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INTRODUCTION

Plant Genome Horizons: Michael Bennett's Contribution to Genome Research

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This Special Issue of *Annals of Botany* celebrates the career of Professor Michael David Bennett (known to all as Mike; Fig. 1). It includes 14 papers covering a diverse range of current genomics research topics, which were solicited to reflect the breadth of his research interests. The Special Issue arises from the meeting entitled 'Plant Genome Horizons – Vistas and Visions' held at the Royal Botanic Gardens, Kew (16–17 April, 2007) and attended by more than 80 colleagues, ex-students and friends representing all stages of his career from 1963 to 2006.

This article gives an overview of some of Mike's most notable work carried out at various stages of his career. It also provides a link by placing his work in the context of the research outlined in the following papers.

In his entry in the *Kew Science Directory* (see Box 1), Mike summarized his research as being 'focused on holistic genomics to improve understanding of the organisation, behaviour and evolution of genomes and their chromosomes', and although this description was written to cover his work at Kew, it actually describes his career from his early days at Aberystwyth and Cambridge, through to his time at Kew to retirement.

Box 1. Entry for Mike Bennett in the *Kew Science Directory* (www.kew.org/science/directory/)

'Research ranged widely over plant karyogenomics since 1963. Work on nuclear DNA and angiosperms has focused on: (1) genome size evolution, (2) reproductive cell biology; (3) higher order genome organisation, and (4) biosystematics. Work at Kew aims to describe and improve understanding of the extent, nature and significance of variation in nuclear DNA amount (DNA C-value and genome size) as fundamental biodiversity characters in flowering plants and other embryophyta. It continues to explore their adaptive significance for plant distribution and behaviour, and to develop the nucleotype hypothesis as a unifying concept, testing its predictive value. The work has produced the "Plant DNA C-values database", greatly improving its taxonomic, geographic and phytoformic representation. Other interests are: polyploidy and wide hybrids, and work to develop and use chromosome painting techniques as powerful tools in plant biosystematic research.'

Mike began his scientific career as an undergraduate at the Department of Agricultural Botany, University College of Wales, Aberystwyth from 1962–1965. During this time he caught the eye of Professor Huw Rees and went on to study for a PhD under his direction. Part of this involved investigating the work of Pierce (1937), who had reported how chromosomes of *Viola conspersa* varied in size by over 300 % depending on the amount of phosphate in the culture solution. In his first paper (Bennett and Rees, 1967), published in *Nature*, Mike showed that in rye (*Secale cereale*) there was no change in genome size despite changes in chromosome volume of 50 % depending on the phosphate level. Further studies on *Allium cepa* (Bennett and Rees, 1969) revealed similar results, and studies on *Vicia faba* showed that chromosomes prepared from the main root were 2–3 times larger than those in small lateral roots, although the DNA content remained constant (Fig. 2; Bennett, 1970). Mike's PhD thesis was entitled '*Experimental control of chromosome structure and behaviour*', and the degree was awarded in 1968 (Bennett, 1968).

From Aberystwyth, Mike went on to work with Sir Ralph Riley at the Plant Breeding Institute, Cambridge (PBI) looking at the mechanisms and timing of meiosis in cereals including diploid rye and barley (*Hordeum vulgare*), hexaploid wheat (*Triticum aestivum*) and hexaploid and octoploid triticale [×*Triticale* (*Triticum* × *Secale*)]. As part of this work he estimated the duration of both male and female meiosis and demonstrated that it was correlated with genome size at the diploid level (Bennett, 1971). He went on to study how factors such as polyploidy, temperature, environment and individual chromosomes could affect the timing of meiosis and discussed some of the possible wider implications for plants (Bennett, 1977*b*). Arising from this he became interested in the consequences of genome size variation on developmental processes and life cycles of plants, leading him to coin the term 'nucleotype' to define those conditions of the DNA that affect the phenotype independently of the encoded information in the DNA. Since then the term has been extensively used in the field of genome size research. Indeed, in two papers in this Special Issue, the consequences of genome size variation at the cellular (Francis *et al.*, 2008) and phenotypic level (Knight and Beaulieu, 2008) are discussed and reviewed, demonstrating the far-reaching consequences that variation in DNA amount can have on an organism.

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FIG. 1. Professor Mike Bennett.

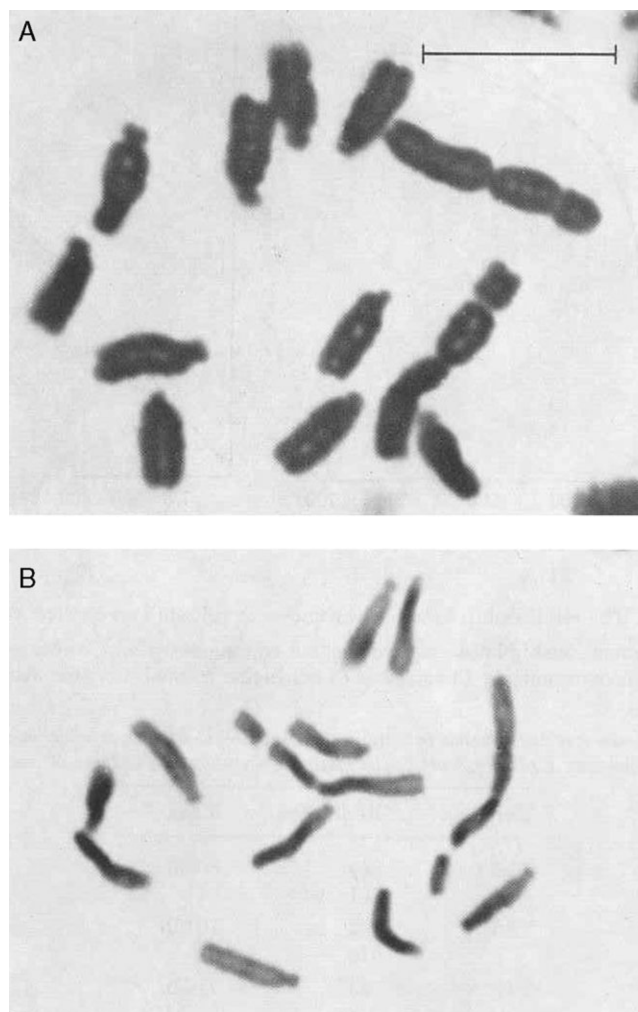

FIG. 2. Metaphase chromosomes of *Vicia faba* prepared from (A) the main root and (B) lateral roots. The difference in volume between the two is three-fold although no difference in DNA amount was found (from Bennett, 1970). Scale bar = 10 µm.

His interest in nucleotypic effects of genome size variation led him to collate widely scattered genome size data into a usable database. In 1976 the first of eight lists was published (Bennett and Smith, 1976); this was, of course, in hard copy only. With the rapid development of computer and database technologies, the electronic Plant DNA C-values database (www.kew.org/genomesize/homepage.html) went live in 1997, and subsequent updates have been invaluable to the genome size community, enabling broad analyses of the data. Mike, together with colleagues, has used the database to analyse large-scale patterns of genome size evolution across angiosperms (Leitch *et al.*, 1998; Soltis *et al.*, 2003) and land plants (Leitch *et al.*, 2005), the relationship between genome size and weediness (Bennett *et al.*, 1998) and seed weight (Beaulieu *et al.*, 2007), and patterns of genome size change following polyploidy (Leitch and Bennett, 2004). Others have also made use of the database (e.g. Jasienski and Bazzaz, 1995; Knight and Ackerly, 2002; Vinogradov, 2003; O'Meara *et al.*, 2006; Ross-Ibarra, 2007). Two additional analyses are included in this volume (Francis *et al.*, 2008; Jones *et al.*, 2008).

Jones and his colleagues review the results of an analysis looking at the relationship between genome size and occurrence of B-chromosomes in angiosperms (Palestis *et al.*, 2004; Trivers *et al.*, 2004; Levin *et al.*, 2005). They show that the presence of B-chromosomes is positively correlated with genome size (Jones *et al.*, 2008). In addition, Jones *et al.* provide an overview of B-chromosome research in the century since they were first discovered in 1907.

Mike's interest in the nucleotypic relationship between genome size and cell cycle time led him to team up with Francis to investigate possible relationships between replicon size, rates of DNA replication, duration of S-phase and genome size (e.g. Francis *et al.*, 1985; Kidd *et al.*, 1987). In this Special Issue, Francis *et al.* (2008) present results of a new analysis from 'data mining' of the literature. In total 110 measurements of cell-cycle time for species with genomes sizes ranging 290-fold were combined to generate the largest cell-cycle time survey to date. This revealed a strong positive relationship between genome size and cell-cycle time independent of ploidy level and life cycle type. The relationship held whether all species were analysed together or if monocots and eudicot subsamples were analysed separately, although eudicots appeared to be characterized by a narrower range of cell-cycle times than monocots of equivalent DNA amount. Further, mean cell-cycle duration was seen to be significantly shorter in annuals than in perennials. The relationship was non-linear, with a striking increase in cell-cycle time in perennial monocots with C-values greater than approx. 25 pg. Although more data are needed to confirm this trend, the apparent threshold at approx. 25 pg is intriguing since a similar DNA amount was noted by Mike to be important in determining life cycle strategies in angiosperms: species with 1C values greater than approx. 25 pg were observed to be obligate perennials (Bennett, 1972; Bennett, 1987). Potential explanations for the observed correlations are discussed in the light of molecular studies. They point to the possibility that as DNA amount increases the amount of heterochromatin also

increases, accompanied by conformational changes in the chromosome structure. This in turn may reduce the frequency of DNA replication origins and results in a longer DNA synthesis phase and hence longer cell-cycle time. While intriguing, these explanations do not explain the sudden and dramatic increase in cell cycle time in species with C-values greater than approx. 25 pg, and further work is clearly needed.

Throughout his career, genome size has remained one of Mike's major interests, woven through many other areas of research, and he has contributed to the field immensely. His thorough understanding of the principles of Feulgen staining (one of the main techniques used to estimate genome size) led him to make suggestions for best practice as early as 1976 (Bennett and Smith, 1976). With the advent of flow cytometry in the 1980s as an additional technique for genome size estimation, Mike pursued this with the same attention to detail. In particular, the potential for inhibitory cytosolic compounds to interfere with the quantitative binding of fluorochromes (essential for accurate genome size estimation) became a focus for some of his more recent research, leading to his paper published in this issue (Bennett *et al.*, 2008) investigating the effects of anthocyanin on genome size estimation in *Euphorbia pulcherrima*. Overall, his contribution to this area of genome size research is reflected in the paper presented by Greilhuber (2008) who provides an overview of nuclear DNA content measurements in plants with a particular focus on technical difficulties.

Polyploidy has been another recurring theme in Mike's research career. Initially, this was focused on the impact of ploidy on the duration of meiosis in cereals (e.g. Bennett and Smith, 1972; Finch and Bennett, 1972; Bennett and Kaltsikes, 1973), showing that the duration of meiosis in polyploids was shorter than for diploids with corresponding genomes sizes (Bennett, 1977*b*). Since then his interest has expanded into many areas including studies of chromosome origin, behaviour and spatial organisation in the polyploid nucleus (e.g. Bennett, 1984*b*; 2004). These studies have been considerably enhanced by the development and application of genomic *in situ* hybridization (GISH; Le *et al.*, 1989; Schwarzacher *et al.*, 1989), which enables different genomes within a polyploid nucleus to be distinguished (Bennett *et al.*, 1992; Bennett, 2004). Indeed, Mike's group was the first to use GISH to analyse the genomic structure of a wild allopolyploid, *Milium montianum* (Fig. 3; Bennett *et al.*, 1992).

The effect of polyploidy on genome size evolution has also been studied by Mike. A large-scale analysis of DNA amounts in 2185 diploid and 823 polyploids showed that loss of DNA following polyploidy was a widespread, although not universal, phenomenon (Leitch and Bennett, 2004). This result was supported by previous studies analysing genome size evolution in individual polyploid species (reviewed in Leitch and Bennett, 2004), and more recent data coming from genome sequencing that shows extensive loss of DNA in polyploids such as maize (*Zea mays*; Messing *et al.*, 2004) and rice (*Oryza sativa*; Wang *et al.*, 2005; Bruggmann *et al.*, 2006). This Special

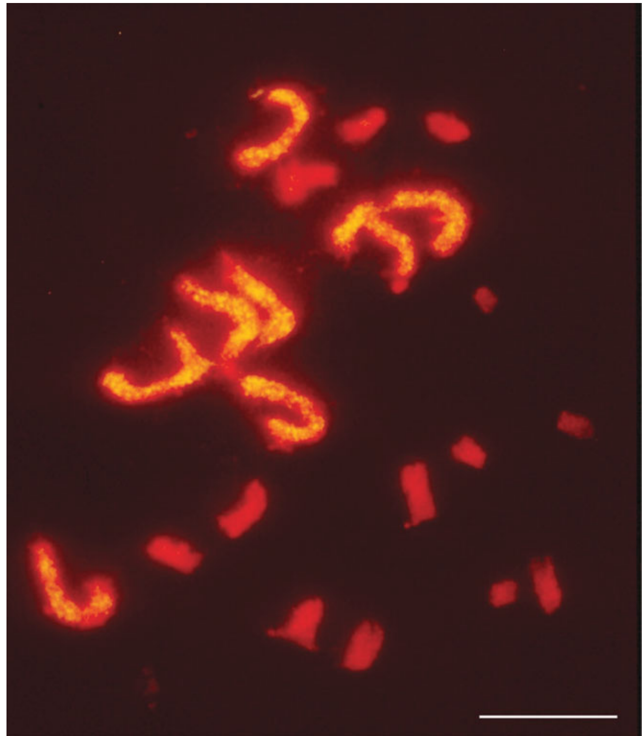

FIG. 3. Use of genomic *in situ* hybridization to distinguish different genomes in the allopolyploid *Milium montianum* ($2n = 22$; Poaceae). Scale bar = 10 μm. From Bennett *et al.* (1992).

Issue includes a paper by Leitch *et al.* (2008), who report recent research on genome size evolution in the genus *Nicotiana*. Here, genome size changes were documented in nine allopolyploids, ranging in age from <200 000 years to approx. 4·5 million years. Although genome downsizing occurred in four polyploids, in the remaining five increases in genome size were apparent, with the size of the increase being positively correlated with increasing age of the polyploid species. Assuming that the apparent changes in the polyploids are not artefacts caused by the incorrect choice of putative parental species used for comparison or by subsequent genome size changes in the parental diploids following polyploid formation, then the results provide new insights into how genome size may evolve following polyploidy.

At the molecular level, research into both naturally occurring and synthetic polyploids has shown that combining different genomes in the same nucleus can have dramatic effects, leading to changes at the level of the genome, transcriptome, proteome and metabolome (reviewed by Chen, 2007). Mike's interest in the molecular evolution of polyploids is reflected in three papers in this Special Issue.

The first of these concerns the evolution of ribosomal DNA (rDNA) sequences in allopolyploid *Nicotiana* species by Kovarik *et al.* (2008). Here, the links between chromosomal organization, rDNA sequence homogenization, concerted evolution and nucleolar dominance are discussed within a temporal and comparative framework by taking advantage of *Nicotiana* polyploids formed over

widely different time-frames (thousands to millions of years). The results suggest that establishment of nucleolar dominance through epigenetic silencing (even as early as in the F_1 hybrid) plays a significant role in influencing the subsequent evolution of rDNA sequences. Active rDNA sequences appear vulnerable to homogenization leading to concerted evolution at such loci. In contrast, inactive, epigenetically silenced rDNA sequences do not appear to undergo homogenization. Because selection cannot act on such silenced genes, they accumulate mutations and are eventually eliminated from the genome. Based on the time-frames involved, results of this study suggest that sequence elimination is detectable in polyploids $\geq$1 million years.

Ma and Gustafson (2008) report dynamic and genome-specific changes occurring after the formation of synthetic hexaploid and octoploid triticale (polyploids containing both wheat and rye genomes). More changes were apparent in the rye genome than in the wheat genome (based on analysis of AFLP fragments), a result that is congruent with some of Mike's earlier work with Gustafson on chromosomal evolution in triticale in which spontaneous changes in the telomeric rye C-bands were reported (Gustafson and Bennett, 1982; Gustafson *et al.*, 1983). Genome-specific changes as observed in triticale have also been reported in some other polyploids (e.g. Song *et al.*, 1995; Zhao *et al.*, 1998; Ozkan *et al.*, 2001; Skalicka *et al.*, 2005).

Understanding endopolyploidy, particularly the development of endosperm (which is initially triploid, although later higher polytriploid levels are found), is important given that the endosperm of a range of species is a major source of food. However, the origin, significance and development of endosperm is still poorly understood (Bennett, 2004). Mike has contributed to this area of research through his detailed studies of the timing and cytological changes associated with endosperm development in cereals, such as wheat (Bennett *et al.*, 1973) and rye (Bennett *et al.*, 1975), and of how this is altered in triticale (Bennett, 1974; 1977*a*; Gustafson and Bennett, 1982). In particular, he noted a relationship between the presence of late-replicating sub-telomeric heterochromatin on particular rye chromosomes and grain shriveling, and suggested that this heterochromatin needed to be eliminated for successful triticale breeding (Gustafson and Bennett, 1982).

In an attempt to understand endosperm development more fully, one area of research has focused on unravelling the role that genomic interactions play, given the inbuilt genomic imbalance in the endosperm (combining one paternal and two maternal genomes). To this end, molecular tools have been applied using, for example, reporter lines and gene expression approaches to examine the consequences of creating endosperms with maternal and paternal genomic excesses and hence the role that gene dosage, genomic imprinting and the combining of two sets of chromatin-remodeling machinery play in the development of a functional endosperm. In this Special Issue, Pennington *et al.* (2008) use such approaches together with morphological analysis to examine how maize endosperm development is influenced by maternal and paternal genomic excesses, uncovering the importance of parental genomic imprinting (in which alleles of a particular gene are differentially expressed, depending on whether they originated from the male or female parent) among other factors, in normal endosperm development.

At Cambridge, Mike worked primarily with plant breeders and much of the focus of his research was to understand better the biology of crop plants, especially in Poaceae. In addition to his work on the importance of organized endosperm development in triticale, (mentioned above) he carried out detailed analyses of meiosis and gametophytic development to shed light on factors affecting seed development in cereals (Bennett *et al.*, 1975). His interest in crops is reflected in this Special Issue by two papers. King *et al.* (2008) describe the development of microsatellite markers for perennial ryegrass (*Lolium perenne*; an important forage and amenity grass worldwide) and their potential application in gene isolation, analysis of genes involved in the control of target traits and marker-assisted selection in breeding programmes.

Together with a knowledge of the genetics of cultivated forms of crop plants, plant breeders also depend on an understanding of the origins of these forms and of diversity in progenitors and wild relatives (e.g. Vaughan *et al.*, 2007). An example of this is illustrated in the paper by Saeidi *et al.* (2008) in this Special Issue in which genetic diversity of *Aegilops tauschii* ($2n = 2x = 14$), the D-genome progenitor of bread wheat, is examined in Iran using IRAPs (inter-retrotransposon amplified polymorphisms), which detect retrotransposon insertional polymorphisms (Kalendar and Schulman, 2006; Schulman, 2007). These data are used to provide insights into the patterns of genomic diversity, evolutionary relationships and phylogeography of the species.

Perhaps Mike's most significant contribution to plant breeding is his work on wide hybridization and uniparental chromosome elimination. In plant breeding the ability to produce doubled haploids (dihaploids) considerably speeds up plant breeding as it produces homozygous lines. In the early 1970s it was shown that dihaploid barley could be generated by crossing barley with its wild relative *Hordeum bulbosum* as this led to the elimination of the entire *H. bulbosum* genome. Some of Mike's early work involved studying the timing and rate of chromosome elimination in such hybrids (Fig. 4; Bennett *et al.*, 1976). Doubling the chromosome number produced homozygous dihaploids in a single generation, much more quickly than by back-crossing for at least eight generations as in conventional plant breeding. The first commercial barley cultivar made using this approach was called 'Mingo' (Ho and Jones, 1980). Although it was hoped that a similar method would be applicable to wheat breeding, studies revealed that this was not to be the case mainly due to dominant alleles of one or two crossability genes (*Kr1* and *Kr2*) present in most breeding lines and commercial varieties of winter wheat (Snape *et al.*, 1979). However, inspired by a preliminary report suggesting that embryos could be produced by pollinating wheat with maize (Zenkteler and Nitzshe, 1984), Mike and Laurie (also at the PBI) went on to show that it was possible to overcome

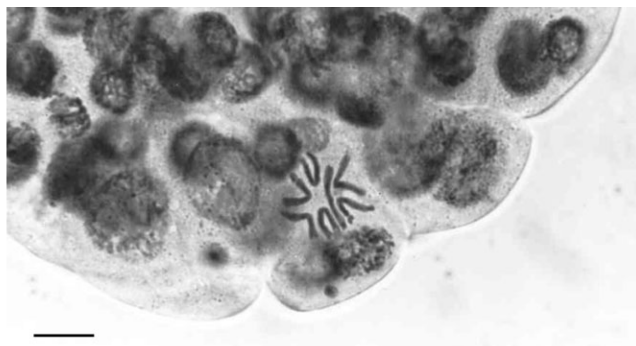

FIG. 4. Haploid metaphase nucleus showing the seven chromosomes of *Hordeum vulgare* 'Vada' following elimination of the *H. bulbosum* genome in the hybrid embryo, 72 h post-pollination (from Bennett *et al.*, 1976). Scale bar = 10 μm.

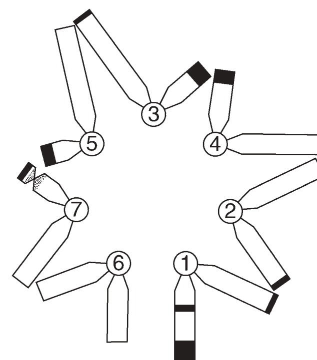

FIG. 6. The natural karyotype of *Secale africanum* ($2n = 14$) ordered according to the Bennett model (from Bennett, 1982).

crossability problems by crossing wheat with maize to generate wheat × maize hybrids (Fig. 5; Laurie and Bennett, 1988; see also Laurie and Bennett, 1986; 1989). Within three cell cycles all maize chromosomes were eliminated, resulting in a haploid wheat genome that could then be doubled to generate dihaploid wheat. This method is still used in plant breeding research (Forster *et al.*, 2007). Mike went on to analyse chromosome elimination in a number of other cereal hybrids (reviewed in Bennett, 1995*b*) and to examine disposition of parental genomes in such hybrids.

Understanding nuclear organization was a central theme in Mike's research from the late 1970s to the 1990s, including investigations of the somatic association of homologous chromosomes, genome separation and the arrangement of heterologous chromosomes (e.g. Heslop-Harrison and Bennett, 1983*a*, *b*; 1990). Arising from this work was the proposal of the 'Bennett model' as a means to predict the mean spatial order of chromosomes in a simple haploid genome (Fig. 6; Bennett, 1982; see also Bennett, 1981, 1983). This model was used to predict the arrangement of chromosomes in various cereals (Bennett, 1982; Heslop-Harrison and Bennett, 1983*a*, *b*), leading Mike to suggest that there were fundamental mechanisms controlling nuclear architecture and chromosome order (Bennett, 1982, 1984*a*). Given that there appeared to be common principles determining the spatial order of chromosomes, Mike proposed that the term 'natural karyotype' should be used to define such order (Bennett, 1984*a*). In 1986 Mike, with Heslop-Harrison, won a major grant from the BP Venture Research Unit (a branch of BP with a philosophy for 'blue skies' research). This enabled them to extend research on genome organization and in particular to develop and apply fluorescent *in situ* hybridization to plant chromosomes (e.g. Fig. 7; Leitch *et al.*, 1991; see also Schwarzacher *et al.*, 1989; Heslop-Harrison and Bennett, 1990; Leitch *et al.*, 1990).

More recently, identification of extensive synteny and colinearity in several grass genomes and their alignment into a circularized 'ancestral grass genome' (Moore *et al.*, 1995) led Mike to question to what extent such circularized genomes related to the natural karyotype predicted by the Bennett model (Bennett, 1996). Addressing such a question was, however, only possible for maize as accurate cytological data were not available for the other grasses studied by Moore *et al.* (1995). The data from Moore *et al.* supported previous cytogenetic studies that maize is a tetraploid

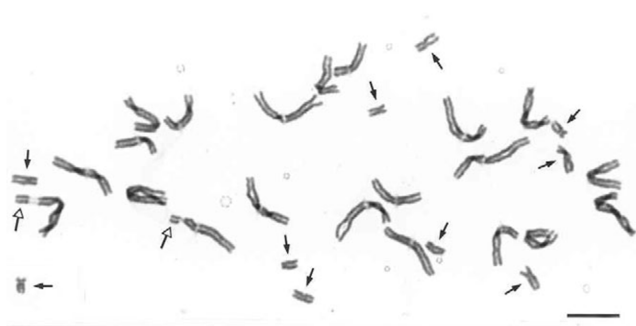

FIG. 5. Metaphase in a hybrid zygote 24 h after pollination of wheat (*Triticum aestivum* 'Chinese Spring', $2n = 42$) with maize (*Zea mays* 'Seneca 60', $2n = 20$). Solid arrows point to the ten maize chromosomes. The remaining larger 21 chromosomes come from wheat (open arrows indicate the wheat satellites; from Laurie and Bennett, 1988). Scale bar = 10 μm.

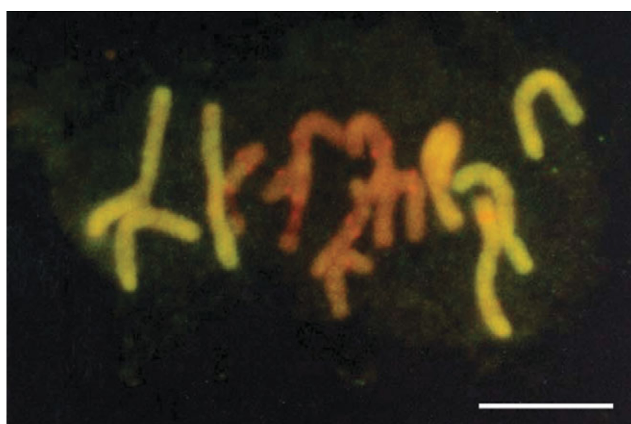

FIG. 7. Metaphase chromosome spread of the hybrid barley × wild rye (*Secale africanum*) following genomic *in situ* hybridization (GISH) showing seven barley chromosomes (orange fluorescence) surrounded by seven wild rye chromosomes (yellow fluorescence; from Leitch *et al.*, 1991). Scale bar = 10 μm.

comprising two sets of five chromosomes each. By applying the rules of the Bennett model, Mike showed that he was able to predict the same order of chromosomes for the larger of the two maize genomes (comprising maize chromosomes 1, 4, 2, 3 and 6) as that shown in the circularized ancestral maize genome of Moore *et al.* (1995). With the smaller maize genome (comprising chromosomes 5, 7, 10, 8 and 9) there was just one difference between the order predicted and that given by Moore *et al.* (1995). Further work is clearly needed to extend these studies to the other cereals studied by Moore *et al.* as this will allow their natural karyotypes to be predicted and compared with the ancestral grass genome. Such wider comparisons may then establish to what extent the natural karyotype, conserved syntenic blocks and ancestral genome order are related.

Understanding the mechanism by which homologous chromosomes recognize each other and pair at meiosis has long intrigued biologists, including Mike, especially in polyploids in which the potential for pairing between homoeologous chromosomes can be high. Given the economic importance of wheat, the control of pairing here has received particular attention. This species contains $2n = 42$ chromosomes comprising three ancestral genomes (each $2n = 14$) known as the A, B and D genomes. Thus there are seven sets of six related chromosomes. The major locus controlling the correct pairing between only homologous chromosomes is the *Ph1* locus, a single dominant locus located on chromosome 5B that was discovered by Riley and Chapman (1958). Since its discovery, its mode of action has received intense scrutiny. Indeed, Mike was originally employed by Riley at the PBI to investigate the problem of pairing in wheat and to understand the *Ph* genes. As part of this work, Mike became interested in premeiotic development and carried out detailed studies of the timing and ultrastructural developmental changes that occurred during this stage in several species including wheat, *Lilium longiflorum* and *Trillium erectum* (Bennett *et al.*, 1973; Bennett, 1976). For example, he noted that the duration of successive premeiotic cell cycles increased in wheat from 25 to 55 h in the three cycles preceding meiosis (compared with 12·5 h in root-tip meristem cells; Bennett *et al.*, 1973). Such mitotic cell divisions occur asynchronously in wheat, *L. longiflorum* and *T. erectum*, and yet meiosis proceeds synchronously. Thus one important aspect of premeiotic interphase involves synchronization via a developmental hold that accumulates meiocytes at the G1 stage. This is followed by synchronous DNA synthesis (S phase), which is again longer than in root-tip cells (e.g. 12–15 h compared with 3·8 h in root tips of *Triticum aestivum*; Bennett, 1976). Studies have also shown that activities during premeiotic interphase may be critical for correct chromosome alignment, and through electron microscopy Mike and colleagues revealed the presence of fibrillar material that was only present in the premeiotic interphase (and early stages of meiosis) of pollen mother cells and not in somatic cells surrounding the pollen mother cells of 19 members of Poaceae examined (Fig. 8; Bennett *et al.*, 1979; see also Bennett *et al.*, 1974). He went on to suggest that the fibrillar material may play a role in establishing or maintaining spatial co-orientation of chromosomes in the premeiotic interphase as a prerequisite for normal meiotic pairing, perhaps through movement of telomeres at the nuclear membrane formed after premeiotic mitosis (Bennett *et al.*, 1979).

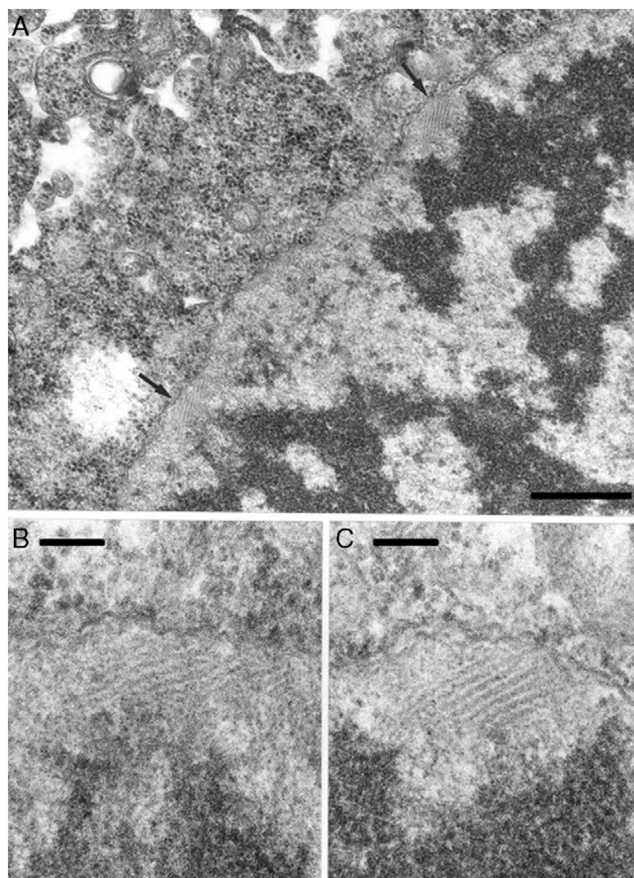

Fig. 8. Electron micrographs of pollen mother cells of *Triticum aestivum* 'Chinese Spring' at premeiotic interphase showing (A) two bundles of fibrillar material (FM; arrowed) apparently linking chromatin to nuclear membrane; (B, C) FM from (A) at higher magnification showing bundles composed of microfibres (image taken from Bennett *et al.*, 1979). Scale bars: (A) = 0·5 µm; (B, C) = 100 nm.

Further insights into the control of chromosome pairing have recently come to light through the use of molecular tools to dissect and characterize the chromosomal region containing the *Ph1* locus. Griffiths *et al.* (2006) used deletion line mapping to localize the *Ph1* locus to a 2·5 Mb region on chromosome 5B of wheat and found a segment of subtelomeric heterochromatin inserted into a cluster of *Cdc2* (*Cdk*-like) -related genes. Further characterization of the deletion lines using deletion mutants, together with expression profiling of genes in the region of the *Ph1* locus forms the focus of the paper by Al-Kaff *et al.* (2008) in this Special Issue, leading to the suggestion that the *Ph1* locus may be defined to a *Cdk*-like gene cluster related to *Cdk2* in humans. Such genes in humans are involved in meiosis (Marston and Amon, 2004; Cohen *et al.*, 2006), perhaps in licensing origins of replication and chromatin remodelling, essential for the onset of meiosis (Alexandrow and Hamlin, 2005).

Most of our understanding of meiosis at the molecular level has come from the study of model organisms, and in plants much of this knowledge originates from *Arabidopsis thaliana*, given the wealth of genetic resources available (Mezard *et al.*, 2007; Wijeratne and Ma, 2007). However, to what extent information from *A. thaliana* is representative of other plants remains to be determined. To address this issue, Phillips *et al.* (2008) use a comparative proteomic approach to study meiosis in rye by analysing the organization of two synaptonemal complex-associated proteins and two recombination-related proteins throughout meiotic prophase using antibodies isolated from *A. thaliana*. The results demonstrate that resources available for *A. thaliana* can be used to study meiosis in cereals, with elements in common and striking differences being highlighted. Such studies, although still in their infancy, clearly emphasize the importance of applying such approaches to enable unifying features of meiosis to be identified and distinguished from species-specific events.

In 1987 Mike moved to Kew to become the Keeper of the Jodrell Laboratory. Surrounded by researchers whose focus was systematics, evolution and conservation rather than plant breeding, he expanded his research further. Techniques such as karyotype analysis and genomic *in situ* hybridization (GISH), which had been used to analyse material of plant breeding interest, were now applied to study organization, evolution and diversity of genomes of wild species (Parokonny *et al.*, 1992; Bailey *et al.*, 1993; Kenton *et al.*, 1993; Bennett, 1995*a*; Takahashi *et al.*, 1999). Nevertheless, in reality this only represented a natural extension of his understanding of the need for genomic data for biosystematics (e.g. see Bennett, 1984*a*).

In his role as Keeper, Mike was instrumental in embedding the novel fields of molecular systematics and conservation genetics in the work programme of the laboratory and of Kew as a whole. Since its establishment in 1992, the Molecular Systematics Section of the Jodrell has become an internationally renowned centre for phylogenetic and related studies, leading to the publication of a new classification of the angiosperms as a result of a major international collaboration (APG, 1998; APG II, 2003). The papers by Kovarik *et al.* (2008) and Leitch *et al.* (2008) in this Special Issue illustrate the application of phylogenetic analyses to questions of ribosomal DNA evolution and genome size in *Nicotiana* allopolyploids, respectively, and de Lange *et al.* (2008) use a combination of phylogenetic, cytogenetic and morphological studies as the basis for conservation recommendations in *Crassula* species from New Zealand.

Through his supervision of Tony Cox's PhD (Cox, 1995), Mike was directly involved in one of the first conservation genetics studies at Kew, focusing on the lady's slipper orchid (*Cypripedium calceolus*). Pulling together the themes of conservation genetics and genome-size measurement, one product of the Conservations Genetics Group in the Jodrell (now part of the Genetics Section) has been the demonstration that AFLP (amplified fragment length polymorphisms; Vos *et al.*, 1995) are not readily applicable to wild species with large genomes, including *C. calceolus* (Fay *et al.*, 2005). Following the work of Garner (2002), who found a correlation between increasing genome size and decreasing amplification success with nuclear microsatellites in animals, Barbará *et al.* (2007), based in the Jodrell, found a significant negative effect of genome size on cross-species amplification of nuclear microsatellites in a wide range of eukaryotes, including plants.

In his analyses of conservation status and genome sizes from the Plant DNA C-values database, Vinogradov (2003) found a 'spectacular "dose-dependent" relationship', with threatened species having larger genomes on average than their less-threatened relatives. Thus it appears that large genomes can be a double disadvantage: species with large genomes are likely to be rare/threatened and, at the same time, assessing genetic diversity in these species is problematic.

A summary of Mike's time at Kew would not be complete without mention of his reputation for being an effective manager of major scientific infrastructure development projects (two extensions to the Jodrell Laboratory and the Millennium Seed Bank at Wakehurst Place). These provide a physical legacy of his contribution to the work of the Royal Botanic Gardens, Kew, at both sites (Fig. 9).

Mike Bennett retired in August 2006, and we hope that this Special Issue provides a snapshot of his scientific

FIG. 9. Views of (A) the Millennium Seed Bank at Wakehurst Place (completed 2000) and (B) the Wolfson wing of the Jodrell Laboratory (completed 2006).

career, with links to many of his scientific publications. We wish Mike a long and happy retirement, although we suspect that he has not finished writing yet!

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