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SYNAPTONEMAL COMPLEX FORMATION AND DISTRIBUTION OF RECOMBINATION NODULES IN PACHYTENE TRIVALENTS OF TRIPLOID COPRINUS CINEREUS

by

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Synaptonemal complex formation and distribution of recombination nodules were analyzed in trivalents of triploid Coprinus cinereus. The analysis of 14 completely reconstructed nuclei covering the period from early pachytene to mid diplotene has permitted the following conclusions: at pachytene, chromosome pairing and synaptonemal complex formation were almost exclusively in the form of trivalents. All three homologues were frequently associated at the same site, two central regions combining the three lateral components. The three homologues were never paired with three central regions. The trivalent configurations were maintained unaltered throughout pachytene and at least the centromeres remained associated at early and mid diplotene. At mid-late pachytene, unpaired chromosome arms were frequently associated with central region material in some cases containing recombination nodules. The free face of such central regions was occasionally bound to an electron dense rod resembling a lateral component. Both central regions of the double complexes in the trivalents were able to bind recombination nodules. An analysis of the distribution of recombination nodules along the trivalents indicated that nodules were distributed independently between the two central regions of the trivalents.

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1. INTRODUCTION

Chromosome synapsis in triploid organisms might a priori be expected to result in pairing either of all three homologues at the same region or in pairing of only two of the three homologues at a particular site.

On the basis of light microscopic studies of pachytene and diakinesis nuclei of triploid Hyacinthus and Tulipa, NEWTON and DARLINGTON (23) and DARLINGTON and MATHER (9) came to the conclusion that pairing was exclusively by two's at a given site with frequent shifts of pairing partners, a result supported by MCCLINTOCK (18) in triploid maize. More recently, ultrastructural studies of synaptonemal complexes at pachytene in tri- and tetraploid organisms (1, 19, 20, 25, 27, 31) have confirmed this concept by showing that synaptonemal complex formation as a rule is between only two of the homologues at a given site with occasional shift of pairing partner. Today, the contention that only two chromosomes can pair at the same site in polyploid organisms is considered a well established fact.

A number of genetic and cytological reports have, however, challenged this view. An initial indication on the mode of chromosome pairing in triploid Drosophila oocytes was presented in 1925 by BRIDGES and ANDERSON (6), who, in a study of crossing over in the X chromosomes, showed that among the 25 double crossovers recorded, 15 involved the same two chromosomes (recurrent type) and 10 were between different combinations of X chromosomes (progressive type). Hence, a crossover in one region does not markedly prejudice the chromosomes involved in additional crossovers in the trivalent and BRIDGES and ANDERSON concluded that all three X chromosomes had to be paired to explain this observation.

These observations and conclusions were later supported by REDFIELD (29), who, among 132 double crossovers in chromosomes III in triploid females of Drosophila melanogaster, found 63 recurrent and 69 progressive. Finally BEADLE (2), analyzing crossing over in attached X triploids, obtained similar results, 98 of the double crossovers being recurrent and 96 progressive. It was concluded (3), that pairing either involved all three homologues or, if pairing was exclusively between two of the three homologues at any site, changes of pairing partner must be relatively frequent to account for the observed equality between the two types of double crossovers. The latter conclusion was supported by MATHER (17) who showed, using REDFIELD's (29) data, that expected crossover frequencies provided a better fit to the observed frequencies when based on the assumption that pairing was between only two of the three homologues at the same site.

Observational support for the contention that all three homologues could pair was obtained by light microscopic investigations of pachytene nuclei from several triploid organisms (e.g. Hyacinthus, 4; Nicotiana, 24; and Gossypium, 30). Partial »triple synapsis« was found in all these organisms. In triploid Nicotiana, for example, OLMO (24) reported preferential triple synapsis in telomere and centromere regions as well as in regions with large chromomeres. All three homologous chromosomes were, however, never observed to be paired throughout their entire length.

Ultrastructural studies of synaptonemal complexes in triploid chicken (8) and triploid oocytes of the silkworm, Bombyx mori (25) have confirmed these observations. In both organisms, all three homologous lateral components were often lying side by side held together by two central regions. In triploid Bombyx oocytes, the double synaptonemal complexes were less frequent than in the triploid chicken and restricted to telomere regions, most of the complement at early pachytene being paired two by two with occasional shift of pairing partners.

The present paper describes chromosome pairing and the distribution of recombination nodules between the homologues of the trivalents in triploid meiocytes of the basidiomycete Coprinus cinereus analyzed by serial sectioning and three dimensional reconstruction of synaptonemal complexes.

2. MATERIALS AND METHODS

The material used in the present study was obtained from a cross between the strain JR52 (ATCC 26055) and strain 410–11. As described previously strain JR52 is haploid (13). Hence, the two additional genomes must have originated from stain 410–11.

The culture procedures and the methods for

Table I

Chromosome associations at meiotic prophase and total number of chromosomes in triploid Coprinus.

Stage	Nucleus number	Univalents	Bivalents	Trivalents	Total number of chromosomes
Early pachytene	10	0	2	11	37 (3n–2)
	11	0	1	12	38 (3n–1)
	12	0	1	12	38 (3n–1)
	14	1	2	11	38 (3n–1)
Mid-late pachytene	1	0	0	11	33 (3n–6)
	4	0	0	13	39 (3n)
	6	0	0	13	39 (3n)
	9	1	1	12	39 (3n)
	13	0	1	12	38 (3n–1)
Early diplotene	2	4 centromere regions		10	–
	3	13 centromere regions			–
	8	0	0	13	39 (3n)
Mid diplotene	5	13 centromere regions			–
	7	13 centromere regions			–

Table II

Mean absolute and relative lateral component length and centromere index (± standard deviation) of the chromosomes at mid-late pachytene in triploid Coprinus.[a]

Chromosome number	Absolute length (μm)	Relative length (%)	Centromere index
1	3.9 ± 0.6	11.4 ± 1.8	31 ± 4
2	3.5 ± 0.7	10.3 ± 2.1	42 ± 3
3	3.2 ± 0.4	9.4 ± 1.2	38 ± 3
4	2.9 ± 0.4	8.5 ± 1.2	38 ± 1
5	2.8 ± 0.2	8.2 ± 0.6	40 ± 7
6	2.7 ± 0.6	7.9 ± 1.8	29 ± 3
7	2.5 ± 0.6	7.3 ± 1.8	26 ± 6
8	2.3 ± 0.3	6.7 ± 0.9	26 ± 5
9	2.4 ± 0.2	7.0 ± 0.6	44 ± 5
10	2.1 ± 0.2	6.2 ± 0.6	43 ± 5
11	1.9 ± 0.2	5.6 ± 0.6	43 ± 5
12	1.8 ± 0.2	5.3 ± 0.6	46 ± 4
13	2.1 ± 0.3	6.2 ± 0.9	–b
Total	34.1 ± 4.5		

a) Nucleus number 1 is not included as two trivalents were missing.
b) Only the long arm of the nucleolus organizing chromosome was measured.

surgical removal of gills from the fruiting body at different stages of meiosis were the same as those previously described (15). Fixation and embedding was carried out as described by LU (14, 16) and the procedure used for serial sectioning and three dimensional reconstruction as well as the computer techniques used for measuring chromosome length have been described by RASMUSSEN and HOLM (26).

3. RESULTS

3.1. The karyotype

Altogether 14 nuclei were investigated comprising early pachytene (4 nuclei), mid-late pachytene (5 nuclei), early diplotene (3 nuclei) and mid diplotene (2 nuclei). A detailed description of the individual meiotic stages and the karyotype (n = 13) in Coprinus are given by HOLM et al. (13). Reconstruction of the entire chromosome complement was possible in ten of the analyzed nuclei and demonstrated unequivocally that the nuclei were triploid (Table I). Five of the nuclei contained only 37 and 38 chromosomes and were thus aneuploid for one or two chromosomes (Table I). One nucleus (number 1) contained 11 trivalents only.

Classification of the individual chromosomes were performed on the basis of lateral component length and centromere index at mid-late pachytene according to the criteria given by HOLM et al. (13). Unlike the diploid crosses, the present cross did not contain translocations and thus provides a »normal« pachytene karyotype of Coprinus cinereus (Table II and Figure 1). As pointed out in the previous paper, the chromosomes can be classified into four groups with reasonable certainty while the classification within the groups is less reliable. Only chromosome 1, the longest one, and chromosome 13 which carries the nucleolus organizer region can be identified unambiguously.

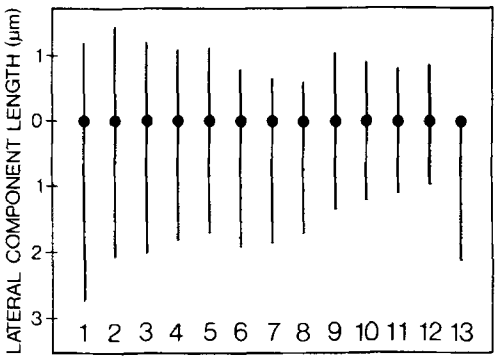

Figure 1. An idiogram showing the mean absolute length and centromere position of the 13 chromosomes of Coprinus cinereus at mid-late pachytene.

The arm of chromosome 13, which possesses the nucleolus organizing region is not included since lateral component continuity is lost within the nucleolar material.

The mean lateral component length of the three homologues ranged at mid-late pachytene from 3.9 µm to 1.8 µm (Table II) which is very similar to the values found in the diploid crosses (13). The same is the case for the total lateral component length of one genome which in the triploid meiocytes amounted to 40.6 µm at early pachytene and 34.1 µm at mid-late pachytene

Table III

Mean lateral component (LC) length and number of recombination nodules (RN) at pachytene and diplotene.

Stage	Number of nuclei	LC length of one genome (µm)[a]	Number of RN's[a]
Early pachytene	4	40.6 ± 2.7	38 ± 2
Mid-late pachytene	5	34.1 ± 4.5	24 ± 5
Early diplotene	3	34.8[b]	22 ± 5
Mid diplotene	2	–	21

a) ± standard deviation.
b) Based on one completely reconstructed karyotype.

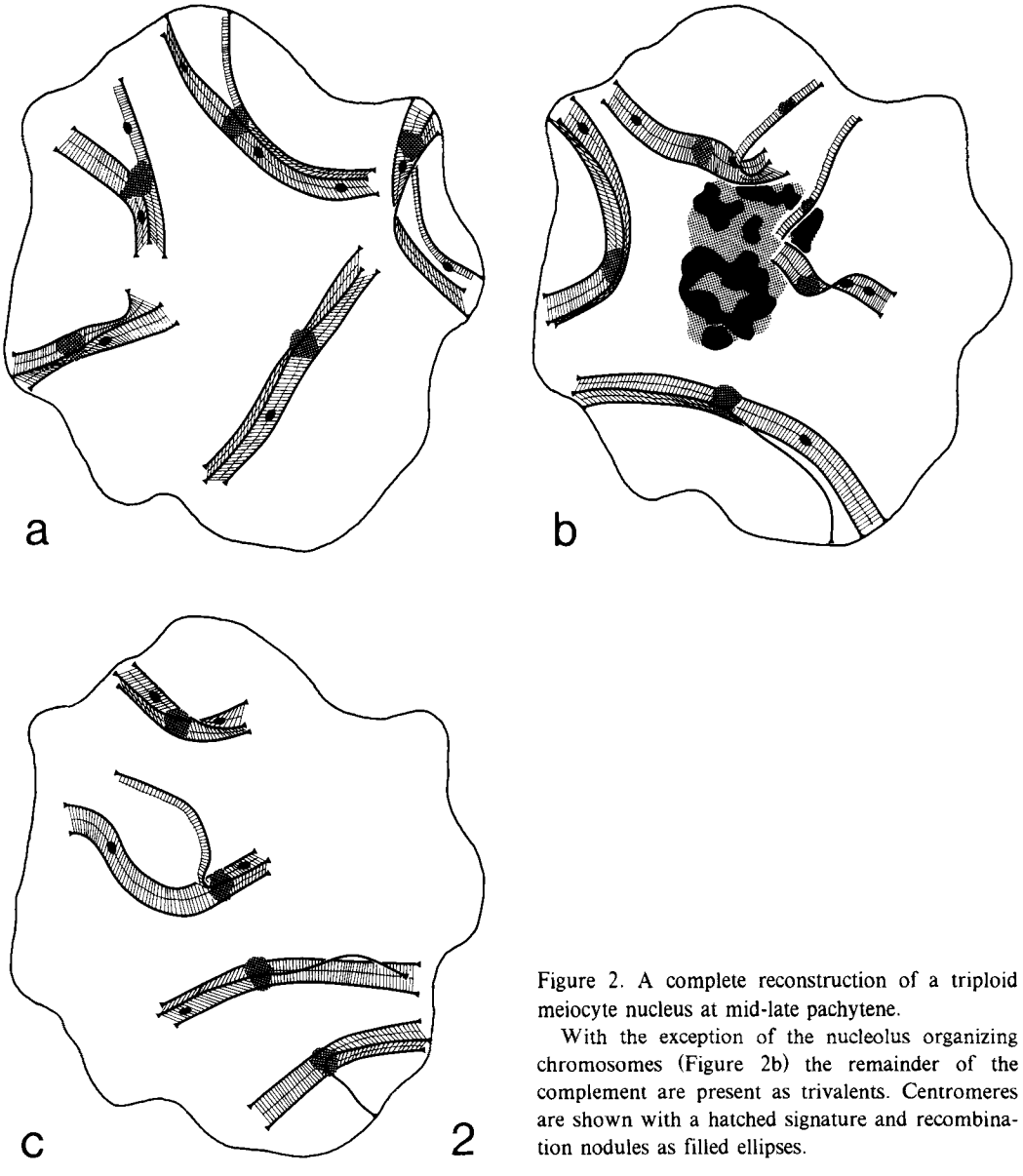

Figure 2. A complete reconstruction of a triploid meiocyte nucleus at mid-late pachytene.

With the exception of the nucleolus organizing chromosomes (Figure 2b) the remainder of the complement are present as trivalents. Centromeres are shown with a hatched signature and recombination nodules as filled ellipses.

(Table III), the corresponding values for the diploid meiocytes being 42.1 μm and 36.0 μm. Hence, the presence of an additional genome in Coprinus does not noticeably affect either the absolute length of the genome or the lengths of the individual chromosomes. This is in accordance with the results from di- and tetraploid yeast (1) while in Bombyx, increasing ploidy level is accompanied by a reduction in the lateral component length of the genome (28).

3.2. Chromosome pairing and synaptonemal complex formation

As shown in Table I, pairing and synaptonemal complex formation involve in almost all cases the three homologues giving rise to exclusive trivalent formation and with only two exceptions (nuclei 14 and 9), the presence of bivalents was a direct result of aneuploidy. The lack of six chromosomes in nucleus 1 is most likely the result of chromosome elimination

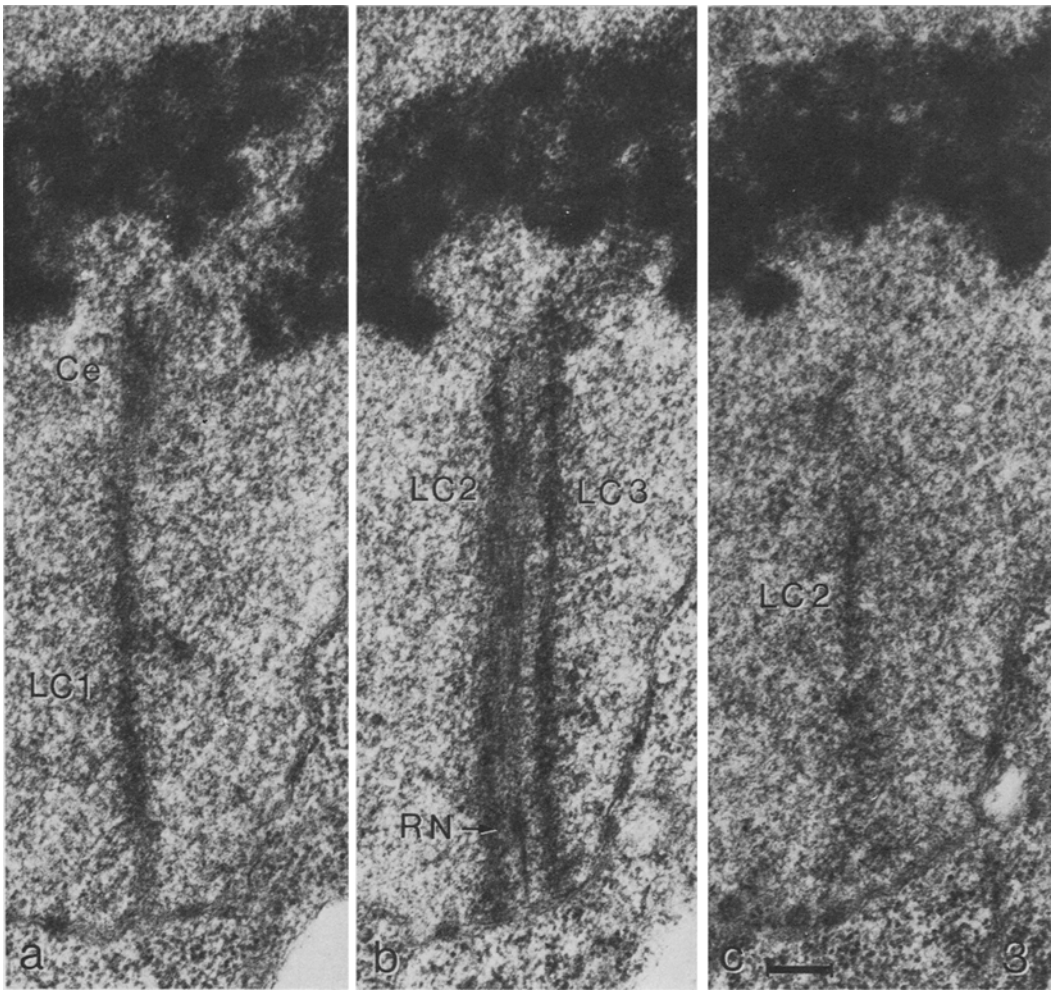

Figure 3. Three consecutive longitudinal sections through the synaptonemal complexes of the long arm of the nucleolus organizing trivalent.

LC1, LC2 and LC3 denote the three lateral components. Ce, centromere; RN, recombination nodule. (Bar = 0.2 μm).

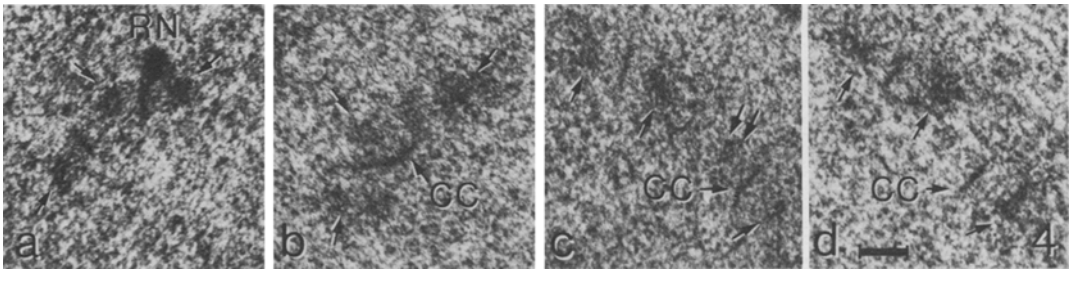

Figure 4. Four cross sections of trivalents. The lateral components are denoted by arrows.

Figure 4a shows a double synaptonemal complex with three lateral components, two by two combined by central regions. In Figure 4b, the two central components (CC) have fused forming a semicircular structure. Figures 4c and 4d show the association between a single lateral component and a fully organized central region. In Figure 4c, the free face of the central region is associated with material resembling a lateral component (double arrow). (A series of sections through this region of the trivalent is presented in Figure 6, Figures 6f and 4c being from the same section). RN, recombination nodule. (Bar = 0.1 μm).

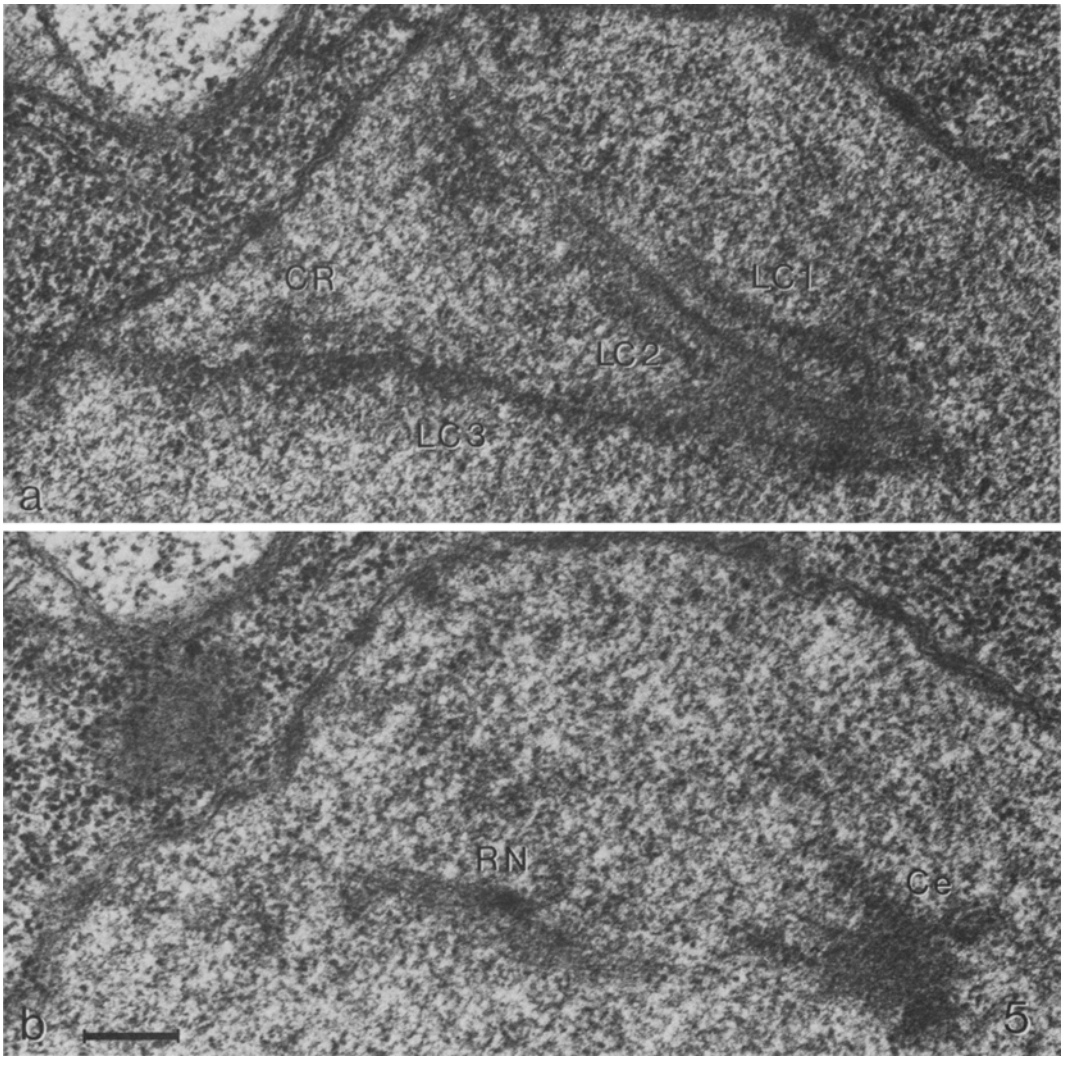

Figure 5. Two consecutive sections through a trivalent.

Two of the lateral components (LC1 and LC2) are paired with a central region distal to the centromere (Ce). The remaining lateral component (LC3) is associated with central region material containing a recombination nodule (RN). (Bar = 0.2 μm).

having occurred after completion of synapsis as evidenced by the presence of 11 homologously paired trivalents in the nucleus.

The complete reconstruction in Figure 2 illustrates the general pairing pattern at mid-late pachytene: synaptonemal complex formation frequently involves all three homologues at a given site, two central regions combining the three lateral components. The three lateral components of the double complex either lie in nearly the same plane (Figures 4a and 8) or form a three-sided prism (Figures 3 and 9). In the latter case, the two central regions were occasionally fused in the central axis of the prism (Figure 4b). Cross sections of completely paired trivalents never revealed more than two central regions per trivalent at a given site, the last potential pairing face without exception being devoid of a central region (Figures 4b and 9). In regions where only two of the three lateral components were

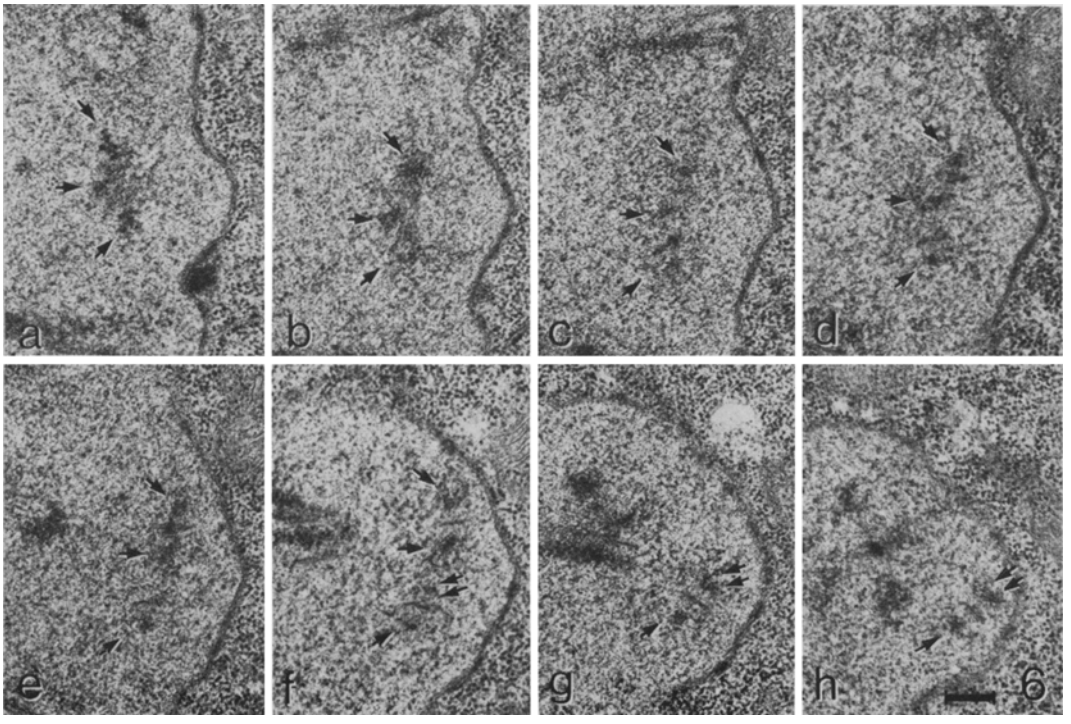

Figure 6. Eight consecutive sections through a trivalent.

In Figures 6a–c all three chromosomes are paired through a double synaptonemal complex. The lower lateral component in Figures 6d and 6e is unpaired and is associated with a central region. In the remaining three micrographs lateral component like material (double arrow) is associated with the free face of the central region in the unpaired chromosome arm. (Bar = 0.2 μm).

engaged in complex formation, the lateral component of the third, free chromosome arm frequently and especially prevalent at mid-late pachytene, combined with either a »half« central region (Figures 2, 4d and 5) or with an apparently intact central region (Figure 4c). Occasionally, the free face of a central region in unpaired chromosome arms was associated with electron dense material resembling a lateral component as illustrated in Figure 4c and by the eight consecutive sections in Figure 6.

Four different types of trivalents were revealed at early and mid-late pachytene (Figure 7). As can be seen from the figure, the frequencies of the various configurations are very similar at early and mid-late pachytene. At both stages, the vast majority of homologues is either completely paired in trivalents with continuous double synaptonemal complexes throughout their entire length (53%) or has one free chromosome arm (30%). Only in 9% of the analyzed trivalents were the three homologues not associated by their contromere regions at pachytene.

At early diplotene, 14, 13 and 13 centromere regions were found in the three analyzed nuclei showing that in virtually all cases the homologous centromere regions remain in close association during synaptonemal complex elimination in diplotene (Table I). The entire chromosome complement of one early diplotene nucleus could be fully reconstructed and revealed 13 trivalents while the disintegration of the synaptonemal complex in the other two nuclei had progressed too far to permit reconstruction of the entire complement.

Association of all three homologous centromere regions was also found in the two mid diplotene nuclei (Table I).

	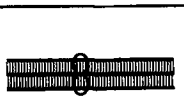	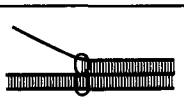	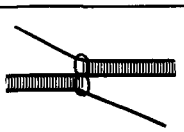	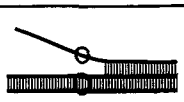
EARLY PACHY-TENE	5 8 6 8	2 4 5 1	1 0 0 2	3 0 1 0
Mean	6.8	3.0	0.8	1.0
MID-LATE PACHY-TENE	5 8 4 5 8	3 3 5 5 4	3 0 1 1 0	0 2 3 1 0
Mean	6.0	4.0	1.0	1.2

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Figure 7. A diagram showing the number of the different trivalent configurations per nucleus.

3.3. Recombination nodules

The total number of recombination nodules per nucleus from early pachytene to mid diplotene is given in Table III. The mean number decreases from 38 at early pachytene to 24 at mid-late pachytene, the corresponding reduction in the diploid (13) being from 37 to 26. Hence, both the number as well as the reduction in the number of nodules between early and mid-late pachytene are almost identical to that observed in diploid Coprinus. Furthermore, the morphology and location of recombination nodules on the central region of the complex appeared similar to that described in diploid meiocytes. Occasionally, recombination nodules were found on the central region of unpaired chromosome arms (Figure 5).

Recombination nodules can attach to both central regions of the trivalent in Coprinus as illustrated by the micrographs in Figures 8 and 9. In Figure 8, the two nodules are separated by a distance of only 0.55 μm and in Figure 9a, the two nodules are both included in the same cross section. Finally, the micrograph in Figure 9b shows that a recombination nodule in rare cases can associate with both central regions of a trivalent simultaneously. This indicates that recombination nodules are distributed independently between the two central regions of the trivalents.

The distribution of recombination nodules among the different combinations of homologues was analyzed by determining the number of trivalents with all nodules between the same two homologues and those in which two or more nodules were located among different combinations of homologues. The values for early pachytene (46 trivalents) and mid-late pachytene (61 trivalents) included both fully paired trivalents and trivalents with one or two chromosome arms unpaired. On the assumption that nodules are distributed independently among the central region of the synaptonemal complexes and that, at a particular site, only two of the three potential combinations of lateral components are capable of receiving a nodule, the expected frequencies of trivalents with all recombination nodules between the same pair of homologues (recurrent type) and trivalents with

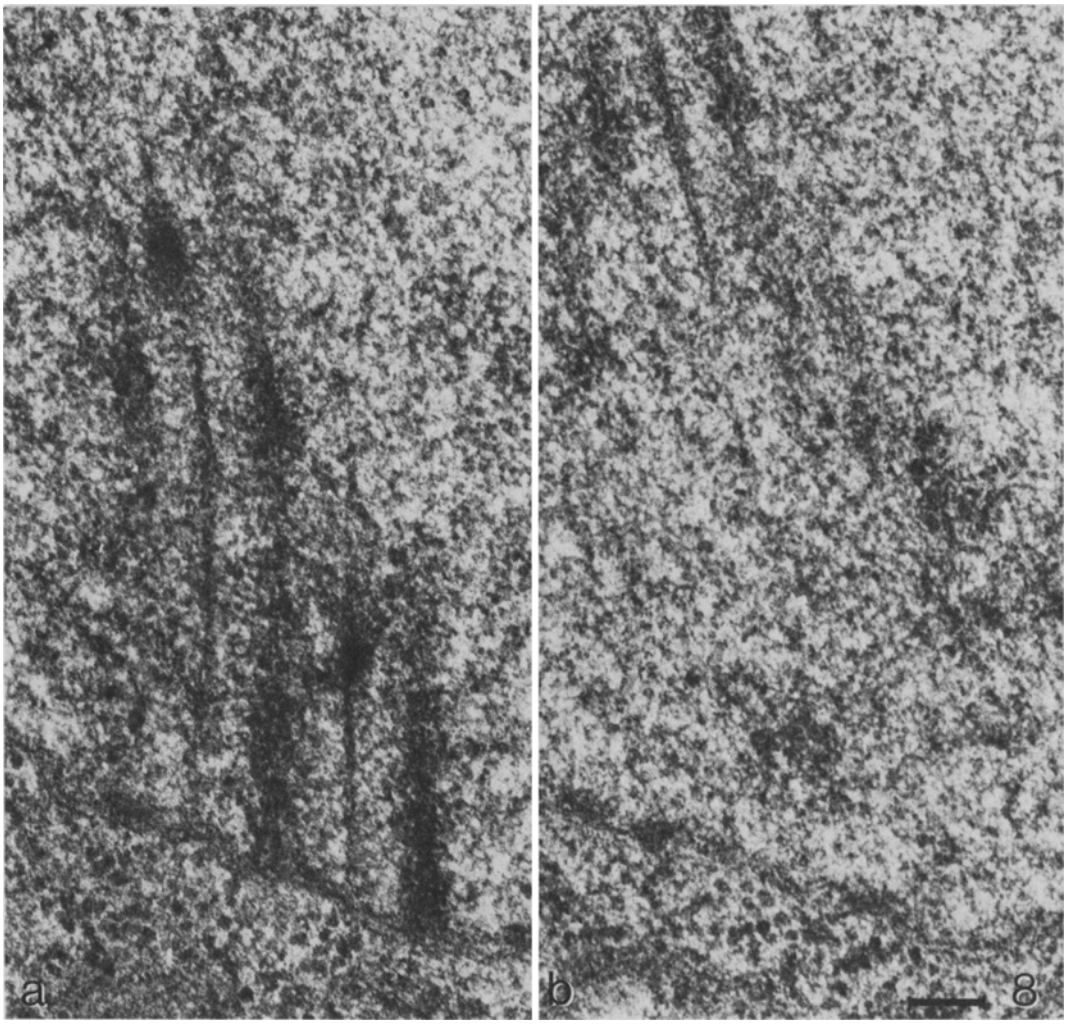

Figure 8. Two consecutive sections through a trivalent paired with a double synaptonemal complex. Note the two recombination nodules between different combinations of homologues. (Bar = 0.1 μm).

recombination nodules between different combinations of homologues (progressive type) are: 50% of each type for trivalents with two nodules, 25% recurrent and 75% progressive for trivalents with three nodules and 12.5% recurrent and 87.5% progressive for trivalents with four nodules. The observed and expected numbers presented in Table IV are almost identical for trivalents with two, three and four nodules which is consistent with the observation that only two central regions join the homologues into trivalents. This furthermore indicates that the placement of recombination nodules occurs independently on the two central regions of a trivalent.

4. DISCUSSION

4.1. Chromosome pairing and synaptonemal complex formation

The present study has unequivocally demonstrated that chromosome pairing and synaptonemal complex formation in triploid Coprinus generally occur by formation of double synaptonemal complexes whereby all three homologues are combined and held in register. This pairing

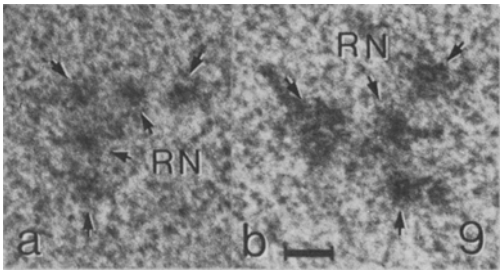

Figure 9. Two cross sections through trivalents with recombination nodules (RN).

Recombination nodules are present at the same level in both central regions of Figure 9a. In Figure 9b, the three lateral components (denoted by arrows) form a triangle with a recombination nodule nearly in the center (Bar = 0.1 μm).

pattern is established during chromosome pairing at zygotene and remains unchanged throughout pachytene as evidenced by almost identical frequencies of the different trivalent configurations at early and mid-late pachytene.

The latter result is at variance with the situation in oocytes of triploid Bombyx (25) where trivalents are regularly formed during the specific pairing phase at zygotene, although at a considerably lower frequency than in Coprinus, most of the pairing being in bivalents and univalents. At mid-late pachytene, however, all trivalents are transformed into bivalents and univalents by dissolution and reassembly of the central region of the synaptonemal complex, followed by a second round of pairing during which the univalents engage in various nonhomologous associations. The same two phase pairing system is operative in tetraploid Bombyx oocytes (27) and in hexaploid wheat (10). In both cases bivalent formation is optimized by transformation of multivalents into bivalents during pachytene. This process has also been inferred from observations in human spermatocytes heterozygous for a reciprocal translocation (12) and mice heterozygous for duplications and inversions (21, 22). It has been hypothesized that correction of chromosome pairing is possible only in regions where crossing over has not taken place. This contention is supported by the fact that, in the recombination proficient tetraploid Bombyx males, the quadrivalents formed during zygotene are maintained up to metaphase I (27, 28).

The existence of a similar two phase pairing system is also inferred from diploid translocation strains of Coprinus (13): In a single case, a translocation quadrivalent was replaced by two heteromorphic, partially nonhomologously paired bivalents. In addition, the distribution of recombination nodules in the arms of the translocation quadrivalents at mid-late pachytene was in agreement with the hypothesis that transformation of translocation quadrivalents into bivalents is prevented if crossing over has occurred distal to the site of pairing partner exchange.

In Coprinus, transformation of trivalents into

Table IV

Observed (O) and expected[a] (E) number of recombination nodules (RN) per trivalent at early pachytene (46 trivalents) and mid-late pachytene (61 trivalents) in triploid Coprinus.

Stage		Mean number of trivalents with 0, 1, 2, 3, 4 and >4 RN's									
		0	1	2[b]	2[c]	3[b]	3[c]	4[b]	4[c]	>4[b]	>4[c]
Early pachytene	O	1	4	5	6	2	11	1	12	0	4
	E	–	–	5.5	5.5	3.3	9.8	1.6	11.4	–	–
Mid-late pachytene	O	1	22	13	11	3	8	1	3	0	0
	E	–	–	12	12	2.8	8.3	0.5	3.5	–	–

a) Assuming equal probability for nodules between two of the three possible combinations of lateral components.
b) All RN's between the same pair of homologues, recurrent type.
c) RN's between different combinations of homologues, progressive type.

bivalents and univalents by dissolution of the central region is theoretically possible in trivalents with 0 and 1 nodule as well as in trivalents in which 2 or more nodules are located between the same combination of the homologues altogether amounting to 53% of the analyzed trivalents. Transformation of trivalents into bivalents and univalents was, however, never observed during pachytene. The presence of 13 centromere regions in all but one of the analyzed diplotene nuclei furthermore shows that all three homologues remain together at least up to late diplotene. Apparently, the trivalents in Coprinus are more stable than for example tri- and quadrivalents of Bombyx oocytes and the multivalents of wheat.

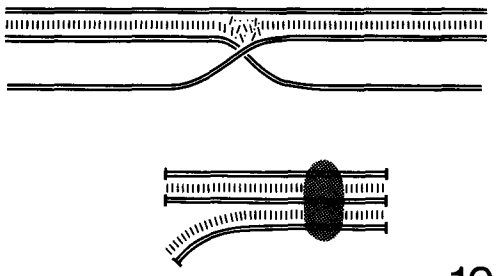

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Figure 10. A diagrammatic representation of trivalent configurations in triploid Bombyx (top) and triploid Coprinus (bottom).

The situation in tetraploid organisms is fundamentally different, as such organisms have the potential of complete bivalent formation. In tetraploid Bombyx oocytes, only few cases of pairing by three's and no cases of pairing by four's were noted (27) and in tetraploid yeast (1), bivalent pairing appeared to be the rule although occasional interruptions of lateral components were interpreted as pairing partner exchanges. Aberrant, five partite synaptonemal complexes, 80 nm in width and with two medial, dense structures resembling central components were reported in tetraploid Allomyces (5). However, by mid-late pachytene, the synaptonemal complexes appeared normal and could be reconstructed. Hence, although less frequent than in triploid organisms, pairing and synaptonemal complex formation in tetraploids may occasionally involve more than two homologues at a particular site.

A difference of possible significance between the multivalents of Coprinus and those of Bombyx and wheat is that all shifts of pairing partners in Bombyx as well as in wheat involve two paired segments with central regions and two segments of unpaired lateral components (Figure 10). The lack of pairing correction in Coprinus is explicable if the more »open« configuration at the site of exchange in Bombyx and wheat acts as the triggering signal for the correction mechanism. The almost perfect pairing and synaptonemal complex formation in the trivalents of Coprinus (Figure 10), in addition to the affinity of homologous centromere regions described previously, may thus be the main factors in preventing initiation of the correction process.

The low amount of DNA per unit lateral component length and the short chromosomes of Coprinus may account for the extensive formation of double complexes. The longer chromosomes with more densely packed DNA of Bombyx and especially of wheat chromosomes may impose physical limitations on the displacement of chromatin required for the exposure of the lateral components prior to assembly of the second central region of the double synaptonemal complexes. Furthermore, the chromosome movements required for the alignment of all three homologues throughout their length may occur more easily in Coprinus and hence facilitate their primary alignment.

The classical concept that pairing in triploids is exclusively by two's has clearly been weakened by this study. The present evidence demonstrates that pairing and synaptonemal complex formation can involve all three homologues at the same site.

The presence of central region material in unpaired chromosome regions along a single unpaired lateral component may either reflect in situ assembly of central regions or may be a result of partial dissolution of central regions of fully paired trivalent arms. The latter possibility is considered less likely in view of the observation in diploid Coprinus (13), human spermatocytes (26), Lilium (11) and Neottiella (33) that central region material can assemble along only one of the lateral components prior to completion of the synaptonemal complex. In situ

assembly of lateral components is furthermore inferred from the observation that lateral component like material in rare cases covers the free face of such central regions, giving the whole segment the appearance of a normal synaptonemal complex.

4.2. Recombination nodules

The mean number of recombination nodules per nucleus at mid-late pachytene is virtually identical to that found in diploid Coprinus (24 nodules versus 26). Hence, the increase in ploidy level does not appear to be accompanied by a corresponding increase in the number of recombination nodules. This is in contrast to the situation in Drosophila, where the frequency of crossing over per chromosome remains unaffected by the increase in ploidy, i.e., the total number of exchanges per triploid nucleus increases by 50% (3,29). The same is the case for the number of chiasmata in triploid Tulipa (9) and Hyacinthus (32).

Further, the present analysis confirms the observations in human spermatocytes (26) and in the meiotic mutant mei-9 of Drosophila (7) that recombination nodules are prerequisites for, rather than the result of, crossing over as shown by the presence of morphologically normal nodules on the central region of unpaired chromosome arms.

The correspondance between the observed and expected distributions of recombination nodules in trivalents with two, three and four nodules is in agreement with the observation that only two of the three possible combinations of homologous chromosomes can pair at the same site and hence are capable of receiving recombination nodules. The almost equal numbers of trivalents with all nodules between the same two homologues and trivalents where nodules are present among different combinations of homologues furthermore indicate that the presence of one nodule between a pair of homologues does not prejudice the placement of additional nodules on the trivalent.

These results may also be relevant for the interpretation of the genetic analysis of double crossovers in triploid Drosophila (2, 3, 6, 29) being indicative of a similar triple pairing with two central regions.

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