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CHROMOSOMA

Synaptonemal complex and recombination nodules in rye (*Secale cereale*)

Mona Abirached-Darmency[1], Denise Zickler[1], and Yvonne Cauderon[2]

[1] Laboratoire de Génétique, Bat. 400, Université Paris-Sud 91405, Orsay Cedex France;
[2] Laboratoire de Cytogénétique, Station d'Amélioration des Plantes, C.N.R.A., Route de St-Cyr, 78000 Versailles, France

Abstract. Meiotic prophase in rye was investigated by serial-section reconstruction of pollen mother cell nuclei. In the mid-late zygotene nucleus, all lateral elements were continuous from telomere to telomere, and 9–20 pairing initiation sites per bivalent were observed. Chromosome and bivalent interlockings detected during zygotene were resolved at early pachytene when pairing was completed. In the three pachytene nuclei, the relative synaptonemal complex (SC) lengths and arm ratios were found to be in good correlation with light microscopic data of pachytene bivalents. Spatial tracing of the bivalents showed that they occupy separate areas in the nucleus. Three types of recombination nodules were observed: large, ellipsoïdal and small nodules at early pachytene and irregularly shaped nodules mainly associated with chromatin at late pachytene. Their number and position along the bivalents correlated well with the number and distribution of chiasmata. The classification of the seven bivalents was based on arm ratio and heterochromatic knob distribution.

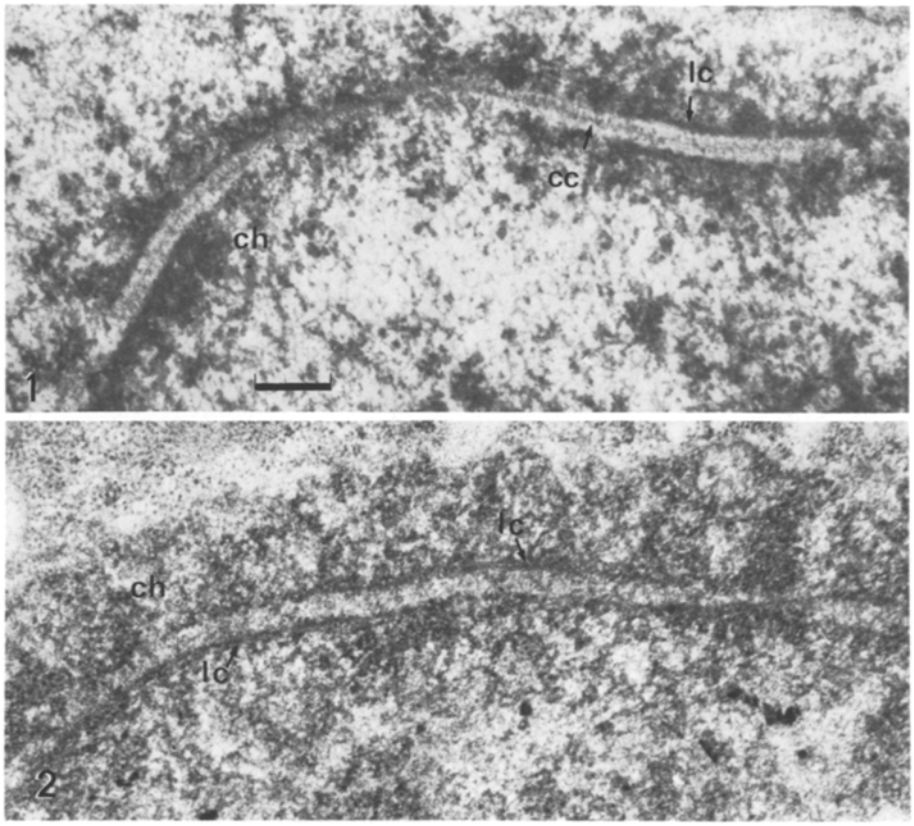
Introduction

Cultivated rye (*Secale cereale* L.) has several agronomical characteristics that would be interesting to transfer to common wheat (*Triticum aestivum*, L. Thell ssp *vulgare* MK). However, when rye and wheat can hybridize, there is nearly no bivalent formation at metaphase I in the F_1 hybrids. Moreover the wheat × rye induced amphiploids (triticales) have a high percentage of aneuploids in their progeny (Gustafson 1976). It has been suggested that the high amount of telomeric heterochromatin in rye chromosomes might be responsible for both the pairing failure and the meiotic instability observed in some triticales (review in Gupta and Priyadarshan 1982). To explain such a prominent effect of the rye chromosomes, it is important to understand first how the rye chromosomes behave during meiotic prophase. Several light microscopic investigations have been performed to identify rye chromosomes (Heneen 1962; Singh and Röbbelen 1975; de Vries and Sybenga 1976; Bennett et al. 1977; Orellana and Giraldez 1981), but only one study has decribed the morphology of the pachytene chromosomes (Lima de Faria 1952).

Chiasmata distribution within bivalents has also been studied and evidence for preferential distal localization has been presented (Jones 1978; Orellana and Giraldez 1981). To study the relationships between the synaptonemal complex (SC), chromosome pairing, and crossing over, we have analyzed serial-section reconstructions of zygotene and pachytene nuclei. The present report focuses on pairing initiation and several features of the pachytene karyotype. It also presents some observations on the distribution and the temporal changes of the recombination nodules.

Materials and methods

The present study was performed on two diploid (2n = 14) varieties of rye *Secale cereale*: the winter rye cultivar Petkus and an inbred line 601, derived from Petkus and kindly provided by A. Berbigier. At tillering stage, the plants were transferred to a greenhouse and kept at 20° C during the day and 15° C at night, with a 16 h:8 h light: dark schedule. As the three anthers of each floret are approximately synchronous in development, one of them was squashed in a drop of aceto-carmine to determine the developmental stage and the other two were used for electron microscopy. To facilitate the penetration of the fixative, the anthers were first slightly excised in a drop of fixative and then fixed in 4% glutaraldehyde in 0.1 M phosphate buffer at pH 7.0 for 4 h at 4° C. After several washes in buffer, the anthers were either postfixed for 2 h in 1% OsO_4 in the same buffer or prestained in 1% phosphotungstic acid (PTA) in absolute ethyl alcohol for 15 h at 4° C (Gillies 1973). The fixed anthers were dissected in buffer under a dissecting microscope, and only the pollen mother cells were embedded between two very thin agar layers on a slide according to the technique of Mole-Bajer and Bajer (1963). The dehydration in a graded alcohol series and the embedding in Epon-Araldite were carried out on the slides. The embedded cells were examined with a light microscope and the desired developmental stages were selected for sectioning. The serial sections were transferred to grids according to the procedure of Wells (1974). Staining in uranyl acetate (5% in water) and lead citrate was performed only on the osmium-fixed material. The number of sections necessary to encompass a nucleus ranged from 100 to 150. Calculation of the SC lengths was carried out as described by Gillies (1973). Seven nuclei from five different plants were serially sectioned and photographed. Four were inbred-line nuclei: one which was at zygotene and was PTA-stained, was reconstructed completely; the other three which were at pachytene and had been osmium-fixed, were reconstructed only



Figs. 1 and 2. Longitudinal section of the synaptonemal complex (SC) of rye in **1** a mid-late pachytene nucleus from a pollen mother cell of the cultivar Petkus (N2) and **2** a partially reconstructed nucleus of the inbred line 601. Note the difference in amount and organization of the chromatin fibers around the SC. *lc* lateral component, *cc* central component, *ch* chromatin. Bar represents 0.3 μm

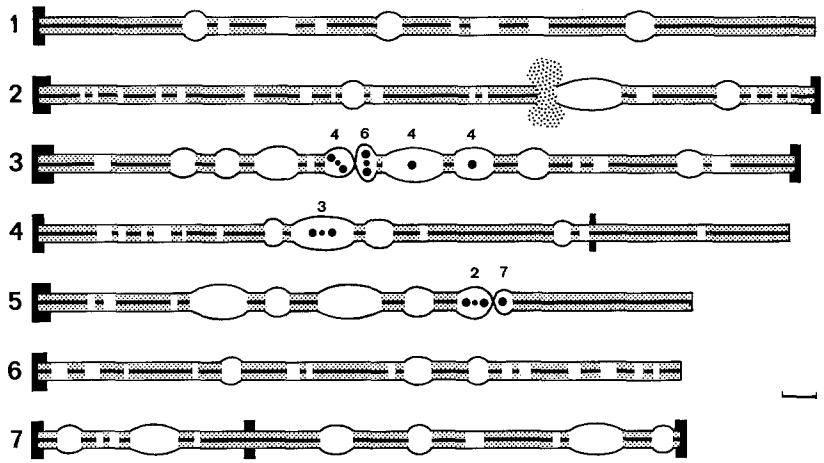


Fig. 3. Seven reconstructed bivalents in a mid-late zygotene nucleus illustrating the multiple pairing initiation sites. Chromosome interlocking is symbolized by a single *filled circle*; bivalent interlocking, by a *triad* of filled circles. The nucleolus organizer region is indicated by a *dotted area*, the heterochromatic knobs by *filled rectangles*. The chromosomes are numbered 1 to 7 according to decreasing length; and the small numbers indicate with which chromosome the interlocking occurs. Bar represents 3 μm

partially. Because the centromeres were difficult to identify in the inbred line, even at pachytene, three completely reconstructed nuclei from Petkus were used to study this stage: one PTA-stained (N3) and two osmium-fixed (N1, N2).

Results

The ultrastructure of the pachytene SC is shown in Figure 1. It is morphologically identical to the SC reported for other plants (Gillies 1973; Holm 1977; Hobolth 1981). The two amorphous lateral elements, approximately 45 nm in diameter, are separated by a central region about 130 nm in width, which contains an amorphous central element of about 35 nm diameter. A progressive condensation of the chromatin fibers surrounding the SC occurred during pachytene. However at mid-late pachytene, the partially reconstructed nuclei of the inbred line clearly showed less compacted chromatin (Fig. 2), and less dense telomeric heterochromatin knobs than the Petkus nuclei.

Zygotene

One zygotene nucleus from the inbred line was reconstructed completely. The PTA staining of this nucleus gave a strong contrast of the lateral components which facilitated their tracing, but probably hindered the identification of the centromeres. The lateral elements of all chromosomes were continuous from telomere to telomere. Twelve of the fourteen telomeres were attached to or located near a re-

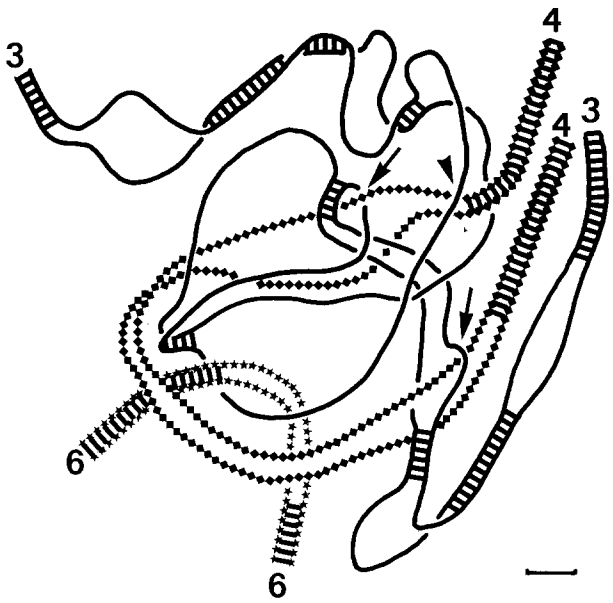


Fig. 4. Part of the reconstructed zygotene nucleus illustrating interlocking between bivalents 3, 4 and 6. Bivalent 4 shows one bivalent interlocking (*arrowhead*) and two chromosome interlockings (*arrows*). Note the wide separation of the homologues of bivalent 3 between the paired regions (*stripes*). Bar represents 0.5 μm

stricted area of the nuclear envelope, giving rise to a bouquetlike arrangement. The two remaining telomeres were free in the nuclear space. The binding of the telomeres to the nuclear envelope occurred in most cases through heterochromatic knobs. The amount of pairing by a completed SC corresponds to 65% of the total lateral element length. All seven bivalents were partially paired (50%–76%). The diagrammatic representation of the chromosomes in Figure 3 shows that the unpaired regions are either separated by a distance equal to the width of the central region or are widely separated. The alignment of the homologous chromosomes throughout their length is, thus, not a prerequisite for SC formation (e.g., bivalents 3 and 5 in Figure 3 where the lateral components joining segments paired with a SC are widely separated).

In each bivalent, central element formation is initiated at the telomere regions, as well as at several (7–18) interstitial sites (Fig. 3). In this mid-late zygotene nucleus, a total of 96 initiation sites was observed. Three chromosomal and four bivalent interlockings were found in which five of the seven bivalents were involved (Fig. 3). In three cases, one lateral element of a partially paired bivalent was trapped between the unpaired lateral components of another bivalent, and four bivalent regions, of which two belonged to the same bivalent, were trapped between unpaired lateral components of another bivalent (Fig. 4).

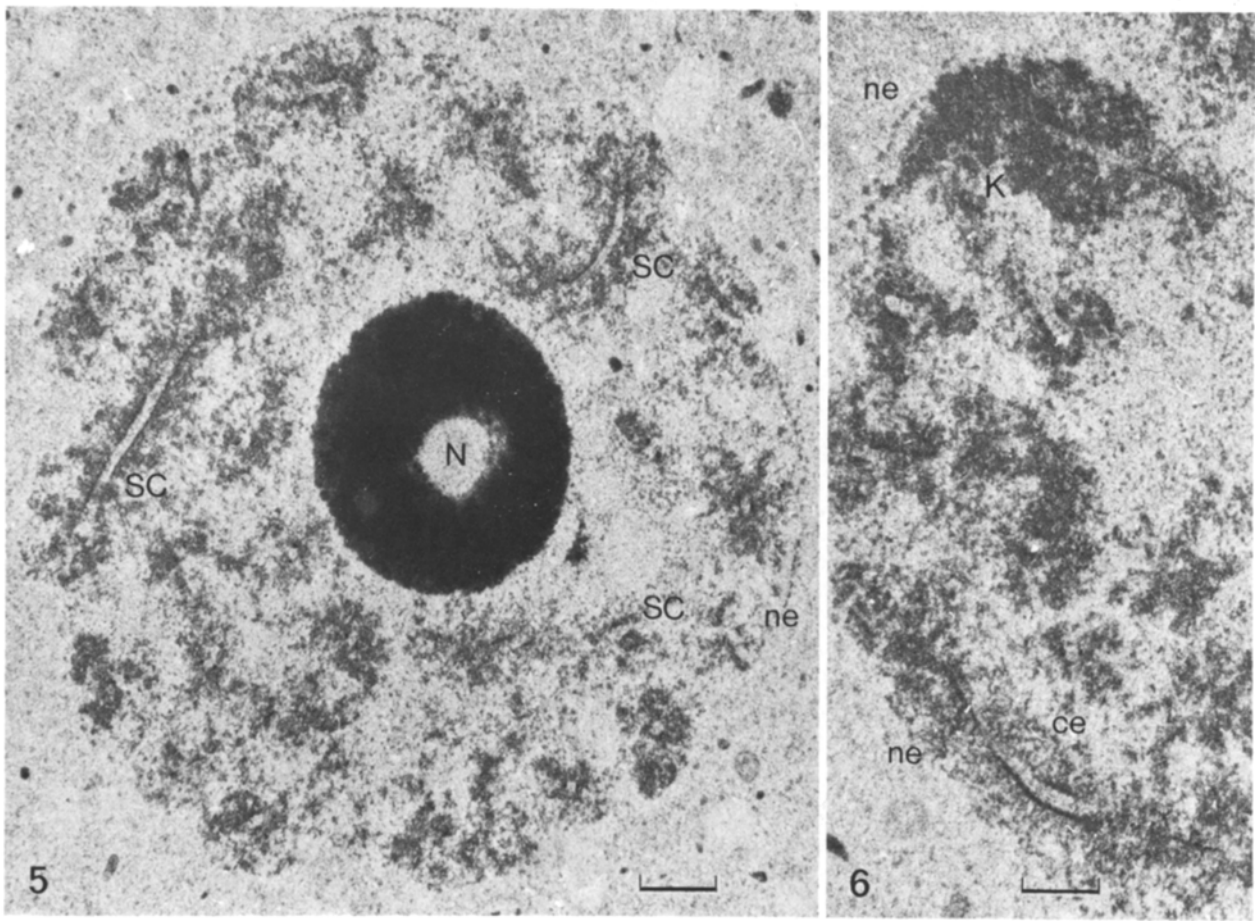


Fig. 5. Survey micrograph of a PTA-stained midpachytene nucleus from Petkus. Note the numerous pieces of synaptonemal complex (*SC*) in longitudinal and cross section. *ne* nuclear envelope, *N* nucleolus. Bar represesents 0.8 μm

Fig. 6. A centromeric region (*ce*) and a telomeric knob (*K*) in a PTA-stained Petkus pachytene nucleus. Note the contact of the centromere with the nuclear envelope (*ne*). Bar represents 0.6 μm

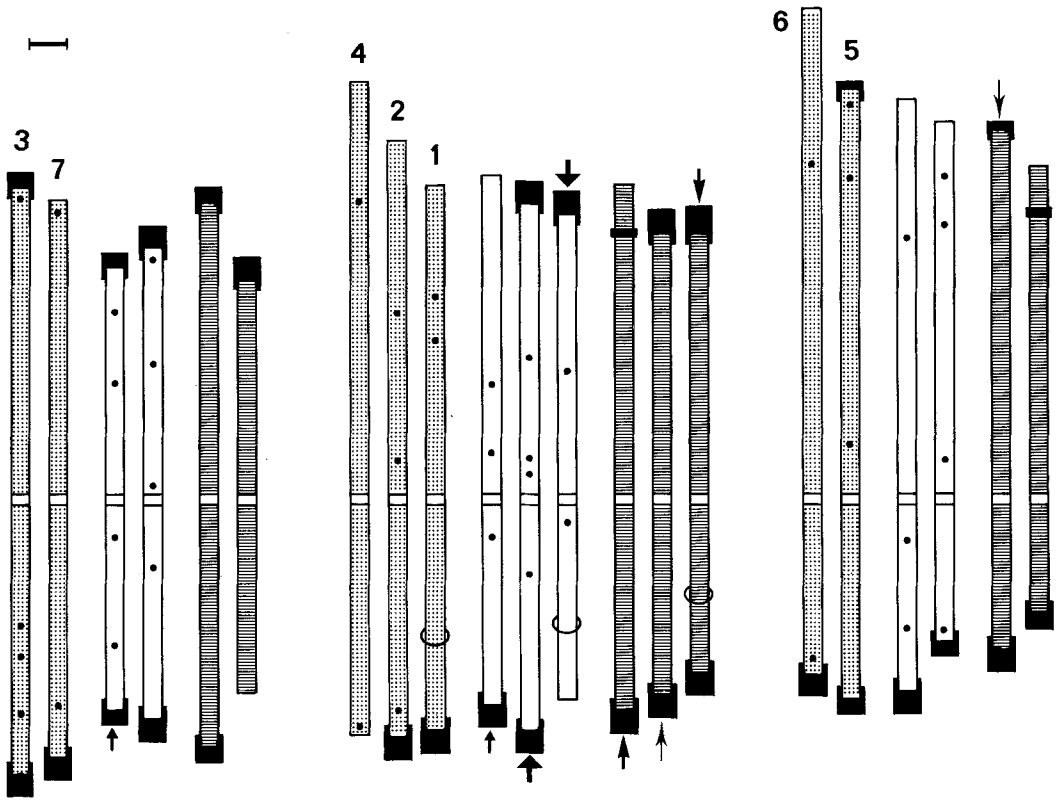


Fig. 7. Idiogram showing the relative SC length of the seven bivalents of Petkus in one early (N1 *dotted* bivalent) and two mid-late pachytene nuclei (N2 *light* and N3 *hatched* bivalent). The bivalents have been grouped according to arm ratio: metacentric (chromosomes 7 and 3); submetacentric (chromosomes 4, 2, and 1); and subacrocentric (chromosomes 5 and 6). Centromeric regions are shown as *light rectangles*, nucleolus organizer regions as *rings* and nodules as *filled circles* (Nodules cannot be detected in the PTA-stained N3). The terminal *filled rectangles* represent the heterochromatic knobs. *Arrows* of equal size indicate two bivalents that are associated by their telomeric knobs (The chromosomes are numbered according to Bennett et al. 1977). Bar represents 5 μm

Pachytene

The three reconstructed pachytene nuclei taken from three different plants of Petkus were characterized by a complete pairing of the 14 chromosomes into seven bivalents, each with a continuous SC from telomere to telomere. No interlocking configuration was observed.

Most of the bivalents terminated close to the nuclear envelope and only three bivalent ends were free in the nucleoplasm in the vicinity of the nucleolus. The polarized aggregation of telomeres found at zygotene was still present in the early pachytene nucleus (N1), whereas in the two mid-late pachytene nuclei (N2 and N3), the telomeres were more scattered and almost uniformly distributed over the nuclear envelope.

The ultrastructure of the pachytene nucleus is seen in Figures 5, 6. The chromatin surrounding the SC shows various degrees of compactness with two distinct regions – the heterochromatic knobs and the centromeres (Fig. 6). A heavily compacted chromatin region (heterochromatin knob) surrounded most of the telomeres and probably constitutes the ultrastructural counterpart of the C-bands, routinely identified in light microscopy since the pioneering work of Sarma and Natarajan (1973). The heterochromatic knobs ranged in diameter from large (approximately 1.5 μm) to medium-sized (1 μm) to small (0.3 μm) and were distributed as shown in Figure 7. N1 had five large, two medium and one small knob; N2 had seven large and three small knobs; and N3 had seven large, three medium, and one small knob. Only two subterminal knobs were oberved, both in N3. In two nuclei, fusion of knobs of different bivalents was detected. In three of these four cases the short arm of one bivalent and the long arm of a second bivalent were involved (see arrows in Fig. 7).

The centromeric regions were readily distinguishable by their lower density and their fibrous substructure (Fig. 6). The SC passed through the centromeric chromatin without interruption or structural modification. The length of the centromere region is about 1.4 μm which represents 2% of the bivalent length. The total centromere volume is approximately 2 μm^3 in the early pachytene nucleus and 3 μm^3 in the two late pachytene nuclei. The largest centromeric mass was 1.5 times the size of the smallest in all three nuclei. The seven centromeres were distributed throughout the nuclear space with a preferential localization toward the nuclear envelope. Five centromeres in each of the two mid-late pachytene nuclei, and two in the early-pachytene nucleus were in contact with the envelope (Fig. 6). The centromere regions showed a tendency to be situated in groups of two or three. Moreover, the fusion of two centromeres from different bivalents were observed twice in N2 and once in N3.

Spatial tracing of the seven bivalents in the nucleus showed that most of them appeared to be confined to separate regions of the nucleus as illustrated by the three biva-

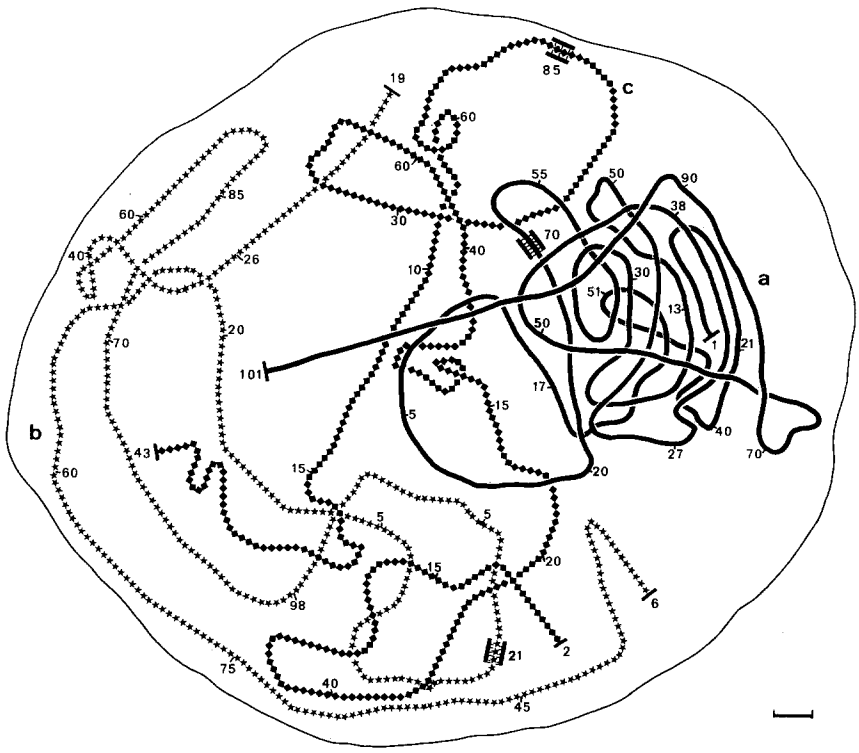


Fig. 8. Spatial tracing of three pachytene bivalents of nucleus N3 (*a*, *b*, *c*) illustrating their arrangement in separate areas. *Numbers* indicate the section numbers. *Bars* at the ends of bivalents indicate termination at the nuclear envelope and *hatched areas* represent centromeres. Bar represents 0.5 μm

Table 1. Absolute and relative length of synaptonemal complex (SC) and arm ratios of *Secale cereale* cv. Petkus (LM light microscopy; EM electron microscopy)

Centromere position	Absolute[a] chromosome length (μm) LM	Absolute SC length (μm)			Relative length				Arm ratio				Karyotyping[c]	
		Early pachytene	Mid-late pachytene			EM				EM			Lima-de-Faria	Bennett et al.
		N1	N2	N3	LM	N1	N2	N3	LM	N1	N2	N3		
Metacentric	88.3	72.4	61.5	53.7	15.5	13	13.3	12.2	1.2	1.1	1.2	1.2	II	7?
	78.8	75.4	58.2	71.3	13.8	13.6	12.6	16.3	1.1	1.2	1.1	1.2	IV	3?
Submetacentric	90.7	78.2	68.6	60.4	15.9	14.1	14.8	13.8	1.4	1.5	1.3	1.3	I	2
	82.3	89.4	68.7	68.5	14.5	16.1	14.8	15.6	1.3	1.5	1.6	1.5	III	4
	69.6[b]	71[b]	62.8[b]	57.7[b]	12.2	12.8	13.6	13.2	1.7	1.4	1.4	1.6	V	1
Subacrocentric	83.2	88.4	65.8	58.3	14.6	15.9	14.2	13.3	2.7	2.8	3	2.9	VII	5
	75.9	79.6	78	68.3	13.3	14.4	16.8	15.6	2.1	2	2.1	2.4	VI	6
Total lengths	568.8	554.4	463.6	438.2										

[a] Values from Lima-de-Faria (1952)
[b] The nucleolus organizing chromosome
[c] N.B. this karyotyping is also based on the distribution pattern of the heterochromatic knobs. The roman numerals correspond to the classification of Lima-de-Faria (1952) and the arabic numerals are those of Bennett et al. 1977)

lents in Figure 8. This pattern occurred almost equally in the zygotene and the pachytene nuclei.

The SC lengths and arm ratios are given in Table 1. To minimize the chromosome length variation in the different nuclei, the relative length of each SC was calculated as a percentage of the total SC complement length. The values are in agreement with bivalent length and arm ratios obtained by light microscopy (Lima-de-Faria 1952). Since the lengths of the individual bivalents were very similar (Fig. 7), the chromosomes were classified into only three groups according to arm ratios. A comparison with the mitotic karyotype established on the basis of arm ratios and C-banding pattern (Bennett et al. 1977) revealed good agreement between the distribution of telomeric knobs and the C-bands especially in the two mid-late pachytene nuclei.

The nucleolus organizer region was located on the short arm of the submetacentric bivalent 1 (Fig. 7) and appeared as a lightly stained region partially embedded in the nucleolus. The SC was disrupted inside the nucleolus organizer region.

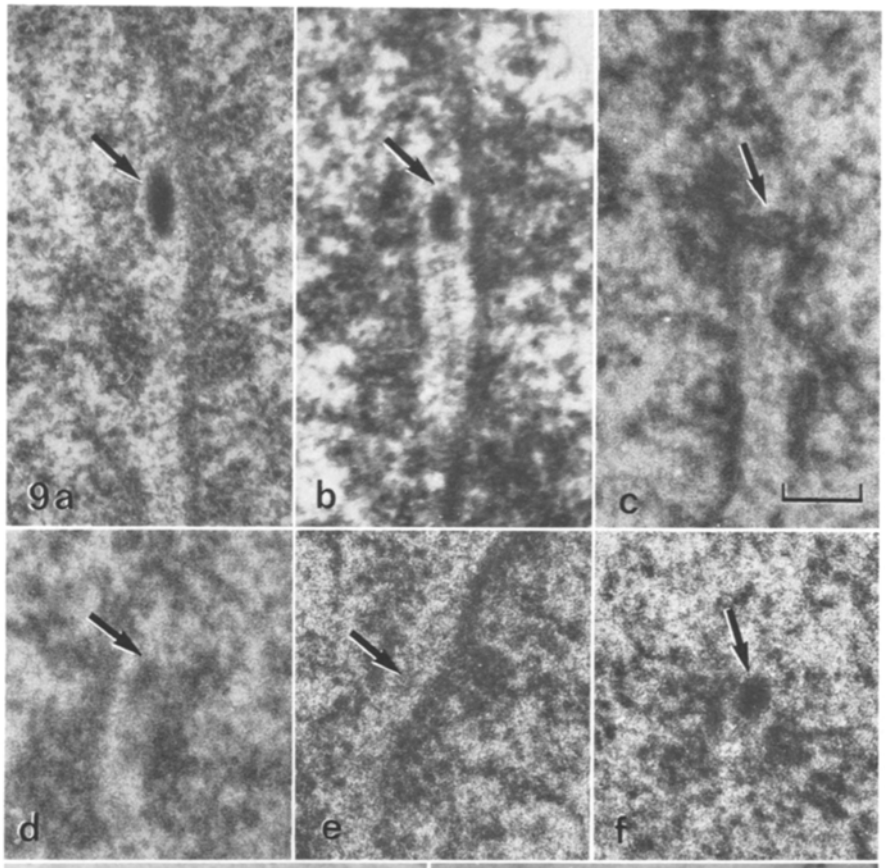


Fig. 9. Longitudinal sections of recombination nodules (*arrows*) at high magnification. Large nodule at early pachytene (**a**), midpachytene (**b**), and late pachytene (**c**). Note the chromatin surrounding the nodule in **c**. Small nodules at early pachytene (**d** and **e**) and in cross section (**f**). Bar represents 0.2 μm

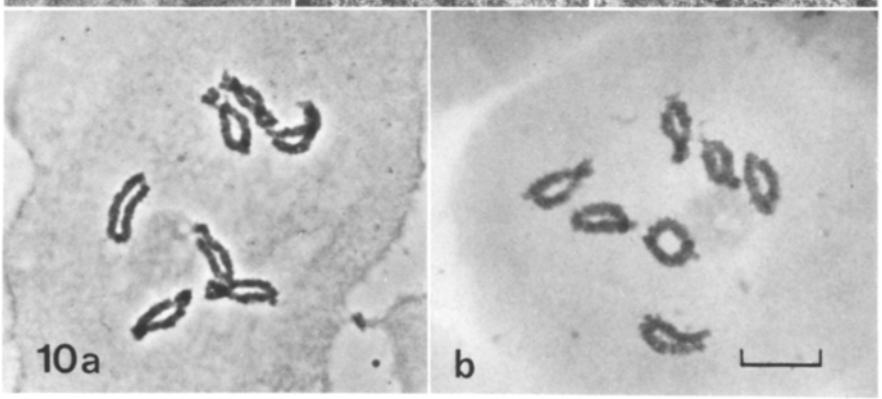


Fig. 10. Light micrographs of late diplotene (**a**) and early diakinesis (**b**) nuclei of pollen mother cell of Petkus. Bar represents 10 μm

Recombination nodules and chiasmata

In the two PTA-stained nuclei, recombination nodules could not be distinguished, whereas all bivalents had nodules in the osmium-fixed nuclei. In the early pachytene nucleus, two different types were observed: large nodules (Fig. 9a) of dense and ellipsoidal morphology (mean size = 100 nm × 210 nm) and small nodules, which were less electron-dense and varied in size and shape (Fig. 9d, e). Both were associated with the central element in the SC central region space. In the mid-late pachytene nuclei, the nodules (mean size = 90 × 140 nm) were more irregular in shape and mainly associated with chromatin fiber (Fig. 9b, c).

The distribution of the nodules on the bivalents is given in Figure 7. In the early pachytene nucleus (N1) only the 18 large nodules, which can be clearly identified even in cross section (Fig. 9f), are shown. All arms except two short ones (including the arm carrying the nucleolar organizer region) have at least one large nodule. The precise number of small nodules was difficult to establish, but was estimated to be around 30. The mid-late pachytene nucleus (N2) has 24 nodules (Fig. 7). All bivalent arms have at least one nodule.

Light microscopy of diplotene and early diakinesis nuclei from the same plants revealed a chiasma frequency of 13–21 per cell (the higher number is for the diplotene nuclei). The mean chiasma number was calculated to be 15–16 at late diplotene (45 nuclei). Most chiasmata were terminal; the interstitial chiasmata were located mainly in the long arms of two bivalents (Fig. 10a, b).

Discussion

Chromosome pairing and recombination nodules

This study has shown that chromosome pairing in rye, *Secale cereale*, follows the general pattern described for a

number of organisms (review in Rasmussen and Holm 1980):

a) The polarized distribution of telomeres in a distinct bouquet arrangement at zygotene is followed by uniform distribution of the bivalent ends during pachytene.

b) Interlocking of chromosomes and bivalents is a regular feature of the zygotene pairing and is especially prevalent in species with long chromosomes.

c) Pairing is often initiated from the telomere regions but occurs also at several sites along the chromosomes. Such multiple-site pairing initiation appears to be a common feature of fungi and higher plants in contrast to the telomeric initiation usually found in animal species (review in Zickler 1977; Rasmussen and Holm 1980). The observation that in rye SC formation occurs at many interstitital sites is especially interesting because exclusive telomeric initiation of pairing, together with the presence of heterochromatic knobs around the telomeres, have been used to explain pairing failure between rye and wheat chromosomes and between homologous rye chromosomes in triticales (review in Gupta and Priyadarshan 1982).

A second important point to emerge from the present work is the characterization of the recombination nodules associated with the central element of the SC. There are two morphologically different types at early pachytene, and only one at late pachytene. Nodules of two sizes have been reported previously and related respectively to crossing over and conversion (review in Carpenter 1979). No functional relationship can be concluded here. The dense early pachytene nodules in rye, like in *Paeonia* (Kehlhoffner and Dietrich 1983) and wheat (Hobolth 1981) are larger than in fungi (Zickler 1977; Holm et al. 1981) and animal species (Carpenter 1979; Holm and Rasmussen 1980), and the SC length per nodule is also much longer.

In rye, the distribution of chiasmata within bivalents has been the subject of several studies, and it is well established that despite considerable differences in chiasma frequence between different inbred lines and cultivars, the chiasmata are predominantly terminal (review in Jones 1978; Orellana and Giraldez 1981). At the SC level, the number of nodules (18–24) correlate well with the number of chiasmata seen in the light microscope at diakinesis (12–21 with a mean of 15–16). In the two nuclei analyzed 10 of the 14 bivalents had at least one distal nodule. This supports the hypothesis that nodules are present at sites where crossing over occurs and where chiasmata form later (Holm and Rasmussen 1980).

Chromosome arrangement within the nucleus

Premeiotic chromosome arrangement has often been evoked as a prerequisite for meiotic chromosome pairing (review in Avivi and Feldman 1980; Yacobi et al. 1982). Bennett (1982) has provided evidence in rye for a somatic chain arrangement of the chromosomes depending upon arm length. The present study has unequivocally shown that such an ordered chromosomal arrangement in the somatic nuclei does not prevent the frequent occurrence of chromosome or bivalent interlocking during chromosome pairing at zygotene, and thus confirms that interlocking is a normal feature of synapsis. Moreover, reconstruction of three pachytene nuclei failed to reveal interlocking configuration which implies that in rye they are already resolved at pachytene as in other organisms (Review in Holm and Rasmussen 1980).

The observation that during pachytene, the different beivalents tend to be localized in limited regions of the nucleus is probably not related to chromosome pairing at zygotene because it is more prominent in the three pachytene nuclei than in the zygotene nucleus.

Pachytene karyotyping

Attempts to recognize individual rye chromosomes on a morphological basis had limited success until the discovery that characteristic telomeric hetrochromatin could be vizualized by C-banding (Sarma and Natarajan 1973). The classification of rye chromosomes by cytogenetic parameters has also been performed and their corresponding C-banding patterns described by Darvey and Gustafson (1975). Karyotype analyses have revealed considerable polymorphism in the banding patterns of varieties of the same species and even of plants from the same population (Weimarck 1975; Singh and Röbbelen 1975; Bennett et al. 1977). Such variability is also detectable between the ultrastructural pachytene karyotype of winter Petkus and the pachytene bivalents of a different cultivar of *Secale cereale* investigated by light microscopy (Lima de Faria 1952). The knob fusion observed here as well as the fact that the pattern of knob distribution could depend on the pachytene substages probably produce the heterogeneity in knob pattern of the three pachytene nuclei. The knob distribution in N2 and N3, which were both in mid-late pachytene, was more similar than in N1, which was in early pachytene. In spite of this variability, it was possible by combining the arm ratios with the distribution of the heterochromatic knobs, to correlate the seven bivalents to the mitotic chromosomes of spring Petkus classified by C-banding (Bennett et al. 1977; see Table 1 and Fig. 7).

The centromere volumes have also been shown to be useful chromosome markers (Bennett 1981). However, in rye the centromere volumes are very similar and cannot be used to identify the individual bivalents.

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