necrosis, and his remarkably astute observations were published in 1965.[2]

Early work in Queensland on cell death

In early 1965 Kerr returned to his home city of Brisbane and joined the University of Queensland Pathology Department as a Senior Lecturer. Other members of the department at that time included Professor George Christie, who had also studied under Sir Roy Cameron in London, Dr J. A. Inglis as Reader, and Dr T. H. Vickers and Dr P. S. Bhathal, both Senior Lecturers.

The University of Queensland Pathology Department in 1967 acquired its first electron microscope and Kerr was thus able systematically to explore the ultrastructural evolution and morphological features of shrinkage necrosis.[3] This was a pivotal stage in the development of what was to become the apoptosis concept. Kerr initially received technical assistance from David Collins and later from Brian Harmon. The stereotypical changes that were described as occurring in the rat liver were later replicated in many other tissues and also, the features that Kerr observed were similar to those seen in recently published electron microscopic studies, which included so-called Councilman or acidophilic bodies known to occur in the liver in various natural diseases.

For these ultrastructural studies, the models of ischaemic liver injury and chemically induced liver injury were used. The small, rounded or ovoid bodies of condensed parenchymal cell cytoplasm which still lay in the extracellular space, were both membrane-bounded and contained closely packed well preserved cytoplasmic organelles. Because the cytoplasmic masses were often seen in clusters, with some of the masses being extremely small, it was felt that rather than occurring as a degenerative process that they most likely arose by a process of active budding off of protuberances that had formed on the surface of the apparently condensing cells. Some of these cytoplasmic bodies contained condensed chromatin. Before fragmentation of the cell there had been condensation and margination of the nuclear chromatin, with sharp edges and which abutted the nuclear envelope. There was phagocytosis of these membrane-bounded cytoplasmic fragments by both Kupffer cells and hepatocytes with their subsequent degradation within phagolysosomes.[4]

The ultrastructural features of hepatocyte necrosis were very different, with swelling of both the cytoplasm and mitochondria, breaking down of plasma membranes, the dissolution of cellular constituents and eventual ingestion by mononuclear phagocytes, but not by epithelial liver cells.

Three conclusions were drawn by Kerr at this stage of his research: first, that while severe cellular injury causes necrosis, more mild injury may increase a degree of shrinkage necrosis in a tissue; second, that the cellular condensation and budding is a metabolically active process and not a degenerative one; and third, that shrinkage necrosis represents at least one type of cell death that can be seen in normal tissues.

Kerr's initial observations about cell death were derived through experimental animal models; the next stage in the growing understanding of the cell death story concerned the relevance of his findings to malignant tumours in humans. In around mid-1970 Kerr attended a seminar given by a student on tumours in which the paradoxically slow rate of growth of basal cell carcinomas of the skin, despite their intrinsically high rate of mitoses, was discussed. This prompted Kerr to recall the recent comments of Jeffrey Searle, then a pathology registrar at the Royal Brisbane Hospital. Searle had noticed that the histological features of shrinkage necrosis could be seen in basal cell carcinomas, a common neoplasm of the skin, frequently seen in Queensland. Kerr and Searle undertook a light and electron microscopic study of basal cell carcinomas, which confirmed that shrinkage necrosis was indeed common in basal cell carcinomas, with the ultrastructural features observed being similar to those seen in the previous experimental liver samples.[5] And, of particular interest, was

[2]Kerr (1965).
[3]Kerr (1971).
[4]Kerr (1969).
[5]Kerr and Searle (1972).

that rather than being ingested by mononuclear phagocytic cells, many of the condensed tumour cell fragments were ingested and broken down by other tumour cells. Kerr and Searle were to deduce that cell death by shrinkage necrosis was likely to be a significant element in the kinetic equation of these cancers. They also observed that shrinkage necrosis, often quite extensive, could be seen by light microscopy in a range of tumour types. Additionally, it was thought that while mild ischaemia may have been a contributing factor to this, that shrinkage necrosis could also be observed in very thin trabeculae of tumour cells, for example, only two cells wide, meant that mild ischaemia was unlikely to always be the primary cause of shrinkage necrosis. Furthermore, by that time, instances of shrinkage necrosis were identified in different tissues of healthy animals, the process in those circumstances deemed to most likely represent an aspect of normal cell turnover. Interestingly, a human squamous cell carcinoma specimen, which had been surgically excised during a course of radiotherapy, had an increased level of shrinkage necrosis present compared with what might usually be expected in such a tumour. The preliminary conclusion in that instance was that radiotherapy may be eliciting shrinkage necrosis in tumours.

The apoptosis story

At about that time in Scotland, another pathologist, Alastair Currie (later Sir Alastair), noticed small fragments of cells in the adrenal cortices of rats, but he was not then aware of their significance. Currie was born in 1921 in Islay in the Inner Hebrides. He studied medicine in Glasgow and in 1947 joined the Royal Infirmary of Glasgow as a Lecturer in Pathology, in 1954 becoming an honorary Consultant Pathologist in that same department. He had an early interest in endocrine pathology, particularly that of the anterior pituitary and the adrenal cortex. Later, when he was head of the Division of Pathology at the Imperial Cancer Research Fund Laboratories in London, he developed a model of endocrine-dependent mammary gland tumours, the Huggins rat mammary carcinoma. The tumour was induced by the polycyclic hydrocarbon 9,10-dimethyl-1,2-benzanthracene (DMBA), and would often regress after oophorectomy. Currie had noticed that rats that had been given low doses of DMBA acquired cell fragments in the inner cortices of their adrenal glands. Later, as Regius Professor of Pathology at the University of Aberdeen, he, together with his PhD student, Andrew Wyllie, noticed similar-appearing fragments, also in the inner cortices of adrenal glands, on this occasion occurring in newborn rats which had been depleted of adrenocorticotropic hormone (ACTH). Similarly, Wyllie and Currie observed the death of scattered, single cells in the inner adrenal cortices of rats that had been treated with glucocorticoid, which had suppressed the secretion of the trophic hormone, ACTH.

In late 1970, Currie visited Brisbane for a month, as the Mayne Guest Professor in Pathology at the University of Queensland. This was to be a very important meeting of minds.

Kerr showed Currie images of shrinkage necrosis, including his electron micrographs of the process occurring in the liver, as well as discussing with him his plans to study basal cell carcinoma. Currie was very excited at seeing these images of shrinkage necrosis, as he had observed instances of cell death with similar light microscopic features in his endocrine experiments. Kerr undertook an electron microscopic examination of the DMBA-induced adrenal cortical changes and as predicted, the single dead cells he identified had the ultrastructural features of shrinkage necrosis.[6]

Kerr was due to take study leave from the University of Queensland and Currie suggested this be spent in Aberdeen in his Department. Kerr arrived in Aberdeen in September 1971. There had been several animal experiments underway in the department and following Kerr's arrival, electron microscopic studies were performed on tissues acquired from many of these. In all instances where single cell death was identified, the ultrastructural features of shrinkage necrosis were observed.

Wyllie, further exploring single cell death in the inner adrenal cortex due to a reduction in circulating ACTH levels, either in adult rats induced experimentally, or foetal rats, where this occurs physiologically, noted in both instances that the concurrent administration of ACTH could prevent the decrease in cell size and the cell death.[7] Additionally, after removal of the ovaries the apparently hormone-dependent DMBA-induced rat tumours also decreased in size, and large numbers of tumour cells were seen to have undergone shrinkage necrosis.

Another PhD student in the Aberdeen Pathology Department at the time of Kerr's visit was Allison Crawford, a developmental biologist. She was studying the teratogenic effects of 7-hydroxymethyl-12-methylbenz(a)anthracene, a major metabolite of DMBA, and this was associated with encephalocoele and spina bifida in the mature rodent foetus, when injected into Sprague-Dawley rats in mid-gestation.[8] Within 24 hours of the injection, there was tissue deletion from pronounced, but localised, cell death, and this accounted for the changes that developed. With electron microscopy, the ultrastructural features were those of shrinkage necrosis.

One of the final pieces in the jigsaw of what was to become the apoptosis concept came when Crawford told Kerr and his Scottish colleagues about cell death in normal embryonic and foetal development, a very precisely controlled

[6] Kerr (1972)
[7] Wyllie and others (1973).
[8] Crawford and others (1972).

process. Electron micrographs of cell death in normal development were available for review and the ultrastructural features identified were the same as those seen in shrinkage necrosis in post-natal life.

The key features of this distinctive and specialised form of cell death that was fundamentally different to necrosis could be enumerated. These included the specific light microscopic and ultrastructural features that could be observed in a wide variety of biological circumstances. The process appeared to be active and programmed and not a degenerative change as occurs in what was usually meant by necrosis, and there was no accompanying inflammation. The process occurred in normal adult tissues, most likely involved in normal cellular turnover and it also occurred in physiological involution and pathological atrophy. Additionally, it was also implicated in the finely controlled, focal deletion of specific tissues during normal development. The process occurred in malignant tumours and appeared enhanced by at least some non-surgical treatments. Often it appeared to function as the opposite of mitosis in regulating cell populations.

Professor James Cormack of the Department of Greek at the University of Aberdeen suggested the term 'apoptosis'. While it meant 'falling off' or 'dropping off' as with petals from flowers or leaves from trees in autumn, it also implied a relationship with mitosis. The ground-breaking paper 'Apoptosis: a basic biological phenomenon with wide-ranging implications in tissue kinetics', by Kerr, Wyllie and Currie, was published in the *British Journal of Cancer* in 1972.[9] That cell death could be an important aspect of the normal development of animals had already been proposed, but it was only this landmark paper that clearly and explicitly distinguished between this conserved and apparently programmed, normal, physiological cell death and the quite different features of acute pathological cell death which characteristically has an accompanying acute inflammatory response. What are now well known and characteristic morphological features of apoptosis, both at the light and electron microscopic levels, were both very well described and illustrated in that paper. In the first stage, the formation of apoptotic bodies included striking condensation of both the nucleus and the cytoplasm together with nuclear fragmentation and the separation of cytoplasmic protrusions that have formed on the cell surface to produce membrane-bounded cell remnants of varying sizes. Once formed, the majority of apoptotic bodies that had been seen to date were found within the cytoplasm of intact cells, including histiocytes, epithelial cells and neoplastic or carcinoma cells, this suggesting that they were rapidly phagocytosed. As well as enunciating and reviewing the many and varied biological circumstances in which apoptosis had been documented to have occurred, the likely implications of the presence of apoptosis as well as possible initiating factors were discussed. Showing penetrating insight, the authors established apoptosis 'not only as a distinctive morphological process but also an important basic biological phenomenon, which plays a complementary but opposite role to mitosis'.[10]

While there had been earlier descriptions of a type of cell death different to that of necrosis, these had mostly been published in the German literature and were not readily accessible to the English-speaking scientific community. The authors of the 1972 inaugural apoptosis paper were not then aware of this work. Additionally, these earlier papers tended to describe these instances of cell death as isolated phenomena, rather than as part of a unifying hypothesis as described by Kerr and others.[11]

Alistair Currie moved to Edinburgh in April 1972 to become Head of the Department of Pathology at the University, and Andrew Wyllie joined him there in October of that year. Currie was a very distinguished and highly regarded pathologist. He reorganised the departments of pathology both in Aberdeen and in Edinburgh, turning the latter, in particular, into a centre of excellence, both nationally and internationally. In time, Currie became increasingly involved in the strategic planning of medical research and health services at a national level. His interest in apoptosis did not wane, especially as its considerable significance began to be appreciated particularly with the early characterisation of genes involved in facilitating or inhibiting the process. Currie died in January 1994.

Andrew Wyllie, the son of a doctor, was born in Aberdeen in 1944, studied medicine at the University of Aberdeen and, after working with Currie and also Kerr in Aberdeen, spent three years as a Lecturer in Pathology in Edinburgh. Later, he worked in the Laboratory of Molecular Biology at Cambridge University, where he experienced the excitement of Roger Kornberg's discovery of the nucleosome. Wyllie returned to Edinburgh, and in 1980 he demonstrated that glucocorticoid-induced apoptosis of thymocytes was associated with endogenous endonuclease activation.[12] This gave a characteristic ladder pattern of oligonucleosomal fragments on DNA electrophoresis, quite unlike the diffuse smear seen on electrophoresis after cells undergo necrosis. Wyllie became Professor of Experimental Pathology in Edinburgh, and from 1998 until 2011 he was Professor of Pathology at the University of Cambridge. He died in 2022.

The University of Queensland

After the period of sabbatical leave in Aberdeen, Kerr returned to Brisbane and the University of Queensland,

[9] Kerr and others (1972).
[10] Kerr and others (1972).
[11] Cummings (2017).
[12] Wyllie (1980).

Fig. 2. John Kerr (courtesy of the University of Queensland).

where, together with co-workers, he continued to explore the role of apoptosis in diverse biological and clinical situations (Fig. 2). And in the process, many long-lasting personal and professional friendships were formed, in particular that with Dr Jeffrey Searle, a distinguished anatomical pathologist who specialised in diseases of the liver and the kidney in particular, and who for many years was Director of Anatomical Pathology of the Royal Brisbane Hospital. Kerr and Searle described the deletion of cells by apoptosis during castration-induced involution of the rat prostate,[13] and also the apparently spontaneous occurrence of apoptosis in cases of squamous cell carcinoma of the uterine cervix.[14] They both, together with Dr Brian Harmon, also undertook an electron-microscopic study of cell death by apoptosis in the anuran tadpole tail during spontaneous metamorphosis.[15]

With Professor Lawrie Powell AC (1934–2022) and others, apoptosis was proposed as the type of liver cell death that occurs in chronic active hepatitis, then commonly referred to as piecemeal necrosis. Powell was an internationally recognised hepatologist and medical researcher, and from 1990 to 2000 was the Director of the Queensland Institute of Medical Research.[16] Kerr, Powell and others also proposed apoptosis to be the mode of cell death in antibody-dependent lymphocytotoxicity.[17]

Other collaborators of Kerr, and then members of the University of Queensland Department of Pathology included Dr Neal Walker, an esteemed gastro-intestinal pathologist, Dr Glenda Gobé, a renal biology research scientist, and Clay Winterford, an electron-microscopist and histologist. Kerr was also supportive of Japanese pathologists, including Dr Hideaki Ishii and Dr Tomio Arai, who were visiting research fellows in the department.

A review of the nature of apoptosis, and the implications of its role in dermatopathology, was undertaken with Professor David Weedon AO, an eminent dermatopathologist, former President of the Australian Medical Association and former President of the Royal College of Pathologists of Australasia.[18]

The final two PhD students supervised by Kerr were Dr Trevor Forster, a Senior Lecturer in Applied Science at the Queensland University of Technology, and Dr Margaret Cummings, who later became the Director of Anatomical Pathology at the Royal Brisbane and Women's Hospital.

Kerr wrote about apoptosis and its kinetic role with respect to radiation biology for a book co-edited by his particular friend Professor H. Rodney Withers AO (1933–2015), also a medical graduate of the University of Queensland, and later a radiation biologist and oncologist in the United States.[19] Withers, who was a recipient of the Enrico Fermi Award, worked at the MD Anderson Cancer Centre and also at the University of California, Los Angeles.

In 1973 Kerr became a Reader in the Department of Pathology, and in 1975 he became Professor of Pathology, a position he held until his retirement twenty years later in January 1995. In July 1996, the title of Professor Emeritus was conferred by the University of Queensland.

Teaching

As well as being well known internationally for his groundbreaking research, Kerr was also acknowledged as 'one of the most popular and significant teachers in the history of the Faculty of Medicine'.[20] His inspirational teaching provided a generation of medical students with a solid

[13] Kerr and Searle (1973).
[14] Searle and others (1973).
[15] Kerr and others (1974).
[16] Kerr and others (1979).
[17] Stacey and others (1985).
[18] Weedon and others (1979).
[19] Kerr and Searle (1980).
[20] Pearn (2023).

foundation in the pathological basis of disease.[21] Though quietly spoken and unassuming, his otherwise serious lectures would be enlivened by his quick sense of humour and his very distinctive and infectious laugh.

As described by Jeffrey Searle at an occasion marking Kerr's retirement in 1995, 'John Kerr taught us all'. He would 'show you something he has just found at a PM, or remarking on an association between a clinical sign and a pathological finding with such enthusiasm that one could never forget it'. Kerr was also a physician and 'his practice of regarding pathology as an extension of clinical medicine was one of the keys to making him the great teacher he is'.[22] The inaugural University of Queensland Award for Excellence in Teaching was bestowed upon Kerr in 1988.

Pathology Museum

Kerr made an enormous contribution to the University of Queensland's Pathology Museum, then known as the James Vincent Duhig Museum of Pathology. At the time of his retirement in 1995, the museum housed 4000 documented specimens, many of which Kerr had collected, dissected and described (Fig. 3).[23] For many years Kerr was assisted by the museum curator, Alexander (Sandy) Powell, who prepared the specimens for display (Fig. 4). The museum has been regarded as one of the best collections of teaching specimens in Australia. It formed a uniquely valuable learning resource for many thousands of medical students.

Royal Brisbane Hospital

As well as Kerr's university work, from 1974 until his retirement, he was a Pathologist at the Royal Brisbane Hospital, as it was then known. During that time, the directors of the department were Dr Robert (Robin) Cooke and Dr Jeffrey Searle (Fig. 5). Rather than general surgical pathology reporting, Kerr mostly focused on diseases of the liver, in part a reflection of his earlier PhD studies in London. Every Friday afternoon, he and others from the hospital department met with gastroenterologists, including in particular, Professor Lawrie Powell, to review that week's clinical cases.

Each week, during the university teaching terms, Kerr performed a teaching autopsy, where a rostered group of students could see the dissection occurring while learning about the clinicopathological correlation of the case at hand. Kerr also attended the weekly registrar teaching session where the pathology registrars were shown a series of unknown histology slides for which they had to work out the diagnosis in front of various senior members of the department. While often a rather nerve-wracking experience for the registrars, they did appreciate Kerr's timely and insightful comments about the diseases being discussed.

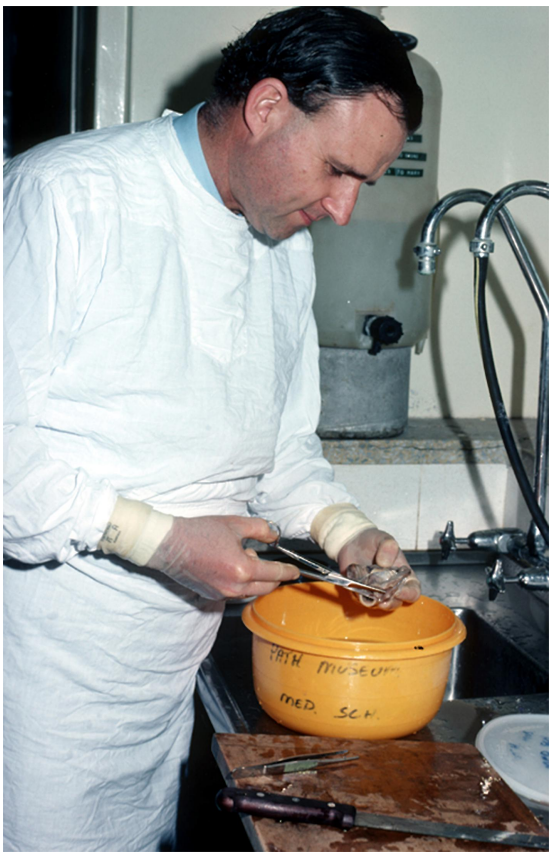

Fig. 3. John Kerr dissecting a specimen (courtesy of Robin Cooke).

Service to professional bodies

As well as his university and hospital work, Kerr made many significant contributions to a range of other professional bodies. These included being a member of the Council for the Queensland Institute of Medical Research. From 1988 until his retirement, Kerr was also an Adjunct Senior Principal Research Fellow at the Queensland Institute of Medical Research. He was a member of the Anti-Cancer Council of the Queensland Cancer Fund, and was grateful on relinquishing that position in 2001 to have received a kind note of acknowledgement from Paul de Jersey AC, then the Chief Justice of Queensland. Kerr was a member of the Queensland State Committee of the Royal College of Pathologists of Australasia, and also had been the Royal College of Pathologists of Australasia representative on

[21] Cummings (2017).
[22] J. Searle, pers. comm.
[23] Anonymous (1995).

Fig. 4. John Kerr and Sandy Powell (courtesy of Robin Cooke).

Fig. 5. John Kerr, with Jeffrey Searle (left) and Robin Cooke (right) (courtesy of Margaret Cummings).

the Postgraduate Medical Education Committee of the University of Queensland. He had also been a member of the Pathology Advisory Committee of the Queensland Department of Health. Helping to promote medical research in general, Kerr was a member of the National Council of the Australian Society for Experimental Pathology and was also a member of the Queensland State Committee of the Australian Society for Medical Research. And, because of all his earlier research work, being a founding member of the editorial board of the journal *Cell Death and Differentiation*, established in 1994, was especially cherished by him.

Fig. 6. John and Maureen Kerr, on a butterfly expedition (courtesy of the Kerr family).

Family and friends

In 1973 Kerr met Maureen Field, then a secretary in the University Pathology Department, who later became a neuropsychologist (Fig. 6). They married in 1994 and Kerr became step-father to Giovanna Field. He remained close to his sister Robyn's family, including his niece, Robina Rueger and nephew, Ross Rueger. He was also very attached to the family dogs, each a dachshund, and each one named Charlie.

A particular friend from medical student days and beyond was Dr Michael O'Rourke (1935–2022), a distinguished surgeon, who was Medical Superintendent at the Ipswich Hospital (1967–71) and later, senior surgeon at the Mater Hospital (1973–91) as well as a Senior Lecturer and Clinical Tutor in Surgery at the University of Queensland.[24]

Kerr's national and international apoptosis colleagues including Professor Sharad Kumar, Emeritus Professor Kay Ellem (1931–2013), Professor Gerry Melino and Professor Richard Lockshin, were also esteemed friends. And in quite a different world, Kerr had many long-term, valued friends in the lepidoptera community.

Lepidoptera

Kerr's lifelong interest in butterflies and moths began through serendipity. With the heightened fear of a Japanese invasion of Northern Queensland in World War 2, many civilians, especially women and children, were evacuated. Kerr and his mother had the great good fortune to stay with the family of Dr Gustavus (Athol) Waterhouse (1877–1950) in Killara in Sydney. Athol Waterhouse, who was born and lived in Sydney, had graduated from the University of Sydney with a Bachelor of Science in 1899 and a Bachelor of Engineering (mining) in 1900, and was awarded a Doctor of Science in 1924 for his research on the butterfly genus *Tisiphone*. He was an assistant assayer with the Sydney branch of the Royal Mint from 1900 to 1926, but he was best known as an entomologist. He began collecting butterflies in 1893, and was renowned for his meticulous taxonomic studies. With George Lyell, in 1914, he published the book *The Butterflies of Australia*, the first comprehensive work on Australian butterflies in western literature.[25]

Athol Waterhouse was the uncle of Douglas Frew Waterhouse (1916–2000), Chief of the CSIRO Division of Entomology for over twenty years, and recipient of many awards and Fellowship of the Australian Academy of Science. Before Douglas Waterhouse was even ten years old, Athol took him on many collecting trips in the Sydney region, instilling in him a considerable understanding of Australian butterflies and other insects from an early age.

In a similar spirit, Waterhouse inspired in the young Kerr an earnest enthusiasm for butterflies that was to remain

[24] O'Rourke and Ellem (2000).
[25] Waterhouse and Lyell (1914).

with him lifelong. As Kerr himself recollected in 2013 on the occasion of his own butterfly collection being donated to Australian National Insect Collections (ANIC), a major scientific collection managed by CSIRO: 'I developed a passion for butterflies at an early age under the guidance of the legendary Dr G. A. Waterhouse. Despite my youth he managed to implant the notion that collecting is not merely a diverting pastime but should involve scientific study. Throughout my adult life most holidays were devoted to collecting trips to various parts of Australia'.[26]

After finishing his school years in Sydney, Kerr returned to Brisbane, where he met Jack Macqueen (1900–86) and they became good friends. Macqueen was a dairy farmer by profession and at that time lived near Millmerran in Queensland. He had a very extensive and meticulously labelled insect collection that included 25,000 Lepidoptera and 7000 Coleoptera, and which he donated to the ANIC in 1975. Kerr went on many collecting trips, but two particularly special ones were those undertaken with Macqueen to the Iron Range on the Cape York Peninsula. On their first trip in May 1961 when they were fortunate to be guests of the mining company BHP, they discovered two New Guinean butterfly species (*Hypochrysops hippuris* and *Toxidia inornata*), which had not been previously known in Australia.[27] Their second trip to the Cape York Peninsula occurred in April and May in 1966, and this trip elicited *Philiris ziska*, *Philiris diana papuana*, *Allora major*, and a special subspecies of *Candalides consimilis*.[28] Soon after Kerr made his early butterfly discoveries, he corresponded with Dr Ian Common, the curator of Lepidoptera in the ANIC at CSIRO in Canberra. With initial guidance from Common, Kerr developed the delicate skill of dissecting and mounting the fragile male genitalia of small Lepidoptera, demonstrating how to interpret the difference in species based on micro-structures, and referring to these differences when describing and publishing species which were new to the scientific community.

In December 1964, Kerr was introduced by his friend Tom Guthrie to Edward (Ted) Edwards AM (1945–2023) and they spent a wonderful day collecting in the Blue Mountains. Edwards, an eminent Australian lepidopterist, worked at the ANIC for over forty years where he was manager of the Lepidoptera collections, and later in retirement, was an Honorary Research Fellow. He was renowned for both his encyclopaedic knowledge and his support of fellow lepidopterists. Edwards was first able to see Kerr's very impressive collection in February 1969. He highlighted the importance of Kerr's trip to Iron Range, or the Claudie River, as the area is also called, and how this became a nexus for butterfly and moth collectors because of the important findings of this exploratory trip.[29]

In 1967, Kerr and Macqueen collected a specimen of a jewel butterfly, together with many more specimens of what was thought to be the same species, all from the area which included Leyburn and Millmerran. Later, with the involvement of Don Sands OAM, they were able to describe the butterfly as a new species: the bulloak jewel *Hypochrysops piceatus*.[30] Macqueen moved to Toowoomba in 1976 and on the Great Dividing Range, Kerr and Macqueen collected many more lepidoptera of interest, and were sometimes joined in these ventures by Don Sands. In their early paper, Kerr, Macqueen and Sands were able to show that a small butterfly, *Acrodipsas illidgei*, known to have predatory larvae that fed on ants, and as a subspecies of *Acrodipsas* (then *Pseudidpsas*), was actually a distinct species and not a subspecies of a well-known species, *Acrodipsas myrmecophila*.[31]

Don Sands is an entomologist who worked for the CSIRO for thirty years, where he focused on the taxonomy, ecology, and conservation of insects. He investigated the natural enemies of insects and weeds, solutions to major pest problems and also, biological control projects, and in 2010 was awarded the Australian Natural History Medallion. He was awarded a PhD (1982) and also a DSc (2023) from the University of Queensland. Living in Brisbane, he and his wife Susan were to be greatly treasured, life-long friends of Kerr and his family.

In July 1975, on his third visit to the Cape York Peninsula, Kerr joined a trip to a rainforest area east of Heathlands. This was part of an Australian Biological Resource Study, a programme of Environment Australia, and was organised by Geoff Monteith and Jiro Kikkawa. There they caught the impressive and distinctive orange-brown *Lexias aeropa*.[32] Kerr enjoyed himself enormously on this trip. His fourth trip to Cape York was in July 1993, when together with Sands, they collected specimens on Mt White.

Kerr was involved in the discovery of six new native Australian species and these were described by him along with his various collaborators. The species included: *Trapezites macqueen* (with Sands),[33] *Hesperilla fuva* (with

[26] Edwards (2013).
[27] Kerr (1966).
[28] Kerr (1967). Sands and Kerr (1978).
[29] Edwards (2013).
[30] Kerr and others (1969).
[31] Kerr and others (1968).
[32] Monteith and Kerr (1977).
[33] Kerr and Sands (1970).

Sands),[34] *Candalides geminus* (now *Erina geminus*) (with Edwards),[35] *Jalmenus pseudictinus* (with Macqueen),[36] *Hypochrysops piceatus* (with Macqueen and Sands),[37] and *Acrodipsas mortoni* (with Sands and C. G. Miller).[38] Indeed, as Edwards described, Kerr, Sands, and Macqueen 'pioneered a butterfly "enlightenment" during the 1960s, which endures to this day.'[39]

Kerr's collection was housed in nine, twelve-drawer beautiful cedar cabinets in a specially constructed butterfly house in the backyard of his long-term home in Hamilton in Brisbane. His collection included one holotype, 71 paratypes of 16 species of butterflies, and in addition, some unique and historical specimens too. Several new genera of moths were included as well as many undescribed species. And as described by Sands, Kerr was 'meticulous with his pinning and spreading the wings of specimens … without even the tiniest of marks'.[40] His collection was both extraordinary for its breadth and for its immaculate preparation.

Kerr's collection of moths was similarly very impressive. Housed in more than 140 store boxes, they were in immaculate condition and were the culmination of twenty five years of collecting, mostly in southeast Queensland, including at the Sunshine Coast and Upper Brookfield. A female *Taurometopa haematographa* (Odontiinae, Crambidae) from Mission Beach, was particularly precious, having been previously unrepresented in the ANIC.[41]

Kerr's collections of butterflies and moths were donated to the CSIRO for lodgement with the ANIC in 2013 and 2015 respectively.

Invited international presentations

As the importance of apoptosis came to be appreciated in the scientific community, Kerr was invited to present at a number of international meetings. Highlights of these included giving the keynote opening lecture at a three-day meeting on Apoptosis at the Banbury Centre, Cold Spring Harbor Laboratory, New York, in April 1990, and in May 1993, giving the Twelfth Milford D. Schulz Lecture at the Department of Radiation Oncology at the Harvard University Medical School. Kerr gave the opening lecture at the Paris Conference on Apoptosis in AIDS and Cancer in December 1993, the opening lecture at the First International Conference in Skeletal and Cardiac Muscle in Padua in June 1996, the keynote lecture at the International Symposium on Biodefence Mechanisms in Chiba, Japan in September 1996, and in June 1998, in San Diego, the Ramon Guiteras Lecture at the Annual Meeting of the American Urological Association.

Fig. 7. John Kerr holding the Charles IV Prize medallion in Prague in 2002 (courtesy of the Kerr family).

Honours and awards

Kerr was the recipient of many awards, local, national and international and each award was of special importance to him. The awards are listed here: University of Queensland Award for Excellence in Teaching (1988); Royal College of Pathologists of Australasia Distinguished Fellows' Award (1989); Life Governor, Australasian Postgraduate Federation in Medicine (1991); Bancroft Medal, Queensland Institute of Medical Research (1992); Bancroft Medal, Australian Medical Association (1993); Fred W. Stewart Award, Memorial Sloan-Kettering Cancer Centre (1995); Officer in the General Division of the Order of Australia (1996); Fellowship of the Australian Academy of Science (1998); Doctor of Science *Honoris Causa*, the University of Queensland (1998); the especially prestigious Paul Ehrlich and Ludwig Darmstaedter prize (with Robert Horvitz), Frankfurt am Main (2000); Tall Poppy in Science Award, the Australian Institute of Political Science (2001); the University of Queensland Medical Alumnus of the Year (2001); International Cell Death Society Award for the creation of

[34] Sands and Kerr (1973).
[35] Edwards and Kerr (1978).
[36] Kerr and Macqueen (1967).
[37] Kerr and others (1969).
[38] Sands and others (1997).
[39] Edwards (2013).
[40] Sands (2024).
[41] Edwards and Turco (2016).

the concept of apoptosis (2002); the International Charles IV Prize, Charles University and the City of Prague (2002); the Centenary Medal, Australia (2003); the Australia and New Zealand Society for Cell Developmental Biology President's Medal (2003) and Fellow of the Institute, the Queensland Institute of Medical Research (2005) (Fig. 7). Very nicely, at the University of Queensland Medical School at Herston, where Kerr spent the great majority of his working life, there is now a room (Room 320A), which is called the Emeritus Professor John Kerr Room, with a plaque outlining his main achievements and contributions to the University.

Significance of work and legacy

Kerr is best known for his ground-breaking work on apoptosis. In the seminal *British Journal of Cancer* paper of 1972, Kerr along with Wyllie and Currie 'were the first to collate and define the distinct morphological features of controlled cell death in different contexts'.[42] The paper of 1972 currently has 13,813 citations. Now, more than fifty years since its publication, a PubMed search for the term 'apoptosis' reveals 612,849 journal articles. However, the 1972 paper is not just of interest for historical reasons, 'but is also very much alive in current studies focused on the analysis of apoptosis in both normal physiology and multiple forms of disease'.[43] Additionally, subsequent work on apoptosis, including its complex molecular mechanisms, has led to the identification of several additional forms of programmed cell death, and also the development of a new class of drugs that trigger apoptosis in certain forms of cancer.[44] The bibliography of John Kerr is provided as supplementary material.

After his retirement Kerr did not undertake any active research in the field of apoptosis, but he watched its progress with great interest. When a new finding was made in the field of cell death, he typically sent hand-written letters of congratulations from his home in Hipwood Avenue to his national colleagues.

In a completely different sphere, but still very much involving scientific research and meticulous attention to detail, was Kerr's extensive Lepidoptera collection, which he kindly donated to the ANCI, a part of the CSIRO and which forms a valuable part of their collection.

Although Kerr retired a little over thirty years ago, his pathology lectures and tutorials are still fondly remembered by a large contingent of what are now senior medical practitioners working throughout Queensland and beyond. It was not just the very logical and clearly elucidated scientific explanations that they remember, although these were greatly valued. More, it was his inherent good nature that came across to the students. The all-encompassing tremendous rapport he had with people inspired each individual he was in contact with to try to do their best.

Kerr was also quietly benevolent. Over the years he made numerous, generous and very unobtrusive philanthropic gifts in support of a variety of causes at the University of Queensland.

Kerr died in Brisbane on 4 June 2024, after a long illness.

Supplementary material

Supplementary material can be accessed from the article page online.

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