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The effect of *Ph* gene alleles on synaptonemal complex formation in *Triticum aestivum* × *T. kotschyi* hybrids

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Summary. Chromosome pairing at zygotene-pachytene was studied in *Triticum aestivum* × *T. kotschyi* hybrids ($2n = 5x = 35$, genomic constitution $ABDC^US^V$) by electron microscopy of synaptonemal complexes in spread microsporocyte nuclei. Hybrids carrying either the *Ph* allele or the *ph* allele, which differ markedly in metaphase I pairing, are both capable of greater than 90% pachytene pairing, although pairing in the *Ph* hybrids appeared slower or less synchronised. In both genotypes branched synaptonemal complexes were formed by intra- and interchromosomal pairing. The *Ph* gene control on homoeologous pairing does not act on the ability to pair into synaptonemal complexes. It may act on the rate of pairing or the time of crossing over.

Key words: *Triticum* hybrids – Homoeologous pairing – *Ph* gene – *ph* mutant – Synaptonemal complexes

Introduction

Cytogenetic studies dating back 65 years have established that common bread wheat (*Triticum aestivum* L.) is an allohexaploid (Sears 1976) derived from three diploid species whose genomes were designated AA, BB and DD. It has also become clear that these three genomes share considerable genetical identity, and are composed of homoeologous chromosomes (Sears 1952). Although homoeologous chromosomes from different genomes have the potential to pair and undergo crossing over during meiosis, only bivalent associations of homologues are seen at metaphase I in the hexaploid. Riley and Chapman (1958) showed that genetic control of this behaviour resides in the long arm of a chromosome subsequently shown to be chromosome 5B, and the locus involved has been designated *Ph* (Wall et al. 1971 b).

In the absence of the normal *Ph* locus (eg. nullisomic 5B – Riley 1960) hexaploid wheat homoeologues can form multivalent associations of 3, 4, 5 or 6 at metaphase I. Riley (1960) also found that euhaploid *T. aestivum* ($2n = 3x = 21$) had a mean of 1.15 bivalents and 18.67 univalents per metaphase I cell, while the nulli 5B haploid ($2n = 20$) had a mean of 3.83 bivalents, 1.50 trivalents and 7.50 univalents per metaphase I cell, with occasional associations of 4, 5 or 6 chromosomes. The absence of the 5B locus also had the effect of increasing the chiasma frequency in hybrids between *T. aestivum* and other species (Riley and Chapman 1963; Riley 1968).

Several induced mutations at the *Ph* locus have been obtained (Wall et al. 1971 a; Sears 1977; Giorgi and Barbera 1981) and mapped to the long arm of 5B (Sears 1976; Jampates and Dvorak 1986). The effect of these *ph* mutants has usually been monitored by observing metaphase I chromosome associations in hybrids between *T. aestivum ph* and other species of *Triticum*, *Aegilops* and *Secale*. Sears (1977) showed that the *ph* mutant he produced with X-rays increased metaphase I pairing in the hybrid with *T. kotschyi* ($2n = 4x = 28\ C^UC^US^VS^V$) from 1.03 bivalents per cell to 7.65 bivalents, 2.70 trivalents, 0.75 quadrivalents and 0.40 pentavalents per cell. This *ph* mutant hybrid had about 50% greater chiasma frequency than found in the nulli 5B hybrid. The effectiveness of this *ph* mutant in inducing homoeologous pairing amongst wheat chromosomes was confirmed by Dhaliwal et al. (1977) in a wheat X rye hybrid. Giorgi and Barbera (1981) found that a *ph* mutant isolated in tetraploid wheat (*T. turgidum* L. var. *durum* – $2n = 4x = 28$ AABB), and thought to be caused by a deletion (Dvorak et al. 1984;

Jampates and Dvorak 1986), had a similar effect of increasing metaphase I associations in hybrids with *Aegilops kotschyi* (= *T. kotschyi*) and *A. cylindrica* (2n = 4x = 28 CCDD).

The mode of action of the *Ph* gene has been the subject of much speculation, and a number of hypotheses have been advanced. The somatic association hypothesis proposed by Feldman and coworkers (Feldman 1968) suggests that homologues and homoeologues tend to be more closely associated than heterologues in premeiotic somatic cells, and that this determined the type of meiotic pairing subsequently observed. Feldman suggested that the wildtype *Ph* gene product in normal wheat acted on spatial distribution of chromosomes and suppressed homoeologue association more than homologue association so that pairing at metaphase I was largely as homologous bivalents. In the absence of *Ph* (nulli 5B or *ph* mutant) there is no effect on somatic association, so that both homologous and homoeologous pairing may occur and metaphase I multivalents are formed. At metaphase I in plants tri-isosomic for $5B^L$ (ie. with six doses of Ph) some homoeologous pairing is observed, but total pairing is reduced and interlocking of bivalents is common. Feldman (1968) concluded that extra doses of the *Ph* gene further suppressed somatic association so that neither homologue nor homoeologues associated premeiotically, and meiotic pairing became more random. Feldman's coworkers have recently presented evidence for separation of genomes during meiosis (Yacobi et al. 1985 a, b), and for the *Ph* gene effect being via action on microtubule components (Ceoloni et al. 1984).

An alternative hypothesis put forward by Riley (1968) to explain the *Ph* gene effect was based on pairing being a two stage process. In the first or attraction stage both homologues and homoloeogues could associate imprecisely. In the second, precise stage only homologues paired. Riley proposed that the *Ph* gene acted to shorten the first stage so that normally only homologues had time to pair. In the absence of *Ph* the attraction phase was longer and both homologues and homoeologues associated. Higher doses of *Ph* terminates the attraction phase even earlier so that pairing is reduced and interlocks are not untangled (Riley 1968).

In order to understand the factors controlling metaphase I associations of wheat chromosomes it is obviously of great interest to study the behaviour of the chromosomes during zygotene and pachytene, when they undergo pairing and crossing over. As light microscopic analysis of these stages is generally almost impossible in wheat, a number of workers have carried out electron microscopic studies of the behaviour of wheat synaptonemal complexes. In serial section reconstruction of a zygotene stage meiocyte of wildtype Chinese Spring wheat Hobolth (1981) found that pairing occurred between homoeologues to form some multivalents. Jenkins (1983) in a similar study confirmed the occurrence of multivalent pairing at early zygotene. When Hobolth reconstructed a pachytene stage nucleus he found only 21 bivalent synaptonemal complexes. He concluded that homoeologous pairing is a regular feature of zygotene synaptonemal complex formation in hexaploid wheat, but that crossing over is delayed until homoeologously paired multivalents are transformed into strictly homologously paired bivalent synaptonemal complexes, and consequently only bivalents are found at metaphase I. Holm (1986) used a spreading technique to confirm that multiple chromosome associations regularly occurred at zygotene in most hexaploid wheat nuclei, but that they decreased in number as pachytene progressed.

As summarised by von Wettstein et al. (1984), the role of the *Ph* gene is to delay crossing over until after resolution of multivalents into homologous bivalents. In the absence of *Ph,* crossing over could occur earlier while homoeologues were still associated in multivalent synaptonemal complexes. This model of *Ph* action can be considered a variant of the timing hypothesis suggested by Riley (1968). A recent electron microscopic study of tri-isosomic $5B^L$ wheat (Wischmann 1986) found that initiation and early progression of pairing was normal, and multivalent synaptonemal complexes were present at zygotene. However, pairing did not appear to proceed beyond about one third of that possible. These results would seem to be partly compatible with the timing hypothesis (von Wettstein et al. 1984), but the effect on overall pairing is also compatible with the expectation of Feldman's hypothesis (Feldman 1968).

To fully understand the action of the *Ph* gene during pairing and crossing over it is obviously desirable to compare the zygotene-pachytene behaviour of plants carrying the wildtype *Ph* allele, and those having the mutant *ph* allele. As a first step towards this, the present study has compared the effect of the two alleles on synaptonemal complex behaviour in *T. aestivum* × *T. kotschyi* hybrids.

Materials and methods

The hybrids used were grown from seed supplied by Dr. K. Shepherd of the Waite Agricultural Research Institute, Glen Osmond, South Australia. To produce the hybrids *Triticum kotschyi* (= *Aegilops kotschyi* = *A. peregrina*) was crossed with Chinese Spring *T. aestivum* homozygous and heterozygous for the *phlb* mutant (Sears 1977). The F_1 progeny of the cross with *phlb phlb* wheat all carry one *phlb* allele and were designated ph hybrids. The F_1 progeny of the cross with *Phlb phlb* wheat should consist of plants carrying either *Phlb* or *phlb* alleles. These plants were screened at metaphase I and those carrying

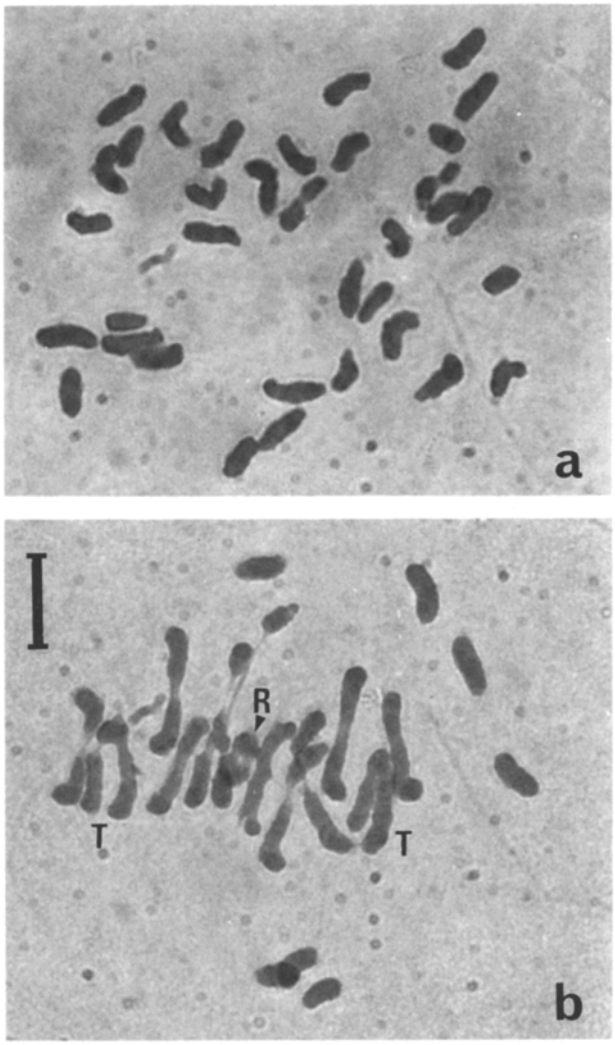

Fig. 1. Aceto carmine squash of metaphase I in *Triticum aestivum*×*T. kotschyi* hybrids carrying **a)** *Ph* allele-35 univalent chromosomes; **b)** *ph* allele-2 trivalents (T), 1 ring bivalent (R), 10 rod bivalents and 7 univalents. Bar = 10 μm

the Phlb allele were identified by their low pairing (designated Ph hybrids).

The plants were grown in pots in a growth chamber under 16 h daylength, with 23/18 °C temperature cycle. Anthers from all plants were examined by light microscopy using acetocarmine squashes, and their metaphase I behaviour noted. Anthers from spikelets at prophase I meiotic stages were spread for electron microscopy by the method previously used for rye (Gillies 1985). The slides were stained by the ammoniacal silver technique (Dresser and Moses 1980), spread nuclei identified, picked up on single hole grids and examined in a Philips EM201A electron microscope. Photographic montages were prepared from electron micrographs of the spread nuclei, at magnifications of 7-10,000X, and the lengths and pairing behaviour of synaptonemal complex lateral elements were analysed using a Graptec digitizer interfaced to a Microbee computer.

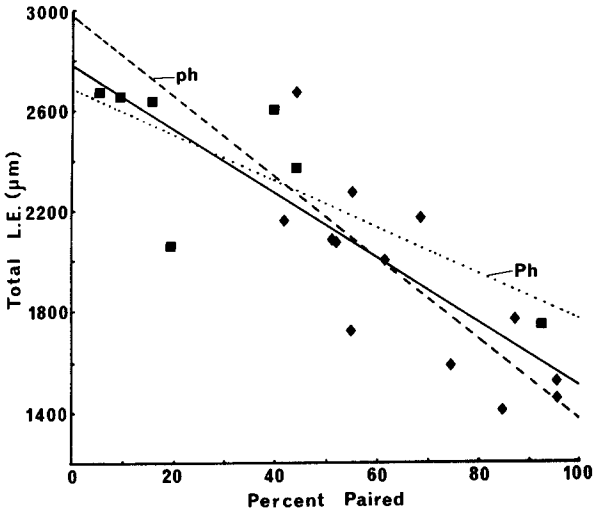

Fig. 2. Plot of total lateral element length versus per cent paired synaptonemal complex for spread nuclei of *Triticum aestivum*×*T. kotschyi* hybrids. ■ 7 Ph nuclei, ◆ 13 ph nuclei. Solid line is regression line for all 20 nuclei (r = −0.843), dotted line is regression line for Ph nuclei (r = −0.772), dashed line is regression line for ph nuclei (r = −0.811)

Results

Four Ph hybrids were identified and used for spreading. At metaphase I these all exhibited very low pairing, with zero, one or two bivalents per cell (Fig. 1 a). All of the ph hybrids exhibited relatively high levels of pairing at metaphase I (Fig. 1 b), with the occurrence of numerous rod bivalents, occasional ring bivalents, trivalents and higher multivalents. The metaphase I behaviour of the two hybrid genotypes was completely in accord with previous reports (Sears 1977).

One hundred and fifty slides of electron microscope spreads were made from 71 spikes – 110 slides from 55 Ph spikes and 40 slides from 16 ph spikes. Spread zygotene-pachytene nuclei from 28 Ph slides and 6 ph slides were successfully stained and picked up on grids. An average of 3.7 nuclei per slide were obtained on Ph slides, and 4.8 nuclei per slide on ph slides. Thirty-two Ph nuclei and 16 ph nuclei were electron micrographed. Most of the Ph nuclei were from early zygotene stages, and only 7 were measured (Ph 1–Ph 7). Of the remaining unmeasured Ph nuclei, 14 were estimated visually to be < 20% paired and 7 were estimated to be 30–50% paired. The remaining 4 Ph nuclei electron micrographed appeared to be well paired, but numerous lateral element breakages caused by an experimental enzyme treatment precluded measurement. Most of the ph nuclei were > 50% paired, and 13 were measured (ph 8–ph 20).

The results from measurement of lateral element and synaptonemal complex lengths in the 7 Ph and 13 ph

Table 1. Analysis of synaptonemal complex pairing in four hybrid nuclei

	Nucleus			
	Ph 6	Ph 7	ph 18	ph 19
% Paired	44.4	92.6	87.6	95.5
Total lateral element length (μm)	2,378.3	1,746.3	1,756.3	1,452.1
Longest lateral element (μm)	76.2	73.8	44.9	72.7
Longest synaptonemal complex (μm)	38.5	53.3	34.3	45.0
Unbranched structures				
– Number[a]	30 (43)	60 (118)	37 (59)	25 (43)
– Mean synaptonemal complex length (μm)	11.58	5.69	7.92	7.55
Branched structures				
– Number[a]	2 (8)	6 (19)	11 (42)	8 (47)
– Mean synaptonemal complex length (μm)	3.70	7.39	7.16	8.09
% Lateral elements in branched structures	5.76	17.93	38.47	53.83
% Synaptonemal complexes in branched structures	5.61	17.35	39.12	56.17

[a] Figures in parenthesis are numbers of discrete synaptonemal complex segments

nuclei are presented graphically in Fig. 2 as a plot of genomic lateral element lengths versus per cent pairing. The lateral element lengths ranged from 2,670 μm in Ph 1, which was 5.4% paired, to 1,405 μm in pH 17, which was 84.85% paired. The 7 Ph nuclei measured ranged from 5.4% to 92.6% paired. The 13 ph nuclei ranged from 42.3% to 95.5% paired. All 20 nuclei seem to be part of a single population with a negative correlation of length versus pairing ($r=-0.843$). The above results also illustrate the fact that most of the Ph nuclei examined (27 out of 32) have < 50% pairing. The spreading technique was identical in each case, and all anthers chosen for spreading were expected to have mid zygotene to pachytene stages.

All of the spread nuclei examined showed evidence of some breakage of synaptonemal complexes and lateral elements (Fig. 3). Because of this it was not possible in any nucleus to determine the precise nature of pairing (bivalents and multivalents), but unbranched bivalent-like synaptonemal complexes could be distinguished from branched synaptonemal complexes which resulted from intra- or interchromosomal switches of pairing (Fig. 4). Breakages of unpaired lateral elements at branch points made estimation of numbers of multivalents difficult. Some broken synaptonemal complexes and lateral elements obviously were caused by stretching forces, and if not unduly displaced during spreading the relationship of broken pieces could be seen. Two Ph nuclei and two ph nuclei were chosen for more intensive analysis of their synaptonemal complex pairing. The results of this analysis are summarised in Table 1, and the idiogram of one nucleus is shown in Fig. 5. The longest lateral element measured was 76.2 μm in Ph 6, and the longest uninterrupted synaptonemal complex was 53.3 μm in Ph 7. The number of unbranched synaptonemal complexes and lateral elements was up to 60 per nucleus. The number of branched pairing structures ranged from 2 to 11 per nucleus. The mean lengths of discrete synaptonemal complex segments were very similar in both branched and unbranched structures in the three highly paired nuclei. Ph 6 (44.4% paired), which had only two identifiable branched pairing structures, had an obvious bouquet with 18 paired synaptonemal complexes clustered on one side of the nucleus. Almost all of these synaptonemal complexes had evenly matched lateral element ends, and the paired stretches ranged from 6.6 to 38.5 μm in length. No bouquet was obvious in the other three nuclei analysed.

As can be seen in Fig. 3 (Ph 7) long stretches of unbranched synaptonemal complex are not uncommon, and numerous evenly matched lateral element ends occur (only some of which are the result of breakage). Unequal and unpaired lateral elements occur at the ends of many synaptonemal complexes. Branch points are usually easily recognised (Fig. 4), but breakage of lateral elements during spreading has often resulted in short lengths of synapotonemal complexes and lateral elements. Three, four or more branch points can be seen in some structures (Fig. 4a, c). Some branch points involve reciprocal lateral element partner exchange (Fig. 4b), but many are non reciprocal (Fig. 4d).

The idiogram in Fig. 5 illustrates the occurrence of up to eight branched pairing structures in ph 19 (M4, M5, and M8 are possibly involved in a single, more complex multivalent). Unfortunately, because of inability to recognise centromeres in the spreads, together with lateral element breakage, none of the chromosomes is identifiable. Based on an average size, the unbranched synaptonemal complexes A to D might represent bivalent pairing between two chromosomes. Several of the longer lateral elements in the branched

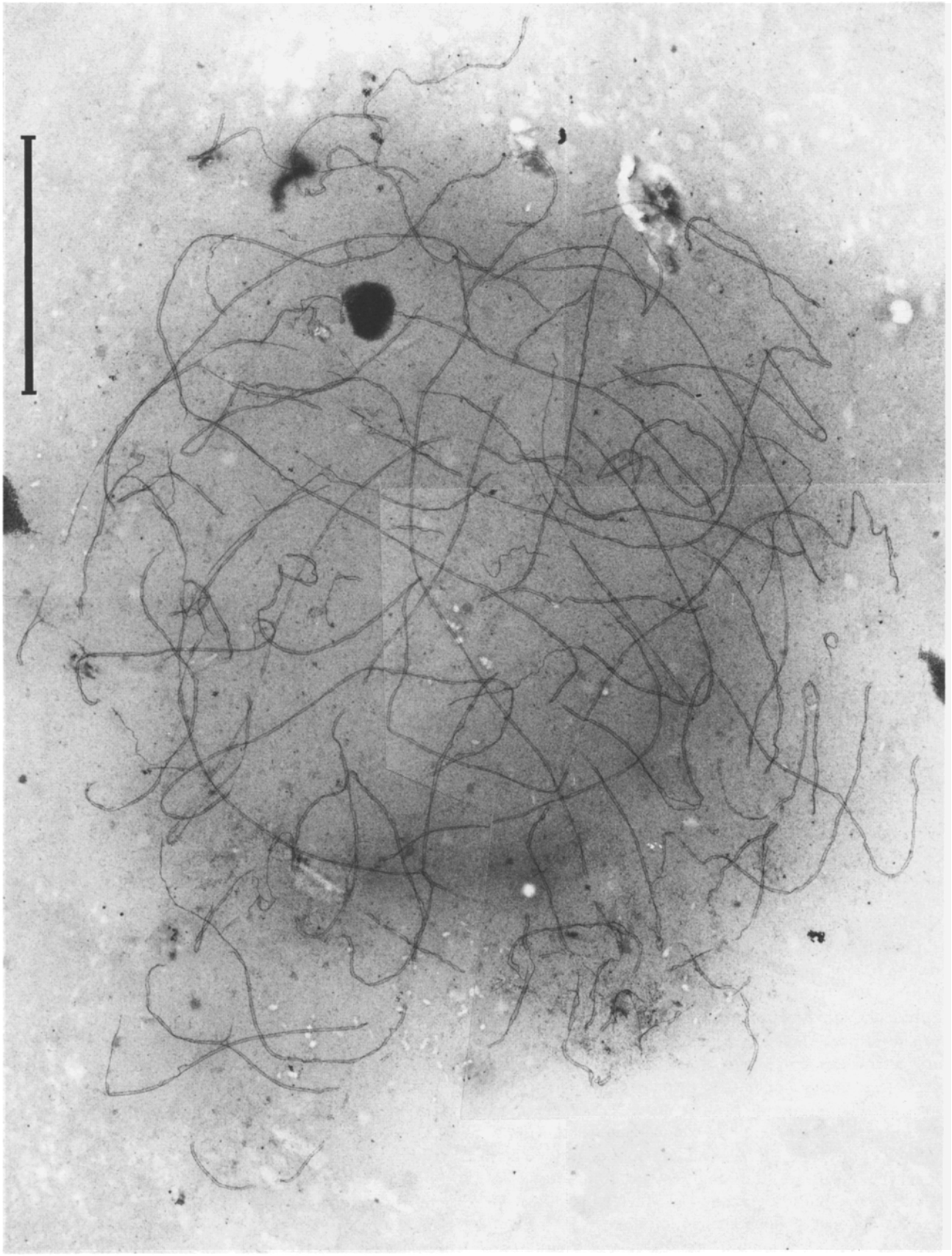

Fig. 3. Electron micrograph of spread pachytene nucleus Ph 7. 92.6% of lateral elements are paired into synaptonemal complexes. Bar = 10 μm

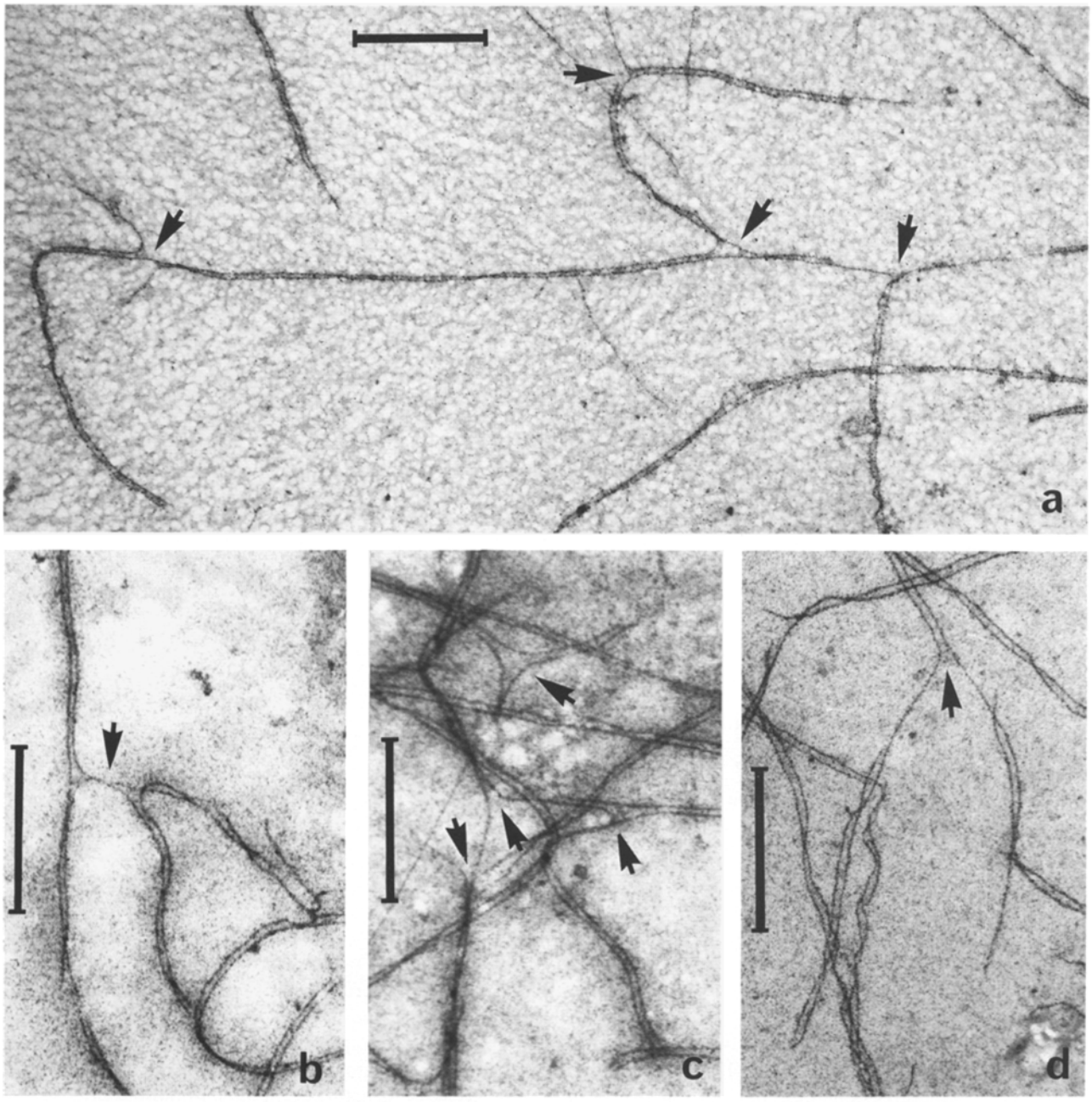

Fig. 4. Higher magnification electron micrographs of pairing switches in synaptonemal complexes from **a)** ph 18 **b)** ph 17 **c)** ph 19 **d)** Ph 7. *Arrows* indicate switch points. Bar = 2μm

structures must also be uninterrupted chromosome axes.

Discussion

The present investigation has attempted to gain information about the mode of action of the *Ph* gene, by comparing the zygotene-pachytene synaptonemal complex formation in hybrids carrying the *Ph* allele with those carrying the *ph* allele. From this comparison the following points emerge.

1. There appears to be no difference between the two genotypes in their abilities to form synaptonemal complexes *per se*. Measurements of lateral elements from all nuclei seem to fit one regression line of pairing versus length (Fig. 2), and the longest synaptonemal

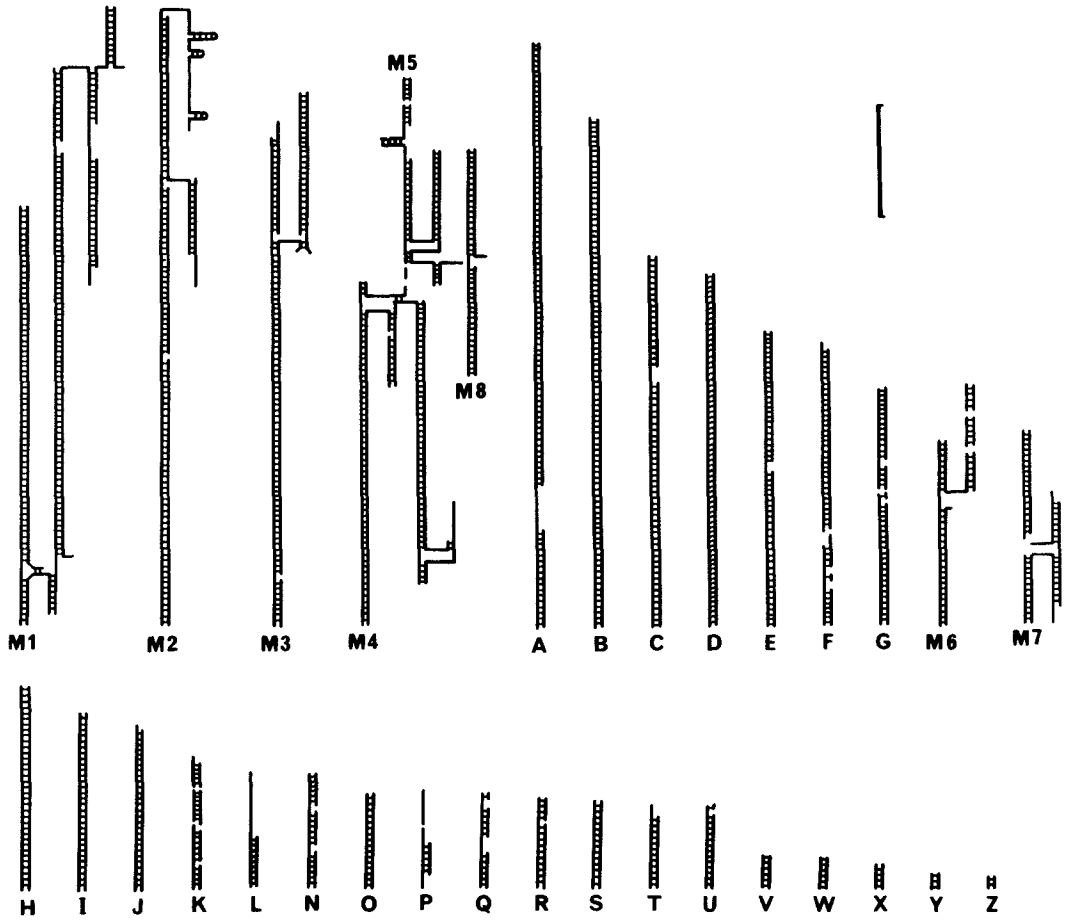

Fig. 5. Idiogram of spread nucleus ph 19 (95.5% paired). Cross bars indicate synaptonemal complexes. Breaks in vertical lines indicate discontinuities in lateral elements. M1 to M8 are branched synaptonemal complexes (multivalents?), and A to Z are unbranched (bivalent?) synaptonemal complexes, ranked by length. M4, M5 and M8 may be associated in one complex multivalent, Bar = 10 μm

complexes and average length were similar in nuclei from the two genotypes (Table 1). The occurrence of a bouquet pairing structure in Ph 6 (44.4% paired), in which approximately two-thirds of the synaptonemal complex length was present as 18 terminally paired unbranched structures, suggests that pairing initiation in these hybrids is similar to that in many other plants, and results in synaptonemal complex formation first near to telomeres (Gillies 1985).

2. The ability of almost all lateral elements to pair completely into synaptonemal complexes is the same in both genotypes. Nuclei from both genotypes were found with > 90% pairing.

3. There appears to be a higher proportion of nuclei with less than 50% pairing amongst the *Ph* genotype, than in the *ph* genotype. This could represent a slower or less synchronised pairing process in the *Ph* genotypes. While preparing the spreads it was noticed that the synchrony of meiotic stages in anthers and florets was more erratic in *Ph* genotypes than in *ph* genotypes, where a more orderly progression of stages was the norm.

4. Both genotypes have the ability for lateral elements to pair into branched (multivalent) synaptonemal complex structures. The type of pairing observed is typical of that in haploids where both inter- and intrachromosomal pairing can occur at pachytene (Gillies 1974). This is not surprising since these hybrids are essentially pentahaploids (genomic formula ABDCS). However, given the homoeologous relationships of the A, B and D wheat genomes (and possibly of the C and S genomes) the chromosomes from different genomes should share some homologous segments. These might be expected to show some preference for forming synaptonemal complex segments which could result in incompletely paired bivalents and multivalents. The well matched telomeric synaptonemal complexes in Ph 6 suggest that either this homology exists near

chromosome ends, or else the initiation process proceeds at telomeres regardless of homology. Similar matching of lateral element ends was noted at zygotene in both triploid and tetraploid hybrids of *Lolium temulentum* × *L. perenne* by Jenkins (1985, 1986).

It should be noted that at least one multivalent might be expected in the present case as a result of a reciprocal translocation which appears to be present in the Chinese Spring *phl* mutant line (Jouve and Giorgi 1986). However, these workers also showed that in plants homozygous for *phl* allele they could identify metaphase I multivalents between chromosomes 7A and 7B, 4A and 4B, and between B and D group chromosomes.

5. A greater proportion of the genome may end up paired as multivalents in *ph* hybrids than in *Ph* hybrids (Table 1). Ph 7 and ph 19 have very similar amounts of pairing, but much less of the Ph 7 genome is present in branched structures. Some caution is necessary in interpreting this result, since Ph 7 has a large number of short synaptonemal complex and lateral element fragments (Fig. 3), many of which could be from broken multivalents.

While these results do not allow a complete answer to the question of how the *Ph* gene acts at pachytene, they do give some indications. It is evident that *Ph* does not affect the ability of chromosomes to associate and form synaptonemal complexes. The effect of *Ph* must therefore be expressed in some mechanism which influences the ability to generate crossovers, since there is a marked difference in chiasma frequency in the two hybrid *Ph* genotypes. This effect could be via a control of the rate of pairing (Riley 1968) or of the time of crossing over (Hobolth 1981). Either of these mechanisms could be a consequence of differences in ability of the two genotypes for fine matching of homologous DNA sequences needed for crossing over.

These findings do not appear to support a mechanism in which chromosome position is an important factor in regulating pairing and crossing over (Feldman 1968). It could be argued that in hybrid *Ph* nuclei, because of fixed chromosomal and genomic positions, chromosome associations which lead to synaptonemal complex formation are essentially random, usually not homoeologous, and therefore do not lead to crossing over and chiasmata formation. In the hybrid *ph* nuclei the chromosomes might be free to move around and find their homoeologues prior to synaptonemal complex formation. If this were the case a qualitative difference might be expected between the two genotypes in the nature of pairing behaviour and types of zygotene pairing configurations. The relatively minor differences between the two genotypes seen here do not support this idea.

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