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www.publish.csiro.au/journals/hras *Historical Records of Australian Science*, 2011, **22**, 277–290

Spencer Smith-White 1909–1998

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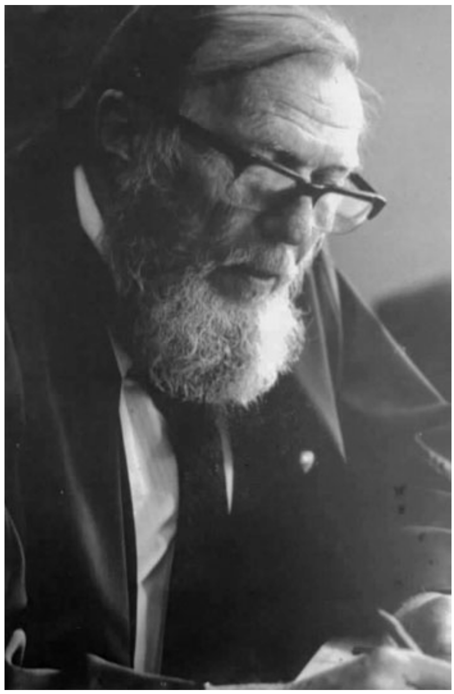
Spencer Smith-White's research group at the University of Sydney was for many years the foremost laboratory studying the cytology, cytogenetics and cytoevolution of the Australian flora. He pioneered this field with his chromosomal studies on major Australian families, such as the Rutaceae, Myrtaceae, Proteaceae and Epacridaceae. His cytogenetic analyses underpinned his discussions of the origins and distribution of the major elements of the Australian flora.

When Emeritus Professor Spencer ('Spinny') Smith-White died quietly in hospital on 26 March 1998, Australia lost one of its most original and creative plant science academics. He had been elected to the Australian Academy of Science in 1962. His research group at the University of Sydney was for many years the foremost laboratory studying the cytology, cytogenetics and cytoevolution of the Australian flora. He pioneered this field with his chromosomal studies on major Australian families, such as the Rutaceae, Myrtaceae, Proteaceae and Epacridaceae. His students complemented his studies with analyses in several other woody and herbaceous endemic Australian families. Smith-White's cytogenetic analyses provided the principal data for his deliberations on the origins and distribution of the major elements of the Australian flora.



Early Life

Spinny's father, also named Spencer, arrived in Australia from Ifield, Sussex, in 1891 at the age of 19. He married Alice Johnson at St Paul's Church, Redfern, on 10 April 1905. 'Spinny' was born the elder of twin boys (by 15 min) in the Sydney suburb of Forest Lodge on 14 April 1909. Spinny's sister, Margaret Anne, was born in 1917. Margaret passed away on 3 February 2011 in Bowral, New South Wales, aged 93 years. The Smith-White family spent their early years at Summer Hill, New South Wales, and Spinny, following an early interest in biological matters, entered Hurlstone Agricultural High School and then later studied at Hawkesbury Agricultural College. He had fond memories of Hawkesbury College and often returned to Old Boys' functions and maintained friendships with several of his colleagues who took up positions in academia, the agricultural research community and the bureaucracy in various states of Australia.

 10.1071/HR11007 0727-3061/11/020277

Smith-White then studied agriculture at the University of Sydney, graduating with Honours in 1932. His early academic achievements paralleled, at the University, those of his twin brother Bill who excelled in mathematics, winning the University Medal and a scholarship to Cambridge. Spinny was always intensely proud of his twin's achievements and later of their dual careers at the University of Sydney, where Bill eventually rose to the position of Associate Professor of Mathematics. Bill died in 1986.

After graduation, Smith-White worked at Griffith Research Station in rural New South Wales. He then became Science Master at Scotch College in Adelaide. He was not highly motivated in this position and it came to an end when he had a serious motorcycle accident and was invalided back to Sydney, after which he no longer had an interest in school teaching as a career. In 1935 he took up a position as Plant Breeder with the New South Wales Department of Agriculture at Glen Innes and in February 1937 he was appointed Economic Botanist at the Museum of Applied Arts and Technology in Sydney.

Spinny met his future wife 'Mabs' Halliwell whilst holidaying at Jervis Bay, New South Wales, in January 1939. They became engaged in July and married on 15 December 1939. Mabs and her parents and siblings had arrived in Australia from England in 1921 following the end of the First World War. Her secondary education in a country high school was curtailed somewhat by the developing Great Depression of the 1930s, necessitating her entry into a business college to help ease the family's finances. After her marriage she became interested in her husband's career and was able to put her secretarial skills to good use in deciphering his rough notes and typing these for publication. She also accompanied Spinny on many field trips to central Australia and on overseas sabbaticals.

An Interest in Evolutionary Genetics

During Smith-White's early years, chromosome biology emerged as a new and powerful tool in the study of evolutionary biology. In the USA, T. H. Morgan had successfully shown the relationships of genes and chromosomes and linked these to Mendel's laws of heredity. It was thought that the study of chromosomes would be an ideal way to explore the genetic affinity between different species. This was, at least to first order, a reasonable assumption.

Initially the techniques for studying chromosomes were difficult and time-consuming and very few people were involved around the world. What changed this was the publication of two books, both of which originated from the John Innes Horticultural Research Institute in the UK. These were *Recent Advances in Cytology* by Cyril Darlington (1932) and *The Handling of Chromosomes* by Darlington and L. F. La Cour (1942). The earlier work provided the first intellectual basis for the interpretation of chromosome architecture and behaviour in mitosis and meiosis in relation to genetic systems. The later, complementary book described simple techniques for the preparation of mitotic and meiotic chromosomes for microscopic study.

Smith-White was profoundly affected by these works, so much so that he made the decision to take up a career in cytogenetic research. He obtained a position in the New South Wales Department of Agriculture at Glen Innes to work on *Nicotiana* (tobacco). Papers by an American, H. M. Wheeler, on the cytology of *Nicotiana* further stimulated his interest in cytogenetics. Smith-White put together a collection of Australian *Nicotiana* species, some of which he obtained from the Russian collection, in preparation for making some observations on the indigenous species of the genus. This did not, however, lead to any publications.

In 1937 Smith-White moved to the Museum of Applied Arts and Technology in Sydney, his first research appointment, where he was to work on the genetics of essential oils of eucalypts. He did carry out some research in this area but it was very slow going and he had plenty of opportunity to begin what was to become his lifelong focus in research—cytological studies on Australian plants.

Career at the University of Sydney

Smith-White began publishing his chromosomal work in the *Proceedings* of the Linnean Society of New South Wales. His early studies attracted the attention and support of other scientists including Newton Barber and David Catcheside, two geneticists who had come to Australia from England, Barber to a lectureship at the University of Sydney and Catcheside to a professorship at the University of Adelaide. Ten years after he started work on the chromosomes of some of the major Australian families of flowering plants, working essentially by himself, Smith-White at last found himself with colleagues who had broad knowledge in this field, so that he could have significant communication with them about his developing subject. Newton Barber moved from the University of Sydney to the University of Tasmania to become Professor of Botany and Genetics and in 1948 Smith-White took up his position at the University of Sydney. Smith-White put genetics on the map at the University of Sydney and it was fitting that he subsequently was appointed as the Foundation Professor of Genetics there. He remained at the University of Sydney until he retired in 1974. He was awarded the degree of Doctor of Science in Agriculture in 1956.

Spinny played an important role in the Science Faculty in the University of Sydney and was widely recognised for his active encouragement in undergraduate and graduate teaching and research training. After he retired, the staff of the School of Biological Sciences established a fund supporting an annual ‘Professor Spencer Smith-White Prize’, awarded to the student with the most outstanding work in Biology Honours in the field of genetics.

On a perhaps more emotional level, Derek Anderson, Pro-Vice Chancellor in 1996, conducted a naming ceremony for the new tea-room in the Botany building that became ‘The Spencer Smith-White Room’ in recognition of Spinny’s insistence that everything stops for tea!

At the University, Smith-White was able to continue and expand his cytological and evolutionary research on families of Australian plants. Over the years, he built a strong coterie of research students in this area and made major contributions to the cytology of the Australian flora and to ideas on its evolutionary history.

Apart from his courses in cytology and genetics, Smith-White lectured in systematic biology. The practical sessions associated with his lectures in this area were heavily flavoured with his thoughts on the genetic systems of the groups of plants being studied. This aspect of the Australian flora was very important in the discussions he had with other staff working on the ecology and physiology of Australian plant communities. Smith-White thus had a significant impact through a range of activities of the botany department.

His genetics lectures to first-year classes were quite extraordinary, with excellent genetic content, and although genetics perhaps was not of the greatest interest to all students in the class, the way Smith-White delivered the lectures, with heavy breathing into the microphone, made for an interesting experience for the students. His lectures to upper-level students on cytology and cytogenetics were absolutely first-class.

Apart from his own research efforts and his lecturing responsibilities, Smith-White from the outset of his appointment began building a group of research students who worked in similar ways to himself on various groups of the Australian flora. These students included Helen Ramsay, Alison McCusker, Barbara Briggs, Bryan Barlow, Sid James and Jim Peacock. These and later students such as Helen Stace, Charlie Carter and Judy Ford were given enormous freedom by Smith-White, but it was a freedom with extensive mentoring in the practice of first-class science and in reasoning on genetic systems. His research group began to be noticed in Australia and elsewhere and they made many contributions to the Genetics Society of Australia. Smith-White was a major personality in the Genetics Society; along with Newton Barber, David Catcheside, Michael White and two CSIRO Chiefs, James Rendel and Otto Frankel. He was a foundation member of the Society. The Society provides an annual Smith-White Travel Prize to assist a postgraduate student to attend an international conference.

He enthused about cytogenetics and genetic systems with his students and imbued a love of research in cytology and genetics into each one of them. He urged his students to work hard, to question everything and to strive for understanding and for excellence in their work. His students went on to fill several leading botanical and genetic positions in Australian universities, in CSIRO, and in the national herbaria of Australia. Additionally, Alison McCusker became a valuable staff member of the International Plant Genetic Resources Institute of the Consultative Group of International Agriculture Research in Rome and Jim Peacock was a Board member and chairman of the Institute for several years. Spinny made a contribution greater than most university academics through the students coming out of his laboratory, and this continued through a second generation. Sid James had a very important influence on research on native plants of Australia and his many students included Stephen Hopper, now Director of the Royal Botanic Gardens at Kew, while many of Bryan Barlow's graduate students moved to research positions in Australian botanical institutions.

Spinny's interactive style with students was unique. Often his voice would reverberate through the laboratories as he called out 'come and tell me what you think of this'. Spinny would be looking down the microscope, his beloved Lumipan, at some peculiarity of meiosis in the Epacridaceae and the summons to his students was for them to give an interpretation of what was going on in that particular cell. Initially we all used to dread the call in case we made absolute fools of ourselves but, in retrospect, this is where we learned most from him.

All of us who were his students enjoyed and profited enormously from our field-work with Spinny in the bush. He had a wide knowledge of the flora and had thought deeply about the evolutionary implications of the features and distribution of the species in focus at the time. He was immensely proud of his students and was always modest about his contribution to their development and to their success.

It was during excursions to the University Research Station at Pearl Beach, to Betts Camp at Mount Kosciuszko, or in inland Australia that his students saw that his scientific enthusiasm was combined with a deep Australian larrikin streak. He entertained us with stories, reminiscences and party tricks, along with enjoying a whisky or a good red wine.

It was to his great credit that Smith-White initiated first-class research programmes and built up his laboratory in such academic isolation. After Catcheside and Barber came to Australia, genetics and cytogenetics began to grow, and with Michael White returning to the University of Melbourne and CSIRO building up its strength in animal genetics under the leadership of James Rendel, Smith-White then had fertile ground in which to operate. Apart from his earlier, quite amazing achievements, he was also remarkable in keeping up with the fast-moving development of the knowledge and technologies of genetics beginning in the 1950s and extending into the 1970s. His mind reached far beyond the cytological technologies that he worked with himself. He kept abreast with the experiments and new understanding that flowed from the rise of molecular biology. He urged his students to do the same and we all participated in energetic discussions of the latest results in the study of the characteristics of DNA and the central genetic information system of living organisms.

There is no doubt that the crowning achievement in Smith-White's career in cytology and genetics was his being invited to address the Cold Spring Harbour Symposium in 1959. Here, he presented the first major synthesis of the evolution of the Australian flora based on an integration of cytogeographic data of the many native Australian plant families studied by himself and his students. His paper had a major influence for some time on the views held by Australian biogeographers on the origins and evolution of the Australian flora. As data on continental drift and plate tectonic movements came to the fore in the mid-1960s, Smith-White began to realise that his interpretation of chromosome relationships in the various families would require a somewhat different interpretation from those he had given, which assumed that the flora had been derived from successive invasions of the flowering plants into a relatively isolated Australian continent. In fact, as Barlow in his 1981 essay in the introductory volume of the *Flora of Australia* pointed out, Smith-White's initial analysis probably delayed the acceptance in Australia of the role of Gondwanan plate movements in Australian biogeography. Nevertheless, his data provided major sources for the conceptualization of an autochthonous element of the Australian flora.

International Influences

An experience that stood out as being seminal in Smith-White's development was a period of sabbatical leave that he spent with Darlington in the UK in 1956. As mentioned above, Darlington was one of the leading lights in plant cytogenetics and it was his writings that first kindled Smith-White's passion for this field. Darlington was regarded by many, and certainly by Smith-White, as *the* authority of the field.

Spinny's time with Darlington did not go completely smoothly. They were both strong characters and they clashed on many things, but both of them had remarkable minds and Smith-White left the Darlington laboratory with amicable relationships. Later when Darlington visited Smith-White's Australian laboratory, we, the students, were left in no doubt that Smith-White still almost hero-worshipped Darlington for his contributions to cytogenetics. The time that he spent with Darlington and the way he was able to interact with many other cytologists and cytogeneticists in leading European laboratories convinced Smith-White that greater emphasis needed to be placed on international communications in his science and on fostering exchanges between countries, this being very rare in Australia in the late 1950s and early 1960s. He developed his interactions with several European and American scientists through letters concerning his own work and with comments on their work. Of course, he emphasised to his students the importance of keeping up with other people's findings.

He later spent a sabbatical period with Professor Harlan Lewis at the University of California at Los Angeles and was greatly impressed by the work that Lewis was doing with *Clarkia*. There is no doubt that these two sabbatical periods and his discussions in those two major laboratories and with other international cytogeneticists and geneticists were a major factor in Smith-White's scientific journey.

Harlan Lewis had developed a strong research programme on experimental cytoevolution in the field and this provided Smith-White with an opportunity to study the desert floras of Arizona and California, and gave him new insights into chromosome evolution and species relationships in the flora of the extensive arid regions of central Australia. This strongly influenced the direction of his research, particularly in his last period of research with students such as C. R. Carter and a visiting Japanese scientist, K. Watanabe, focusing on *Brachyscome* species of the arid inland.

Retirement

Although he formally retired from the University of Sydney in 1974, Smith-White remained active in science—especially in discussions with his students, many of whom had by then taken up research positions in Australia, advancing further the frontiers of cytoevolution in the Australian flora, while others moved from cytogenetics into molecular genetics and other fields.

In retirement, his research was somewhat limited because of the rather disappointing decision of the University of Sydney that Emeritus Professors were best located in another university. The University of New South Wales provided Smith-White with laboratory facilities and the opportunity to interact with other geneticists, but he probably would have been happier and more productive if he had been able to remain at the university to which he had contributed so much.

The Smith-White Laboratory

To be a student in Spinny's laboratory meant total involvement, working extremely hard and participating fully in a vigorous, open academic atmosphere for research. Many of us were also close to Spinny and his family. His sons Spencer and Tony and his daughter Stephanie were friends and, most of all, we were close to his wife Mabs, who was a wonderful, graceful and gentle complement to our University experience. Spinny was a man who was larger than life, who loved his science and who loved life, and who worked and lived to the fullest. Mabs commented once, when Jim Peacock recalled that Spinny had been a trial at times, 'but there was only one Spinny!' He was eccentric but was a great professor with a highly creative mind. The University of Sydney was rightly proud of him.

Research Achievements

It was the mark of an unusual mind that a science teacher at Scotch College in Adelaide chose to read C. D. Darlington's highly technical and advanced book, *Recent Advances in Cytology*. Smith-White was deeply impressed by the work and it generated a determination in him to leave teaching to seek a research career built around the genetics and cytology of plants.

Early Research on Essential Oils

Smith-White's first research appointment was at the Technological Museum in Sydney and his responsibilities related to the breeding of essential oils in eucalypts – a tough problem for someone beginning in genetic research. However his first paper, published in 1940 (1), concerned not *Eucalyptus* but the Tung Oil tree, a member of the family Euphorbiaceae. Tung Oil had several valuable industrial uses and there was a good deal of interest in Australia in establishing Tung plantations. Smith-White carried out a fine study of the trees that had been introduced into Australia from a series of different locations, with the underlying objective of determining an optimal way of breeding for increased yield of Tung Oil. His paper, which dealt with the climatic requirements of the tree as well as its vegetative and reproductive development, showed a keen appreciation that both asexual reproduction and sexual reproduction modes could be important in breeding. Smith-White identified and documented the existence of considerable variation in yield in individual trees and determined that future plantations should be established from the highest-yielding trees. He discussed a method of asexual budding into existing stock for short-term expansion of high-yielding trees, but his principal conclusion was that controlled crosses with selection for high yield was a better strategy for the ultimate establishment of high-yielding plantations.

In the same year he published his first note on oil yields in *Eucalyptus*. This paper (2) described variation in yields from individual trees of *Eucalyptus dives*. He made some comments on the silviculture of *E. dives* plantations but even in this short paper it was evident that Smith-White had already realised that genetic selection and improved yield were both desirable and possible.

In 1942 Smith-White was a co-author on the variation and chemical analysis of the essential oils of another myrtaceous species, *Leptospermum citratum* (3). This paper on sub-species differences in oil composition marked the end of Smith-White's research career in the breeding for essential oils in the Myrtaceae. He was then able to pursue his primary interest in chromosome behaviour and chromosome evolution in the family Myrtaceae, as the Technological Museum wisely gave him the freedom to follow the passion that had been stimulated by Darlington's treatise.

Chromosomal Surveys in Major Australian Plant Families

For the next six years, Smith-White spent most of his research time on cytological studies in the Myrtaceae whilst still giving some attention to his long-term study of the genetics of the essential oils of eucalypts. It was the cytology that captured his primary research interest and he published two papers on this topic whilst he was employed at the Technological Museum. The first dealt with several genera in the tribe Leptospermoideae (4) and the second, some six years later, on chromosome numbers in the Leptospermoideae and Myrtoideae, another major group in the family (5).

The first of these papers marks the beginning of a life-long study of the cytology and cytogenetics of endemic Australian plants. Smith-White built his whole career, including the development of a large group of students and colleagues, around this major contribution to knowledge of the Australian flora.

Smith-White studied eight species of *Eucalyptus* and thirty other species in the Leptospermoideae. The haploid chromosome complement in all species he found to be 11 and although the chromosomes were small and relatively homogeneous in appearance, Smith-White's keen observations led him to recognise that some secondary pairing, particularly in *Eucalyptus gummifera,* was possibly an indication of a derived tetraploid constitution of the genus. Although male meiosis in all of these species was highly regular and without any apparent polyploidy, he was acutely aware that occasionally some anaphase laggards occurred in the first meiotic division. This was an early indicator of Smith-White's understanding of the potential genetic significance of such lagging chromosomes, which were to become of great interest in some of his subsequent studies.

In the second paper, published in 1948, Smith-White reported chromosome numbers in a large number of species in two of the subfamilies in the Myrtaceae, the Leptospermoideae and Myrtoideae (5). He found that most species appeared to be normal diploids with a haploid chromosome set of 11, but he did find that two species of *Syzygium* and one of *Acmena,* all then known as *Eugenia,* were tetraploid. The chromosome behaviour of these tetraploid species at meiosis was perfectly regular. He did not offer any consideration of the origin of the tetraploids except to note that they were species at the extreme geographical range of the sub-tribe. He did not address whether this was genetically controlled regular chromosome behaviour in an autotetraploid or evidence of an allopolyploid origin of the species. The paper established the cytogenetic characteristics of all of the taxonomic groupings in these two sub-families, many of the species having major representation in a wide range of ecosystems in Australia. Once again, he commented on secondary association of chromosomes and interpreted it to indicate that there may have been a primitive condition of six haploid chromosomes and that the 11 chromosome haploid set was of secondary polyploid origin and had been generated at an early stage in the evolution of the family.

Smith-White continued his cytological studies on the Myrtaceae after he took up his position in the Botany Department at the University of Sydney. He published two more papers, one on cytology and phylogeny in the tribe Chamaelaucoideae in 1950 (8) and the second on the subtribe Euchamaelaucinae in 1954 (10). He was aware that cytology, particularly chromosome number, had been used in several research studies to indicate the phyletic relationships between groups of plants and to cast light on the nature of genetic processes that might have controlled speciation. He was interested to see whether he could reach any conclusions on these matters from the cytological studies in the three tribes of the Myrtaceae. It was in the third tribe, the Chamelaucioideae that Smith-White first found chromosome numbers that were not based on the haploid number of 11 chromosomes. This must have caused him considerable excitement and it enabled him for the first time to think about the evolution that may have occurred in the tribes and sub-tribes within this iconic Australian family of plants.

In the genus *Darwinia* he found a haploid number of 6 chromosomes (10). This observation, together with the fact that there was a good deal of pollen sterility in the species of this genus, set Smith-White thinking seriously about the genetic systems that applied in *Darwinia*. Importantly, he speculated on the significance of small isolated populations of plants within the different species. He thought there could well be segmental chromosome rearrangements that he could not observe but that he knew could lead to lack of regularity in the meiotic behaviour of the chromosomes through interference in chiasma formation.

In another genus, *Verticordia*, he found a haploid number of 8, but in some plants that had been collected for him he found a haploid number of 11. He was cautious in his interpretation of these results and noted that it was essential to have accurate taxonomic and collection data before any postulates in regard to evolution within the species could be put forward. In other genera in the family he once again found the inevitable haploid number of 11 chromosomes.

This paper strengthened his previous suggestions that the original haploid number in the Myrtaceae may well have been 6 chromosomes, and that the predominant haploid number of 11 chromosomes had been derived by polyploidy and that this must have happened at the beginning of a major era of diversification and evolution in the family. He cited *Darwinia* as a representative of the primitive chromosome constitution and that the family presented an impressive case of secondary polyploidy in its evolution. It was in this paper, on the basis of this research, that Smith-White began commenting on hypotheses that had been presented by previous workers on the evolution of the family.

Later, in his fourth paper on cytological studies in the Myrtaceae (10), Smith-White had to retract his own major hypothesis concerning the primitive nature of the genus *Darwinia* and agree with others that the haploid number of 11 was probably the primitive number and that the other haploid numbers $n = 6$ and $n = 8$ were specialized derivations from that basal chromosome set. This paper represents an important acceptance by Smith-White of the progression of science through hypotheses erected on existing facts that could later be struck down as new facts became available. It was a strong mark of his scientific honesty and his acceptance of the progressive building of understanding based on new knowledge.

Prior to his move to the University of Sydney, Smith-White extended his cytological observations of native Australian plants to the heath family Epacridaceae (6),[1] another major woody family in the Australian flora. In contrast to his work in the Myrtaceae, Smith-White found that chromosome numbers in the Epacridaceae were exceptionally variable and concluded that the

[1] Here and elsewhere, the nomenclature current at the time and used by Smith-White is generally retained.

haploid number of 4, very common in *Styphelia* and *Leucopogon* species, was the basal number for the family. In interpreting the array of different chromosome numbers, particularly in the Styphelieae, he proposed that there was a complex set of evolutionary changes in chromosome number, through both increases in chromosome number and the production of reductional series. He was not able to attribute any phylogenetic significance to these changes in chromosome number.

Smith-White's subsequent studies in the Epacridaceae were extensive, and in 1955 he reported on chromosome numbers and pollen types in the family (14). This paper established him up as a leader in cytogenetic thinking both in Australia and elsewhere in the world. He elucidated the triploid genetic system of *Leucopogon juniperinus* (see below). In presenting an extensive survey of chromosome numbers in the family he discussed the difficulty of being too dogmatic about hypothesising phyletic relationships. He found such a striking array of chromosome numbers in different groups in the family that his major conclusion was that the family must have had an ancient origin and that there must have been periods of fundamental chromosome instability leading to a diverse array of effective genetic systems.

Following his work on the Myrtaceae and Epacridaceae, Smith-White worked on the Rutaceae, the family of *Boronia* and many other well known native plants (11). He reported chromosome numbers in 69 species and determined that the primary basic chromosomes number was almost certainly 9. He again found variation in haploid numbers and was able to show that the patterns of chromosomal evolution involved both aneuploidy and polyploidy. In all the diploid and polyploid species, chromosome pairing in male meiosis was regular. He concluded that the polyploids were essentially allopolyploid in origin, derived from hybridization between chromosomally different progenitors. He recognised that the more ancient transitions to polyploidy were recognisable at the level of genera and that more recent development of polyploid conditions were seen at the specific, or even sub-specific, level. It was this third family of Australian plants, the Rutaceae, that catalysed his thoughts about the correlation of geographical and cytological data and led him to his conclusions about the historical development of the major groups that he had studied.

Smith-White's cytological analyses thus covered three major families of woody plants of the Australian flora. Concurrently, through the 1950s, his attention to evolution in the Australian flora was expanding through the studies of the group of students he built up. Alison McCusker worked with him on some aspects of the Epacridaceae, while Helen Ramsay worked on genera of the Proteaceae, Barbara Briggs studied ecogenetics of the *Ranunculus* group, Bryan Barlow worked on another woody family, the Casuarinaceae and Sid James researched *Callistemon* (Myrtaceae), particularly on one apomictic genetic system. Sid James and Jim Peacock were his first students to specialize their efforts into more herbaceous families of the Australian flora. James worked on an intriguing genetic system of reciprocal translocations and its relation to inbreeding/outbreeding balances in *Isotoma* (Lobeliaceae), and Peacock studied the genera and species of the Goodeniaceae including *Brunonia australis* (32).

In 1970, Smith-White and his students Charlie Carter and Helen Stace reported cytological observations on 37 species and varieties of *Brachyscome* as well as undescribed species. The great variety of chromosome numbers and the presence of B-chromosomes in many of the species suggested that the taxonomy of this species group needed to be re-examined (22). They postulated that the complex series of chromosomal rearrangements that were evident were probably of importance in adaptation to the arid regions of the Australian continent where this species group is currently found. This was the first paper in a numbered series of detailed studies of cytogenetic systems in this genus (see below).

All these studies, his own and those of his students, led Smith-White to develop a broad thesis on the probable evolution of the Australian flora in geological and continental time scales. He synthesised his cytoevolutionary insights with the contemporary knowledge of the geographical distribution of the families, genera and species across Australia, and of the climatic and geological evolution of the continent in the Tertiary and Quaternary periods. His major conclusion was that the chromosomal diversity of the native plant groups was due to episodic diversification during their geographic expansion on a continental scale and under progressively different climatic conditions through geological time. His conclusions led him to interpret a general pattern of development of the characteristic Australian flora since the mid-Cretaceous period through to the Quaternary.

This synthesis of cytological, cytogenetic, geographic and climatic data resulted in a major paper that he presented at the Cold Spring Harbour Symposium of 1959 (17). His address on 'Cytological Evolution in the Australian Flora' established an important new way of thinking about the origins and evolution of the flora that has been subsequently built on and refined by many other botanists. He largely concentrated on the major woody taxa and discussed the patterns of chromosomal change, involving aneuploidy and polyploidy; but he also referred to the significance of secondary chromosomal pairing associations. He recognised different time scales in cytoevolution, particularly as indicated by polyploidy being significant at the generic level for the earlier events and at the species level in the more recent events. He was able to reflect on the changes over the geological periods from the mid-Tertiary to the present and was also able, very usefully, to compare the endemic groups with introduced groups. This showed him probable times and entry points and subsequent geographical patterns of spread and chromosomal change. His presentation gave him an enviable international reputation in the fields of cytoevolution and floristic palaeogeography, especially in respect of the Australian flora.

Some years later, in 1982, Smith-White provided the summary and conclusions from a conference on 'Evolution of the Flora and Fauna of Arid Australia' (34), in itself a powerful and learned paper. It comprised a second major statement of the conclusions that he had come to from his own research, as well as the synthesis of the work of the contributors, dealing with both plants and animals, on the way in which elements of the Australian flora and fauna had developed over geological epochs following the break-up of Gondwana. He identified the largely Tertiary timing of the increasing aridity of southern-central Australia that gradually extended northwards. He discussed the different examples of entry of different floral and faunal elements from more mesic environments into the arid zone and commented that there are only very few examples of apparent movements from the arid into the more mesic and montane areas, these occurring largely in the Quaternary.

Apart from this consideration of the radiation, evolution and continental dispersal of the Australian biota, Smith-White's paper presented an incisive consideration of canalized evolution in which he pointed out that genetic history and the environmental opportunities open up a non-random set of evolutionary possibilities that differ for each taxon. He also considered the evidence, particularly in the entry of species from the mesic into the arid zones in Australia, of cases of episodic evolution under relaxed selection pressures, with new and extensive environments permitting the rapid development of a characteristic and somewhat unstable composition of both flora and fauna.

This paper is one of the most important treatises on floral and faunal evolution at a continental level through geological time extending through the Tertiary and Quaternary into the Recent. Together with his Cold Spring Harbour Symposium paper of 1959, this paper, less well known, represents an impressive epilogue to a distinguished period of research by one of Australia's earliest and foremost geneticists.

Intensive Studies of Unusual or Unique Plant Cytogenetic Systems

As mentioned above, Smith-White had a remarkable ability to recognise unusual plant developmental features that were associated with chromosomal behaviour. This was first demonstrated in his studies in the Epacridaceae. At an early stage in this work, in the late 1940s, he also came across a very unusual cytogenetic phenomenon in *Leucopogon juniperinus* (7). This obviously fascinated him and he carried out a series of quite brilliant cytological studies on both the development of the male and female gametes and the generation of the functional embryo sac, published in two papers in *Heredity* in 1948 (7) and 1955 (13). This species was revealed to be a stable triploid with a diploid chromosome number of 12. At meiosis there is regular pairing of eight of the chromosomes into four bivalents, leaving four unpaired univalent chromosomes. In the male the four univalent chromosomes undergo a polarized segregation in the development of pollen and are excluded from any viable nuclei. In the female gametophyte the four univalents are included in the functional embryo sac mother cell. In this way fertilization re-establishes a triploid number of 12. This is one of the very few cases of a stable triploid species in the plant world. It is not an apomictic species but has developed through the remarkable behaviour of the chromosome sets, presumably of allopolyploid origin in the past, resulting in a highly unusual but stable reproductive genetic system. This remarkable piece of cytogenetic work contributed greatly to Smith-White's international standing, facilitating his period of study in Darlington's laboratory in the UK.

A significant outcome of Smith-White's studies in Epacridaceae (6) was his recognition of an unusual polarized development of pollen grains in *Styphelia* and other genera. In the related northern hemisphere family Ericaceae there is a pattern of tetrad pollen development, where all four products of male meiosis remain together instead of separating into individual pollen grains. He showed that the usual situation in *Styphelia* is the production of a viable monad through non-development of the other three pollen grains of the tetrad. He noted that the pollen development system did show some irregularities, and this became a major fascination as in subsequent work he analysed the patterns of tetrad development in the family.

As the study expanded, Smith-White showed there were some genera where tetrad pollen was the rule, where all four monads remained associated in a tetrad group. Most fascinating for him was finding, in some species, segregating tetrad pollen where there was an array of viable monads, dyads, triads and tetrad pollen grains. Smith-White realised that this undoubtedly was the result of chromosomal and genetic instability in these species. He was to carry out some fascinating detailed studies on segregating tetrad pollen in two species, *Astroloma pinifolium* and *Acrotriche fasciculiflora* (16).

Smith-White realised that the patterns of pollen development that he came across in the Epacridaceae were indicative of nuclear/cytoplasmic interactions operating in a regularized fashion in development of the functional gametes. He published his thoughts on cytoplasm–nucleus interactions as a major treatise in his Presidential Address to the Linnean Society of New South Wales in 1959 (15). This was a tour-de-force on the operation of intracellular gradients that he deduced must apply to the cytoplasm-nucleus interactions during pollen grain development. At this time he had already noted that the breakdown of this monad pattern into variable tetrad pollen was likely to be mirroring some underlying genetic instability, which he later studied to great effect in some species of the family. His inductive analysis of pollen development in the tribe Styphelieae was of world-leading standard in cytogenetic thinking.

In his work on the segregating tetrads, largely in *Astroloma pinifolium* and to some extent in *Acrotriche fasciculiflora* (16), the basic observation that Smith-White had in front of him was a frequency distribution of the mature pollen types ranging from a situation where all four grains were viable, a full tetrad, to where no products of meiosis were viable, a so-called nullad. Because the geometry of development was tetrahedral he did not have the advantage genetically of working with an ordered tetrad. He was not able to discern the products of the first and second divisions of meiosis, and in his attempts to explain the phenomena he had to do this on the basis of unordered tetrads.

His analyses in 1959 (16) and 1960 (18) represented one of the most sophisticated lines of genetic research in Australia at that time. He was able to erect hypotheses of causative factors based on independence of the two meiotic divisions, and was able to fit the distribution satisfactorily to a trinomial square expectation. He noted the presence in some plants, and especially in some populations, of departures from the trinomial square form, and recognised that interactions with cytoplasmic factors and/or environmental factors were also involved.

By chance one of his graduate students, Jim Peacock, working in a completely different family of plants, the Goodeniaceae, found a tetrad mode of pollen development in *Lechenaultia* and again came across tetrad segregation driven by various pollen lethal systems. For Peacock and his Adelaide mentor at that time, Peter Martin, the interaction with Smith-White was very important. They published on pollen development and sterility in the same year as Smith-White's more extensive work in the Epacridaceae.

Smith-White's second paper in his study of tetrad segregation was with a student, Alison McCusker. In this paper he was able to bring observations on chromosome breakage into the variable tetrad system (18). Not all the tools that he would have liked to have were available to him in this analysis but nevertheless their paper, published in 1960, was yet another confirmation of the high level of Smith-White's research capacity in elucidating the cytogenetics of endemic Australian plant species.

His final paper in this series was published in 1963 (19) and concerned the variable tetrad situation he found in *Astroloma conostephioides*, particularly in the Grampian Mountains in Victoria. Here he was able to develop a sophisticated analysis based on proposed lethal systems, without defining the nature of the lethality. One can sense the frustration that Smith-White felt in dealing with these genetic systems in native plants in that he was limited by the difficulty of their cultivation and lack of other basic genetic information to develop hypotheses as to the adaptive value of their unique genetic behaviours.

Chromosomal Systems of an Arid-zone Genus of the Compositeae

In 1968 Smith-White published a paper (21) that was to lead to a series of related papers dealing with the cytology, chromosomal evolution and genetic systems of species of *Brachycome* (now *Brachyscome*), a member of the Compositeae. He had discovered that *B. linearifolia* had a haploid chromosome number of only 2. He realised how unusual this was in flowering plants and suggested that it could well develop that this 2-chromosome species might be a valuable model species for cytogenetic and genetic research. He thought that since the plant was an ephemeral annual it should be readily cultivated and suitable for experimental cytogenetics.

In this first paper he also noted that supernumery B-chromosomes were sometimes present and he described the behaviour of the B-chromosomes. In the subsequent eleven papers on this and related species, Smith-White and his colleagues found a richness of chromosomal change in terms of haploid numbers. Not until late in the series, in paper number 10 (34) with his Japanese colleague, Kuniaki Watanabe, were the more experimental aspects of *Brachycome* cytogenetics addressed with the attempted construction of artificial hybrids. In fact, the floral structure and breeding system in this group of plants has discouraged researchers from developing it as a cytogenetic/genetic model plant.

The first paper in the numbered series, reporting cytological observations on 37 species and varieties of *Brachycome*, is described above. In the next paper (23) Smith-White and Carter concentrated on the $n = 2$ species then included in *B. lineariloba* but subsequently described by Carter as *B. dichromosomatica*. They documented the behaviour of B-chromosomes in the different chromosomal races that they found. They followed this with a more detailed description of the behaviour of B-chromosomes, identifying two size classes of these accessory chromosomes (25).

Paper four is probably the most important paper in the whole series (26). Along with Carter and a visiting researcher, D. W. Kyhos, Smith-White studied the cytogenetic system of a 10-chromosome quasi-diploid species. The extraordinary genetic system of this accession of *Brachycome* mirrored the earlier powerful analysis that Smith-White had carried out in *Leucopogon juniperinus*. In this *Brachycome* variety the somatic chromosome complement consisted of a diploid set of 4 chromosomes with an additional 2 non-homologous accessory chromosomes. The accessory chromosomes are inherited only through the pollen. The pollen grains that do not receive the copies of the B-chromosomes as a result of lagging behaviour in the second meiotic division were nonfunctional. The embryo sacs, the development of which is described in the paper, do not transmit these univalent accessory chromosomes. This is remarkably reminiscent of the triploid genetic system of *Leucopogon juniperinus* except in this case, in *Brachycome*, the transmission of the full haploid set of the regular and accessory chromosome is paternal.

Papers five, six and seven in the series report on the meiotic behaviours of several the *Brachycome* species group (27, 29, 30). The pairing of chromosomes in several the lines or species led the authors to make suggestions as to the phyletic relationship between the members of the species group.

In paper seven (30) the suggestion is made that the evolution of the various chromosome races may well be related to the increasing aridity in southern central Australia in the late Pleistocene and through recent geological epochs.

In the tenth paper of the series (34), Smith-White and his colleague Watanabe provided a synthesis of all of the cytological and geographical information assembled in this extensive series of papers. This paper considered the phyletic and evolutionary relationships of *Brachyscome lineariloba*. The authors commented again on the remarkable transmission of the accessory B-chromosomes through the pollen and their exclusion from functional embryo sacs.

In the eleventh and final paper of the series (35), Smith-White and colleagues reported that they had developed artificial hybrids between outbreeding *Brachyscome dichromosomatica*, the haploid 2-chromosome species, and *Brachyscome goniocarpa* which is inbreeding and has a haploid number of 4. The meiotic behaviour suggested that the additional chromosomes in *B. goniocarpa* showed no homologous pairing with the chromosomes of *B. dichromosomatica* but their work suggested that the then current recognition of the placement of the two species into different super-species was not warranted. This paper emphasised the difficulty of controlled crossing and hybrid formation in these daisy plants and the recognition that this represented a hurdle for the wide use of these species in a study of cytogenetic breeding systems.

In a paper co-authored with Carter in 1981 (33), Smith-White published a powerful theoretical analysis on the maintenance of B-chromosomes in *Brachyscome dichromosomatica*. In earlier work on pollen lethality, particularly in the Epacridaceae, Smith-White had demonstrated his skills in the segregational mathematics involved in unusual genetic systems, and the paper on B-chromosomes demonstrated his ability to present possible explanations for unusual chromosomal behaviour at the population level.

Carter had earlier concluded that the fitness of plants with one or two accessory B-chromosomes is greater than the fitness of plants without any accessory chromosomes when the plants were subjected to water stress and dryer conditions. In their 1981 analysis he and Smith-White concluded that this inference appeared to be justified although in non-stress conditions the fitness of plants containing an accessory B-chromosome was lower than that of plants without the B-chromosome. They noted that the observed non-disjunction and preferential segregation in pollen grain mitosis should lead to a fixation of B-accessory chromosomes at a higher frequency, but this did not occur, so they concluded there must be balancing negative selection permitting the establishment of a stable equilibrium, capable of environmental modification. The paper presents sophisticated analyses, but the authors noted that the models they considered were simplistic and that without extensive experimental work their hypothetical conclusions must remain just that—hypothetical.

Other Research Achievements

Smith-White's unbounded interest in genetic systems is reflected in other research achievements, not confined to native flora, that he made whilst continuing his mainstream research, and that were of considerable interest in their own right.

In 1950 (9) he published on non-reciprocal fertility matings between sub-species of mosquitoes. This and a subsequent paper in 1954 (12) originated from his friendship with a colleague, A. R. Woodhill, from the Department of Zoology at the University of Sydney. Behaviours that Woodhill had identified in his mosquito research programme led Smith-White to conclude that this genetic system must be dependent on either nucleus-independent cytoplasmic factors or anomalous meiosis in oogenesis in the mosquito. He and Woodhill concluded that this unusual genetic system has had significance in generating incipient speciation in mosquitoes.

Another research area quite removed from his focus on the cytogenetics of the Australian flora was a study on human chromosomes in 1963 (20). B. Turner, a human cytogeneticist in a Sydney hospital, asked Smith-White and Jim Peacock to examine the unusual cytology in a male patient who was mentally and physically retarded. This collaborative piece of research resulted in the first report of a ring-shaped autosome in humans.

Smith-White's facility in the mathematical analyses of unusual genetic systems was also shown in a paper with his former student George Miklos in 1971 (24) in which they presented a method of analysis of the instability of segregation-distorter in *Drosophila*.

Summary

Spencer Smith-White's research career can be largely thought of in two major phases. The first and most important of these involved his cytological studies of major endemic groups of the Australian flora. His studies encompassed three of the largest families of angiosperms that had representative species in all regions of the continent of Australia. This was his work on the Myrtaceae, the Epacridaceae and the Rutaceae, from which he formed some major hypotheses as to the origin and pan-continental spread of the Australian flora.

This phase coincided with exquisite analyses of many unusual or unique cytogenetic situations that he found in native plant species (and in some animals), including permanent triploidy and variable tetrad segregation, featuring nuclear-cytoplasmic interactions, genetic lethals and non-random chromosomal segregation.

The second phase was his work in *Brachyscome*, stimulated by his discovery that *Brachyscome lineariloba* has a haploid chromosome number of only 2. This discovery initiated an extensive body of work on the species complex related to *B. lineariloba*, leading to further conclusions about chromosomal evolution and its relationship to periods of climatic change through geological eras. In both phases, therefore, he recognised some very unusual genetic systems. His sustained research in these two major areas was a mark of the integrity and commitment that Smith-White had in his quest to use cytogenetics as a means of understanding the evolution of the Australian flora.

Acknowledgements

We should like to acknowledge the helpful suggestions made by Spinny's widow, Mabs Smith-White, and his son Tony Smith-White, and also the excellent taxonomic suggestions made by Dr Barbara Briggs.

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