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A JOR special section devoted to the 100th anniversary of Michael James Denham White's birth

Preface

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Long ago, as one of us (CJB) started research towards a PhD dissertation on the population cytogenetics of some South American grasshoppers, he had already been strongly influenced by the first Spanish translation (by Francisco A. Sáez, 1951, the pioneer of orthopteran cytogenetics in South America) of Michael White's 'Animal Cytology and Evolution' (1945). CJB had also been fortunate to attend lectures on chromosomes by Sáez, and Sáez had been fascinated by a lecture delivered by Clarence McClung on grasshopper chromosomes at La Plata University (Argentina) in the late twenties' of the XXth century. Sáez was a friend of Michael White's; they had met at the 12th International Congress of Genetics (Tokyo). CJB will always remember a photograph kept in the room of his major professor, Juan H. Hunziker, at Buenos Aires University, in which Michael White, Francisco Sáez, Theodosius Dobzhansky and Bruce Wallace enjoy a good time in Japan.

In 1982 CJB travelled to Maracay, Venezuela to an international entomological meeting. Michael White was one of the outstanding featured speakers and CJB was eager to meet the man in person. Unfortunately, Michael did not appear. By that time, he had been stricken by the liver cancer that shortly afterwards caused his death, at the height of his extraordinary career. Unaware of Michael's health problems, CJB had prompted E.R. Hasson to send our new manuscript on *Leptysma argentina* population cytogenetics (Bidau & Hasson 1984) to Michael, in order to get an expert evaluation before trying to publish. Michael's comments and criticisms were invaluable and the paper was published shortly after; the letter and his kind comments on our beginners' manuscript will never be forgotten.

At that time, CJB had bought, with his meagre doctoral student income, both essential books by White: the third edition of '*Animal Cytology and Evolution*' in its 1977 paperback edition and '*Modes of Speciation*' (1978). Attracted, as so many others, by White's clear and didactic writing style, even when discussing the more complicated cytogenetic and evolutionary problems, CJB too had been captured by the stasipatric model of speciation created by White. That same year, CJB met Godfrey M. Hewitt, who had been a visiting researcher at the Australian National University at White's Department, and orthopterists and cytogeneticists Alejo Mesa and Amilton Ferreira, both having been students of White at Melbourne. Through them, CJB felt closer to this admired biologist.

When CJB moved to Misiones National University to lead an evolutionary genetics team, the younger of us (DAM) was an undergraduate, who quickly became fascinated by the intricacies of what was (and still is) our main orthopteran cytogenetic model for population cytogenetic studies (Bidau & Martí 2002): the melanopline *Dichroplus pratensis*. On this species he later developed his PhD thesis and published his first scientific work on female meiosis. We agree that Michael White's enduring influence has moulded to a great extent, our thinking on cytogenetic and evolutionary matters. Yet one more evidence of our acknowledgment is Michael White´s portrait, hanging in our laboratory for many years, along with that of Prof. Ricardo Ronderos, founding member and past president of the Orthopterists' Society.

For these reasons, it is an honor and great pleasure for us, that through the generosity of the Orthopterists' Society, its President María Marta Cigliano and JOR Editor Glenn K. Morris, we are able to pay homage to the extraordinary work of this great scientist. Our colleagues, some of whom were friends or students of Michael's, and others indirectly influenced by his work, have all to be commended for their excellent collaboration that jointly has produced this special section that we feel Michael would have liked. We now briefly comment on each contribution and its relation to Michael White's scientific interests.

The life of Michael James Denham White was marked not only by itinerant and fruitful scientific achievement but also by adventures. White worked in many countries and institutions and influenced the cytogenetic, biological and evolutionary thinking of many scientists around the world, either directly through his students and collaborators, or indirectly through his publications and books; these books well summarized an incredible amount of knowledge about the chromosomes of animals (White 1973a,b; 1978). Peacock and McCann's (2010) biography clearly demonstrates White's qualities as scientist, his vast output that was not limited to grasshoppers, but extended to orthopteroids in general, to vertebrates, and also impressive studies on Cecidomyidae (White 1950).

White loved Italy where he had spent most of his boyhood between 1915 and 1927. Throughout his academic life he returned many times to that country where he established solid scientific ties and was elected to the Accademia Nazionale dei Lincei, an honor he especially appreciated. White's last (posthumous) paper was published in Italy (White 1985). In this context Prof. Ernesto Capanna writes here about his friendship with White, whose influence was decisive at the onset of Capanna's distinguished career in cytogenetics and evolution (Capanna 2010). Capanna's short paper shows in an affectionate way, the man and friend behind the famous scientist.

Michael White's distinguished career spanned more than 50 y of the biological history of the twentieth century; he lived from a time when problems that today seem matter-of-fact were then controversial and actively discussed (*e.g.*, crossing over and chiasmata), through the birth of the modern evolutionary synthesis, to which he contributed through the publication in 1945 of the first edition of '*Animal Cytology and Evolution*'. In his last years, he saw the impact of chromosome-banding techniques on the evolutionary study of chromosomes, and the beginnings of molecular cytogenetics (White *et al*. 1981, 1982). In this issue, Bidau and Martí (2010) examine the history of orthopteran cytogenetics from McClung's classic paper (1899) to the current day, highlighting Michael White's contributions to the field in such diverse subjects as sex chromosomes, anomalous meiotic systems and population and evolutionary cytogenetics.

Although neo-sex chromosomes of Orthoptera were described early in the history of cytogenetics (McClung 1905, Castillo *et al.* 2010), it was Michael White who performed the first comparative studies and systematized the analysis of neo-sex systems in acridids, eumastacids and mantids. His work pioneered a large number of studies on the origin, significance, cytogenetics and evolution of insect sex chromosomes. White's tradition is honored in this special section by three papers. Mesa *et al.* (2010) report the discovery of an exceptional karyotype including a neo-XY system of recent origin in the phaneropterine *Scaphura nigra*, a Batesian mimic of wasps. Ferreira and Mesa (2010) analyze the cytotaxomomic aspects of the neo-$X_1X_2Y/X_1X_1X_2X_2$ sex chromosomes of the melanopline genus *Dichromatos*. Finally, Castillo *et al.* (2010) review the history of the discovery of sex chromosomes in the Orthoptera, its impact on the chromosome theory of heredity, and the relevance of neo-sex chromosomes in the interpretation of sex-chromosome evolution, as well as the fate of neo-sex chromosomes over evolutionary time.

All his life, Michael White was fascinated by anomalous and hard-to-explain meiotic systems, such as the bizarre mechanisms of gall midges, or the achiasmate male meiosis of some mantids and eumastacids (White 1965a,b; 1970). A related problem was grasshopper species with strong localization of chiasmata in males. Although cases of strict localization of chiasmata were known from the beginning of cytogenetics [*e.g.*, the grouse locusts, Harman (1915, 1920)], its real meaning was discussed first by White in a cytogenetic and evolutionary context and in relation to the Haldane-Huxley rule (Bidau & Martí 2010). In fact, one of White's early papers (White 1936) was on the meiotic process in two orthopterans with chiasma localization, in particular *Mecostethus grossus* (*Stethophyma grossum*), which became a classic model in studies of chiasma localization and its relationship with synapsis. Viera *et al.* (2010) in this special section, review past studies on *S. grossum* meiosis, and report new discoveries regarding the mechanisms involved in pairing, synapsis and chiasma formation of this species, using state-of the-art molecular cytogenetic techniques.

White's first large-scale studies of chromosomal polymorphisms on natural populations of grasshoppers took place while he stayed in the USA at the University of Texas, where he also studied the cytology of gall midges. He chose an exceptional group of Acrididae for his cytogenetic work, the Oedipodinae genera *Trimerotropis* and *Circotettix* (White 1949, 1951); in these he pioneered studies on the effects of pericentric inversions (and other rearrangements) on meiosis and on racial and specific differentiation in grasshoppers. In this issue, Guzmán and Confalonieri (2010) report on a new phylogeographic analysis of *Trimerotropis pallidipennis*, a species showing clinal variation of polymorphic pericentric inversions in South America, using modern molecular techniques. It is a tribute to White's insights that his proposals on phylogenetic relationships and migratory routes of trimerotropines, based only on cytology and geographic distributions, have passed the test of time, and were supported by these modern analyses.

B chromosomes have played a fundamental role in population studies of many grasshopper species, due to their diversity of origin and structure, due also to the ease with which one could study their mitotic and meiotic behavior, initially in males and later in females. Although Bs were not a main theme of White's cytogenetic work, he studied some cases in *Trimerotropis* and produced an excellent review chapter in '*Animal Cytology and Evolution*' (White 1973). Bakkali *et al.* (2010) report a study of B chromosomes in a grasshopper species, *Eyprepocnemis plorans*: this species has become a classic model for the study of B-chromosome evolution and of the parasitic nature of these chromosomes. In this paper, the authors analyze components of reproductive success in temporal and geographic samples of the species and in relation to the presence of parasitic B chromosomes, which they found to decrease female fertility in B carriers. Showing another aspect of supernumerary heterochromatin in grasshoppers, Rosetti *et al.* (2010) analyze B chromosomes and supernumerary segments in the Neotropical *Dichroplus elongatus* (Melanoplinae) using fluorescent banding, and correlate observed frequencies with geographic and climatic variables.

Study of the cytogenetics of Morabinae grasshoppers of Australia confronted White with a diversity of evolutionary problems, among them the existence of a parthenogenetic grasshopper of hybrid origin (*Warramaba virgo*), and the extraordinary chromosomal diversity of the genus *Vandiemenella,* formerly, the '*viatica*' group of morabine grasshoppers. Within this group, White identified a number of parapatric narrow zones of overlap (hybrid zones) between chromosomally differentiated taxa. The nature of these contact zones and the special characteristics of *Vandiemenella* chromosomal variation and geographic distribution, were the basis of White's stasipatric model of speciation (White 1974, 1978; Mrongovius 1979). This model has always been controversial and even White's close collaborator, the taxonomist KH.L. Key had a different interpretation of speciation in the morabines (Key 1974, White 1985). Controversies notwithstanding, hybrid zones were of permanent interest to White who recognized their central role in speciation. In this issue, Bella *et al.* (2010) report on the Pyreneean hybrid zone between *Chorthippus parallelus parallelus* (continental subspecies) and *C. p. erythropus* (endemic of Spain), unknown in White's time. The authors study *Wolbachia* infection, endosymbiotic bacteria that affect reproduction in insects in populations of this hybrid zone, and reveal evidence that *Wolbachia* are producing a significant reproductive barrier within the zone and thus may be involved in speciation.

White was well aware of the importance of knowing not only the meiotic process of organisms, but the whole gametogenesis cycle. In many instances of chromosomal re-arrangement, aneuploidy, B chromosomes or hybridism, meiosis may proceed in a relatively normal fashion, but consequences for fertility are carried by the immature gametes and understanding of the gametes' mechanisms of maturation are central for the assessment of the impact of an altered meiosis on evolutionary processes. For example, in a classic paper, White (1955) studied the patterns of spermatogenesis in 66 acridoid grasshopper species of several families and subfamilies, in what constituted the first comparative analysis of its kind. Gosálvez *et al.* (2010) depart from the traditional focus of orthopteran evolutionary studies that is the meiotic chromosomes, to consider the structural modifications in sperm DNA which are a consequence of changes in the chromosomes themselves and their behavior during male meiosis. The analysis of DNA quality using a range of modern molecular techniques is a promising new field for studies of evolutionary cytogenetics and clearly indicates grasshopper chromosomes still have a lot to say.

As mentioned above, one of the most controversial hypotheses of White was the stasipatric mode of speciation, largely based on his extensive studies of karyotypic differentiation in the '*viatica*' group of the genus *Vandiemenella* (White 1978). Many were the objections directed toward this model (Kearney & Hewitt 2009), but recently, a series of studies using molecular phylogeographic methods, rescued the *Vandiemenella* system after 30 y. The results of Kawakami *et al.*

(2009) do not support the stasipatric model *sensu stricto* but, as Kearney and Hewitt (2009) say, recent theoretical work on the effect of inversions may throw a light on the fixation of chromosomal rearrangements, one of the problems of White's model. Kearney and Hewitt (2009) wonder what Michael White would have done in view of these new results. White was a man of strong convictions but also of great scientific honesty. As he had done when a new and plausible model for the origin of the parthenogenetic *Warramaba virgo* was proposed (Hewitt 1975), he would have started a series of new experiments and then change his view accordingly if the results so indicated. Finally, quoting Kearney and Hewitt (2009): '*White tended to dismiss mating behaviour as a major factor in Morabine speciation—'they are rather primitive'—and the hybridization between deeply diverged taxa would support this view.[…]. But the role of mating behaviour of* Vandiemenella *in this process deserves study, and White would probably have had a go.*'

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