CSIRO PUBLISHING

Historical Records of Australian Science, 2017, **28**, 183–193
https://doi.org/10.1071/HR17011

Geoffrey Bruce Sharman 1925–2015

Hugh Tyndale-Biscoe[A,C] *and Jennifer A. Marshall Graves*[B]

[A]114 Grayson Street, Hackett, ACT 2602, Australia.
[B]School of Life Science, La Trobe University, Melbourne, Vic. 3086, Australia.
[C]Corresponding author. Email: hughtb@bigpond.com

Geoff Sharman was one of the most important figures in the post-war renaissance of research into the indigenous mammals of Australia. He discovered the remarkable phenomenon of delayed development, or embryonic diapause, in kangaroos. He pioneered marsupial cytogenetics, making seminal contributions to chromosome evolution, sex determination, and X chromosome dosage compensation in female marsupials. He inspired a whole generation of younger biologists to make the investigation of Australian mammals the primary objective of their professional careers. Fifty years before he began there had been a brief but highly fruitful period of investigation into the native fauna based at the University of Sydney Medical School.[1] When the four pioneers departed to Chairs in Britain and Fellowship of the Royal Society, further research in the field languished until the 1950s. Sharman's research built on that pioneering work, particularly of J. P. Hill and his associates on the reproductive anatomy and development of marsupials, and then extended it into the new field of cytogenetics.

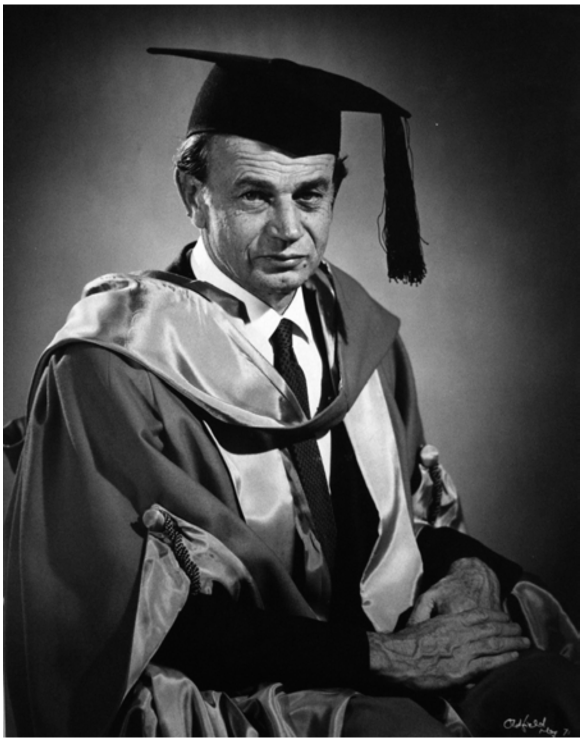
Published online 31 August 2017

Early Years

Geoff was fond of saying that he came from very humble stock and, but for the opportunity provided after the Second World War for returned servicemen to attend university, he might never have had a scientific career. On the other hand, he must have nursed dreams of academic fame and fortune, as one of us [JMG] recalled him saying, on a visit to La Trobe University in the 1990s, 'I knew at age 16 that I wanted to be a Professor of Zoology.'

Despite his humble beginnings he could trace his antecedents back to the Swing Rioters of 1830 Britain. These were country ploughmen who feared that they would lose their livelihood to new agricultural machinery and so they smashed up the swing winnowers being introduced. For this action, 755 of them were condemned to transportation to New South Wales and Van Diemen's Land. After the Reform Bill of 1832, however, they were pardoned and, while some returned to Britain the majority remained and, as Geoff wrote, 'became the founders of present day Australian families.' His father, Clifford Alfred Valentine Sharman, born in 1893, was the fourth generation from the founding family of George and Mary Sharman who migrated to Tasmania in 1853. His mother, Jean Hope (née Ralston) was also from Tasmania. Geoff's parents had a dairy farm, *Solmont*, at Dunorlan ~60 km from Launceston.[2] Geoffrey Bruce, the second child in a family of four girls and two boys, was born on 13 January 1925 in Launceston. Due to the severe conditions of the Great Depression he was obliged to leave school at 15 and become a carpenter's apprentice in Launceston. On reaching 18 he joined the Royal Australian Naval Reserve in June 1943 and his naval medical record states that the first joints of the index and second finger of his right hand were missing. Not quite correct, according to his son John; he lost the nail of the index finger and part of the second finger in a timber planer during his former employment.

Geoff served on HMAS *Huon* and HMAS *Burdekin* as an Ordinary Seaman on convoy duty between Papua New Guinea and the Philippines and was demobilized on 24 May 1946 in Hobart. Initially he resumed his former trade, taught woodwork at the Launceston Technical College and worked on his parents' farm. He presumably



completed the school leaving-certificate at this time because a Commonwealth Returned Servicemen's Traineeship enabled him to enrol at the University of Tasmania in Hobart at the beginning of 1949.

He found study very hard and nearly gave up in his second year. But then he came under the guidance of Professor Newton Barber in botany, which introduced him to the new field of cytogenetics. Geoff must have been an exceptional student for in December 1950, while still an undergraduate, he co-authored a letter to *Nature*[3] on multiple sex chromosomes in the marsupial, *Potorous tridactylus*, the long-nosed potoroo, that lives around the Hobart campus. This was a harbinger of his subsequent scientific career; the cytogenetics and reproduction of macropod marsupials. The full list of Geoff Sharman's scientific publications is available as Supplementary Material to this paper. Three more papers on cytogenetics were published from his Hobart studies[4] by the time he graduated with a BSc Hons from the University of Tasmania at the end of 1952. These articles won him a Nuffield Fellowship to continue research on marsupials with Professor Harry Waring at the University of Western Australia. A condition of the Fellowship was that he not enrol for a PhD degree. Instead Geoff was awarded a DSc ten years later from the University of Western Australia on his published work.

While at Hobart, Geoff met Barbara Veale, who was working in the Library of the Royal Society of Tasmania. As he later remarked, 'You would be surprised at the number of scientists who meet their wives in libraries.' Barbara's father, Raymond James Veale, born in New Zealand in 1904, was an agronomist in Tasmania and her mother was Nellie Maude (née Greenhill) and distantly related to the Sharmans. Geoff and Barbara had a shared interest in tramping and on the 1951 Easter weekend were in a party that revisited the Old Crotty [Fincham] Track to the Franklin River and Mt Fincham. At the remote Tahune Hut by the Franklin they were greeted by Olegas Truchanas, whose beautiful photographs later saved the river from being dammed. They all celebrated Barbara's 21st birthday there.[5] Barbara and Geoff were married in February 1952 and moved to Western Australia at the end of that year.

University of Western Australia, 1952–4

The renaissance of Australian Mammalogy had begun in 1948 when Harry Waring became the first Professor of Zoology at the University of Western Australia. Harry came from Aberdeen University where he had been influenced by Lancelot Hogben and the rise of comparative physiology in Europe. He immediately directed attention to the marsupials as worthy objects of study in their own right and began to attract lots of young biologists to study them, based on two sorts of questions: How does a marsupial compare with a eutherian in respect to physiological functions? And how does a particular aspect of physiology relate to function and survival in a field situation?

On nearby Rottnest Island there was an abundant population of the small wallaby, the quokka (*Setonix brachyurus*), and when Geoff and Barbara arrived at the end of 1952 research was being actively prosecuted on adrenal function, temperature regulation, water balance, digestive physiology and kidney function of this handy species. Geoff 's task was to study its reproduction and he wasted no time; January is the start of the breeding season and he was collecting material that month.[6]

He began the first systematic study of the oestrous cycle and pregnancy of any Australian species of marsupial and only the second of any marsupial; Carl Hartman had studied the Virginia opossum (*Didelphis virginiana*) 30 years before.[7] Using the changing cytology of the vaginal epithelium, as Hartman had, Geoff determined that the quokka is polyoestrous with a cycle length of 27–28 days and that fertilization occurs one day after oestrus and birth occurs 25–26 days later. Pregnancy is thus one day shorter than the oestrous cycle and birth is followed by a post-partum oestrus and another pregnancy. However, no further birth occurred until lactation ceased, either because of the storage of sperm—as hitherto thought—or because of the delayed development of the next embryo. By ligating the oviducts of lactating quokkas Geoff proved that stored sperm were not involved and demonstrated conclusively that the egg is fertilized at post-partum oestrus and lies dormant in the uterus as a 100-cell blastocyst during the succeeding lactation. This major discovery was submitted to *Nature* on 9 August 1953 and published early in 1954.[8] The three definitive papers on the anatomy, histological changes in the uterus and vaginae, and normal and delayed pregnancy, were submitted to the *Australian Journal of Zoology* in June 1954 and appeared the next year.[9] They were followed by a brief note confirming delayed implantation in another macropod marsupial, the tammar, *Macropus eugenii*, and the prediction that the phenomenon may be common to all kangaroos and rat kangaroos,[10] which proved to be largely correct. These papers established Geoff 's reputation as an independent and original scientist.

At the beginning of 1955, the Sharmans left for Britain and a year at the Medical Research Council Radiobiology Unit at Harwell to pursue Geoff 's other interest, cytogenetics. He arranged for six male long-nosed potoroos to be sent live from Hobart to Harwell so that he could investigate the effect of radiation on mammalian chromosomes.[11] The low number and large size of potoroo chromosomes made this a good species in which to investigate the topic, then of acute interest to Harwell. While this was his main project he was also intrigued by a report of sex chromosome polymorphism in the common European shrew, *Sorex araneus*. In the autumn of 1955 he collected five specimens that showed that the diploid number varied from 22 to 25 in different individuals.[12]

More significantly for his later work on X chromosome inactivation, he met Mary Lyon, the discoverer of X chromosome inactivation,[13] who moved from Edinburgh to Harwell during that year.

By the end of 1955 Geoff was giving his address as Department of Zoology, University of Adelaide where he would take up a lectureship in 1957. However, the Sharmans remained in London through 1956 at the Department of Physiology, Royal Veterinary College, where Geoff examined the foetal membranes and placentation of the quokka under the guidance of Professor E. C. Amoroso FRS. Four years previously Amoroso had published a comprehensive review of mammalian placentation,[14] and was the acknowledged master of the field. Geoff wrote to HTB,

> I enjoyed working with Amoroso very much. I was able to work up fairly thoroughly a series of *Setonix* intra-uterine embryos and thanks to Amoroso was able to get orientated on foetal membranes. My lecturer in embryology didn't tell me that mesoderm wasn't really red, like on the blackboard![15]

This visit resulted in a major paper five years later on embryonic membranes and placentation in marsupials.[16]

Waring had hoped Sharman would return to Perth and to that end he had arranged the finance for a Senior Lectureship to be offered to him while he was in Britain. However, Geoff was already committed to a lectureship in Adelaide, which he took up in 1957. In the same letter to HTB he wrote, 'My only objection to Perth was its poor library facilities and its great distance from the rest of Australia. However, I am afraid I didn't get on so well with Waring and I like [Professor WP] Rogers (whom I have known for a long time) very much.' This would not have pleased Waring who had a long memory on such matters, as will become evident.

The University of Adelaide, 1957–61

During their time in Adelaide, Barbara and Geoff 's two sons were born. John Andrew was born in 1958 and Robert James in 1960. In later life John's main career has been English language teaching and Robert is an aircraft pilot and flying instructor.

In Adelaide, Geoff continued his two primary research interests in marsupial cytogenetics and marsupial reproduction. It was during this period that Geoff was closely involved with a few other mammalogists in developing the idea for an Australian Mammal Society, which took form at the ANZAAS Congress in Adelaide in 1958 and was inaugurated a year later at the subsequent Congress in Perth.[17]

Marsupial Chromosomes

Geoff now became seriously involved in tackling some of the great questions about DNA and chromosomes. An age-old question, still unanswered, is why mammal genomes—about a metre of DNA that shares overwhelming genetic homology in all vertebrates—is cut up into different numbers of short or long pieces (that we see as chromosomes) in different species. The distribution of chromosome numbers among eutherian mammals is very wide, with a diploid number (2n) of between 6 and 92 with a single mode at 40–45.

Marsupial genomes are much the same size as eutherian genomes, but they are arranged as fewer, larger chromosomes; the smallest kangaroo chromosome is about the size of the largest human chromosome. Geoff had studied species in which the females had the smallest number ($2n = 10$) of any species of mammal described at the time (marsupials were later bounced from the Guinness Book of Records by the Indian muntjac (*Muntiacus muntiac*),[18] which has only 6 chromosomes). Sharman was the first to point out that the distribution of chromosome numbers among marsupial species was rather narrow, and, unusually, bimodal, with strong peaks at $2n = 14$ and $2n = 22$.[19] He proposed that the $2n = 22$ mode was likely to be an ancestral number, because it was shared by American species (thought to have been the first to diverge), and some Australian species. Fusion of these smaller chromosomes would have occurred to make the 14 larger chromosomes.

This was the beginning of a long and sometimes heated debate with his colleagues at the University of Adelaide, David Hayman and Peter Martin, who argued strongly that $2n = 14$ was ancestral, and fission of these fewer larger chromosomes in South American lineages accounted for the $2n = 22$ karyotypes.[20] They made a good argument for it being basic at least to Australian lineages because it is shared by at least some species of all Australian marsupial superfamilies.

Little more than arguing could be done with the crude cytological techniques of the day that offered no information on the gene and DNA sequence content of chromosomes. An important improvement was the development of treatments that revealed a transverse set of bands. Building on the huge body of observations on chromosome size and shape by Hayman and Martin, their student Ruth Rofe discovered that the detailed banding pattern of the $2n = 14$ karyotype was shared by some members of all Australian families as well as two families of South American marsupials.[21]

New techniques enabled direct comparisons of DNA content. Chromosome 'paints' could be prepared by physically separating chromosomes on the basis of size and DNA content, preparing DNA from each, tagging with a fluorochrome and hybridizing to the chromosomes of the same or other species.[22] These single chromosome probes painted homologous regions in dazzling colours—Geoff was impressed! Painting showed that, indeed, the $2n = 14$ karyotypes were all the same, but also that the few Australian $2n = 22$ and 20 karyotypes were unrelated to those of American marsupial superfamilies, a blow for the ancestral $2n = 22$ hypothesis.

The debate took a new twist, however, when Brazilian cytogeneticist Marta Svartman used probes that lit up the ends of chromosomes (telomeres). They studied seven South American species including *Caluromys philander*, *Metachirus nudicaudata*, *Microureus cinereus* and *Marmosops incanus*, all with 14 large chromosomes. They detected telomeric sequences in the middle of the large chromosomes and suggested that they mark where smaller chromosomes of a $2n = 22$ individual had fused secondarily into the $2n = 14$ configuration.[23] Geoff 's $2n = 22$ ancestor was back in business.

Most recently, however, new techniques for gene mapping were used to show that the gene content and order over Svartman's proposed fusion points on these large marsupial chromosomes was conserved in outgroups: eutherian mammals and even chicken and frog, so it must be ancestral.[24] This implied that the large chromosomes of $2n = 14$ species were ancestral to all marsupials.

Marsupial Reproduction

In his first years in Adelaide, Geoff also focussed on reproduction in the common brushtail possum, *Trichosurus vulpecula*, a common species in the suburbs. It provided a useful contrast to the pattern of reproduction in the quokka and other macropod marsupials because the 17-day gestation was considerably shorter than the oestrous cycle of 24 days and the species did not display post-partum oestrus or embryonic diapause.[25] In this respect it was similar to the pattern of the American opossum described by Hartman in 1923. What he did show was that, at day 17 after oestrus, the unmated brushtail possum was capable of suckling a newborn young transferred to one of the two teats in her pouch, thereby demonstrating that no additional hormones were involved during pregnancy in the preparation of the mammary gland for lactation.[26] With Phyllis Pilton he began the first studies on the hormones of reproduction that supported this conclusion; the excretory product of progesterone, pregnanediol, was assayed in the urine of pregnant and non-pregnant possums and found to be the same concentration, there being no increase during pregnancy.[27] With his students they did the first experiments to test the role of the corpus luteum in maintaining pregnancy in the possum but these were never fully published and only appeared in another paper,[28] on the red kangaroo, which by then dominated his interest.

By 1959 Sharman was the leading figure in the field of marsupial reproduction and was invited to contribute several reviews. At the first symposium held in the new home of the Australian Academy of Science, fittingly to celebrate the centenary of the publication of Charles Darwin's *The Origin of Species by Natural Selection*, Geoff spoke on the evolution of marsupials.[29] He was also invited to contribute to the major volume *Biogeography and*

Ecology of Australia.[30] This was a masterly review of the previous work on marsupial reproduction by J. P. Hill, Carl Hartman and the nineteenth-century scientists, as well as a review of the current Australian work that set the agenda for the field for the next decade. Two years later his review of marsupial placentation, largely based on his own study of the quokka, was published. At the same time a DSc degree was conferred on him by the University of Western Australia for his contributions to marsupial research.

Soon after going to Adelaide, Geoff had become the supervisor for a young wildlife biologist, Alan Newsome, working for the Northern Territory Government on ecology of the red kangaroo, *Macropus rufus*, because the species was regarded as a serious problem for the cattle industry. Newsome soon confirmed Geoff 's conclusion that delayed implantation is common to all kangaroos and also discovered that in severe drought female kangaroos enter anoestrus and rapidly return to oestrus after breaking rains. This was probably the initial incentive for Geoff to redirect his research from the possum to the kangaroos. At the same time the CSIRO Wildlife Survey Section was engaged in two projects on kangaroo ecology for the same reason as the Northern Territory Government; in Western Australia a study of red kangaroos and euros (*Macropus robustus*) had begun in the mid-1950s and another in western New South Wales on red and grey kangaroos, *Macropus giganteus*. The leader of the NSW studies, Harry Frith, had become the Chief of the newly established Division of Wildlife Research in 1961, and he sounded Geoff out on moving to Canberra to lead a much enlarged programme on kangaroo reproduction, including detailed studies on a substantial colony of captive animals.

In September 1961 Geoff wrote, 'It looks as though I will be going to CSIRO so I am beginning to do some intensive natural history on the red kangaroo on which I intend to work in the Section. We have just had two births, from delayed blastocysts, both 235 days from copulation.'[31] With Phyllis Pilton and two young technicians, Jim Merchant and Frank Knight, they determined the length of the oestrous cycle and pregnancy in the red kangaroo and the duration of embryonic diapause when lactation ran its full course.[32] Pilton also published the first study of reproduction in the grey kangaroo in 1961,[33] probably the western grey kangaroo (*Macropus fuliginosus*) although this was not resolved for another ten years when what was thought to be a single species was divided into two species with different reproductive patterns.[34]

The CSIRO Division of Wildlife Research, Canberra, 1962–5

The Sharmans, now with two young sons, moved to Canberra at the beginning of 1962. Geoff brought his two young technicians from Adelaide, and with Frith's technician Bevan Brown, they became the team that handled the captive red kangaroos, an arduous task. They were joined by research scientists John Calaby and Bill Poole and photographer Ederic Slater. Their first task was to examine what factors prevented the development of the dormant blastocyst during lactation.[35] By chance they observed one female kangaroo in the yards suckling her own and another female's young at foot and exploited this to test whether the inhibition of pregnancy was due to the suckling stimulus to the lactating teat.[36] They found that the total amount of time the teat was suckled was greater and the delay was longer when two young at foot were suckling the one teat, and concluded that oxytocin might be the endocrine factor that suppressed the corpus luteum for the longer time. They confirmed this by injections of oxytocin.[37] These early experiments were the first indication of how delay is controlled but twenty years were to elapse before the full story was resolved and prolactin, rather than oxytocin was found to be the hormone involved.[38]

The main project, however, was the analysis of the large body of data collected on kangaroos shot at three sites in Western NSW through 1959 to 1962 by Harry Frith's team. Using the captive colony in Canberra, growth curves of pouch young were developed so that the wild shot young could be aged, and the changing dental pattern was calibrated so that all adult animals could also be aged accurately.[39] With these tools the 3000 adult females and 400 adult males collected were analysed for breeding condition and life expectancy.[40] The conclusion was that the red kangaroo is a nonseasonal breeder, that young are produced in all months of the year, and that the population size is regulated by differential mortality of the young as they become independent of their mothers; in good seasons more of this cohort will survive and in poor seasons most of the cohort will die. A similar conclusion was reached by Newsome in Central Australia at about the same time.[41]

The research of this period that attracted the most public attention was the filming of the birth of the red kangaroo.[42] While biologists had long been aware of the features of marsupial birth, there were several popular myths about how the young of kangaroos were born. Because of the extraordinary small size of the newborn kangaroo one idea was that the young grows as a bud off the teat; another that it is delicately placed in the pouch by the mother and another that the mother licks a path in the fur for it to follow on its way to the pouch. With the increasing knowledge of kangaroo reproduction the team at CSIRO were now in a position to set up in advance the day of birth by removing the previous young from the pouch and so activating the dormant blastocyst in the uterus to develop. In all they watched 24 births, taking clear photos and films of every stage of the process from preparatory behaviour the day before to the attachment of the tiny newborn young to one of the four teats in the mother's pouch.[43] These showed clearly that the young was born still enclosed in the amnion; that it immediately began its independent journey to the pouch with no assistance from its mother; that it reached the pouch within less than five minutes and attached to one of the four teats. The mother's licking followed rather than preceded the passage of the young and was largely concerned in licking up the foetal membranes and fluid. Throughout this time the mother adopted a characteristic position, sitting on her rump with the tail drawn forward. Sharman and Calaby noted that, 'Mated and nonmated females differed in the pro-oestrous and oestrous phases only in that the concentrated burst of pouch cleaning, which appeared to be compulsive, was confined to those mated females which were about to give birth.' From later work on the tammar wallaby it is now known that this compulsive behaviour is directly associated with a brief pulse of prostaglandin from the placenta and uterus,[44] and can be artificially induced in non-pregnant and even male tammars by a single intravenous injection of the hormone.

Because several of the incorrect ideas about kangaroo birth had been published in Europe, Geoff published one account in German,[45] and another in French.[46] The film had wide coverage in Australia and it used to be said in the 1960s that it was for many children the only sex education they ever received at school.

Geoff 's research also came before international audiences in 1963 and 1964 at which he was determined to make outstanding presentations, and did. One American colleague from that time recalled,

> I haven't had any brilliant moments of remembering snippets about Geoff but I do remember that he was smitten by Joan Baez. I remember, too, that he often made a real point of telling people of his humble background in Tasmania and that he started out as a carpenter and that the family was very poor. He talked about how he was able to climb out of this situation and make a name for himself. I always thought that Geoff thrived on being heralded for his scientific accomplishments but was actually a very insecure person.[47]

Her perceptions may have been due in part to the common experience of young Australian scientists at that time making their first visit to America and receiving not a little condescension! The first conference was on 'Delayed Implantation in Mammals', organized by Allen Enders as part of the semi-centennial celebrations of Rice University, Houston. Geoff 's was the opening paper and he presented the whole evidence for delayed implantation in marsupials drawing on his early work on the quokka and later work on red kangaroos,[48] and his was followed by two other papers on delayed implantation in marsupials. In summing up the Houston conference, Amoroso—whom Geoff had worked with in London seven years before—said,

> The great strength of this marsupial work, which I regard as functional morphology, lies in the fact that it has always been considered in the light of the possible course of evolution, and without that reference, I think that morphology is likely to be barren and to fall into errors of homology. Nevertheless, one must caution our Australian friends that it would be prudent to get more of the facts and to explore them more fully before embarking on speculations that may lead us into difficulties.[49]

This provoked Geoff into writing a review on marsupials and the evolution of vivparity for *Viewpoints in Biology*,[50] beginning with the quotation above from Amoroso, and then gave a spirited defence of his ideas, ending with the words,

> It is suggested that marsupial evolution has been accompanied by extension of uterine life, rather than by its curtailment, by evolution of allantoic placentation, in at least two separate lines, instead of its loss and by the begetting of more mature offspring…that the pouch is a marsupial development and that greater elaboration of this structure and extension of pouch life have accompanied marsupial evolution.

A year later in November 1964 in London at the first conference on comparative biology of reproduction in mammals, Geoff reviewed the different patterns of reproduction then known in Australian marsupials.[51] And while in Britain he visited Roger Short at Cambridge to learn his new and highly sensitive method for measuring progesterone in the peripheral circulation of mammals by radio-immunoassay; this was clearly the way to go with research on marsupial reproduction. What was also needed was a smaller, more amenable species than the red kangaroo for critical research, as Amoroso had gently urged.

In 1965, Patricia Berger, an American student from Tulane University, joined Sharman's group at CSIRO to undertake a PhD on marsupial reproduction. He suggested she study the tammar, which was common on Kangaroo Island and had not then been closely studied. Within a year she had discovered that females retain a blastocyst in diapause for eleven months and all give birth within six weeks of the summer solstice.[52] She also established a small colony of tammars at CSIRO, discovered how readily they adapted to captivity and how convenient their size was, and so began research on this handy species, which would eventually become the best studied species of macropod and indeed of any marsupial.

While the tammar work began at CSIRO in 1965, from January 1966 it moved to Sydney when Geoff was appointed to the foundation Chair of Zoology at the University of New South Wales. Research on the large kangaroos, however, continued at CSIRO, especially on the two species of grey kangaroo, by John Calaby and Bill Poole.

Foundation Professor of Zoology, University of New South Wales, Sydney, January 1966 to December 1969

At the University of New South Wales Geoff was charged with establishing Australian mammalogy as a core discipline in the School of Zoology. For this he was initially provided with three new lectureships, which were filled by Terrence Dawson, comparative physiology, just returned from postdoctoral positions at Duke University and Yale; Leon Hughes, reproductive biology, from University of Tasmania and CSIRO Wildlife Research; and Eleanor Russell, animal behaviour, from the University of Cambridge. Of this time Terry Dawson wrote,

> I think the appointments happened rather informally. I heard via the grapevine that Geoff had gone to UNSW and wrote to see if positions might become available and got a job offer by return mail. I accepted Geoff 's offer because I wanted to work on kangaroos especially arid zone species and Geoff was involved in the setting up of Fowlers Gap Research Station in 1966. Initially, 'Geoff 's crew' worked in with him on the population ecology of reds and euros at Fowlers Gap. We spent a lot of time in the field and this was great training and mostly fun. However, within 2–3 years we started to focus on our specific interests and had our own students. Geoff 's enthusiasm for the kangaroo field studies seemed to drop off about then. Never-theless, field trips always rejuvenated him; you could see him obviously unwind once we got west of Dubbo.[53]

As well as establishing the field station in western NSW, Geoff had to develop holding yards for tammars nearby at Cowan Forest and he had a big workload as Head of the new School of Zoology. One of the new students, Randy Rose, recalled his first encounter as an undergraduate with the new professor,

> I first met him in 1966 when we both were waiting for the lift in the BioMed. Building. He was wearing a dirty boiler suit and proceeded to role a cigarette with his fingers. Zoology was on the fifth floor and when I got out so did he. Surprised, I asked if he worked there, thinking he might be the cleaner. He replied with a smile on his face (knowing what I was thinking) that he 'was the Professor Zoology'. Geoff was a great teacher who used plain language.[54]

Meanwhile his own research group concentrated on the tammar wallaby. Initially Pat Berger and Geoff and another PhD student, Meredith Smith, began by addressing critical questions with controlled experiments in the laboratory on the effects of removing the active corpus luteum, injecting steroid hormones at critical times,[55] and demonstrating that adult females that conceive after the winter solstice will retain the blastocyst in diapause without the intervention of lactation until after the next summer solstice.[56]

Meredith Lemon joined Sharman in Sydney and developed the first sensitive assay for measuring progesterone in the peripheral circulation of female tammars.[57]

Geoff moved from UNSW at the end of 1969 and in that last year he published three review papers on marsupial reproduction. With Pat Berger he reviewed the phenomenon of embryonic diapause in marsupials.[58] He gave the Presidential address to ANZAAS Section 11 Zoology on the biology of sex in marsupials in which he traversed the classic studies of Hill and Hartman and the results of the past 20 years and concluded that marsupials and eutherian mammals probably had a common oviparous ancestor.[59] He concluded his other review, in *Science*, with the comment, 'The failure of marsupials to evolve placental secretions, which in eutherians both extends the secretory phase and inhibits ovulation, sets limits to the period of intrauterine development.'[60] In less than two years, evidence for foetal and/or placental endocrine effects in late pregnancy of the tammar was published in *Nature* that challenged that conclusion. The baton on marsupial reproduction was passing to two young scientists who would take the story on to another level by exploiting the advantages of the tammar wallaby: Marilyn Renfree clarified the role of the placenta in intrauterine development,[61] and John Hearn showed how the pituitary gland of the tammar controls embryonic diapause by tonically inhibiting the corpus luteum—quite the reverse of pituitary function in other mammals.[62] Incidentally Geoff considered it was highly irresponsible of HTB, as John Hearn's PhD supervisor, to expect him to investigate the role of the pituitary gland in tammar reproduction.[63]

Although Geoff continued to contribute to textbooks and general reviews,[64] he published no more primary research on reproductive physiology of marsupials after 1969. Nevertheless, when the first monograph on the topic was published eighteen years later it cited 41 of Sharman's papers and its dedication read:

> To three pioneers who recognised the special role of marsupials for the understanding of mammalian reproduction: J. P. Hill, C. G. Hartman, G. B. Sharman.[65]

During the four years he was at the University of New South Wales, Geoff Sharman left his mark on it and the marsupial research group he had set up was strong. Under the leadership of Terry Dawson, who succeeded him as Head of School, it has continued to the present day. The Fowlers Gap Field Station has been pivotal to much of the research produced, as described in Terry's book.[66]

Foundation Professor of Biological Sciences, Macquarie University, Sydney, 1970–85

In January 1970, Geoff took up the Foundation Chair in Biological Sciences at Macquarie University, recognition of the high regard he was held in by then in the Australian scientific community. His close colleagues were expecting him to be elected to the Australian Academy of Science but inexplicably that did not happen for another ten years, the year that Harry Waring died. Whether there was any link between these two events cannot now be checked because the Sharman file can no longer be found in the Academy archives.

At Macquarie, Geoff resumed active research in marsupial sex determination, X chromosome inactivation and cytogenetics, adding chromosomal evolution in rock-wallabies. He proved he could be hands-on in several research projects, as well as running the school. Carolyn Murtagh, who worked for Geoff at Macquarie, wrote,

> Professor Geoff Sharman seized every opportunity to get into the lab, and out into the field. Having dealt with Head of School matters he would arrive in the lab and ask, 'Where are we up to?' Paternal X inactivation in kangaroos was the primary interest so the X-chromosomes of hybrids between macropod species and subspecies (accidental and deliberate) were excitedly perused down the microscope, and autoradiography carried out. He was so obviously enthusiastic and it was infectious.[67]

Sex Determination in Marsupials

Geoff 's work on sex determination in marsupials, begun with observations on some intersexual animals, was to have major repercussions on the field.

Study of intersex humans and mice have been key to many advances in the understanding of sex determination. Sharman was the first to describe intersexual marsupials,[68] summarized in a paper published in 1990.[69] One intersex marsupial had a penis and a pouch with mammary glands, but no scrotum, undescended testes and some disruption of other male characters. This animal had two X chromosomes and a Y. XXY individuals are known in eutherian mammals, but are phenotypically male (for example humans with Kleinfelter syndrome). Sharman also described intersexes with a single X and no Y, which had no testis and a female reproductive anatomy, but a small, empty scrotum instead of mammary glands and a pouch. Again, this contrasts with the female phenotype of XO girls with Turner Syndrome. Many intersex marsupials have been described since.

From these intersexes, Sharman concluded that the Y chromosome was testis determining, as it is in eutherian mammals. However, the hormones made by the embryonic testis do not control other aspects of male development, as they do in humans and mice. The same conclusion was reached by O, Short, Renfree and Shaw from the observation that male tammars have scrotal sacs at birth, two days before the testis differentiates, so presumably in the absence of testosterone.[70]

Geoff recruited Desmond Cooper from La Trobe in 1973 who brought expertise in isozyme detection and marsupial genetics. Des proposed that some secondary sexual characteristics, specifically mammary/scrotal development, were under autonomous control by a gene on the X chromosome.[71] Either the gene on the paternally derived X (present only in females) or the double dosage of the gene on the X in females, was needed to form the pouch. Rare pouch young with half a scrotum on one side and half a pouch on the other had different sex chromosome morphologies on the two sides, which were analysed in an attempt to find the 'pouch gene'.[72]

Again, differences between marsupials and eutherian mammals revealed the evolutionary trajectory by which complex genetic control systems are built up. Indeed, the correct identification of the mammalian sex-determining gene depended on mapping candidate genes in kangaroos and dunnarts. This eliminated the front-running candidate *ZFY*, and led to the correct identification of *SRY* in humans, mice and marsupials.[73]

Marsupial X Chromosome Inactivation

Mary Lyon showed in 1961 that in female mice one X chromosome was genetically inactivated so that XX females and XY males had equivalent activity of X-borne genes ('dosage compensation').[74] This discovery stimulated a search for X chromosome inactivation in marsupials. JMG in David Hayman's laboratory showed that one X in female kangaroos replicates late, a hallmark of inactivation.[75] But which X? In human and mouse the choice of the X to be inactivated is random, so females develop with patches of tissue with one or the other X active.

Three crucial papers in 1971 by Geoff Sharman, Des Cooper and their colleagues, using chromosome or protein markers to distinguish the X chromosomes that came from the male or female parent, showed that marsupials are different. Geoff 's classic cytological demonstration of the origin of the inactive X arose from his observation that the X chromosome of the euro (*Macropus robustus erubescens*) was about one and a half times larger than the X chromosome of the wallaroo subspecies (*M. r. robustus*). Since the two sub-species would readily interbreed, he could identify the origin of each X chromosome in female hybrids. He demonstrated that the late replicating X chromosome was always the paternally derived one.[76] The other two papers showed that proteins coded by only the maternal X were expressed.[77] Together, these three papers, and many more that followed,[78] established that in kangaroos, unlike eutherian mammals, X inactivation was not random, but paternal. Further surprises from the Macquarie group were that in some tissues both X chromosomes were expressed.

X chromosome inactivation remains an important model system to study epigenetic changes in gene expression, now a burgeoning field. Marsupial X chromosome inactivation has been very important for unravelling the complex molecular mechanism by which a whole chromosome can be genetically turned off.[79] Marsupials share many elements of X inactivation with eutherians, such as reactivation in oocytes,[80] but differ in the molecular mechanism.[81] Several epigenetic silencing mechanisms such as histone modification are shared between the mammal groups, but others such as DNA methylation, occur only in eutherian mammals.[82] Remarkably, the locus that controls X inactivation in humans and mice does not exist in marsupials;[83] instead, a completely unrelated controlling element acts in the same way.[84]

Marsupial Chromosome Evolution

At Macquarie too, Geoff's early interest in unusual sex chromosome systems led to major discoveries that would have fundamental impact on our understanding of chromosome function and evolution.

Some of the first work that Geoff Sharman did on marsupial chromosomes turned up an oddity—in some species such as the long-nosed potoroo and the swamp wallaby, *Wallabia bicolor*, males and females had different numbers of chromosomes, differing only in their sex chromosomes.[85] Normally marsupials, like eutherian mammals, have an XX female: XY male chromosomal system of sex determination and the X chromosome is one of the smallest of the complement. But in these species, females had two copies of a large chromosome with two arms (the X), whereas the male had a single X, and two male-specific chromosomes (Y_1 and Y_2) that were equivalent to the two arms of the X. At male meiosis, the autosomes formed normal homologous pairs held together at crossover points, whereas the X and two Y chromosomes formed a chain of three (trivalent) in which the large X paired with Y_1 at one end and with Y_2 at the other. Geoff proposed that the original X chromosome was the short arm of the X, and the original Y was the small Y_1. The multiple sex chromosomes were formed when the original X (but not Y) fused with a large autosome. This has been beautifully confirmed for the swamp wallaby by chromosome painting.[86]

Odder still are the chromosomes of monotreme mammals, the platypus, *Ornithorhynchus anatinus* and the echidna, *Tachyglossus aculeatus*, which had been the subject of confusing earlier reports. Sharman encouraged and championed early work done by Dziunia Bick in Tasmania. Her meticulous drawings of platypus and echidna chromosomes at male meiosis showed a chain of, not just three, but several chromosomes.[87] With Bick and his research assistant and student Carolyn Murtagh, Sharman further characterized the chain in platypus and echidna,[88] and proposed that, like the long-nosed potoroo, this was the product of fusions between sex chromosomes and autosomes. In correspondence to JMG, he wrote,

> Dziunia Bick should at least get a mention because she has always maintained (since she gave up her original XO hypothesis) that the monotreme sex chromosome is a multiple system – like that of *Potorous*…but with more chromosomes in the chain multiple.[89]

Indeed Sharman was right; in enthusiastic correspondence he avidly followed the later work of PhD student (later QEII Fellow) Jacki Wrigley (later Watson) in JMG's laboratory, who used telomere probes to delineate the separate chromosomes, which look at meiosis like a chain of little sausages, whose ends are indistinct. In the same letter Geoff wrote,

> Congratulations on the telomere probe, and one up for Dzunia again! She maintains there are probably only eight chromosomes in the Platypus chain, and your magnificent preparation seems to indicate that to be the case.

Actually Jacki counted ten in platypus and nine in echidna and showed how they lined up at meiosis.[90] Chromosome painting later confirmed that the male platypus has five X chromosomes and five Y, which line up in an XYXYXYXYXY order at meiosis. The X chromosomes all go to one end of the cell, and all the Ys to the other, producing only two kinds of sperm, X-bearing and Y-bearing.[91]

But the situation was even weirder than Sharman could have imagined. Later genome sequencing and gene mapping showed that the platypus sex chromosomes had no homology to sex chromosomes of other mammals; instead, they contained the gene content of the bird sex chromosomes.[92] Geoff was delighted with the fame of platypus sex chromosomes, being delightfully weird, and also defining the origin of our own sex chromosomes, which must be much younger than anyone had anticipated.

Platypus delivered yet another surprise. In the same letter in 1991 Geoff demanded that Jacki find the monotreme sex-determining gene. 'Where does the *ZFY* gene map go to in the echidna genome?' Answer—on chromosome 22, because it is the wrong gene anyway. 'Find which is the male sex determining chromosome in the monotremes,' he insisted. Easier said than done—over several years, three students hunted unsuccessfully for *SRY* in platypus and echidna. 'Surely it can't be on that part of the Y which is homologous to the X?' The identity of the monotreme sex-determining gene is still speculative, but it is clear there is *SRY* (so its non-appearance was hardly surprising). This is important because it dates the origin of the *SRY* gene to after the divergence of monotremes from therians 190 MYA.[93]

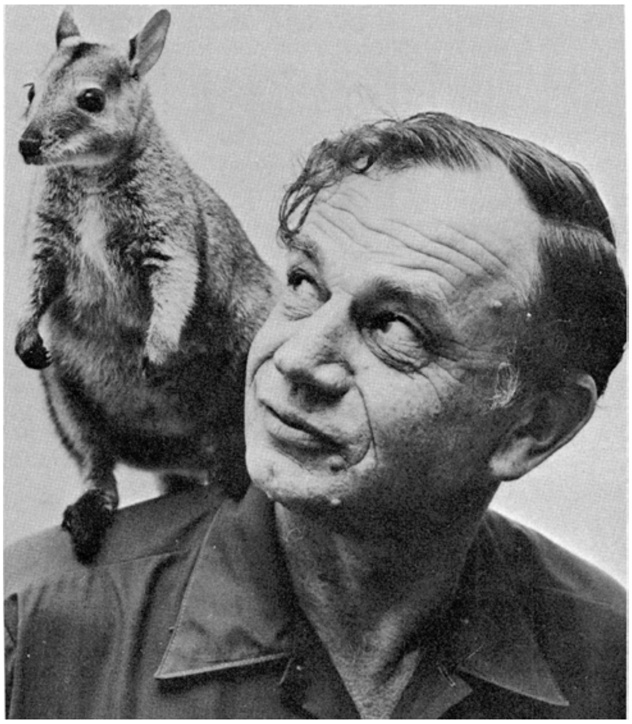


Figure 1. Geoff Sharman in 1977 with an object of his current research, a rock-wallaby, probably *Petrogale godmani*.

Chromosomal Evolution in the Rock-Wallaby Species Complex

The huge marsupial chromosomes offer excellent material for studying chromosome evolution. Marsupials include groups with practically no chromosome change like the 2n-14 dasyurids, and groups like the rock-wallabies that 'seem to change their chromosomes every time they cross a creek.' The rock-wallabies (*Petrogale* species) that inhabit rocky outcrops across Australia display every stage of speciation (Fig. 1). With David Briscoe, Gerry Maynes, Rob Close, and later Mark Eldridge, Geoff explored chromosome and protein variation within this extraordinary species complex,[94] publishing a seminal paper on rock-wallaby speciation.[95] In the second edition of Ron Strahan's *The Mammals of Australia* 13 of 16 species descriptions are by Sharman and his colleagues.[96] One species was named *Petrogale sharmani* by Eldridge and Close in 1992.[97] Mark Eldridge continues the study, using molecular techniques to bear on the questions of genome change and speciation in this unique model system.[98]

Sharman was always interested in what chromosome change could tell us about marsupial relationships and marsupial evolution.[99] And his answer—not much—stands today. Chromosomes are too capricious to be useful except between close relatives like the rock-wallabies, and in special cases, such as the mountain pygmy possum, *Burramys parvus*,[100] and the marsupial mole, *Notoryctes typhlops*.[101] At Macquarie, he became interested in other, better ways to gauge relatedness such as the charge and the sequence of amino acids in proteins like haemoglobin,[102] the forerunner of DNA sequence comparisons that are now the basis for the revolution in constructing phylogenetic trees and dating divergence (for example 166 MY between marsupials and eutherian mammals, and 190 MY between monotremes and therians.[103]

Geoff was now the 'Grand Old Man of Marsupial Biology' and was held in some awe by undergraduates at Macquarie. When they responded to a questionnaire about the staff they wrote that 'Professor Sharman is rude, belligerent and unfair.' Geoff reported this assessment to Barbara who replied, 'Oh Geoffie you're never unfair!' And Geoff delightedly related this to his group.[104]

Due at least partly to Geoff 's efforts, marsupial and monotreme cytology has proved to be a goldmine of new discoveries. Geoff 's network of younger colleagues and students continue to mine the gold, using new molecular technology that Geoff could only dream of. Hardly a paper in any of these fields is published without reference to one or other of Geoff 's seminal publications.

As an acknowledgement of his influence, the first book on marsupial genetics, was dedicated by the Editors, Jenny Graves, Rory Hope and Des Cooper:

> To David Hayman, Peter Martin and Geoff Sharman, who pioneered marsupial genetics, and who were our teachers.[105]

Graceful letters of thanks were received from David and Peter. Geoff wrote a four-page letter detailing several sins of nomenclature and interpretation that he found in the book. But he was never unfair!

Last Years

In 1985, at the age of sixty Geoff retired and he and Barbara moved to Tasmania where they restored an old house in Evandale. For the next ten years or so he maintained links with Macquarie University as an Emeritus Professor. However, his interests in travel proved stiff competition to the world of marsupial genetics. He regretfully declined his invitation to the Boden Conference on marsupial and monotreme genetics because,

> Barbara and I went mad and bought a very expensive 4 wheel drive van which we are having converted to a campervan at further enormous expense. We are leaving Tasmania on Tuesday…And in any case, I don't really think I can contribute very much. …I reckon that there are others who contribute more and I'd really like to go bushwalking in February 1988.[106]

So Geoff and Barbara returned to their roots in Tasmania. His main interest now shifted to research on his family antecedents, especially the Swing Rioters of the 1830s referred to at the beginning of this account. As Barbara's health deteriorated they moved into a retirement home in Launceston and in 2009 he resigned his Fellowship in the Australian Academy of Science. This was ostensibly because he felt he could no longer participate, but there was some other reason he did not disclose; in an email to HTB he wrote, 'I resigned my Fellowship in disgust some time back (and will tell you why later).' But he never did.[107]

Six months later Barbara died, a few months short of their sixtieth wedding anniversary. He lived on at the same place for another four years; he died on 17 August 2015. He is survived by his four sisters, his brother and his two sons.

Acknowledgements

We have been much helped in preparing this memoir of Geoff Sharman, and collating his publications, by his former colleagues

Robert Close, Terry Dawson, Mark Eldridge, Tom Grant, John Hearn, Carolyn Murtagh, Randy Rose, Mary Taylor and Patricia Woolley. We are especially grateful to Geoff 's sons, John and Robert for providing family information and the photographs of Geoff, and for their support.

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