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Place in Science

Michael White put chromosomes into evolutionary thinking and made a primary contribution to the emerging neo-Darwinian evolutionary synthesis. He emphasised cytogenetic systems and argued that genic and chromosomal evolution were of seminal importance in the process of speciation and evolution. His major scientific contribution was *Animal Cytology and Evolution* (19451, a book that summarised, analysed and synthesised current information on animal chromosomes. White held a somewhat parallel place in cytogenetics to C.D. Darlington, whose book *Recent Advances in Cytology (1932*, 1937) had earlier synthesised observations on plant chromosomes. For many years from the late 1930s there was a lively competition between these two industrious, innovative and self-assertive figures. Undoubtedly White found satisfaction greater than that of science alone when *(contra* Darlington) he described an achiasmate meiosis in a mantid during his first period of research in the United States in the late 1930s.

White had an enormous personal capacity for research that was matched by a voracious appetite for the literature of his subject. He had an extraordinary ability to absorb and retain essential technical information, and this contributed towards the integrated approach he achieved in his books. White's contributions to Australian science were largely the result of his own research efforts. He was one of the most consistent and effective participants in meetings of the Genetics Society of Australia and of the Australian Entomological Society. Apart from the impressions that he made on students and other research workers in presenting his results and ideas, he contributed more generally to Australian science by taking a leading role in the Flora and Fauna Committee of the Australian Academy of Science in preparing policies for the development of the biological sciences in Australia. His concerns for taxonomic studies on the Australian fauna eventually led to the fauna work initially carried out by the Australian Biological Resources Study. White worked with colleagues such as Fenner, Waterhouse and Ride on these causes, and later was involved in the early plans for the development of a Museum of Australia. He was a strong advocate of the formation of a Research School of Biological Sciences in the Institute of Advanced Studies in the Australian National University.

Particularly in his later years, Michael White appeared a rather formidable person on first meeting. His unique voice and manner of speaking and somewhat craggy appearance belied what was underneath, an emotional, shy and endearing man for whom many people had a real affection. White was a major figure in the fields of cytology, genetics and evolution. In Australia, where he spent the major part of his scientific life, he was one of the principals in biology, one of a small group of individuals who brought new standards of rigour into Australian cytology and genetics. In presentations to professional societies, he set high standards both as to content and in his mode of delivery. He was a fine example for students and young scientists to emulate, although his manner of presentation was so unique that one was always tempted to listen to the way in which he said things rather than to what he was saying. He liked to be the centre of attention, to create a presence, but he had a wonderful sense of humour and his persona was always softened by mischievous comments and wry smiles. White was an erudite, literate man whose writings even on complex scientific subjects were a pleasure to read. Papers, grant proposals and books were always written longhand in the first draft, and more often than not his first draft was a close approximation to the last.

White's career involved work in many countries, but probably he identified principally with Australia and the country of his boyhood, Italy. In his last years Michael showed particular enthusiasm for Italy. He had been honoured by election to the Accademia Nazionale dei Lincei, but in addition he had active research programmes that took him back to Italy several times. He organised a meeting for the Accademia Nazionale dei Lincei and was obviously delighted to be part of the senior scientific community of that Academy during the meeting, which involved visiting scientists from other parts of the world. His principal leisure activity, one of few, was to read the classics of Italian literature, in the language in which they were first published. It was a unique experience to travel in Italy with White and to benefit from the manifest pleasure he derived in imparting some of his knowledge and observations on the history and culture of the country.

Early Life and Education

Michael White was born in London on 20 August 1910 to James Kemp White and Una Chase White. James White made a modest living tutoring students who were about to enter Oxford and Cambridge universities or the civil service, in mathematics, Greek and Latin. In 1915, when Michael was five years of age, the family migrated to the Tuscany region of Italy. His father, who held fairly bohemian values, did not favour a formal education for Michael and nurtured his education in the home environment. Although, as described in Michael's own writings, his father could not be regarded as having been a successful man in the formal sense, he apparently was a capable teacher and certainly inculcated a desire for the acquisition of knowledge in his son. Michael learned a great deal of natural history in his surroundings in Tuscany and even at the age of seven made some incisive observations on local insects and their life histories, and so gained an early interest in entomology. He was also a keen observer of the native flora and made collections in a systematic manner. His father fostered his developing interest in natural history by providing him with books on appropriate subjects. He admired his father greatly and was distressed when his father died when Michael was only 14 years of age. Before this the family had moved to southern France close to the Italian border, after five years in Italy. They lived a total of seven years in France, although during this period the major cultural influence remained that of Italy. As well as cultivating an interest in natural history, Michael had by this time formed an emotional attachment to Italy and the Italian people. After his father's death, an uncle supported Michael's interest in natural history and provided him with books on botany. His mother, loyal to her late husband's wishes, arranged that his schooling continue through a correspondence course with the University Correspondence College in Cambridge.

In 1927, after almost three years of secondary school studies by correspondence, Michael returned to London to study for a degree at University College (part of the University of London). He was initially disposed towards a botanical career, but under the influence of the Professor of Zoology, D.M.S. Watson, he became enthralled with the possibilities presented in this area of science. In particular, Michael was influenced by Watson's discussions on evolutionary biology and his interest was strengthened by a young lecturer of the College, Richard Palmer, who added a genetic aspect to Michael's thinking about evolution. In his third year of university life White made a special effort in entomological subjects, perhaps because of his childhood interests. He supplemented his University College studies with courses in entomology at the Royal College of Science, where one lecturer, O.W. Richards, had a particular influence. Richards lectured on evolution and discussed problems of the nature of species and speciation. Michael was awarded a prize for excelling in his third year and in choosing his gift made a decision that was to influence the direction of his whole career. Instead of receiving the Gold Medal to which he was entitled to as a top student he chose instead to receive a copy of E.B. Wilson's classic book ***The Cell** in **Development** and **Heredity.*** Wilson's book influenced his choice of his first research topic. In his book Wilson mentioned that there were seeming contradictions between the genetic and cytological data concerning sex-linked inheritance in birds, so White decided to conduct an investigation into the chromosomes of the domestic chicken. Although he encountered technical difficulties in this study, it did confirm his interest in chromosomal and genetic questions. During these and subsequent studies at University College, he was able to take advantage of the University of London system and attend lectures in other colleges in various aspects of biology and evolution. In this way he was exposed to a variety of evolutionary ideas ranging from Lamarckian to Darwinian.

Early Scientific Career

White was awarded a Master of Science degree in 1932 for his cytogenetic studies in chickens. Probably the most important outcome of his Master's degree was that he became convinced that he had special interests and abilities in analysing genetic and evolutionary matters from a chromosomal observational starting point. Given this realisation it was natural that he might turn to the Orthoptera (an insect group including grasshoppers, locusts, crickets, coackroaches etc.) for his subsequent studies because they presented excellent cytological advantages; in particular, large chromosomes.

His first studies also showed that his mind was attuned to the genetical implications of cytological phenomena. He studied the effect of external environmental factors on the frequency of recombination in grasshoppers, first by looking at the influence of temperature on chiasmata frequencies and later at the consequences of x-irradiation. These studies were important because they were *experimental* in character. This emphasis on experimentation was an underlying theme in all of White's subsequent research. However, what attracted him most were the puzzles presented by cytological observations on natural populations. He believed that seemingly anomalous observations were likely to provide a key to understanding the normal and later often referred to his 'treasured exceptions'. The first unusual situation that attracted him was the strict centromeric localisation of chiasmata in *Mecostethus,* a grasshopper found in some of the sphagnum bog areas within striking distance of London. These investigations brought him into contact with a figure who was to have a major influence on him, namely J.B.S. Haldane.

Haldane had arrived at University College in 1932, already a charismatic figure in genetics and evolutionary biology. Although White later denied that Haldane had a strong influence on his work, there is no doubt that he was greatly impressed by him, perhaps as much by his behaviour as by his ideas. White was to develop into a colourful figure himself. Many of White's acquaintances had the pleasure of listening to Michael in some of his memorable feats of story telling, and many of those centred around incidents involving J.B.S. Haldane. Haldane was unquestionably impressed by White and in 1938 invited him to move from the Department of Zoology to the Department of Genetics for his research, but White chose to stay in the zoological milieu, perhaps indicative of his conviction that one always had to study genetic systems in a biological framework. Also, Haldane's department emphasised population and analytical genetics with a mathematical slant which was not one of White's major interests or strong points. However, White maintained close contact with Haldane, who accompanied him on some of his collecting trips. Rigour in analysis of experimental results was certainly one conviction that White absorbed from Haldane's approach to science.

In these first years of study, White cemented the major directions of his research and intellectual interests for the next several decades. It was clear to him that he wanted to work with chromosomes and that the Orthoptera was an ideal group to work with because they were cytologically amenable. Nevertheless, his interest in chromosomes was not in them as cytological objects *per se* but because they provided a key for some incisive thinking about genetic systems and the role of genetic processes in speciation and evolution. His analytical and genetical approach to cytology differed substantially from the more descriptive outlook of most other cytologists of the day. In this early period, too, he worked with grasshoppers, one of the three groups of insects that would be his dominant experimental material throughout his research career. In later research, as a consequence of his first visit to the United States, he would add mantids and gall midges.

1932 was an eventful year in White's life. He married Margaret Thomas, a fellow student with similar scientific and political interests to his own. This was also the year that Darlington's *Recent Advances in Cytology* was published, as too was Haldane's book, *The Causes of Evolution.* Darlington's synthesis of cytological studies in the plant kingdom was of major importance in cytology and cytogenetics. There is no doubt that it had a strong influence on White, probably triggering a desire to make a comparable mark with the chromosomes of animals, particularly insects. Just as White was impressed by Haldane's behaviour he was also impressed by the demeanour of Darlington. Above all, Darlington's book strengthened

White's conviction that chromosomal observations were of value in developing an understanding of genetics and evolution. However, Darlington's approach to cytology, genetics and evolution differed markedly from White's, and several times during their careers they clashed with some relatively intense disputes emerging in the scientific literature.

As a young academic, White briefly became involved politically, and although he was dedicated primarily to his research it is not surprising that, as an intellectually active person, he responded to political concerns of the day. The radical physicist J.D. Bernal had a particular influence in White joining the Communist Party in 1932. Although White was politically concerned, it is clear that he was not a great enthusiast. He was more a supporter than an activist, and was criticised by his political peers for his apparently indifferent attitude. A couple of years later he resigned and joined the British Labour Party.

White went through a troubled period when his marriage effectively ended in 1933, and it was not until 1935 that he fully regained his drive in research and life. At that time he met Sally (Isobel Mary Lunn), whom he would later marry and who for the remainder of his life was an influential and supportive colleague and partner. In 1935, too, he was made a lecturer at University College. In his research he began demonstrating one of his characteristic traits, that of thinking beyond his own immediate experimental studies and placing them in a broader picture, looking for any appropriate generalisations that they indicated. Darlington was of the same conviction but went far beyond the experimental data with many of his generalisations. White was more conservative in this regard and additionally saw the value of experimental cytology in assisting in general understanding. A very good example was work he published on the nature of distributed centromeric activity in the chromosomes of Ascaris, in which he settled contemporary differences of opinion with an unambiguous experimental analysis.
White first synthesised his thoughts about the nature and importance of chromosomes in a small monograph, The Chromosomes, first published in 1937. Although this book did not contain the theoretical insights and major tracks of conceptual thinking that were prevalent in his subsequent book, Animal Cytology and Evolution, it filled a niche in the field at the time and went to seven editions. It was published in several languages and for many years was used extensively in universities throughout the world. In this small monograph White signalled his appreciation of the genetic consequences of meiotic events. The book included what was essentially his first public discussion of the importance of chromosomal systems in evolution. This was quite an achievement for a young scientist of 27 years. The publication of his book undoubtedly contributed to his gaining a Rockefeller Fellowship in 1937 to travel to the United States for a period of research and study.

White went to work at Columbia University with Franz Schrader and Sally Hughes-Schrader, two insect cytologists. He took with him some cytological material and slides from his London studies and carried out an analysis of this material that established that the direction of chromosome coiling was basically random. This contravened generalisations made by Darlington. After the completion of this work, White saw no way to take it any further and began searching for new problems. Through contact with one of the Schraders' students, Kenneth Cooper, he became interested in one of the central cytogenetic problems of the day, the question as to whether meiosis could proceed regularly if there were no chiasmata between homologous chromosomes at metaphase I. Cooper's views differed markedly from those of Darlington, who insisted that chiasmata were essential to the normal and orderly progress of meiosis. White studied meiosis in a male mantid, Callimantis antillarum, and discovered that there was a complete absence of chiasmata in meiosis in the male. White was excited by this discovery and promptly published his findings in the Proceedings of the Royal Society of London, shocking the Schraders with what they viewed as a precipitous approach to science. When reminiscing about working with the Schraders, White always compared their thorough germanic descriptive approach with his own, which was more dynamic and always genetically oriented.

At Columbia, White made another vital contact. Theodosius Dobzhansky was visiting Columbia from the California Institute of Technology where he worked in association with T.H. Morgan and colleagues in Drosophila genetics. Dobzhansky had just published his seminal book Genetics and the Origin of Species, and already it was obvious to White that he was one of the world's most dynamic evolutionary geneticists. Dobzhansky and White quickly established a rapport and, discovering that they both planned to travel to Mexico on collecting trips, arranged to rendezvous in Mexico City. This they did and participated in a lecture series at the Instituto Politécnico Nacional in Mexico City. White had a vivid memory of one of his lectures in which he discussed sex chromosome systems involving either two or three X chromosomes. He was surprised at the enthusiastic applause that punctuated his lecture, not realising at the time that 2 X's and 3 X's signified brand names of popular Mexican beers.

While in the United States, White met a large number of cytologists and geneticists and was clearly influenced by the high level and freedom of academic exchange of ideas. This stimulating period probably strongly influenced his subsequent decision to write what was to become a major book, Animal Cytology and Evolution. His somewhat idyllic academic experience in the United States as a Visiting Fellow also influenced his later decision to return to work in that country. However, the Rockefeller Fellowship required him to go back to England. He returned accompanied by Sally, who had come over to the United States to spend some time with him towards the end of his stay, while he worked at the Woods Hole Laboratory.

Not long after their return to England war broke out. Although for a while his research work continued at University College, the Zoology Department then closed down. After a brief time at an entomological laboratory in Slough, White was placed as a statistician in the Ministry of Food, where he served for the duration of the war. Michael and Sally had married only a few months before war broke out. An amusing episode in an otherwise sombre year of political crises occurred at this time. Michael found himself standing in a queue in order to acquire the marriage licence, and only after some considerable time discovered that he was in fact in the wrong queue. He had unknowingly joined the one for petrol coupons!

So far as his scientific work was concerned, White was frustrated by the inconveniences caused by war-time restrictions. His cytogenetic research languished. He was not intellectually stimulated by his war duties and generally resented the interruption to his career. Nevertheless, this war-time hiatus paradoxically led to one of his most important contributions to science. In the evenings and on weekends he worked on his book, Animal Cytology and Evolution, and he had a manuscript ready by the end of the war. It was published in 1945.

A chapter he wrote for the book Cytology and Cell Physiology (1942) signalled many of the concepts that he further developed in Animal Cytology and Evolution. White recognised that chromosomes were complicated organelles and that ultimately a molecular understanding of them was going to be fundamental to both physiological and evolutionary biology. In the 1942 review he struggled with the fragmentary state of nuclear chemistry and was not able to attach any conceptual meaning to what was then known of nucleic acids and proteins in the chromosome. In this he was not alone. However, this section of his paper was in marked contrast to the masterly sections dealing with structural behaviour of the chromosome. The latter was his field and it is what he understood best. It would not be until the last couple of years of his life that White would fully return again to the recognition that the control of gene expression was central to an adequate understanding of development and evolution. The review was of interest too because, although White had considerable empathy with the wonderful work of the Drosophila geneticists, he was able to question their notion of equating heteropycnotic chromosomes with genetic inertness. White's analysis came from a cytological viewpoint and it was interesting that he did not feel overwhelmed by the genetical studies. His paper contained other important ideas. For example, he concluded that polytene chromosomes of insects' salivary glands and other tissues represented a particular form of endopolyploidy and suggested that there were probably different levels of replication of the chromosome thread in different regions of some polytene chromosomes. Again this was a suggestion stemming from his cytological knowledge of chromosomes, extending far beyond the salivary chromosomes of Drosophila. In this review paper he contributed a penetrating consideration of induced chromosome structural rearrangements in terms of their consequences as mutations. He also emphasised that not all was known in genetics and he pointed to some significant holes in the knowledge fabric.

Animal Cytology and Evolution gathered into a coherent whole a mass of descriptive cytology and conflicting theories of cytogenetics and evolution. In this respect it paralleled Darlington's earlier plant-oriented book, Recent Advances in Cytology. White's Animal Cytology and Evolution was the first critical survey of cytology since E.B. Wilson's The Cell in Development and Heredity published twenty years earlier, the book that initially inspired White to enter the field. It integrated the cytological approaches of Belar, Dobzhansky and Darlington. White's book must be regarded as the foundation of modern animal cytogenetics and it established him as one of the major conceptual contributors to the neo-Darwinian evolutionary synthesis. White examined cytological and evolutionary observations of diverse sources from a genetical viewpoint, and the resulting synthesis probably provided his single most important contribution to the development of modern evolutionary theory.

Animal Cytology and Evolution ranks with Dobzhansky's Genetics and the Origin of Species as one of the seminal treatises in animal evolutionary biology. White's book emphasised that the principles of evolution applied to individual chromosomes and the chromosome complement just as they did to more classical morphological characters. He also stressed that the chromosome complement, principally through its meiotic properties, could influence the course and rate of evolution of any taxon. White had a great understanding of the mechanism of meiosis and its significance, and an almost intuitive grasp of the complexities and consequences of chromosomal rearrangements, especially in regard to speciation. The various chapters of the book testify to what were his major areas of creative study. One of the dominant themes in the book concerned the evolution of sex chromosomes, sex-determining mechanisms, and the phenomenon of thelytoky, the subject on which he concentrated for many of his later research years. Before the war had interrupted White's research, he had published his first papers on sex chromosome mechanisms in both mantids and grasshoppers. He retained an experimental and theoretical interest in sex chromosome systems throughout his career and made many contributions in this area. This topic and his stimulating experiences in the United States were major factors in convincing him to write Animal Cytology and Evolution.

In various editions of the book, as in his research career generally, White's focus was always the chromosome and the chromosome complement. This was true whether he was concerned with a particular aspect of an insect's genetic system, whether he was probing the causes of speciation, or thinking even more widely about mechanisms of consequence for evolution. White personally attached a great deal of importance to the book and put in an enormous effort in later years into producing a second and third edition of comparable quality. The third edition published in 1973 demonstrated that he was attempting to keep abreast of the vast changes that were occurring in genetics with the advent of molecular biology. It revealed his strong interest in molecular analyses of genetic events and showed his determination to embrace these findings within an evolutionary perspective. All three editions of the book bear witness to White's encyclopedic knowledge and familiarity with the published work of animal cytogenetics. White wrote in the preface to his third edition: 'If the present book helps to re-establish chromosomal mechanisms in the centre of the evolutionary stage, the labour of writing it will not have been in vain.

The United States-Science and Politics

In 1946 White was elevated to a readership in University College, but he remained dissatisfied with the scientific community in England. He felt deeply the interruption the war had brought to his research career. While writing *Animal Cytology and Evolution* his ideas were developing rapidly, but he felt he was extremely isolated in the English academic environment. He was becoming increasingly annoyed at what he perceived to be personality cults surrounding a few central figures who dominated the scene in British biology such as Darlington, Mather, Ford, Fisher and to some extent Waddington. As soon as an opportunity presented itself, he travelled again to the United States, looking for a suitable position there. His favourable memories of the stimulating academic environment in the prewar United States were confirmed by his return visit to the Genetics Department of the Carnegie Institute of Washington at Cold Spring Harbour. It was thus not surprising that he accepted an offer of a job at the University of Texas at Austin, one of the strongest centres of genetics research in the United States. In 1947 White spent six months as Visiting Fellow at the Cold Spring Harbor laboratories, then, accompanied by Sally, moved to Texas to begin a new phase of his career.

For most of the time at the University of Texas White was engaged in productive research. He appreciated the opportunity of working with colleagues such as Patterson, Stone, Wheeler, Griffiths and Wagner. It was during this time that he studied the peculiar meiotic systems of the gall midges, Cecidomyidae, a group to which he had been introduced by the Schraders while at Columbia University. White saw that study of the bizarre meiosis of these organisms could further advance the understanding of regular meiotic systems. He also continued work on the chromosomes of grasshoppers which confirmed for him the pleasure to be derived from working with natural populations ***of*** insects, particularly those living in arid environments. While at Texas White commenced regular annual summer collecting trips in the deserts of the south-west. These regular and extensive collecting pilgrimages to outback areas were also to be a feature of his later research work in Australia. In Australia, even in the years of his 'retirement', White mounted major collecting trips into the arid Nullabor Plain in the heat of summer. His wife, Sally, proved to be his only durable companion on these arduous safaris.

Some of the south-west grasshopper taxa had chromosome rearrangements that were polymorphic in various populations. His study of these, particularly in Trimerotropis, kindled his interest in population cytogenetics. During a prolific period, he published not only his own experimental results but also commentaries on a range of other cytological and evolutionary matters.

But White's time at Texas was to be troubled, and this phase of his career was brought to an end by political issues. The McCarthy era of political witch-hunts had begun. Michael was investigated by the US Immigration Authority because of his con-nections with the Communist Party during his student days in England. His problems were acute largely because a state law had been passed that required employees of public universities and other institutions to sign an oath indicating that they had never had any Communist affiliations. Of course, White was unable to do so and this ultimately resulted in his resignation. In the end it was a matter of White either resigning or being deported. During this period he found himself in an untenable situation at Texas. Once again White found safe haven in the intellectual cocoon of the Cold Spring Harbor laboratories. He took sabbatical leave, without pay, and for a year was personally and materially supported and provisioned at Cold Spring Harbor by Miloslav Demerec, Barbara McClintock and others. This gave the White family some respite, allowing them to regain a measure of equanimity before Michael returned to teach again at the University of Texas. However, shortly afterwards this excruciating and deplorable political saga came to a conclusion when in 1953 the White family voluntarily left the United States for Australia.

Australia-An Intellectual and Cultural Home

Through the efforts of Dobzhansky and other colleagues, in 1953 Michael White was offered an appointment in the Genetics Section of the CSIRO Division of Plant Industry in Canberra. Dobzhansky made contact with Otto Frankel, who had recently been appointed Chief of the Division, requesting his help. Frankel, himself a prominent geneticist, was happy to provide a position for White because he was attempting to build up the research strength of the Genetics Section of his Division. Frankel made the full facts of White's predicament known to CSIRO's senior executive officers, Frederick White and Ian Clunies Ross, who had no hesitation in supporting Frankel in his efforts to secure a position for White. There is no doubt that White would have warranted the appointment through his scientific reputation alone, but they were also sympathetic to the unfortunate political intrusions into his career. It was a courageous decision by Frankel and colleagues because anti-Communist sentiment was also raging in Australia. At Canberra, White was put under no pressure to work on plants. Frankel felt that White's presence and active research would be of general benefit to the programme at CSIRO and it certainly proved to be so, with White providing an international perspective and the setting of new standards for other geneticists. He played an important role in raising the standing of the Division's genetics group as a whole.

White spent three productive years in the Canberra laboratories. In 1956, the final year of his appointment, he began working on the morabine grasshoppers. This proved to be a turning-point in his career. This large group of endemic, wingless grasshopper would be his central experimental organisms in subsequent years. one piece of work he carried out in Canberra was an extension of his observations on pericentric inversions in the trimerotropine grasshoppers of the south-west United States. He collaborated with another CSIRO geneticist, Fred Morley, in exploring the genetic consequences of polymorphism for pericentric inversions in populations of a species of local grasshoppers. White was proud of this paper which demonstrated his ability to collaborate with other workers who had complementary skills-in this case, Morley's conceptual mathematical thinking. White also unearthed some other remarkable chromosomal rearrangements in the morabine grasshoppers and this resulted in the first of a series of papers published over many years.

Although his work was stimulating and he was well pleased with his colleagues and the environment, White was not completely satisfied at CSIRO. The CSIRO was a purely research institution and he found himself missing the stimulation and pleasures of teaching. During his time at Canberra he received entreaties to return to the United States where his genetical colleagues fully appreciated his capabilities and his stature as a scientist. No doubt they were anxious to redress the wrongs of the McCarthy period.

With McCarthy's decline in late 1954, the United States returned to a saner political environment and White decided to return to a university position where he hoped to experience the stimulation of both research and teaching. He accepted a position as Professor of Zoology at the University of Missouri, which was one of the strong centres of genetic research in the United States, having an impressive history of both Drosophila and maize genetics. But unfortunately it was not a good choice for White. His particular brand of cytogenetics was not well represented there. Both he and Sally found the general culture and religious environment of Missouri not to their liking. White realised that he and the family had been much more at home in the social and scientific environment of Australia. With the intervention of Frankel and Clunies Ross, an invitation came to White to return to Australia as Professor of Zoology at the University of Melbourne. So, after just eighteen months in Missouri, in 1958 White once again found himself a major figure in the Australian genetics community.

White built up a strong genetics section within the Department of Zoology at the University of Melbourne. In 1964 he became the foundation professor of genetics at the University, moving in 1973 to a separate building of which he was, perhaps uncharacteristically, very proud. He put a considerable effort into raising money for the building and insisted that it made a statement about the importance of genetics as a discipline. White built up a first class genetics department, something much needed in Australia at that time. His personal reputation allowed the department to maintain a strong international flavour, attracting a succession of visiting scientists and scholars. Nevertheless, from the perspective of a dynamic research scientist not all was ideal for him at the University of Melbourne. Particularly onerous were the administrative duties associated with the heavy bureaucracy of the University. White was one of the outstanding scholars in the faculty and this was probably under-recognised by the University. During his professorship he maintained an active research effort and found himself in touch with a wealth of cytogenetic opportunity, particularly with the morabine grasshoppers. He also 'travelled and collected' the Orthoptera of other countries, for example in South Africa and Madagascar.

White had a succession of graduate students during this period, some of whom including Ross Crozier, Jon Martin, John Thomson and Graham Webb, went on to academic and research positions in Australia. However, he personally supervised relatively few postgraduate students. This was perhaps due to his single-minded concern with his own research programme and his lifelong tendency to operate as a lone-worker. He required complete freedom in his own work and thinking and granted the same to others. He was not orientated towards building a strong 'school' as such, although he certainly hoped that this would happen naturally, as a by-product of his own inspiration and devotion to the cause. He was driven on by a desire to uncover yet another piece of the genetic puzzle and fit it into the larger picture. Nevertheless, he made a huge contribution to Australian genetics. Apart from his own students, he also influenced others elsewhere in Australia, primarily through his presentations at the annual meetings of the Genetics Society of Australia. By his later years he had developed into a wonderful example of an idiosyncratic but gifted academic. His addresses at the Genetics Society meetings were inevitably of a high standard with new findings from his experimental programme presented every year. Above all they were colourful and entertaining and fired the imagination of his audience. Along with Otto Frankel, Jimmy Rendel and Spinny Smith-White, Michael White stimulated many of us to aspire to excel in our quests for understanding of the mechanisms and consequences of genome dynamics in plants and animals.

Following his retirement from Melbourne in 1975, White accepted a visiting fellowship in the Research School of Biological Sciences at the Australian National University (ANU) in Canberra. Along with David Shaw he was a major figure in an active cytogenetic team headed by Professor Bernard John, an ex- Darlington student. Even though nominally retired, White attracted, on merit, research grants from both Australia and the United States. He published a substantial part of his total research papers during a very active period at the ANU. During this time he also renewed associations with the CSIRO laboratory at Plant Industry in which he had worked in earlier years. The CSIRO laboratory and the ANU collaborated in seminars and the organisation of journal clubs. Jim Peacock and his colleague, Elizabeth Dennis, molecular biologists in CSIRO, were able to provide him with another set of complementary skills to probe the evolutionary puzzles of the morabines.

In this period in Canberra, his last major period of research, he also renewed his ties with Italy. In 1978 he was elected a Fellow of the Accademia Nazionale dei Lincei, an honour he prized above almost any other, and he took every available opportunity to lecture and conduct research in the country that along with Australia he had identified as homeland territory. It was in Italy, in what proved to be his last visit, that he was stricken with a cancer that not long afterwards ended his life. From his last visit he returned elated because he had been able to visit Corsica and Sardinia, islands he had long wanted to see.

Research on Morabine Grasshoppers

Michael White had an extremely wide knowledge of genetics and evolution. He was a walking encyclopaedia of research in cytology and cytogenetics of the animal kingdom; but to many scientists he was 'the grasshopper man'. Many of his major contributions to science and particularly to an understanding of the modes of speciation and evolutionary change came from his research in the Orthoptera. His particular interest was in the short-horned grasshoppers and particularly the Australian group of Morabine species. He began his work on the Morabines in Canberra, interrupted it when he returned to the USA for the period in Missouri, and then re-established it when he returned to Australia as Professor of Zoology at the University of Melbourne. White's research intensified when he returned to Canberra on retiring from the University of Melbourne.

Population Cytology of Moraba scurra.—In his first paper on the morabine grasshopper Moraba (later Keyacris) scurra, White analysed hybrids of chromosome races in an attempt to explain their distribution in the field, carrying out both laboratory and field experiments. Here we have once again evidence of White's experimental approach to cytogenetics. This *modus operandi* delineated him as a major figure in the field. White analysed the heterotic effect of the polymorphism he had identified and related his work to the extensive studies made in various Drosophila groups. He was intrigued by the positive heterosis that was associated with chromosome rearrangements in Moraba scurra and postulated negative heterosis for hybrids between races with different chromosome numbers, arguing that this could provide a basis for raciation even in small geographic areas. Incidentally, White did often work with the morabines in small geographic areas. He frequently studied these wingless grasshoppers in cemeteries of country towns that provided 'islands' of natural vegetation. More than one citizen in Australia was startled by the figure crawling around on hands and knees in the local cemetery. White summarised his findings on chromosomal polymorphisms and their effects in a major paper in the Cold Spring Harbour Symposium of 1958. This paper marked a milestone in his contributions to primary concepts of population dynamics.

In his prolonged and productive interaction with the morabine grasshoppers, White was fortunate in having a series of col-leagues with complementary sets of expertise. Ken Key, an orthopteran taxonomist in the CSIRO Division of Entomology was associated with White for many years. They first published together in 1957 on the grasshopper genus Austroicetes, a genus of some economic importance in Australia, but the Key-White axis really matured during the long-term collaboration on the subfamily Morabinae that provided a series of papers on the systematics, genetics and evolutionary biology of these remarkable species. In his first period in Canberra, as well as working with Ken Key on the taxonomic side, White formed an association with Fred Morley, a stimulating geneticist in the CSIRO Division of Plant Industry. Morley contributed a quantitative and analytical dimension to White's study of the effect of pericentric inversion polymorphisms in natural populations of Moraba scurra. The White-Morley work was published in 1955.

When White returned to Australia in 1958 to take up the post as Professor of Zoology at the University of Melbourne he continued his analyses of the biological effects of various chromosomal arrangements in Moraba scurra, searching for evidence for heterosis and its basis. In collaboration with Richard Lewontin, he constructed a series of adaptive topographies for various inversion frequencies. They published their results in a strong theoretical paper in 1960. Lewontin, one of the brightest of Dobzhansky's students, provided a link back to the Dobzhansky-White interaction of earlier years. Indeed, Lewontin strongly influenced a number of Australian geneticists during his sabbatical period in the late 1950s in Australia. At a personal level White and Lewontin got on exceptionally well. Before White's work on Moraba scurra it was generally thought that chromosomal polymorphism in natural populations were maintained in equilibrium by simple heterozygote superiority. His research indicated that the situation was far more complex. The research on Moraba scurra, and especially the work carried out in collaboration with Lewontin on adaptive topographies, was extensively cited and discussed in the literature. The Moraba scurra project was one of the most detailed studies of chromosomal polymorphisms in natural populations beyond the standard Drosophila work.

William Atchley, another visitor to Melbourne, provided biometrical analyses in some of the Moraba work, and another visiting scientist, Robert Blackith, collaborated with White in the mid-1960s, applying multivariate analyses to some of the population studies.

Of White's students, probably Graham Webb made the major direct contribution to White's own research area, in particular on the parthenogenetic grasshopper Warramaba virgo. Later, in Canberra, Webb was able to bring molecular-biological analyses to bear on the research through his associations with Liz Dennis and Jim Peacock.

These were fruitful collaborations, and in many cases were crucial in the development of White's scientific work, but throughout there was no doubt in the minds of any of the collaborators that White was in charge! Although his own research work always had priority, he did appreciate the contributions of others and collaborated only with scientists whom he respected and trusted.

Parthenogenesis in Warramaba virgo.—White's tireless fieldwork on the morabines further paid off when he happened on the first example of a parthenogenetic species of grasshopper. On a field trip in western New South Wales in January 1961, White discovered a population of a Moraba (later Warramaba) species and was surprised that he could locate only females. After a fruitless additional search for males by his observant son Nicholas, White became convinced that this was possibly a parthenogenetic species. No mind could have been better prepared to come to such a conclusion. In an earlier study in Austin on the mantid Brunneria borealis White had described an exclusive parthenogenetic reproduction system and had pondered on the genetic consequences of parthenogenesis for a number of years. He sent off a short note to the Australian Journal of Science about his discovery, which was published in August 1962. White enthusiastically took Ken Key, his taxonomist colleague, to look at the all-female population. Key was initially sceptical that this would prove to be a valid species. However, he was soon convinced that no males were present and provided a suitable taxonomic place for the species, with a joint publication in the Australian Journal of Zoology in 1963.

White's first public announcement of his finding of the parthenogenetic grasshopper was at the Genetics Society of Australia meeting in Sydney in 1962. an Australian geneticists have fond memories of Michael describing what was then called Moraba virgo, which he had discovered in two populations by that time, in New South Wales and north-western Victoria. The scientific excitement was accentuated by his presentation, and in particular his enunciation of the word 'femallllllllllle', this word sometimes using many seconds of his valuable presentation time! White was clearly fascinated by thelytoky, as he persisted in calling it in the scientific meetings of that time (perhaps because of the resonance he could give to that particular word rather than because of its precise biological meaning). White studied Warramaba virgo not just for its own sake, however, but because he felt that a detailed study of this unusual species would lead him to an understanding of processes involved in regular speciation events.

Ironically, his initial conclusions about the origin of Warramaba proved to be incorrect. Along with his graduate student, Graham Webb, White studied the patterns of chromosomal replication and concluded that the difficulties they had in recognising homologous pairs of chromosomes in the genome were due to differential heterochromatisation that had occurred since the origin of the parthenogenetic species. It was a prevalent concept in the cytological literature of the day. Another of White's students, David Porter, suggested that perhaps the puzzling chromosome complement was a result of a hybrid origin of the parthenogenetic species. But it was not until 1975 that Godfrey Hewitt, a visiting scientist at the Australian National University, made the convincing suggestion that Warramaba virgo originated as a hybrid between two particular Western Australian sexual species of the grasshopper. Initially White's work on Warramaba uirgo had been only in eastern Australia but he subsequently found that it also occurred on the other side of the arid centre of the continent in Western Australia, where there was a complex of related sexual species. His results were recorded first in 1973 in a paper in Chromosoma. Hewitt, of course, was able to propose a hybrid origin only because of White's extensive data on the sexual species PI69 and PI96 from the Western Australian location. White, who had earlier dismissed a hybrid origin, gradually came to accept this as a real possibility. His experimental hybridisation studies using bisexual relatives led him in 1977 to publicly admit that the hybrid origin was a distinct possibility, and indeed, a high probability.

White had also surmised that the parthenogenetic species undoubtedly had a single origin and he developed elaborate hypotheses as to the probable point of origin and the rate and directions of subsequent migrations to extant localities. But work with Graham Webb on chromosome banding patterns showed two clones of Warramaba virgo which were clearly different, and White was forced to consider the possibility that there had been two separate hybrid origins of Warramaba virgo. This was confirmed in Canberra, following his retirement as Professor of Genetics in Melbourne. He established a collaboration with Jim Peacock and Elizabeth Dennis at the nearby laboratories of CSIRO's Division of Plant Industry. Here, analyses on repeated DNA sequences established beyond any doubt that there had been more than a single origin of Warramaba virgo and that there were probably many.

Michael White's place in the Australian scientific landscape was paralleled by his seamless fit into the Australian physical landscape. Collecting with him in the harsh sunlight, of the Mulga and Cassia country near Broken Hill left an indelible imprint of a dedicated, excited scientist perfectly at home in that demanding, xerophytic ecosystem.

Stasipatric Speciation

In addition to his experimental studies on Moraba scurra and Warramaba virgo, White conducted a third major analysis with morabine species. This was based on the Vandiemenella (formerly Moraba) viatica species group of morabines in the Eyre Peninsula and the surrounding region of central southern Australia. This research sharpened his ideas on the mechanisms by which speciation occurs and provided the stimulus for his last book Modes of Speciation. White's work on Moraba scurra and his other cytogenetic studies had strengthened his conviction that the chromosomal and genetic system of a taxon was of considerable importance to its future. In thinking about how new species developed, White adhered to the basic genetico-biological view that a species was a collection of individual organisms that could be considered to have an interchanging gene pool, so that a species perimeter was drawn by the limits of freedom of exchange of genetic information. Conceptually, he accepted that the gene pool of a taxon could differentiate into two or more subsequent distinct gene pools, that is new species, with genetic mechanisms playing a primary role as isolating mechanisms. He gradually modified his early acceptance of the generally accepted proposition that geographical isolation was a prerequisite to speciation. In several of his publications, White commented on the complexity of biological mechanisms involved in speciation. He recognised that geographic, behavioural, and genetic and cytogenetic mechanisms could all play a role, and in different incipient speciation complexes these factors could have different weightings.

During his studies on the morabines, with their low vagility, he found that he was dealing with taxa associated with small geographic areas, often intimately interdigitated. In his earliest writings on Moraba scurra it is possible to see that he was moving towards the ideas that genetic barriers could be the major isolation mechanism needed for the development of two subsequently independent gene pools. In the viatica species group in the Eyre Peninsula in South Australia, he was confronted with a mosaic of karyotypic chromosomal systems with very little geographical separation. Not only could he find situations where it seemed that new taxa, as defined by the cytogenetic system, arose from an apparent peripheral population isolate of an existing group, but he found other situations where individuals with a new chromosomal system seemed to have arisen within the distribution of another taxon. He coined the term *stasipatric* (stationary place) speciation to describe the latter situation as apparently demonstrated in the *viatica* species group.

Vandiemenella viatica was a regular single species over much of its distribution range, but in the coastal region of central South Australia White found a multitude of chromosomal forms. These forms or races were often contiguous (or *parapatric* in White's terminology). Because the hybrids could be identified cytologically he was able to determine that in many situations the hybrid zones could be extremely narrow, a matter of one or a few metres. This emphasised to him that chromosomal rearrangements could function as strong primary genetic isolating mechanisms. White saw that chromosomal variants with the appropriate properties did not always occur on the geographic peripheries of the species distribution. Rather, White found situations which he interpreted as meaning that the origin had been within the distribution with a subsequent expansion on one or more fronts. This convinced him that geographic isolation was not a mandatory requirement in the speciation process. He developed his stasipatric speciation concept in a lead article in *Science* in 1968, realising that in doing so he was throwing up a challenge to what he considered to be an overly narrow concept of geographically based speciation promulgated by orthodox neo-Darwinian contributors to this field such as Ernst Mayr. White developed his ideas further in his 1978 book, *Modes of Speciation*, where he went to some lengths to explain why we might envisage many different paths of speciation, dependent on chromosomal, genetic, behavioural and other biological factors as well as geographic considerations. In developing his concept of stasipatric speciation, White emphasised his life-long view of the importance and complexity of cytogenetic processes in population dynamics and hence in evolution.

White, an admirer and colleague of Mayr, felt that Mayr had underestimated the importance of genetics related processes in the mechanisms of speciation and evolution. The *viatica* group of the morabines gave him the opportunity to illustrate his view of the many factors involved in speciation. Characteristically, he drew on data derived from his own field collections and experimentation. Although White may not have succeeded in achieving a general acceptance of his views on speciation processes and may not have convinced the broad range of taxonomists and evolutionists that stasipatric speciation may occur, he certainly re-established the importance of genetic mechanisms in the isolation processes involved in the generation of species. Mayr, in a thorough review of *Modes of Speciation* in *Systematic Zoology* in 1978, paid tribute to White in this regard.

Epilogue

Michael White was one of the most distinguished scientists of his generation to work in Australia. Throughout his career he made important contributions to many aspects of cytology and cytogenetics and to evolutionary biology, including speciation theory and systematics. He had an awesome capacity for unremitting hard work and continued his research activities up until a few days before his death. He died from cancer on the 16 December 1983 at age 73, still at the height of his career. At the time of his death he was acknowledged as the world's leading cytogeneticist. His importance to science is indicated by his membership of many of the world's most prestigious academic societies and in the variety of international honours bestowed on him (see below). White was honoured by a Festschrift on his seventieth birthday *(Evolution and Speciation*, 1981; edited by W.R. Atchley and D.S. Woodruff).

Michael is survived by his wife Isobel (Sally), an anthropologist who specialises in research on the Australian aborigines. In addition to her own academic work, Sally had an extensive involvement in Michael's field work. Michael is also survived by his three children: son Nicholas, a virologist, son Jonathan, a university lecturer in humanities, and daughter Charlotte, a medical practitioner. Michael White's passing was a major loss to Australian and international science and to family and friends. His legacy, however, is immense.

Acknowledgements

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Awards and Positions

Degrees

BSc in Zoology and Human Physiology (First Class Honours), University of London, 1931
MSc, University of London, 1932
DSc, University of London, 1940
MSc, University of Melbourne, 1959
Dottore in Science Biologiche honoris causa, University of Sienna, 1979.

Fellowships of Learned Societies

Fellow, Australian Academy of Science, 1955
Member of Council, AAS, 1960-1962
Fellow, Royal Society of London, 1961
Honorary Foreign Member, American Academy of Arts and Sciences, 1963
Fellow of University College, London, 1962
Foreign Member, American Philosophical Society, 1978
Socio Straniero, Accademia Nazionale dei Lincei, 1978 Fellow of the Linnean Society of London honoris causa, 1979
Foreign Associate, U.S. National Academy of Sciences. 1981.

Medals

Mueller Medal, Australian & New Zealand Association for the Advancement of Science, 1965
Silver Medal for Research, Royal Society of Victoria, 1979
Linnean Medal for Zoology, Linnean Society of London, 1983
Minerva Medal of the University of Rome, 1983.

Academic Appointments

1976 Visiting Fellow, Department of Population Biology, Australian National University.
Jan.-Mar. 1968 Visiting Agassiz Professor, Harvard University.
Aug. 1964-1975 Professor of Genetics, University of Melbourne.
July 1958-July 1964. Professor of Zoology, University of Melbourne.
1963 Visiting Fellow, Witwatersrand University, South Africa.
Jan. 1957- June 1958 Professor of Zoology, University of Missouri.
July 1953-Dec. 1956. Senior Research Fellow, CSIRO, Camberra.
Sept. 1947June 1953. Professor of Zoology, University of Texas.
Mar.-Sept. 1947 Guest Investigator, Department of Genetics, Carnegie Institution of Washington, Cold Spring Harbor, N.Y.
Jan.-Mar. 1947 Reader in Zoology, University of London.
1940-1945 Wartime positions as Statistician and Entomologist in British Ministry of Food
1937-1938 Rockefeller Research Fellow, Columbia University
1935-1946 Lecturer in Zoology, University College, London
1932-1935 Assistant Lecturer in Zoology, University College, London.

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1940b. The Origin and Evolution of Multiple Sex Chromosome Mechanisms. Journal of Genetics 40: 303-336.

1940c. A Translocation in a Wild Population of Grasshoppers. Journal of Heredity 31: 137-140.

1940d. Evidence for Polyploidy in the Hermaphrodite Groups of Animals. Nature 146: 132.

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1941b. The Evolution of the Sex Chromosomes. I. The XO and X_1X_2Y Mechanisms in Praying Mantids. Journal of Genetics 42: 143-172.

1941c. The Evolution of the Sex Chromosomes. II. The X-Chromosome in the Tettigoniidae and the Acrididae and the Principle of "Evolutionary Isolation" of the X. Journal of Genetics 42: 173-190.

1942a. The Chromosomes. 2nd ed. London: Methuen.

1942b. Nucleus, Chromosomes and Genes. Chapter 5 in Cytology and Cell Physiology. London: Oxford University Press.

1943. Amount of Heterochromatin as a Specific Character. Nature 152: 536-537.

1945. Animal Cytology and Evolution. 1st ed. Cambridge University Press.

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1946b. The Cytology of the Cecidomyidae (Diptera). II. The Chromosome Cycle and Anomalous Spermatogenesis of Miastor. Journal of Morphology 79: 323-370.

1946c. The Spermatogenesis of Hybrids Between *Triturus cristatus* and *T. marmoratus* (Urodela). Journal of Experimental Zoology. 102: 179-207.

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Note: *when revising the publications of Michael J. D. White we found that a posthumous paper was not included:*

White M.J.D. 1985. Types of hybrid zones. Italian Journal of Zoology 52: 1-20. (The editors).