TETRAD ANALYSIS IN ASPERGILLUS NIDULANS (EIDAM) WINTER.

by

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GENERAL INTRODUCTION.

Genetics is today being studied in organisms ranging from viruses to man but in the majority of these the four products of an individual meiosis are not recovered and so a problem can only be studied by the use of random strands. However, the resolution of some problems requires the recovery of all four products of meiosis (e.g. the study of chromatid interference) thus limiting the range of organisms which can be used. It is occasionally possible to recover two of the four products; for example, by the use of attached-X chromosomes (Emerson and Beadle 1933; Beadle and Emerson 1935; Bonnier and Nordenskiold 1937; Anderson 1925 and Welshons 1955) and by the use of mitotic crossing over in Aspergillus nidulans (Roper and Pritchard 1955). Tetrads which have already been used for genetical work are found in such organisms as Chlamydomonas reinhardi (Smith and Regnery 1950; Hartshorne 1953; Sager 1954); Chlamydomonas moewusii (Lewin 1953); Sphaerocarpus donnellii Allen 1926; Knapp 1936, 1937); Neurospora crassa (Lindegren's 1932 to 1942; Howe 1954; Stadler 1955; Houlahan et al 1949 and many others); Neurospora sitophila (Wilcox 1928; Lindegren 1932; Aronescu 1933; Wulker 1935; Whitehouse 1942; Fincham 1951); yeasts (Winge 1935; Lindegren 1949; Roman, Hawthorne and Douglas 1951; Roman and Sands 1953; Roman,

Phillips and Sands 1955; Bevan 1956); Aspergillus nidulans Hemmons 1952; Pontecorvo 1953); Aspergillus glaucus (Sharpe 1956); Venturia (Boone 1951; Keitt 1952); Glomerella Wheeler 1953); Podospora (Rizet and Engelman 1949); Funaria (Wettstein 1923) and one of the higher plants - Salpiglossis (Reimann-Philipps 1955).

Tetrads offer the advantage that the position and type of the various chromosome exchanges can be more completely ascertained. When three or more markers are used, chromatid and chiasma interference can be distinguished. Further, in crosses involving many loci, the frequency of multiple exchanges is known, making it possible to examine the distribution of exchanges in tetrads.

Two important points that can best be examined by tetrad analysis are whether or not the reciprocal products of an exchange are recovered and also whether allele ratios inconsistent with Mendelian laws occur. In the majority of analysed tetrads, these products are recovered and the allele ratios are consistent with Mendelian laws. However, Mitchell (1955a) has found an example in Neurospora crassa where the reciprocal products of an exchange are not recovered and there are a few instances of 4:0, 3:1, 1:3 and 0:4 ratios where a 1:1 ratio was expected - e.g. Reimann-Philipps 1955; Lindegren 1955 and Mitchell 1955b. Tetrad analyses also

establish the stage of meiosis at which exchanges probably occur (Wettstein 1923; Anderson 1925; Allen 1926).

Centromere positions can be located in either ordered or unordered tetrads. If the tetrad is ordered, the centromere can be mapped in relation to a single marker (Lindegren 1932). For an unordered tetrad it is necessary to have either three independent markers or two linked and one independent marker before the centromeres can be mapped (Whitehouse 1950; personal communication; Papazian 1951, 1952; Perkins 1949). In Aspergillus nidulans the position can be identified by the analysis of mitotic exchanges (Pontecorvo and Kafer 1956) but tetrads must be analysed to estimate the second division segregation frequencies. Tetrad analysis also provides an independent check of the mitotic method.

Tetrads are also useful in demonstrating non-Mendelian segregation of extra-nuclear determinants. By this means non-Mendelian segregation has been found in Chlamydomonas reinhardi (Sager 1954); Aspergillus glaucus (Sharpe 1956) and Neurospora crassa (Mitchell et al 1953). Knapp showed that chromosome aberrations and lethal mutations that are undetectable with random strands may be found by the use of tetrads (cited by Perkins 1953).

Random strands are more efficient than tetrads

for estimating linkage values (Papazian 1952; Perkins 1953). Two random strands give as much information as the four products of a single meiosis (Mather and Beale 1942).

On the other hand if the genotypes of three of the four products of one meiosis are known, the fourth genotype can be deduced or if only two of the products are known and they carry the same allele for all but one of the loci, the other two genotypes can be deduced. This is based on the assumption that meiosis proceeds normally as it does in all but a very few tetrads. In this study, only those tetrads with three or more identified genotypes have been included among the fully classifiable sample. The ascus of Aspergillus nidulans includes four pairs of genetically identical spores so the same amount of information could be extracted from four as from eight spores, if one were to be picked from each pair. Of course, it is obviously impossible to pick one spore from each pair in practice.

PROBLEMS.

The primary objects of this study were to locate some or all of the centromeres and to analyse interference (both chromatid and chiasma) in the BI chromosome of Aspergillus nidulans. The BI chromosome is the best marked chromosome of A.nidulans. The results of these two parts of the work are presented in Sections II and III.

Some of the asci gave allele ratios for particular markers differing from the 1:1 ratio expected from single gene heterozygosis. Also one of the perithecia contained asci carrying a semi-lethal factor while other perithecia contained asci of both selfed and crossed origin. Closely linked markers were included in some of the crosses to check on the recovery of the reciprocal products of exchange. These by-products of ascus dissection are discussed in Sections IV to VI.

Pritchard (1956) found and analysed a duplication of a segment of the BI chromosome. A few asci from a cross involving this duplication were dissected and are briefly discussed in Section VII.

I. MATERIAL AND METHODS.

1. Life cycle of Aspergillus nidulans. As a detailed description of the life cycle of A. nidulans has been given before (Thom and Raper 1945; Pontecorvo 1953) only the main features will be given here.

Aspergillus nidulans (Eidam) Winter is a homothallic ascomycete. The hyphae are branching and divided into "cells" which are multi-nucleate. When grown on solid medium a compact colony is formed. The hyphal strands anastomose quite freely so that heterokaryons are easily obtained.

Some of the hyphal cells differentiate into multi-nucleate conidiophores which terminate in a globose vesicle. From the surface of this vesicle a number of sterigmata are produced and from the tip of each, a chain of asexual conidia is abstricted. The nuclei within a single chain are usually identical but the nuclei of different chains on the same conidiophore may be different. The mature haploid conidia are 3 to 3.5 microns in diameter and the wild type colour is green.

The sexual spores are formed within perithecia - or more exactly, cleistothecia - which contain up to 100,000 asci. The perithecia have hard, dark brown walls and are mature after 8 - 10 days incubation of cultures at 37° C. The asci contain eight ascospores within an

extremely fragile wall.

Cytological analysis of the events occurring during perithecial formation is incomplete owing to the minute size of the nuclei. However, on both cytological and genetical evidence, the eight spores of an ascus are derived from a diploid nucleus which has undergone meiosis followed by a mitotic division. Analyses of single perithecia from heterokaryons show that the asci of any one perithecium are usually all selfed of one or the other parent or all hybrid. Most hybrid perithecia are thus derived from two nuclei which may become associated early in the development of the ascogenous hyphae. If this association occurs, it would be followed by conjugate divisions of the nuclei prior to fusion in pairs in the ascus primordium.

2. Media. Wild type Aspergillus nidulans will grow on a minimal medium containing a carbon source and a few salts. This medium was made up as follows:-

Sodium nitrate 6g.; potassium chloride .52g.; magnesium sulphate ($7H_2O$) .52g.; potassium di-hydrogen phosphate 1.52g.; traces of iron and zinc; dextrose 10g.; distilled water 1000 ml. The pH was adjusted to 6.5 with sodium hydroxide and the medium filtered before sterilization.

Biochemical mutants could be grown on this medium by adding the appropriate growth factors.

Complete medium was made with the same ingredients as the minimal medium above with the addition of:-

Difco Bacto Peptone 2g.; yeast extract "Yeastrel" 1g.; 5 ml. of an hydrolysate equivalent to 200 mg. of casein per ml.; 3 ml. of yeast nucleic acid equivalent to 100 mg. per ml. and 1 ml. of a vitamin solution. The vitamin solution contained:- riboflavin 10 mg.; nicotinamide 10 mg.; p-amino benzoic acid 1 mg.; pyridoxin-HCL 5 mg.; aneurin-HCL 5 mg.; biotin .02 mg.; Ca-pantothenate 20 mg.; choline chloride 20 mg.; inositol 40 mg.; folic acid 1 mg. and distilled water 10 ml. Koch sterilized.

The pH was adjusted to 6.0 to 6.2. The medium was filtered before addition of the vitamin solution and was then sterilized.

Both media as given above were in the liquid state. In order to solidify these media, 1.25% agar was melted in the water before the addition of any of the ingredients.

All ingredients were of analytical reagent standard.

3. Strains used. All the mutants used in the crosses were already available in the Department of Genetics.

Table of mutants used for tetrad analysis.

Mutant	Nature of mutant.	Mutagenic Agent.
ad1	requiring adenine	X-rays
ad8	requiring adenine	U/V
ad20	partially requiring adenine	U/V
ad14	requiring adenine	U/V
ad15	requiring adenine	U/V
ad17	requiring adenine	U/V
an	requiring aneurin	U/V
bi1	requiring biotin	X-rays
met1	requiring methionine	U/V
paba1	requiring p-amino benzoic acid	X-rays
pro1	requiring proline	U/V
pro3	requiring proline	U/V
pyro4	requiring pyridoxine	X-rays
ribo	requiring riboflavin	U/V
sd	requiring thiosulphate	Nitrogen mustard
thi2	requiring "thiazole"	U/V
wn	white conidia	Spontaneous
y	yellow conidia	X-rays.

4. Methods of crossing strains. Strains to be crossed were first purified by isolating a single conidium onto a slope of complete medium. The purified strains were tested for their nutritional requirements. Conidia from the two strains were then streaked together on a Petri dish of minimal medium and a few drops of liquid complete medium were spread along the streak to facilitate germination. The dishes were incubated for three weeks to a month at 37° C. Perithecial and ascus analyses were not carried out until after this incubation period.

Instead of a Petri dish, a slppe of minimal medium in a "boiling tube" was occasionally used.

5. Methods of genetic analysis. The two methods of analysis used in this study were perithecium analysis and ascus analysis.

(a) Perithecium analysis. Hemmons (1952) and Hemmons, Pontecorvo and Bufton (1953) found that the asci within any one perithecium tended to be of one type: all selfed of one or the other parental type or all hybrid. A random sample of spores taken from one hybrid perithecium will therefore be equivalent to a sample of gametes from an individual in higher organisms.

Following their technique, a perithecium was picked and cleaned of hyphal fragments and conidia by rolling it with a needle over a dish containing 3% agar. When the perithecium was clean, it was crushed in .2 ml. of either 1 in 1000 Tween 80 or 1 in 1000 Calzolene oil. The number of spores was estimated by a haemocytometer count and the suspension was then diluted down to a concentration of between 300 to 500 per ml. .1 ml. of this diluted suspension was spread on each of three plates of complete medium giving a sample of 90 to 150 colonies. After 48 hours the plates were examined and the allele ratio for a single pair of "visible" markers was determined. If this allele ratio proved to be 1:1, sufficient of the spores to bring the total number to more than 300 were plated.

These 300 or more colonies were then tested for their nutritional requirements. Firstly, they were inoculated at marked points on further dishes of complete medium. These are called "master plates". Then, using the "multi-wire" replicator devised by Forbes (unpublished) the colonies were replicated from the master plates onto dishes of medium lacking, one at a time, the growth factors in the cross. If a colony failed to grow on a particular plate, then it required the growth factor which was missing. If a colony grew on the same plate, it did not require that growth factor. The inoculations were classified for growth or non-growth after 24 hours and again after 48 hours.

(b) Ascus analysis. The method used initially was that developed by Hemmons (1952). This method is outlined as follows:-

Equipment and instruments used. A micro-loop was constructed from $\frac{1}{8}$" internal diameter soda glass tubing drawn out twice and with the end bent around to form a loop approximately 15 microns in diameter. The shaft of the loop was bent upwards to an angle of approximately 40° so that it would easily enter the ascus suspension (Figure 1). This loop could be used for all the manipulations required. Hemmons used a De Fonbrune micro-manipulator in conjunction

with a binocular microscope (magnification x 360) and micro-loops were made with a De Fonbrune micro-forge. A deep green and an orange filter were used together on the light source.

The dissecting chamber. This was made from $\frac{5}{8}$" internal diameter glass tubing from which a $\frac{1}{4}$" length was taken. A slot $\frac{1}{4}$" wide was then cut out of the side of this circle, thus producing a horse-shoe shape. One end of this horse-shoe was attached to a 3" x 1" microscope slide with the slot facing across the width of the slide. Enough water was introduced to cover the bottom of the chamber (Figure 2).

The ascus suspension. This was prepared by placing a perithecium in a drop of sterile water on a $\frac{7}{8}$" square No. 2 coverslip and then lightly puncturing the perithecium to liberate the contents. The coverslip was then inverted onto the chamber on the microscope stage. The micro-loop could be introduced through the aperture in the side of the chamber.

Ascus dissection. The micro-loop was introduced into the chamber and focussed in a central position. Then the loop was raised into the suspension and manoeuvred into position above an unbroken ascus. The ascus was removed by lowering the loop onto the ascus and then on out of the drop. Care was taken that no conidia or free

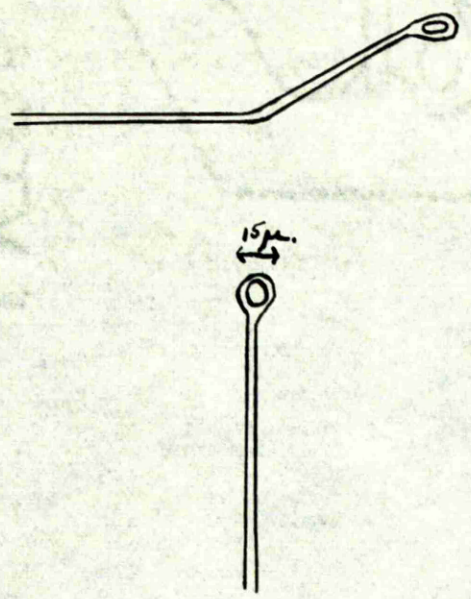

Figure 1. Micro-loop viewed from the side and from above. (Greatly magnified). After Hemmons (1952).

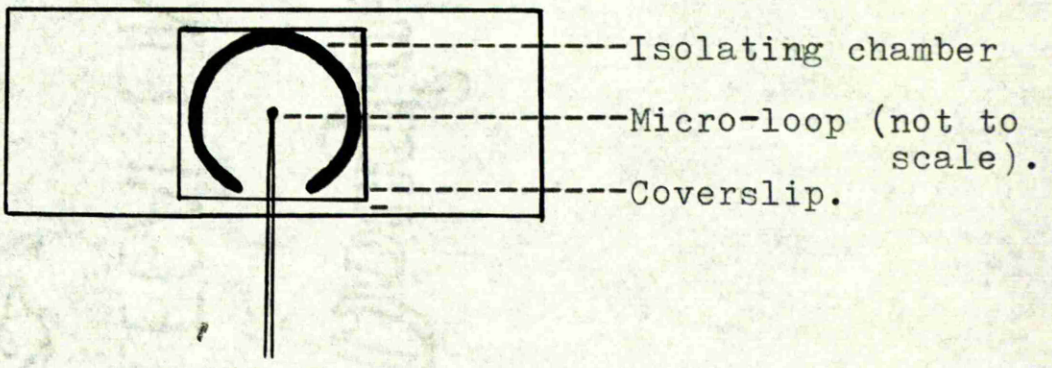

Figure 2. Moist chamber and loop as seen from above. After Hemmons (1952).

ascospores were attached to the loop. The ascus was then transferred to an agar drop on the underside of a second coverslip, substituted for the first. The number of ascospores in the ascus was checked and then by further substitutions, each ascospore was transferred to a separate coverslip. Thus the coverslip carrying the ascus had to be transferred backwards and forwards eight times during the dissection of a single ascus. The numbered agar drop suspensions were then inverted onto specially prepared "depression" slides (see Hemmons 1952) and incubated at 37° C.

A number of modifications of these techniques have since been introduced and are listed below:-

Equipment and instruments used. These were the same as those used by Hemmons except that a Singer micro-manipulator replaced the De Fonbrune and a deep green filter by itself was used on the light source.

The dissection chamber. Instead of continually substituting one coverslip for another during the dissections, a dissecting chamber large enough to hold two coverslips was used. The base of the chamber was a microscope slide 3" x 1" and the sides were three strips of a microscope slide 3/10" in height down both lengths and across one breadth. The other breadth was left open

for the introduction of the micro-loop. Sufficient water to cover the bottom of the chamber was added to prevent dehydration of the preparations. A low ridge across the open breadth prevented the water from running out of the chamber and reduced air currents while dissections were in progress. This chamber was similar to the one used by Lindegren (1949) in the dissection of yeast asci.

The ascus suspension. This was prepared in the manner described by Hemmons except for the following points. Firstly, a ring of vaseline was applied to the edges of the coverslip to keep the drop centred. Secondly, Tween 80 (at a concentration of 1 in 1000) was used in place of water because its lower surface tension enabled the micro-loop to be introduced into the suspension with the minimum of disturbance. Thirdly, the isolation of asci was made easier by transferring most of the suspension to a second coverslip and then diluting the remainder of the suspension on the first coverslip. This diluting process was repeated from the second to a third cover-slip and so on. Since the asci and free spores, etc. were well spread out on the diluted remainders, intact asci were more easily separated from free conidia and ascospores.

Ascus dissection. The diluted suspension was inverted and placed at one end of the dissecting chamber. A thin layer of medium was then poured into a Petri dish

and cut up into approximately 3/10" x 6/10" rectangles. One of these rectangles was placed on a $\frac{7}{8}$" square No. 2 coverslip and further divided into eight pieces. The coverslip was then inverted onto the dissecting chamber adjacent to the ascus suspension. Asci were removed from the suspension as described by Hemmons. Isolated asci were transferred from the ascus suspension to one of the eight pieces of medium by moving the microscope stage instead of the coverslip. At this point the number of ascospores was checked. IF the ascus was not to be dissected, the eight spores were left on this one piece. IF the ascus was to be dissected, seven of the ascospores were again picked up by the loop, and distributed one by one to the remaining seven pieces of medium. The coverslip was then removed and the eight pieces were slid off onto marked positions on a Petri dish of medium. Twelve undissected asci or five dissected asci could be fitted into a Petri dish (Figures 3 and 4).

Classification for colour and nutritional requirements of the germinated spores from the dissected asci was done as described for perithecium analysis.

The modifications of Hemmons' techniques described here have enabled the speed of ascus dissection to be appreciably increased.

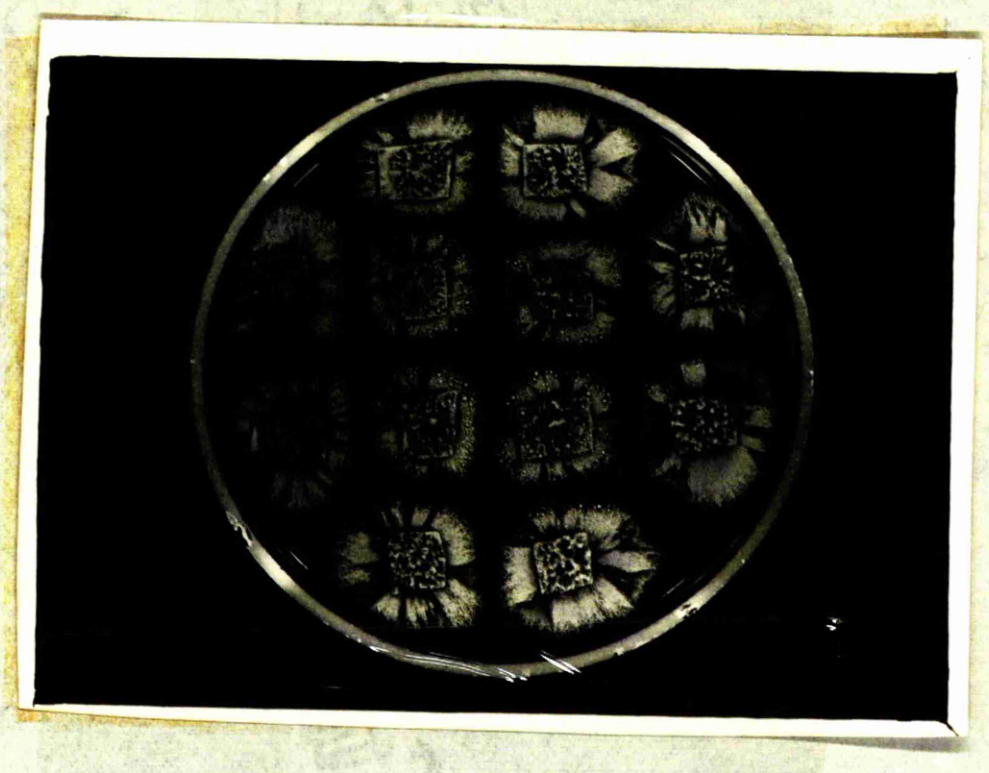

Figure 4. The arrangement of twelve undissected asci on a Petri dish of complete medium.

II. LOCATION OF CENTROMERES.

1. Methods of analysis. When dealing with an organism such as Neurospora which has ordered tetrads, it is possible to distinguish the products of the first and second meiotic divisions by the positions of the spores in the ascus. The centromeres may then be mapped in relation to a single gene for each chromosome. However, in unordered tetrads, the products of the first and second divisions cannot be distinguished and it is necessary to have either three independent loci or two linked and one independent locus before the centromeres can be mapped. Formulae have been given by Whitehouse (private communication; 1950); Papazian (1951; 1952) and Perkins (1949). The formulae as given by Whitehouse are used in this instance.

Whitehouse (1949) and Perkins(1949) showed that if two loci are unlinked, the proportion of tetratype asci (in the absence of interference) is:-

$$p = x + y - 3xy/2$$

where p is the proportion of tetratypes and x and y are the proportions of second division segregations at the loci A and B respectively. Since there are two variables x and y and only one equation, it is not possible to solve for both x and y. By introducing a third

independent locus C and hence a third variable z, it is possible to obtain three equations which may then be solved for the three unknowns x, y and z.

Thus $q = y + z - 3yz/2$ and $r = x + z - 3xz/2$

where q and r are the proportions of tetratypes with respect to B and C and A and C respectively and z is the proportion of second division segregation at the C locus. The solution of these three equations gives:-

$$x = \tfrac{2}{3}\left(1 \pm \sqrt{\frac{4 - 6p - 6r + 9pr}{4 - 6q}}\right) \quad \text{---------- (1)}$$

$$y = \tfrac{2}{3}\left(1 \pm \sqrt{\frac{4 - 6p - 6q + 9pq}{4 - 6r}}\right) \quad \text{---------- (2)}$$

$$z = \tfrac{2}{3}\left(1 \pm \sqrt{\frac{4 - 6q - 6r + 9qr}{4 - 6p}}\right) \quad \text{---------- (3)}$$

When two real solutions are obtained for any one of these formulae, one will be greater than $\frac{2}{3}$ and one will be less than $\frac{2}{3}$ but since proportions of second division segregation greater than $\frac{2}{3}$ are likely to be rare (Mather 1938), the smaller value is probably the correct one. Perkins (1955) has, however, collected several instances where the frequency of tetratype asci is greater than the maximum $\frac{2}{3}$ expected in the absence of interference. The frequencies of the tetratype asci in the cases cited ranged from 74.6% to 98.8%.

If two of the loci are linked and the third locus is independent, it is still possible to locate the centromeres as follows:(Whitehouse.private communication):-

Let A, B and C be three loci; A and B linked and C independent.

Let x, y and z be their respective second division segregation frequencies.

Let 2P, q and r be the tetratype frequencies of A and B; B and C and C and A respectively. Therefore P is the recombination frequency of A and B (if there are no 4-strand double exchanges).

Then, as in the previous case:-

$q = y + z - 3yz/2$

$r = x + z - 3xz/2$

and also $2P = x + y$ or $x - y$ or $y - x$ ----------(4)

Solving for x, y and z gives:-

$2P =$	$x + y$	$x - y$	$y - x$
$x =$	$2.\frac{2P - q + r - 3Pr}{4 - 3q - 3r}$	$\frac{2}{3}.\frac{3Pr - q + r - 2P}{r - q}$	$\frac{2}{3}.\frac{3Pr + q - r - 2P}{q - r}$
$y =$	$2.\frac{2P + q - r - 3Pq}{4 - 3q - 3r}$	$\frac{2}{3}.\frac{3Pq - q + r - 2P}{r - q}$	$\frac{2}{3}.\frac{3Pq + q - r - 2P}{q - r}$
$z =$	$\frac{q + r - 2P}{2 - 3P}$	$\frac{q - r + 2P}{3P}$	$\frac{2P - q + r}{3P}$

It should be noted that owing to double exchanges, equation (4) is only true if A and B are near the centromere. Thus, if A and B are remote from the centromere, they may have almost identical second division segregation frequencies although they are known to be 10 or 20 units apart.

The proportion of ditype to tetratype asci with respect to any two markers will be dependent on the number of exchanges between the markers and their respective centromeres. When both or one of a pair of markers are segregating independently of their centromeres, the proportion of tetratype asci will be $\frac{2}{3}$ in the absence of interference. Therefore a tetratype frequency of $\frac{2}{3}$ can still mean that one of the pair of markers is linked to its centromere (Whitehouse 1949).

In the first three crosses analysed, full dissection and classification of the asci was carried out. A method for detecting close linkage of a marker to its centromere, without complete ascus dissection, was later developed. This method depends on the availability of a "visible" marker already known to be closely linked to its centromere and the ability to select automatically against the marker whose relationship with its centromere is to be determined.

This rapid method is most conveniently illustrated by describing an actual example. In Aspergillus nidulans the marker determining white conidia (wn) was found to be 18.5 units from its centromere. A large number of nutritional mutants was available and in the following example pro1 was used in an attempt to find its second division segregation frequency. It is not linked

to wn. From the cross wn pro1//+ +, whole undissected asci were placed on medium which selected against those spores requiring proline. This made it possible to distinguish the different types of asci as follows:-

Ascus type.	Ascospores		Colour of colony from whole ascus.
	Growing	Not growing	
Parental ditype.	++ and ++	wn pro1 and wn pro1	Green
Non-parental ditype.	wn+ and wn+	+pro1 and +pro1	White
Tetratypes.	wn+ and ++	wn pro1 and +pro1	Green & White.

Thus the frequency of tetratypes can be determined simply by examining the colour of colonies originating from whole asci.

In this method, there is a systematic source of error because a tetratype may be classified as a parental or a non-parental ditype if one of the colours accidentally fails to show up. This could happen when some of the ascospores either fail to germinate or germinate but are overgrown by hyphae from other ascospores. If large, this kind of error could simulate close linkage to a centromere where none exists. Consequently, this method is useful only for a quick screening of a number of mutants and must be followed, where linkage to a centromere is suggested, by complete analysis of fully dissected asci for the actual estimation of linkage.

This screening method can also detect close linkage between two markers. An excess of parental ditypes over non-parental ditypes would indicate such linkage.

2. Experimental. Six crosses were used in this part of the work. All eight spores in a tetrad did not invariably germinate. The proportions of asci with one, two or three and four spores with different genotypes growing are given in Table 1. If meiosis was assumed to be normal in tetrads with only three genotypes among the germinating ascospores, the fourth genotype could be inferred. Therefore, tetrads with three or four genotypes among the germinating ascospores have been pooled. S_{12}

The first two crosses analysed (namely y sd// bi1 pyro4; and ad1//y sd pyro4) were chosen so that all the markers except y and bi1 were located on different chromosomes. With the exception of y and bi1, the frequency of tetratype asci with respect to all pairs of markers did not deviate from .67 in any case, indicating that not more than one of each pair of markers could be linked to their centromeres (Tables 2 and 3).

The third cross wn ad1 pro1 paba1 y//y pyro4 was chosen because the analysis of mitotic crossing over (Pontecorvo and Kafer 1956) had indicated that a centromere was fairly close to pro1 and because wn, pyro4 and pro1 were located on different chromosomes. Furthermore, wn and ad1, although located on the same chromosome, segregated independently.

Table 1.

Number of hybrid asci dissected and the number of genotypes recovered from the germinated ascospores.

Cross	Number of genotypes recovered. 3 & 4	2	1	Total.
y sd//bi1 pyro4	37	5	6	48
ad1//y sd pyro4	27	4	1	32
wn ad1 pro1 paba1 y//y pyro4	107	7	2	116
wn ad14 y//y sd	24	-	-	24
wn ad14 y//bi1 thi2	11	-	-	11
wn ad14 y//bi1 met1	48	4	-	52

N.B. Abnormal asci have not been included in this table.

Table 2.

Numbers of parental ditypes, non-parental ditypes and tetratypes recovered from the fully classifiable, normal asci of the cross y sd//bi1 pyro4.

Numbers with respect to:-	Number of ditypes (D)		Number of tetratypes (T)	Probability of a 1:2 ratio of D:T.
y & sd	P.D.	9	24	N.S.
	N.P.D.	4		
y & bi1	P.D.	33	3	<.001
	N.P.D.	1		
y & pyro4	P.D.	11	20	N.S.
	N.P.D.	6		
sd & bi1	P.D.	11	21	N.S.
	N.P.D.	5		
sd & pyro4	P.D.	5	26	N.S.
	N.P.D.	6		
bi1 & pyro4	P.D.	11	19	.05 - .04
	N.P.D.	7		

Table 3.

Numbers of parental ditypes, non-parental ditypes and tetratypes recovered from the fully classifiable, normal asci of the cross ad1//y sd pyro4.

Numbers with respect to:-	Number of ditypes (D)		Number of tetratypes (T)	Probability of a 1:2 ratio of D:T.
ad1 & y	P.D.	6	17	N.S.
	N.P.D.	4		
ad1 & sd	P.D.	3	20	N.S.
	N.P.D.	4		
ad1 & pyro4	P.D.	7	16	N.S.
	N.P.D.	4		
y & sd	P.D.	6	16	N.S.
	N.P.D.	5		
y & pyro4	P.D.	5	17	N.S.
	N.P.D.	5		
pyro4 & sd	P.D.	2	19	N.S.
	N.P.D.	6		

It will be seen from Table 4. that the ratio of ditypes to tetratypes with respect to wn and pro1 differs from the 1:2 ratio expected in the absence of linkage of one or both markers to a centromere. Although the ratio of ditypes to tetratypes with respect to wn and paba1 does not differ significantly from the 1:2 ratio expected, the tetratype frequency is used in the calculation of centromere distances as paba1 is known to be 8 to 10 units from pro1 (Forbes 1956).

Ratios of parental to non-parental ditypes which differ significantly from 1:1 indicate linkage when the parental ditypes are in excess. This is seen in the case of the bi1 and y markers in the cross y sd//bi1 pyro4 (Table 2) and in the case of the pro1 and paba1 markers in the cross wn ad1 pro1 paba1 y//y pyro4 (Table 4). The recombination frequency of the former was calculated to be .068 ± .034 and of the latter to be .084 ± .018.

The unlinked marker wn and the two linked markers pro1 and paba1 have been mapped in relation to their centromeres using the formulae given by Whitehouse (private communication). The application of these formulae to these data gave the following recombination frequencies:-

pro1 - centromere = .180 ±

paba1 - centromere = .265 ±

wn - centromere = .187 ±

Table 4.

Numbers of parental ditypes, non-parental ditypes and tetratypes recovered from the fully classifiable, normal asci of the cross wn ad1 pro1 paba1 y//y pyro4.

Numbers with respect to:-	Number of ditypes (D)	Number of tetratypes (T)	Probability of a 1:2 ratio of D:T.
wn & pro1	P.D. 31 N.P.D. 21	55	<.001
wn & paba1	P.D. 22 N.P.D. 21	64	.2 - .1
wn & pyro4	P.D. 10 N.P.D. 16	81	.04
wn & ad1	P.D. 15 N.P.D. 17	75	N.S.
ad1 & pro1	P.D. 12 N.P.D. 20	75	N.S.
ad1 & paba1	P.D. 11 N.P.D. 17	79	N.S.
ad1 & pyro4	P.D. 23 N.P.D. 20	64	N.S.
pro1 & paba1	P.D. 89 N.P.D. -	18	<.001
pro1 & pyro4	P.D. 17 N.P.D. 15	75	N.S.
paba1 & pyro4	P.D. 16 N.P.D. 14	77	N.S.

The recombination frequencies were obtained by halving the second division segregation frequencies. The calculation of standard errors of these recombination fractions poses a difficult problem. An attempt to solve the problem is not justified by these small data which are intended to give no more than an indication of centromere positions.

It was fortunate that one of these markers i.e. wn was "visible" as this enabled the quick method for screening further markers to be used. The method was first checked by selecting against pro1 in the cross wn ad1 pro1 paba1 y//y pyro4 analysed above by full dissection. The results (Table 5) did not differ from those obtained by full dissection, showing the method to be reliable. A number of markers were therefore examined by this method. In each case a small number of asci were fully dissected to check the viability of the ascospores (Table 1). Using the quick method, parental ditypes, non-parental ditypes and tetratypes were determined in the various crosses by the colour of the colony (Table 5 and Figure 5). In all cases except the cross wn ad14 y//bi1 met1 the ratios of ditypes : tetratypes did not differ from the expected ratio of 1:2. This cross was therefore further analysed by complete ascus dissection (Table 6), and the unlinked markers wn, ad14

Table 5.

Types of colonies produced by the three ascus types in four crosses to which the quick screenir method was applied. The numbers are those of each ascus type found. Abbreviations are:- M.M. = minimal medium. ad = adenine. paba = para-amino benzoic acid. pyro = pyridoxine. bi = biotin.

Medium used	Selection against:-	Parental ditype (P.D)	Non-parental ditype (N.P.D)	Tetratype (T)	Total asci	Probability 1:2 ratio of P.D + N.P.D:
		(1) wn ad1 pro1 paba1 y//y pyro4				
M.M. + ad + paba + pyro	pro1	yellow 24	white 20	white & yellow 46	90	<.01
		(2) wn ad14 y//y sd				
M.M. + ad	sd	white 2	yellow 4	white & yellow 25	31	N.S.
		(3) wn ad14 y//bi1 thi2				
M.M. + ad + bi	thi2	white 10	green; yellow; green & yellow 6	white & yellow; white & green 32	48	N.S.
		(4)wn ad14 y//bi1 met1				
M.M. + ad + bi	met1	white 16	green; yellow; green & yellow 21	white & yellow; white & green 21	58	<.001

Table 6.

Number of parental ditypes, non-parental ditypes and tetratypes recovered from the fully classifiable , normal asci of the cross wn ad14 y//bi1 met1. The biotin requirement was not classified.

Numbers with respect to:-	Number of ditypes (D)		Number of tetratypes (T)	Probability of a 1:2 ratio of D:T.
wn & ad14	P.D.	14	26	.1 - .05
	N.P.D.	8		
wn & met1	P.D.	12	25	.05 - .02
	N.P.D.	11		
ad14 & met1	P.D.	10	25	.05 - .02
	N.P.D.	13		

and met1 were mapped in relation to their centromeres using the formulae given by Whitehouse (1950). The recombination frequencies obtained by the application of these formulae to the data were as follows:-

wn - centromere = .478 ± or .184 ±

ad14 - centromere = .478 ± or .184 ±

met1 - centromere = .502 ± or .165 ±

The recombination frequencies were again obtained by halving the second division segregation frequencies. The latter values are probably in each case the correct ones as the former would indicate second division segregation frequencies greater than .67.

The incomplete asci from the two crosses showing centromere linkage (Table 1) constitute such a small fraction of the total that they have been ignored. Perithecial analyses of all the crosses were done before ascus analysis in order to detect any gross abnormalities of behaviour.

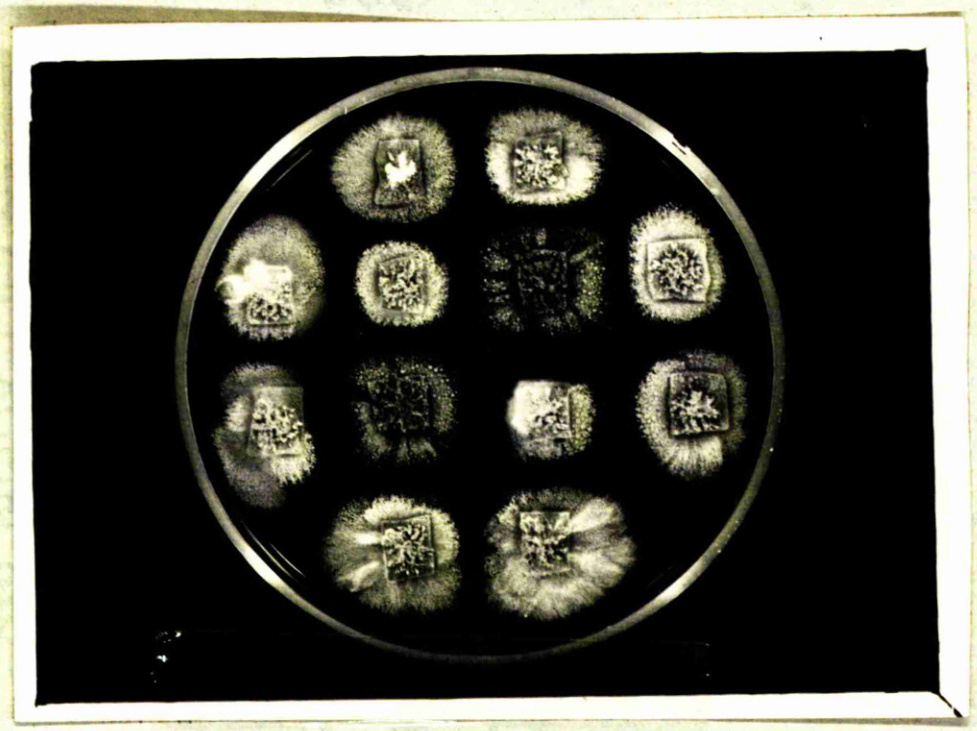

Figure 5. Visual determination of parental ditypes, non-parental ditypes and tetratypes with respect to the markers wn and thi2 in the cross wn ad14 y//bi1 thi2. The whole undissected asci were placed on minimal medium + adenine + biotin thus selecting against ascospores requiring "thiazole". Starting in the top row and reading from right to left in each successive row, the colonies are counted as 1 to 12. The colonies showing only white conidia are parental ditypes (Numbers 3 and 5); the colonies showing yellow conidia only, green conidia only or a mixture of yellow and green conidia are non-parental ditypes (Numbers 2, 4 and 9); and the colonies showing either a mixture of white and green or white and yellow conidia are tetratypes (Numbers 1, 6, 7, 8, 10, 11 and 12)

3. Correction of recombination frequencies.

As pointed out by Spiegelman (1952) it has often been assumed that $p_{AB} = \frac{1}{2}P_{AB}$ where p_{AB} refers to recombination frequency between two loci A and B and P_{AB} to the corresponding second division segregation frequency. This assumption has been made in calculating the recombination frequencies between the centromeres and the various markers in Section II - 2. The justification usually offered for this formula is that in random strand analysis only half of the exchanges are recovered since in a large population only one strand is recovered from each tetrad. Both Rizet and Engelmann (1949) and Papazian (1951) have made use of this conversion factor but have pointed out that, except over short map distances, it is at best an approximation. This is because the limit approached by p_{AB} as the number of chiasmata between A and B increases is .5, whereas the limit of P_{AB} is .67. For long map distances the conversion factor would yield a value of .33 instead of the .5 expected.

Spiegelman has calculated a conversion factor which, assuming no interference, takes account of this discrepancy. This is:-

$$p_{AB} = \tfrac{1}{2}\left(1 - \left(1 - \tfrac{3}{2}P_{AB}\right)^{\frac{2}{3}}\right) \qquad \text{----------(5)}$$

This formula has been used to recalculate the

recombination frequencies between the centromeres and the linked markers - wn, ad14, pro1 and met1. For the cross wn ad1 pro1 paba1 y//y pyro4 the recombinations frequencies were altered to:-

pro1 - centromere = .202 ±

paba1 - centromere = .326 ±

wn - centromere = .211 ±

and for the cross wn ad14 y//bi1 met1, the recombination frequencies were altered to:-

wn - centromere =.207 ±

ad14 - centromere = .207 ±

met1 - centromere = .183 ±

III. ANALYSIS OF MULTIPLE EXCHANGES.

1. Introduction. The analysis of multiple exchanges presents two distinct problems:- (a) the relationship of the chromatids involved in two or more exchanges and (b) the distribution of the exchanges along the chromosomes. If the chromatid relationships in the multiple exchanges are not random, the phenomenon is generally referred to as "chromatid interference" and if the distribution of the exchanges is not random, the phenomenon is generally referred to as "chiasma interference". In order to avoid confusion in terminology these terms are used in this thesis although "type interference" and "position interference" seem more exact (Carter and Robertson 1952).

Both chromatid and chiasma interference may be studied by cytological observations, by whole tetrad analysis, and by half tetrad analysis. If the assumption is made that chromatid interference does not occur, then random strand analysis provides information on chiasma interference. The assumption of no chromatid interference must be made because the results of the two types of interference cannot be separated by random strand analysis.

Cytological evidence of chromatid interference can be obtained either by direct study of various stages of meiosis or by observing bridges and fragments in

inversion heterozygotes. Direct study has shown an excess of compensating over non-compensating double exchanges in Stenobothrus (Darlington and Dark 1932), Melanoplus femur-rubrum (Hearne and Huskins 1935), and Trillium erectum (Huskins and Newcombe 1941). Work on inversion heterozygotes indicates that compensating double exchanges are more frequent than non-compensating double exchanges in Fritillaria (Frankel 1937); equally frequent in Gasteria (Giles 1944) and less frequent in Tulipa (Upcott 1937).

The data from the attached-X chromosomes of Drosophila show that 2-, 3- and 4-strand double exchanges occur with a frequency of 1:2:1 (Anderson 1925, Emerson and Beadle 1933 and Beadle and Emerson 1935). On the other hand Bonnier and Nordenskiold(1937) found that 4-strand double exchanges occurred more frequently than 3- and 2-strand double exchanges, but that this interference diminished with increasing distance from the centromere. Recently, Welshons (1955) has repeated the experiments of Bonnier and Nordenskiold and has found no evidence of chromatid interference.

Morgan (1933) used a closed-X chromosome of Drosophila and Weinstein (1936) applied a mathematical treatment to some Drosophila data obtained from various sources to show that exchanges occurred at random between non-sister chromatids.

Reviews of the tetrad data analysed for interference have been presented by Whitehouse (1942), Papazian (1952) and Perkins (1955). Lindegren (1933, 1936a, b) presented data from tetrad analysis of Neurospora crassa but in all three papers, there were insufficient numbers of double and multiple exchanges to allow any conclusions on chromatid and chiasma interference to be drawn. Lindegren and Lindegren (1937, 1939) reported ratios of 2-:3-:4-strand double exchanges of 27:14:8 in the "sex" chromosome and of 20:17:4 in the second chromosome of Neurospora crassa. They later discovered that 15 of the 2-strand type in the second chromosome could have been either 2- or 4-strand doubles (Lindegren and Lindegren 1942). The recalculated values were therefore 24 2- or 4-strand : 17 3-strand double exchanges and this ratio does not differ from the expected 1:1. In the same paper (Lindegren and Lindegren 1942)they found locally specific patterns of chromatid and chiasma interference in four regions of the "sex" chromosome of Neurospora crassa. Across the centromere they found a high degree of both negative chromatid interference and negative chiasma interference. Some or all of this negative interference may be ascribed to centromere mis-assortment (Perkins 1955). When other pairs of intervals were considered, varying patterns of chromatid and chiasma interference emerged. Whitehouse (1942)has pointed out a

number of errors made by Lindegren and Lindegren (1937, 1939) in the analysis of their data and has carried out the necessary recalculations. Whitehouse further showed that in these data of the Lindegren's, passing of the centre nuclei at the second division of meiosis could account for less than 1% of the asci. Recent work by Howe (1954, 1956) and Stadler (1955, 1956) on Neurospora crassa showed no interference across the centromere. These authors used an independent marker to detect meiotic nuclear passing or errors in dissection. The data of Houlahan, Beadle and Calhoun (1949) included insufficient numbers of double exchanges to assess significance.

Wulker (1935), working with Neurospora sitophila recovered 8 2-strand : 28 3-strand : 8 4-strand double exchanges but this ratio is only significant at about the 7% level.

Tetrads of Sphaerocarpus donnellii (Knapp 1937) gave no indications of chromatid interference but very long intervals were used and interference may have been obscured.

Wettstein (1923) described a cross in the moss Funaria hygrometrica with four linked factors where parental and non-parental ditypes but no tetratypes were observed. These results could be explained by positive chromatid interference or by exchange at the 2-strand stage of meiosis.

In summary, the available data on chromatid

interference does not give any conclusive answer. In most of the cytological work there are excesses of compensating over non-compensating double exchanges. Excluding the results of Bonnier and Nordenskiold (1937) which were not confirmed by the comparative work of Welshons (1955), the attached-X data of Drosophila show that the relationship of the strands taking part in multiple exchanges is random. Except for the work of Lindegren and Lindegren (1937, 1939, 1942) which has been extensively corrected and criticized, the same conclusion is reached from the tetrad data. The data of Wettstein (1923) may or may not indicate chromatid interference.

The presence or absence of chromatid interference is important in relation to the conclusions drawn from random strand analysis about chiasma interference. There is general agreement that in Drosophila melanogaster there is no chiasma interference across the centromere and positive chiasma interference in the arms of the chromosomes (e.g. Weinstein 1918; Anderson and Rhoades 1930; Graubard 1934 and Stevens 1936), but in all these examples the assumption was made that there was no chromatid interference. By the analysis of random strands, the effects of chromatid and chiasma interference cannot be separated. If there is chromatid interference in the chromosomes of Drosophila melanogaster the conclusions on chiasma interference may well be wrong.

(2) Methods of analysis.

(a) Linkage estimates. For the tetrad data, these were made by the method of Mather and Beale (1942).

(b) Tests for the homogeneity of the exchange distributions from the different perithecia. The tests were made by the following method:-

Let there be 0 -------- k perithecia.

Let s_i = number of exchanges in the i^{th} perithecium.

Let n_i = number of asci sampled in the i^{th} perithecium.

If s_i is Poisson with mean $n_i\lambda$, (and $n_i\lambda$ is large) then s_i is approximately normal with mean $n_i\lambda$ and variance $n_i\lambda$ and $\frac{s_i - n_i\lambda}{\sqrt{n_i\lambda}}$ is approximately normal with mean 0 and variance 1.

Also $\frac{(s_i - n_i\lambda)^2}{n_i\lambda}$ is $\chi^2_{(1)}$

Therefore $\sum_{i=1}^{k} \frac{(s_i - n_i\lambda)^2}{n_i\lambda}$ is $\chi^2_{(k)}$

If λ is replaced by the estimate $\frac{\sum s_i}{\sum n_i} = \frac{S}{N}$ then,

$$\sum_{i=1}^{k} \frac{(s_i - n_i\frac{S}{N})^2}{n_i\frac{S}{N}} \text{ is } \chi^2_{(k-1)}$$

Therefore $\sum_{i=1}^{k} \frac{n_i(p_i - p.)^2}{p.}$ is $\chi^2_{(k-1)}$ where p_i

is the mean of the i^{th} perithecium and p. is the overall mean. By multiplying out:-

$$\frac{1}{p.}\left[\sum_{i=1}^{k}\left(n_i p_i^2 - 2 n_i p_i p. + n_i p.^2\right)\right]$$

$$= \frac{1}{p.}\left[\sum_{i=1}^{k} n_i p_i^2 - N p.^2\right]$$

$$= \frac{1}{p.}\left[\sum_{i=1}^{k} s_i p_i - N p.^2\right]$$

$$= \left[\frac{\sum_{i=1}^{k} s_i p_i}{p.}\right] - N p.$$

(c) Estimation of the expected number of 4-strand double exchanges within the genetically marked intervals of the crosses. If only two markers are available in a cross, then three classes of tetrad are detectable. These are:-

Class (1). Those tetrads with no exchange in the interval between the two markers.

Class (2). Those tetrads with a single exchange in the interval between the two markers.

Class (3). Those tetrads with a 4-strand double exchange in the interval between the two markers.

However, in tetrad analysis, the 3-strand double exchanges within intervals are included in Class (2) and the 2-strand double exchanges within intervals are included in Class (1).

In the absence of interference, the distribution of the exchanges within the intervals is multinomial with probabilities:-

P_0 (non-exchange tetrads) $= e^{-m} + \frac{1}{4}(1 - e^{-m} - \frac{m\, e^{-m}}{1!})$

P_1 (single exchange tetrads) $= \frac{m\, e^{-m}}{1!} + \frac{1}{2}(1 - e^{-m} - \frac{m\, e^{-m}}{1!})$

P_2 (4-strand double exchanges) $= \frac{1}{4}(1 - e^{-m} - \frac{m\, e^{-m}}{1!})$

where m is the mean number of exchanges and is small.

Hence approximately, since m is small:-

$P_0 = 1 - m + \frac{5}{8}m^2$

$P_1 = m - \frac{3}{4}m^2$

$P_2 = \frac{1}{8}m^2$

Solving for m in terms of P_1:-

$m = \frac{2}{3}(1 - \sqrt{(1 - 3\,P_1)})$

Therefore $P_2 = \frac{1}{8}\, P_1^2\, (1 + \frac{3\, P_1}{2})$ (approximately) ----------(5a)

This formula (5a) is similar to that given by Papazian (1952). Papazian's formula was $N = \frac{F^2}{8}(1 + \frac{2\, F}{3})$ where N is the 4-strand double exchange class and F is the single exchange class. It was pointed out by Dr. D.D.Perkins (private communication) that Papazian's formula is incorrect.

(d) Correction of the frequencies of the 2-, 3- and 4-strand double exchanges between two intervals A and B by the use of tetrads with a 4-strand double exchange within either A or B and accompanied by a single exchange in B and A respectively (Whitehouse 1956, private communication

Whitehouse showed that for a pair of intervals:-

$$d = x - \frac{nxy}{z} + \frac{ny^2}{2z} \quad \text{or} \quad d = x + \frac{ny}{z}\left(\frac{y}{2} - x\right) \text{ ------(6)}$$

$$e = y - \frac{ny^2}{z} + \frac{ny(1 - y)}{z} \quad \text{or} \quad e = y + \frac{ny}{z}(1 - 2y) \text{ --(7)}$$

$$f = z - \frac{nyz}{z} + \frac{ny^2}{2z} \quad \text{or} \quad f = z + \frac{ny}{z}\left(\frac{y}{2} - z\right) \text{ ------- (8)}$$

where x, y and z are the actual proportions of 2-, 3- and 4-strand relationships between exchanges and $x + y + z = 1$; d, e and f are the observed proportions of 2-, 3- and 4-strand relationships between exchanges and $d + e + f = 1$; and n is the ratio of those tetrads with a 4-strand double exchange within one of the intervals and a single exchange in the other interval to the frequency of $d + e + f$.

Now from equation (7)

$$z = \frac{ny(1 - 2y)}{e - y} \text{ ----------(9)}$$

and from equation (8)

$$f = z + \frac{ny^2}{2z} - ny$$

$$\text{or } 2z^2 - 2z(f + ny) + ny^2 = 0 \text{ ----------(10)}$$

Hence $f = \frac{ny(1 - 2y)}{e - y} + \frac{y(e - y)}{2(1 - 2y)} - ny$

Multiplying this expression by $2(1 - 2y)(e - y)$

gives $sy^3 + ty^2 + uy + v = 0$ ----------(11)

where $s = 4n + 1$

$t = 4en - 2(e + 2f + 3n)$

$u = e^2 + 4ef + 2f + 2n - 2en$

$v = - 2ef$

$\underline{z}$ is then found from equation (9) and $\underline{x} = 1 - y - z$.

It was pointed out (Whitehouse -private communication) that where $e = .5$, then $y = .5$ and that it is then possible to find $\underline{z}$ from the quadratic equation (10).

The cubic equation (11) has three solutions (theoretically) while the quadratic equation (10) has two solutions (theoretically). However, not all of these solutions will be real.

3. Experimental. Among four crosses used for interference analysis, the markers in the first were confined to the right arm of the BI chromosome and a region .3 units in length was included in the hope that some information on exchange in such a short region would be obtained. However, it soon became apparent that with the methods of ascus dissection available at the time, analysis of such a short region was impractical. The second cross was therefore set up with markers covering approximately 69 units of the BI chromosome. The independent marker pyro4 was included in the second cross to assist in the detection of abnormalities of development of the ascus. Techniques of ascus dissection became so improved later on that an analysis of a short region was again attempted. The choice of this third cross was unfortunate as the distribution of the exchanges from the different perithecia proved to be heterogeneous (Table 10). The cross was therefore abandoned and a fourth cross which included two short regions was analysed. All the asci used in interference analysis were fully dissected and classified for conidial colour and nutritional requirements.

The four crosses which will hereafter be referred to as Cross 1, Cross 2, Cross 3 and Cross 4 were:-

Cross 1. pro1 bi1//paba1 y ad8.

Recombination frequencies calculated from the ascus analysis.

.070	.154	.049
pro1 +	+ +	bi1
+	paba1 y	ad8 +

Cross 2. ribo ad14 paba1 y//an pro1 bi1 pyro4.

Recombination frequencies calculated from the ascus analysis.

.164	.070	.254	.063	.093	.047	
ribo +	ad14	Centro- +	paba1	y	+	+
+	an +	mere	pro1 +	+	bi1	pyro4

Cross 3. pro1 paba1 y//ad17 bi1.

Recombination frequencies calculated from the ascus analysis.

pro .103	.123	.046
pro1 +	paba1	y +
+	ad17 +	+ bi1

Cross 4. pro3 bi1//pro1 ad15 paba1 y.

Recombination frequencies calculated from the ascus analysis

.003	.073	.002	.127	.044
pro3 +	+	+	+	bi1
+	pro1	ad15	paba1 y	+

The pro1 and pro3 markers can be recognized visually by their growth on minimal medium. The pro1 marker determines a fair degree of growth after 3 days incubation at 37° C. while the pro3 marker determines distinctly less growth after 3 days incubation at 37° C. (Figure 6).

Analyses of Crosses 1, 2 and 3 by the use of random strands from single perithecia were carried out before dissection was started. The perithecial analysis of Cross 4 was done by Dr.E.Calef and he has kindly allowed me to use his results. In all four crosses, perithecia used for perithecial analysis and for ascus analysis were obtained from the same Petri dish. Details concerning the markers used can be found in Section I - 3. The perithecial analyses of all four crosses gave no evidence of chromosomal re-arrangements but the markers an and ad14 in Cross 2 gave

a reduced viability significant at the 5% level. In the ascus analysis the ribo marker (Cross 2) had a reduced viability significant at the 5% level, but the viability of all the other auxotrophs was as good as that of their corresponding prototrophs.

In order to test whether the incomplete asci from each cross constituted a selected sample, the recombination frequencies obtained from the "fully classifiable ascus samples" were compared to the recombination frequencies obtained from the perithecial analyses (Table 7). This procedure was adopted because the incomplete asci from each cross constituted such a small fraction of the total (Tables 12, 13, 14 and 15). Table 7 shows no differences between the recombination frequencies obtained from ascus analysis and from random strand analysis.

The exchange distribution among the asci from different perithecia proved to be homogeneous in Crosses 1, 2 and 4 but not in Cross 3 (Tables 8, 9, 10 and 11). Cross 3 has therefore not been considered any further.

Table 7.

Recombination fractions in Crosses 1, 2 and 4 as obtained by random strand analysis and by ascus analysis. The random strand estimates of Cross 4 were kindly supplied by Dr. E. Calef.

Cross 1 (pro1 bi1//paba1 y ad8).

Interval	Recombination fractions estimated by:- Random strands.	Asci.
pro1 - paba1	.109 ± .0184	.070 ± .0108
paba1 - y	.113 ± .0187	.154 ± .0126
y - bi1	.060 ± .0140	.049 ± .0079

Cross 2(ribo ad14 paba1 y//an pro1 bi1 pyro4).

Interval	Recombination fractions estimated by:- Random strands.	Asci.
ribo - an	.165 ± .0131	.164 ± .0154
an - ad14	.066 ± .0087	.070 ± .0103
ad14 - pro1	.295 ± .0161	.254 ± .0182
pro1 - paba1	.057 ± .0082	.063 ± .0102
paba1 - y	.093 ± .0102	.093 ± .0123
y - bi1	.042 ± .0071	.047 ± .0094

Cross 4 (pro3 bi1//pro1 ad15 paba1 y).

Interval	Recombination fractions estimated by:- Random strands.	Asci.
pro3 - pro1	Not scored.	.003 ± .0015
pro1 - ad15	.063 ± .0122	.073 ± .0078
ad15 - paba1	.003 ± .0025	.002 ± .0012
paba1 - y	.139 ± .0173	.127 ± .0096
y - bi1	.028 ± .0083	.044 ± .0061

Table 8.

Tests of homogeneity of exchange frequencies between the perithecia of Cross 1 (pro1 bi1//paba1 y ad8). Perithecia with 5 or fewer exchanges have been pooled.

Perithecium Number	Number of fully classifiable asci (ni)	Number of exchanges (si)	Mean number of exchanges (pi)
1	31	15	.4839
2	28	13	.4642
3	25	15	.6000
4, 14 & 15	42	13	.3095
5	13	8	.6154
6	24	11	.4583
7	28	21	.7500
8	27	14	.5185
9	This perithecium carried a semi-lethal (dwarf).		
10	27	13	.4815
11	26	18	.6923
12	28	18	.6429
13	29	21	.7241
16	30	15	.5000
17	22	14	.6364
18	12	6	.5000

Total number of asci (N) = 392

Mean number of exchanges (p.) = .5485

$X^2_{(14)}$ = 11.42 Probability = .70 - .50

Table 9.

Tests of homogeneity of exchange frequencies between the perithecia of Cross 2 (ribo ad14 paba1 y//an pro1 ~~paba1~~ bi1)/. pyro4

Perithecium Number	Number of fully classifiable asci (ni)	Number of exchanges (si)	Mean number of exchanges (pi)
1	24	36	1.5000
2	23	35	1.5217
3	26	35	1.3462
4	29	43	1.4828
5	24	38	1.5833
6	17	19	1.1176
7	13	13	1.0000
8	10	14	1.4000
9	24	31	1.2917
10	74	93	1.2568

Total number of asci (N) = 264

Mean number of exchanges (p.) = 1.3500

$X^2_{(9)} = 5.87$ Probability = .80 - .70

Table 10.

Tests of homogeneity of exchange frequencies between the perithecia of Cross 3 (pro1 paba1 y//ad17 bi1). Perithecia with 5 or fewer exchanges among the tetrads have been pooled.

Perithecium Number	Number of fully classifiable asci (ni)	Number of exchanges (si)	Mean number of exchanges (pi)
1	54	18	.3333
3	26	15	.5769
4	19	16	.8421
5	20	15	.7500
2, 6, 7, 8 & 9	32	18	.5625

Total number of asci (N) = 151

Mean number of exchanges (p.) = .5430

$X^2_{(4)}$ = 9.17 Probability = .05

Table 11.

Tests of homogeneity of exchange frequencies between the perithecia of Cross 4 (pro3 bi1//pro1 ad15 paba1 y).

Perithecium Number	Number of fully classifiable asci (ni)	Number of exchanges (si)	Mean number of exchanges (pi)
1	20	5	.2500
2	16	7	.4375
3	94	53	.5638
4	79	47	.5949
5	49	28	.5714
6	168	74	.4405
7	147	71	.4830

Total number of asci (N) = 573

Mean number of exchanges (p.) = .4974

$X^2_{(6)}$ = 6.47 Probability = .50 - .30

Table 12.

Summary of the data obtained from Cross 1 (pro1 bi1//paba1 y ad8).

Non-exchange tetrads		223
Single exchange tetrads.		
pro1 - paba1	28	
paba1 - y	86	
y - bi1	18	
Total		132
Double exchange tetrads		
4-strand double within pro1 - paba1	1	
4-strand doubles within paba1 - y	6	
4-strand double within y - bi1	1	
pro1 - paba1; paba1 - y	9	
pro1 - paba1; y - bi1	4	
paba1 - y; y - bi1	6	
y - ad8; ad8 - bi1	1	
Total		28
Triple exchange tetrads		
pro1 - paba1; paba - y; y - bi1	2	
4-strand double within pro1 - paba; single y - bi1	2	
4-strand double within pro1 - paba1; single paba1 - y	3	
4-strand double within paba1 - y; single y - bi1	1	
4-strand double within y - bi1; single paba1 - y	1	
Total		9
Incomplete asci		55
		392
Perithecium No. 9 carrying semi-lethal (dwarf)		62
Abnormal asci		3
GRAND TOTAL		512

Distribution of the exchanges in the sample of asci.

	Number of exchanges.				
	0	1	2	3	Total
Observed	223	132	28	9	392
Expected	226.2	124.1	34.0	7.7	392

Table 13.

Summary of the data obtained from Cross 2 (ribo ad14 paba1 y// an pro1 bi1 pyro4).

Non-exchange tetrads		67
Single exchange tetrads		
ribo - an	27	
an - ad14	4	
ad14 - pro1	39	
pro1 - paba1	5	
paba1 - y	11	
y - bi1	3	
Total		89
Double exchange tetrads		
4-strand double within ribo - an	1	
4-strand doubles within ad14 - pro1	4	
4-strand double within an - ad14	1	
ribo - an; ad14 - pro1	16	
ribo - an; pro1 - paba1	3	
ribo - an; paba1 - y	4	
ribo - an; y - bi1	2	
an - ad14; ad14 pro1	4	
an - ad14; pro1 - paba1	1	
an - ad14; paba1 - y	3	
an - ad14; y - bi1	1	
ad14 - pro1; pro1 - paba1	7	
ad14 - pro1; paba1 - y	8	
ad14 - pro1; y - bi1	2	
pro1 - paba1; paba1 - y	2	
pro1 - paba1; y - bi1	1	
paba1 - y; y - bi1	3	
Total		63
Triple exchange tetrads		
4-strand double within ribo - an; single ad14 - pro1	1	
4-strand double within ribo - an; single y - bi1	1	
4-strand doubles within ad14 - pro1; single ribo - an	7	
4-strand double within ad14 - pro1; single paba1 - y	1	
4-strand double within paba1 - y; single pro1 - paba1	1	
4-strand double within y - bi1; single ad14 - pro1	1	
ribo - an; an - ad14; ad14 - pro1	5	
ribo - an; an - ad14; paba1 - y	1	
ribo - an; ad14 - pro1; pro1 - paba1	5	
ribo - an; ad14 - pro1; paba1 - y	5	

Table 13 continued.

Triple exchange tetrads		
ribo - an; ad14 - pro1; y - bi1	1	
an - ad14; ad14 - pro1; pro1 - paba1	1	
an - ad14; ad14 - pro1; paba1 - y	1	
an - ad14; ad14 - pro1; y - bi1	3	
ad14 - pro1; pro1 - paba1; paba1 - y	2	
ad14 - pro1; pro1 - paba1; y - bi1	1	
ad14 - pro1; paba1 - y; y - bi1	1	
pro1 - paba1; paba1 - y; y - bi1	1	
Total		39
Quadruple exchange tetrads		
4-strand double within an - ad14; singles ad14 - pro1 and y - bi1	1	
4-strand double within ad14 - pro1; singles pro1 - paba1 and y - bi1	1	
ribo - an; ad14 - pro1; pro1 - paba1; paba1 - y	2	
ribo - an; ad14 - pro1; paba1 - y; y - bi1	1	
Total		5
Quintuple exchange tetrad		
4-strand double within ribo - an; singles an - ad14 and ad14 - pro1 and paba1 - y	1	
Total		1
Incomplete asci		25
Selfed green asci		1
Abnormal asci		3
GRAND TOTAL		293

Distribution of the exchanges in the sample of asci.

	Number of exchanges.					
	0	1	2	3	4 & 5	Total
Observed	67	89	63	39	6	264
Expected	68.4	92.4	62.4	28.1	12.7	264

Table 14.

Summary of the data obtained from Cross 3 (pro1 paba1 y// ad17 bi1.

Non-exchange tetrads		93
Single exchange tetrads		
pro1 - ad17	15	
ad17 - paba1	0	
paba1 - y	16	
y - bi1	5	
Total		36
Double exchange tetrads		
pro1 - ad17; paba1 - y	7	
paba1 - y; y - bi1	4	
pro1 - ad17; y - bi1	4	
4-strand double within pro1 - ad17	1	
4-strand doubles within paba1 - y	4	
Total		20
Triple exchange tetrads		
pro1 - ad17; paba1 - y; y - bi1	1	
4-strand double within pro1 - ad17; single paba1 - y	1	
Total		2
Incomplete asci		6
Abnormal asci		3
GRAND TOTAL		160

Relationship of adjacent exchanges.

	2-strand	3-strand	4-strand
pro1 - ad17; paba1 - y	2	3	3
paba1 - y; y - bi1	1	4	-
pro1 - ad17; y - bi1	2	1	2
Total	5	8	5

Distribution of the exch anges in th e sample of asci.

	Number of exchanges.				
	0	1	2	3	Total
Observed	93	36	20	2	151
Expected	88.0	47.8	13.0	2.2	151

$X^2_{(3)} = 6.97$ Probability = .10 - .05

Table 15.

Summary of the data obtained from Cross 4 (pro3 bi1// pro1 ad15 paba1 y)

Non-exchange tetrads		340 × 4
Single exchange tetrads		
pro3 - pro1	3	
pro1 - ad15	49	
ad15 - paba1	2	
paba1 - y	105	
y - bi1	32	
Total		191 × 2
Double exchange tetrads		
pro1 - ad15; paba1 - y	18	
pro1 - ad15; y - bi1	4	
paba1 - y; y - bi1	8	
4-strand double with in pro1 - ad15	3	
4-strand double within paba1 - y	5	
Total		38
Triple exchange tetrads		
pro1 - ad15; paba1 - y; y - bi1	3	
4-strand double within pro1 - ad15; single y - bi1	1	
4-strand double within y - bi1; single pro1 - ad15	1	
Total		5
Quadruple exchange tetrad		
4-strand double within paba1 - y; singles pro1 - ad15 and y - bi1	1	
Total		1
		575
Incomplete asci		34
Abnormal asci		2
GRAND TOTAL		611

Distribution of the exchanges in the sample of asci.

	Number of exchanges.				
	0	1	2	3 & 4	Total
Observed	340	191	38	6	575
Expected	347.5	172.9	43.0	11.6	575

$X^2_{(3)} = 3.83$ Probability = .30 - .25

4. Strand relations in multiple exchanges. The information on these relationships from Crosses 1, 2 and 4 has been summarized in Tables 16 to 21.

In a hypothetical case, when two intervals A and B are marked on a chromosome, various tetrad classes can be detected. (Whitehouse 1942). These are as follows:-

Class	Type of exchange.	
	Interval A.	Interval B.
1	None	None
2	Single	None
3	None	Single
4	Single	Single
5	4-strand double	Single
6	Single	4-strand double
7	4-strand double	None
8	None	4-strand double
9	4-strand double	4-strand double

It cannot be excluded that the 4-strand doubles which occur within intervals (Classes 5 to 9) were caused by exchanges at the two strand stage of meiosis. The tetrad class normally used in the evaluation of chromatid interference is Class 4. This class will include 2-, 3- and 4-strand double exchanges in a ratio of 1:2:1 if chromatid interference is absent. Classes 5 and 6 cannot be used as the relationship between the two adjacent exchanges is

indeterminate. However, the omission of Classes 5 and 6 may introduce an error into the proportions of 2-, 3- and 4-strand double exchanges observed in Class 4.

When the two intervals are short, the size of Classes 5 and 6 is small and the error introduced by their omission is negligible. However, as the intervals become longer, the size of Classes 5 and 6 will increase and the error will no longer be negligible.

The error introduced by the omission of these two classes is really caused by the fact that the comparable class with a 3-strand double exchange within one interval and a single exchange in the other interval is inevitably included in Class 4, while the class with a 2-strand double exchange within one interval and a single exchange in the other interval will be included in either Class 2 or 3. Furthermore, the type of "double exchange" observed between the two intervals (actually arising from a single exchange in the one interval and a 3-strand double exchange in the other interval) will give the relationship of the single exchange and the furthest exchange of the 3-strand double. This will be different from the relationship of the single exchange and the closest exchange of the 3-strand double. The latter gives the important strand relationships.

Using the method of Whitehouse (1956, private communication) (see Section III - 2 - d), the frequency of

Classes 5 and 6 in the present data could be used to correct for the proportions of tetrads in Class 4 which arose from three exchanges and which therefore showed the wrong strand relations. There were no tetrads in Class 9, showing that tetrads with four or more exchanges in the two intervals did not occur. When the frequency of tetrads with four or more exchanges in the two intervals is high, then the correction factor cannot be used.

There were a number of methods by which the data could be analysed. These were:-

(1) The relationship of all pairs of exchanges were considered, regardless of the position of the centromere, the intervals in which the exchanges occurred and whether or not there was another exchange between the two being considered. The disadvantages of this method were that it was assumed that the mechanism of exchange was uniform along the length of the chromosome and that an intervening exchange had no effect on the relations of the strands involved in the two bounding exchanges. Crosses 1, 2 and 4 were examined by this method but Whitehouse's correction factor was not used. This correction factor cannot be used when no allowance is made for possible effects of intervening exchanges.

(2) The assumption that an intervening exchange had an effect on the strand relations of the bounding

exchanges could, of course, be almost overcome by considering only adjacent exchanges. (The only intervening exchanges which are then not recovered by tetrad analysis are the 2-strand double exchanges within intervals). These adjacent exchanges were considered regardless of the interval in which they occurred and regardless of the centromere position. This type of analysis was extended by ignoring the exchanges which occurred in 1, 2 or more intervals at one or other end of the marked region or at both ends simultaneously. The effect of this analysis was to consider the strand relationships of adjacent exchanges when varying lengths and regions of the chromosome were used. Crosses 1, 2 and 4 were examined by this method and since the frequency of undetected intervening exchanges must be so low as to be negligible, Whitehouse's correction factor was [redacted] applied to the data.

(3) It was quite possible that the centromere had a differential effect as was observed by Lindegren and Lindegren (1942). Therefore, if the centromere was included in the marked region, the data were analysed in relation to it. In Cross 2 the strand relationships of those pairs of exchanges which fell wholly in one or the other of the chromosome arms and also the strand relationships of those pairs of exchanges where one fell in one arm and the other fell in the other arm were considered.

Only Cross 2 was analysed by this method and exchanges in the ad14 to centromere to pro1 interval had to be ignored, as it was not known on which side of the centromere they occurred. No allowance was made for intervening exchanges and so, again, Whitehouse's correction factor was not used.

In the present study the data picked out of the three crosses as a result of the use of any one of these methods were referred to as "a sample", or more specifically "a sample of double exchanges", "a sample of adjacent exchanges", etc.

The analysis was complicated by small numbers of pairs of exchanges recovered in some of the samples. Therefore, the samples in which the total number of pairs of exchanges was less than 20 were ignored. This meant that the following samples were ignored in the analysis:-

Table 16. Cross 1. pro1 bi1//paba1 y ad8. The samples of adjacent exchanges found in the chromosome lengths pro1 to y and paba1 to bi1.

Table 17. Cross 2. ribo ad14 paba1 y//an pro1 bi1 pyro4. The samples of adjacent exchanges found in the chromosome lengths an to pro1; ad14 to paba1; ribo to ad14; pro1 to bi1; pro1 to y and paba1 to bi1.

Table 18. Cross 4. pro3 bi1//pro1 ad15 paba1 y. The sample of adjacent exchanges found in the chromosome length paba1 to bi1.

The remaining data of Crosses 1, 2 and 4 (Tables 16 to 21) were considered according to each of the methods outlined above. If all four chromatids participated at random in double and multiple exchanges, the ratio of 2-: 3-:4-strand double exchanges should have been 1:2:1. This ratio was broken down into four components, namely:-

(1) The ratio of compensating (2-strand + 4-strand doubles) : non-compensating (3-strand doubles) should have been 1:1.

(2) The ratio of 2-:4-strand doubles should have been 1:1.

(3) The ratio of 2-:3-strand doubles should have been 1:2.

(4) The ratio of 4-:3-strand doubles should have been 1:2.

The UNCORRECTED samples were compared first to these ratios:-

(a) Cross 4. Three samples were available with total numbers of double exchanges greater than 20 (Table 18) and in all of them, the ratios of 2-:3-:4-strand doubles were 1:2:1. The component ratios were:-

(1) Compensating:non-compensating double exchanges --------- 1:1.

(2) 2-:4-strand double exchanges -------- 1:1.

(3) 2-:3-strand double exchanges -------- 1:2.

(4) 4-:3-strand double exchanges --------- 1:2.

(b) Cross 2. Twelve samples were available with total numbers of double exchanges greater than 20 (Table 17) and in all of them, the ratios of 2-:3-:4-strand doubles were 1:2:1. The component ratios were:-

(1) Compensating:non-compensating double exchanges --------- 1:1

(2) 2-:4-strand double exchanges -------- 1:1 except for two samples -------- i.e. the sample of adjacent exchanges in the chromosome length an to bi1 and the sample of adjacent exchanges in the chromosome length ad14 to bi1. In both samples there were excesses of 2-strand double exchanges.

(3) 2-:3-strand double exchanges -------- 1:2.

(4) 4-:3-strand double exchanges -------- 1:2.

(c) Cross 1. Only two samples were available with total numbers of double exchanges greater than 20 (Table 16) and in both of them, the ratios of 2-:3-:4-strand doubles were 1:2:1. The component ratios were:-

(1) Compensating:non-compensating double exchanges -------- 1:1.

(2) 2-:4-strand double exchanges -------- 1:1.

(3) 2-:3-strand double exchanges -------- 1:2.

(4) 4-:3-strand double exchanges -------- 1:2.

Secondly, the CORRECTED samples were compared to these ratios.

(a) Cross 4. There were two samples with numbers greater than 20 which could be corrected by Whitehouse's formulae (Tables 18 and 21). In both of them, the ratios of 2-:3-:4-strand doubles were 1:2:1. The component ratios were:-

(1) Compensating:noncompensating double exchanges -------- 1:1.

(2) 2-:4-strand double exchanges -------- 1:1.

(3) 2-:3-strand double exchanges -------- 1:2.

(4) 4-:3-strand double exchanges -------- 1:2.

(b) Cross 2. There were nine samples with numbers greater than 20 which could be corrected by Whitehouse's formulae (Tables 17 and 20). In all of them, the ratios of 2-:3-:4-strand doubles were NOT 1:2:1. The component ratios were:-

(1) Compensating:non-compensating double exchanges -------- 1:1.

(2) 2-:4-strand double exchanges -------- NOT 1:1 -------- too many 2-strand double exchanges.

(3) 2-:3-strand double exchanges -------- NOT 1:2 with one exception. Barring the exception, which may have been the consequence of sampling error, there were too many 2-strand doubles. The exception involved the sample of adjacent exchanges found in the chromosome length from ribo to pro1.

(4) 4-:3-strand double exchanges -------- NOT 1:2 -------- too few 4-strand double exchanges.

(c) Cross 1. There was only one sample with numbers greater than 20 which could be corrected by Whitehouse's formulae (Tables 16 and 19). In this one sample the ratio of 2-:3-:4-strand double exchanges was NOT 1:2:1. The component ratios were:-

(1) Compensating:non-compensating double exchanges -------- NOT 1:1 -------- too many compensating double exchanges.

(2) 2-:4-strand double exchanges -------- NOT 1:1 -------- too many 2-strand double exchanges.

(3) 2-:3-strand double exchanges -------- NOT 1:2 -------- too many 2-strand double exchanges.

(4) 4-:3-strand double exchanges -------- 1:2 -------- N.B. Numbers very small.

Table 16.

Strand relationships of double exchanges in Cross 1 (pro1 bi1//paba1 y ad8)

	OBSERVED (i.e. UNCORRECTED)	Classes 5 & 6 (n)	RECALCULATED (i.e. CORRECTED)
Any two exchanges	2-str. = 9 = .3462 3-str. =12 = .4615 4-str. = 5 = .1923	7 = .2692	
Any adjacent exchanges in the interval pro1 to bi1.	2-str. = 9 = .3750 3-str. =11 = .4583 4-str. = 4 = .1667	7 = .2917	2-str. =12.9 = .5393 3-str. = 6.5 = .2691 4-str. = 4.6 = .1916 ***
Any adjacent exchanges in the interval pro1 to y.	2-str. = 4 = .3636 3-str. = 5 = .4545 4-str. = 2 = .1819	3 = .4545	
Any adjacent exchanges in the interval paba1 to bi1.	2-str. = 2 = .2500 3-str. = 5 = .6250 4-str. = 1 = .1250	2 = .2500	

*** indicates a probability of less than .001 that the data agree with a ratio of 1:2:1.

Table 17.

Strand relationships of double exchanges in Cross 2 (ribo ad14 paba1 y//an pro1 bi1 pyro4).

	OBSERVED (i.e. UNCORRECTED)	Classes 5 & 6 (n).	RECALCULATED (i.e. CORRECTED)
Any two exchanges.	2-str. =40 = .2407 3-str. =84 = .5247 4-str. =38 = .2344	19 = .1173	
Any two exchanges within arms (excluding the ad14 to pro1 interval).	2-str. = 5 = .2174 3-str. =14 = .6087 4-str. = 4 = .1739	2 = .0870	
Any two exchanges between arms(excluding the ad14 to pro1 interval).	2-str. = 6 = .1538 3-str. =21 = .5385 4-str. =12 = .3077	3 = .0769	
Any adjacent exchanges in the interval ribo to bi1.	2-str. =35 = .2742 3-str. =66 = .5323 4-str. =24 = .1935	15 = .1210	2-str. = 60.7 = .4845 3-str. = 55.9 = .4475 4-str. = 8.4 = .0671 ***
Any adjacent exchanges in the interval ribo to y.	2-str. =27 = .2571 3-str. =55 = .5238 4-str. =23 = .2191	13 = .1238	2-str. = 48.8 = .4651 3-str. = 49.4 = .4701 4-str. = 6.8 = .0648 ***
Any adjacent exchanges in the interval ribo to paba1.	2-str. =17 = .2361 3-str. =37 = .5139 4-str. =18 = .2500	12 = .1667	2-str. = 31.2 = .4334 3-str. = 35.0 = .4864 4-str. = 5.8 = .0802 ***
Any adjacent exchanges in the interval an to bi1.	2-str. =25 = .3165 3-str. =41 = .5190 4-str. =13 = .1645	5 = .0633	2-str. = 40.5 = .5122 3-str. = 35.2 = .4460 4-str. = 3.3 = .0418 ***
Any adjacent exchanges in the interval ribo to pro1.	2-str. =13 = .2549 3-str. =24 = .4706 4-str. =14 = .2745	10 = .1961	2-str. = 19.3 = .3785 3-str. = 26.8 = .5257 4-str. = 4.9 = .0958 *

Table 17 continued.

	OBSERVED (i.e. UNCORRECTED)	Classes 5 & 6 (n).	RECALCULATED (i.e. CORRECTED)
Any adjacent exchanges in the interval an to y.	2-str. =17 = .2742 3-str. =33 = .5323 4-str. =12 = .1935	4 = .0645	2-str. =31.8 = .5137 3-str. =28.0 = .4513 4-str. = 2.2 = .0350 ***
Any adjacent exchanges in the interval ad14 to bi1.	2-str. =19 = .3276 3-str. =31 = .5345 4-str. = 8 = .1379	4 = .0690	2-str. =33.5 = .5770 3-str. =22.2 = .3822 4-str. = 2.3 = .0408 ***
Any adjacent exchanges in the interval ad14 to y.	2-str. =11 = .2619 3-str. =24 = .5714 4-str. = 7 = .1667	3 = .0714	2-str. =24.2 = .5762 3-str. =16.4 = .3900 4-str. = 1.4 = .0338 ***
Any adjacent exchanges in the interval an to paba1.	2-str. = 8 = .2353 3-str. =18 = .5294 4-str. = 8 = .2353	2 = .0588	2-str. =16.8 = .4927 3-str. =16.0 = .4702 4-str. = 1.2 = .0371 ***
Any adjacent exchanges in the interval an to pro1.	2-str. = 5 = .3333 3-str. = 5 = .3333 4-str. = 5 = .3333	1 = .0667	
Any adjacent exchanges in the interval ad14 to paba1.	2-str. = 4 = .2222 3-str. =11 = .6111 4-str. = 3 = .1667	1 = .0556	
Any adjacent exchanges in the interval ribo to ad14.	2-str. = - = - 3-str. = 4 = .6667 4-str. = 2 = .3333	1 = .1667	
Any adjacent exchanges in the interval pro1 to bi1.	2-str. = 5 = .3125 3-str. = 9 = .5625 4-str. = 2 = .1250	1 = .0625	
Any adjacent exchanges in the interval pro1 to y.	2-str. = 1 = .1429 3-str. = 5 = .7143 4-str. = 1 = .1429	1 = .1429	

Table 17 continued.

	OBSERVED (i.e. UNCORRECTED)	Classes 5 & 6 (n).	RECALCULATED (i.e. CORRECTED)
Any adjacent exchanges in the interval paba1 to bi1.	2-str. = 2 = .3333 3-str. = 3 = .5000 4-str. = 1 = .1667	-	

*** indicates a probability of less than .001 that the data agree with a ratio of 1:2:1.
** indicates a probability of .01 - .001 that the data agree with a ratio of 1:2:1.
* indicates a probability of .05 - .01 that the data agree with a ratio of 1:2:1.

Table 18.
Strand relationships of double exchanges in Cross 4 (pro3 bi1//pro1 ad15 paba1 y).

	OBSERVED (i.e. UNCORRECTED)	Classes 5 & 6 (n).	RECALCULATED (.i.e. CORRECTED)
Any two exchanges	2-str. =12 = .3000 3-str. =17 = .4250 4-str. =11 = .2750	4 = .1000	
Any adjacent exchanges in the interval pro1 to bi1.	2-str. =11 = .3056 3-str. =16 = .4444 4-str. = 9 = .2500	4 = .1111	2-str. =11.8 = .3265 3-str. =14.9 = .4139 4-str. = 9.3 = .2596
Any adjacent exchanges in the interval pro1 to y.	2-str. = 5 = .2381 3-str. = 9 = .4286 4-str. = 7 = .3333	1 = .0476	2-str. = 5.0 = .2381 3-str. = 8.8 = .4192 4-str. = 7.2 = .3427
Any adjacent exchanges in the interval paba1 to bi1.	2-str. = 5 = .4545 3-str. = 5 = .4545 4-str. = 1 = .0909	1 = .0909	

Table 19.

RECALCULATED strand relationships of double exchanges in Cross 1 (pro1 bi1//paba1 y ad8).

	2-str:3-str. (Column 1)	4-str:3-str. (Column 2)	2-str:4-str. (Column 3)	Compensating:Non-compensating (Column4).
Any adjacent exchanges in the interval pro1 to bi1.	12.9: 6.5 **	4.6: 6.5	12.9: 4.6 *	17.5: 6.5 *

* indicates a probability of .05 - .01 that the data agree with a ratio of 1:2 in Columns 1 and 2 and with a ratio of 1:1 in Columns 3 and 4.
** indicates a probability of .01 - .001 that the data agree with a ratio of 1:2 in Columns 1 and 2 and with a ratio of 1:1 in Columns 3 and 4.

Table 20.

RECALCULATED strand relationships of double exchanges in Cross 2 (ribo ad14 paba1 y//an pro1 bi1 pyro4).

	2-str:3-str. (Column 1).	4-str:3-str. (Column 2).	2-str:4-str. (Column 3).	Compensating:Non-compensating. (Column 4).
Any adjacent exchanges in in the interval ribo to bi1.	60.7:55.9 ***	8.4:55.9 ***	60.7: 8.4 ***	69.1:55.9
Any adjacent exchanges in the interval ribo to y.	48.8:49.4 ***	6.8:49.4 ***	48.8: 6.8 ***	55.6:49.4
Any adjacent exchanges in the interval ribo to paba1.	31.2:35.0 **	5.8:35.0 **	31.2: 5.8 ***	37.0:35.0
Any adjacent exchanges in the interval an to bi1.	40.5:35.2 ***	3.3:35.2 **	40.5: 3.3 ***	43.8:35.2
Any adjacent exchanges in the interval ribo to pro1.	19.3:26.8	4.9:26.8 *	19.3: 4.9 **	24.2:26.8

Table 20 continued.

	2-str:3-str. (Column 1).	4-str:3-str. (Column 2).	2-str:4-str. (Column 3).	Compensating:Non-compensating. (Column 4).
Any adjacent exchanges in the interval an to y.	31.8:28.0 **	2.2:28.0 **	31.8: 2.2 ***	34.0:28.0
Any adjacent exchanges in the interval ad14 to bi1.	33.5:22.2 ***	2.3:22.2 *	33.5: 2.3 ***	35.8:22.2
Any adjacent exchanges in the interval ad14 to y.	24.2:16.4 ***	1.4:16.4 *	24.2: 1.4 ***	25.6:16.4
Any adjacent exchanges in the interval an to paba1.	16.8:16.0 *	1.2:16.0 **	16.8: 1.2 **	18.0:16.0

* indicates a probability of .05 - .01 that the data agree with a ratio of 1:2 in Columns 1 and 2 and with a ratio of 1:1 in Columns 3 and 4.
** indicates a probability of .01 - .001 that the data agree with a ratio of 1:2 in Columns 1 and 2 and with a ratio of 1:1 in Columns 3 and 4.
*** indicates a probability of less than .001 that the data agree with a ratio of 1:2 in Columns 1 and 2 and with a ratio of 1:1 in Columns 3 and 4.

Table 21.

RECALCULATED strand relationships of double exchanges in Cross 4 (pro3 bi1//pro1 ad15 paba1 y).

	2-str:3-str. (Column 1)	4-str:3-str. (Column 2)	2-str:4-str. (Column 3)	Compensating:Non-compensating (Column 4).
Any adjacent exchanges in the interval pro1 to bi1.	11.8:14.9	9.3:14.9	11.8: 9.3	21.1:14.9
Any adjacent exchanges in the interval pro1 to y.	5.0: 8.8	7.2: 8.8	5.0: 7.2	12.2: 8.8

(5) Discussion of chromatid interference.

(a) The essential features to be noted in the data.

(α) Cross 4. There were NO DIFFERENCES between the corrected and the uncorrected samples involving the strand relations of adjacent exchanges in the chromosome lengths pro1 to bi1 and pro1 to y. Apparently all four chromatids participated at random in double and multiple exchanges.

(β) Cross 2. There were MANY DIFFERENCES between the corrected and the uncorrected samples involving the strand relations of adjacent exchanges in the chromosome lengths ribo to bi1; ribo to y; ribo to paba1; ribo to pro1; an to bi1; an to y; ad14 to bi1; ad14 to y and an to paba1. It will be noted that these chromosome lengths included the chromosome lengths used in Crosses 1 and 4.

In the uncorrected data most of the samples suggested that the four chromatids participated at random in double and multiple exchanges. There was a slight hint that this might not be correct in so far as there were the two samples with more two than four strand doubles. The corrected samples brought this feature out quite clearly. In all nine corrected samples there were more 2- than 4-strand doubles. The corrected samples also showed that the ratios of 2-:3-strand doubles were NOT 1:2 (with one

exception) ---- in fact, the frequencies of 2- and 3-strand doubles agreed very well with a 1:1 ratio. The ratio of 2-:3-strand doubles in the exception which involved the strand relations of adjacent exchanges in the chromosome length ribo to pro1, could equally well have been 1:1 or 1:2. The exception was probably the result of sampling error.

(γ) There were MANY DIFFERENCES between the uncorrected samples and the one corrected sample involving the strand relations of adjacent exchanges in the chromosome length pro1 to bi1. The uncorrected samples suggested that the four chromatids participated at random in double and multiple exchanges. The corrected sample was entirely different. As in the corrected samples of Cross 2 there were more 2- than 4-strand doubles and the ratio of 2-:3-strand doubles was NOT 1:2. However, in the corrected samples of Cross 2 the ratios of 2-:3-strand doubles were very close to 1:1. In the corrected sample of Cross 1 there were twice as many 2-strand as 3-strand doubles (the probability of equality was, however, fairly high at .15). The ratio of 3-:4-strand doubles could not be determined with any reasonable accuracy owing to small numbers.

(b) Comparison of the results with those expected from some possible theoretical models of exchange. The

simplest model of exchange is that all four chromatids of the first meiotic division are involved at random in double and multiple exchanges. In a large sample of double and multiple exchanges, the outcome of this model would be that 2-, 3- and 4-strand double exchanges occurred in a ratio of 1:2:1. In the present study the uncorrected data did not disagree with this ratio.

However, the uncorrected data were subject to errors caused by undetected double exchanges within intervals. Whitehouse (1956) has realized that if such undetected double exchanges occur at all frequently, they may constitute an important source of error and he has devised a method which corrects for them. The correction is based on the number of 4-strand double exchanges within either of a pair of intervals which occur together with a single exchange in the other interval. The logic is that if this type of triple exchange is occurring, then triple exchanges with either a 3-strand double or a 2-strand double within either of the intervals together with a single exchange in the other interval are also occurring. The tetrad type with a 3-strand double within one of the intervals may cause an error.

A 3-strand double exchange within an interval is detected by tetrad analysis as a "single exchange".

Furthermore, the OBSERVED strand relations of this 3-strand double exchange within an interval to a single exchange in another interval are those of the single exchange and the furthest exchange of the 3-strand double. These strand relationships will be different from those of the single exchange and the closest exchange of the 3-strand double and it is this latter relationship which is important. A 2-strand double exchange within an interval is not detected at all.

Although in the present study Whitehouse's correction formulae were used in the analysis of the strand relations between adjacent exchanges, there were two reasons for proceeding with caution. As stated above, his correction is based on the occurrence of 4-strand double exchanges within intervals. Now, firstly, if these 4-strand double exchanges within intervals were caused by exchanges at the two strand stage of meiosis, then the use of the formulae was wrong. Secondly, his formulae assume that the proportions of 2-, 3- and 4-strand double exchanges were the same within and between intervals. If this assumption was not valid for the three crosses analysed in this study, then again the use of the formulae was wrong.

Therefore, while ALWAYS bearing in mind that the use of Whitehouse's correction formulae may have been wrong,

the data from the three crosses were corrected. The question then was whether the corrected data remained in the ratio of 1:2:1. TO REPEAT, this was the ratio expected on the simplest hypothesis that all four chromatids of the first meiotic division were involved at random in double and multiple exchanges.

(α) Cross 4. In the two corrected samples involving the strand relations of adjacent exchanges in the chromosome lengths pro1 to bi1 and pro1 to y, the ratios of 2-:3-:4-strand doubles had remained at 1:2:1.

(β) Cross 2. In the nine corrected samples involving the strand relations of adjacent exchanges in the chromosome lengths ribo to bi1; ribo to y; ribo to paba1; ribo to pro1; an to bi1; an to y; an to paba1; ad14 to bi1 and ad14 to y, the ratios of 2-:3-:4-strand double exchanges were no longer 1:2:1. 2- and 3-strand double exchanges were equally frequent in eight of the nine corrected samples and there were too few 4-strand double exchanges in ALL nine corrected samples. The exception with respect to the 2- and 3-strand double exchanges involved the strand relations of the adjacent exchanges in the chromosome length ribo to pro1. In this sample the ratio of 2-:3-strand double exchanges could equally well have been 1:1 or 1:2. This exception was probably the consequence of sampling error.

(γ) Cross 1. In the single corrected sample involving the strand relations of the adjacent exchanges in the chromosome length pro1 to bi1, the ratio of 2-:3-: 4-strand double exchanges was also no longer 1:2:1. There were too many 2-strand doubles and too few 4-strand doubles. In this case there were also twice as many 2-strand as 3-strand doubles but the total number of 2- + 3-strand doubles was low and the probability of a 1:1 ratio was high at .15.

At first sight the three crosses seemed to be entirely inconsistent. However, considering only Crosses 1 and 2 for the moment, one salient point was apparent. This was that TWO OF THE STRANDS WERE PREFERENTIALLY INVOLVED IN ADJACENT EXCHANGES.

Therefore, this "simplest model" was rejected as inadequate since it was defined as "all four chromatids of the first meiotic division were involved at random in double and multiple exchanges".

The problem now was to find a model which would allow variation in the frequencies of 2-, 3- and 4-strand doubles from a point where most of the adjacent exchanges involved only two of the four strands to a point where the adjacent exchanges involved the four strands at random. A two phase model built up by several workers seemed most

attractive in the present study because a slight extension of the model allowed the required range of variation in the frequencies of the 2-, 3- and 4-strand double exchanges to be obtained.

It was first postulated by Belling (1931) that exchanges occurred only between the two new chromatids during the process of their formation ("new strand" exchanges). Naturally if these were the only exchanges that occurred, then only 2-strand double exchanges would be possible. This is obviously incorrect and Lindegren and Lindegren (1937) and Schwartz (1953, 1954, 1955) then suggested that sister strand exchanges superimposed on Belling's system would give the required 3- and 4-strand double exchanges. If sister strand exchanges occurred so often that even and odd numbers were equally frequent in the mean distance between adjacent new strand exchanges, then the ratio of 2-:3-:4-strand double exchanges would be 1:2:1. That is, the ratio obtained would be the SAME as that obtained from the "simplest model". However, the ratio obtained by the two phase model (i.e. a combination of sister strand and new strand exchanges) would change if the mean frequencies of sister strand exchanges in the mean distance between adjacent new strand exchanges decreased to a point where even and odd numbers did not

occur in equal frequencies. (Since there is no general agreement on the occurrence of sister strand exchanges, the available evidence is presented in Appendix 1).

IMPORTANT NOTE. For the remainder of this discussion, the "frequency of sister strand exchanges" is understood to mean the "frequency of sister strand exchanges in the mean distance between adjacent new strand exchanges" except where specifically stated to the contrary.

If there were no sister strand exchanges in the mean distance between adjacent new strand exchanges, a 2-strand double would be the result; if there was one sister strand exchange, then a 3-strand double would be the result; and if there were two sister strand exchanges, (one in each pair of sister chromatids) then a 4-strand double would be the result. It is immediately obvious that the ratios of 2-:3-:4-strand double exchanges would be determined by the MEAN "frequency of sister strand exchanges". The possible range would be from 1:0:0 (no sister strand exchanges) to 1:2:1 (even and odd numbers occurring with equal frequency).

Lindegren and Lindegren (1937) obtained an excess of 2-strand double exchanges in the "sex" chromosome of Neurospora crassa and explained their results by

postulating the two phase model of exchange. They proposed that sister strand exchanges in the mean distance between adjacent new strand exchanges were not sufficiently numerous to allow even and odd numbers to occur with equal frequency. Hence there was an excess of 2-strand double exchanges.

Now a possible extension of this two phase model is that the MEAN "FREQUENCY OF SISTER STRAND EXCHANGES" CAN BE VARIABLE. If this is so, the mean "frequency of sister strand exchanges" determines the proportions of 2-, 3- and 4-strand double exchanges recovered.

There are two variables which may affect the mean "frequency of sister strand exchanges". If the mean distance between adjacent new strand exchanges is kept fixed, then an increase in the mean "frequency of sister strand exchanges" will shift the ratio of 2-:3-:4-strand double exchanges towards 1:2:1 while a decrease in the mean "frequency of sister strand exchanges" will shift the ratio towards 1:0:0. On the ~~contrary~~ other hand, if the mean "frequency of sister strand exchanges" is kept fixed, then an increase of new strand exchanges will shift the ratios of 2-:3-:4-strand exchanges towards 1:0:0 while a decrease of new strand exchanges will shift the ratios towards 1:2:1. Of course, all combinations of the two will be theoretically

possible.

However, the MAIN POINT is that the proportions of 2-, 3- and 4-strand double exchanges will be dependent on the mean "frequency of sister strand exchanges" no matter how that particular frequency arose.

It is on this frame of reference that the corrected data of Crosses 1, 2 and 4 can be harmonized into one model. According to the extended two phase model postulated, Cross 4 had the highest mean "frequency of sister strand exchanges"; Cross 2 had an intermediate frequency; and Cross 1 MAY have had the lowest frequency.

To be more precise, it is now postulated:-

(1) that the mean"frequency of sister strand exchanges" was sufficiently high in the samples from Cross 4 that an even and an odd number occurred with equal frequency. The ratios of 2-:3-:4-strand double exchanges were therefore 1:2:1.

(2) that in the samples from Cross 2, most of the tetrads had either no sister strand exchanges in the mean distance between adjacent new strand exchanges (giving the 2-strand doubles) or one sister strand exchange (giving the 3-strand doubles). The small number of 4-strand double exchanges would be given by a small number of tetrads with more than one sister strand exchange in the mean distance between adjacent new strand exchanges.

(3) that (assuming the difference between Crosses 1 and 2 to be real) in the single sample from Cross 1, most of the tetrads had no sister strand exchanges in the mean distance between adjacent new strand exchanges (giving the 2-strand doubles) while a small proportion had either one or more sister strand exchanges in the mean distance between adjacent new strand exchanges (giving the small number of 3- and 4-strand double exchanges.)

(c) Conclusions. IF it is accepted that the corrected data fitted the two phase model of exchange, the following conclusions are reached:-

(1) The proportions of 2-, 3- and 4-strand double exchanges were the same in the two corrected samples of Cross 4. These samples involved the adjacent exchanges in the chromosome lengths pro1 to y and pro1 to bi1. Since these two samples involved practically the same chromosome lengths, there was no point in drawing comparisons between them.

(2) The proportions of 2-, 3- and 4-strand double exchanges were the same in eight of the nine corrected samples of Cross 2. These eight samples involved the adjacent exchanges in the chromosome lengths ribo to bi1; ribo to y; ribo to paba1; an to bi1; an to y; an to paba1;

ad14 to bi1 and ad14 to y. THEREFORE, by the two phase model, the mean frequency of sister strand exchanges found in the mean distance between adjacent new strand exchanges was constant in these chromosome lengths. The exceptional sample involved the adjacent exchanges in the chromosome length ribo to pro1 and was probably the result of sampling error.

(3) Nothing can be said about the constancy or otherwise of the mean frequency of sister strand exchanges in the mean distance between new strand exchanges in Cross 1 because only the sample of adjacent exchanges in the chromosome length pro1 to bi1 was corrected.

(4) The proportions of 2-, 3- and 4-strand double exchanges were different between Crosses 1, 2 and 4, although the difference between Crosses 1 and 2 did NOT reach statistical significance. THEREFORE, by the two phase model of exchange, the mean frequency of sister strand exchanges in the mean distance between adjacent new strand exchanges was different in Crosses 1 and 4 and different in Crosses 2 and 4. It MAY also have been different in Crosses 1 and 2.

Before considering whether or not these conclusions were biologically reasonable, it must be emphasized that the data provided absolutely no direct evidence for or against the occurrence of sister strand exchanges. Also the

reader must CONSTANTLY bear in mind the possibility that the use of Whitehouse's correction formulae was wrong.

That there should have been a variation in the mean "frequency of sister strand exchanges" between crosses seemed reasonable. The strains used as parents for these three crosses came directly from a number of other crosses and it was likely that there were many factors, both chromosomal and environmental, which could have affected the "mean"frequency of sister strand exchanges".

That there should have been a constant mean "frequency of sister strand exchanges" in the samples from the different chromosome lengths within Cross 2 was perhaps remarkable but the explanation may have lain in the method of analysis. There were insufficient numbers of double exchanges to allow the adjacent exchanges in any one pair of intervals to be analysed. The result was that the adjacent exchanges from a "combination of intervals" were invariably used in the analysis. The exchanges from each interval were used in more than one "combination of intervals" so any differences in the mean "frequency of sister strand exchanges" between one section of the chromosome and another may thus have been obscured.

FINALLY, it seemed that:-

(1) The variations in the mean "frequency of sister strand exchanges" between Crosses 1 and 4 and between

Crosses 2 and 4 were likely to be real.

(2) The variation in the mean "frequency of sister strand exchanges" between Crosses 1 and 2 may or may not have been real.

(3) On the contrary, the constancy of the mean "frequency of sister strand exchanges" within Cross 2 was probably the result of using the exchanges from each interval more than once in the "combinations of intervals" used for analysis.

(6) Chiasma interference. The data obtained in the present study offered three ways of detecting the occurrence of chiasma interference.

The first way was by measuring the frequency with which an exchange occurred simultaneously in each of two genetically marked intervals. In the absence of chiasma interference, exchanges in the two intervals should have been independent. The present data showed that exchanges were independent, no matter which pair of intervals was considered. (Table 22). In the calculation of the theoretical number of double exchanges, a 4-strand double exchange within either of a pair of intervals was counted as a single exchange. This was done because interference must be calculated from the effect of two adjacent exchanges upon each other.

The second way was to follow the distribution of the exchanges among the tetrads. In the absence of chiasma interference this distribution should have been Poisson. As can be seen in Tables 12, 13 and 15, the observed distributions of the exchanges among the tetrads from Crosses 1, 2 and 4 were Poisson, again showing the absence of chiasma interference.

Finally, interference could have been detected by using the double exchanges within intervals. (Only one of the three types of double exchanges within intervals could be detected by tetrad analysis ---- i.e. the 4-strand

Table 22.

Number of double exchanges observed and expected from different pairs of intervals of Crosses 1, 2, and 4.

Cross 1 (pro1 bi1//paba1 y ad8).

Pair of intervals	Observed	Expected
pro1 - paba1; paba1 - y	14	14.2
pro1 - paba1; y - bi1	8	4.5
paba1 - y; y - bi1	10	10.5

Cross 2 (ribo ad14 paba1 y//an pro1 bi1 pyro4).

Pair of intervals	Observed	Expected
ribo - an; an - ad14	7	8.5
ribo - an; ad14 - pro1	45	39.0
ribo - an; pro1 - paba1	10	10.7
ribo - an; paba1 - y	14	15.1
ribo - an; y - bi1	5	7.5
an - ad14; ad14 - pro1	16	12.7
an - ad14; pro1 - paba1	2	3.4
an - ad14; paba1 - y	6	4.9
an - ad14; y - bi1	5	2.5
ad14 - pro1; pro1 - paba1	19	16.0
ad14 - pro1; paba1 - y	22	22.5
ad14 - pro1; y - bi1	12	11.3
pro1 - paba1; paba1 - y	8	6.1
pro1 - paba1; y - bi1	4	3.1
paba1 - y; y - bi1	6	4.4

Cross 4 (pro3 bi1//pro1 ad15 paba1 y).

Pair of intervals	Observed	Expected
pro1 - paba1; paba1 - y	22	20.0
pro1 - paba1; y - bi1	9	7.1
paba1 - y; y - bi1	12	12.2

double exchange type.) In the absence of interference, the exchanges within one interval should have been distributed among the tetrads in a Poisson distribution and the number of 4-strand doubles should have been $\frac{1}{4}$ of the total double exchanges (i.e. $\frac{1}{4}$ of the third term of the Poisson distribution). This $\frac{1}{4}$ of the double exchanges could be expressed in relation to the frequency of single exchange tetrads observed and so an estimate of the number of 4-strand double exchanges within any one interval was obtained (see Section III - 2 - c). This method showed that there was an excess of 4-strand double exchanges in one of the intervals of Cross 1 (the pro1 to paba1 interval with a recombination frequency of .07 $\pm$ .010); an excess of 4-strand double exchanges in the total data of Cross 1 but not of Crosses 2 and 4; and an excess of 4-strand double exchanges in the total pooled data of Crosses 1, 2 and 4. This excess of 4-strand double exchanges in the total pooled data was present regardless of whether or not the data from the interval ad14 to centromere to pro1 were included (Table 23). Excesses of 4-strand double exchanges within intervals have previously been observed by Hemmons (1952) in Aspergillus nidulans and by Ebersold (1956) in Chlamydomonas reinhardi.

Table 23.

Expected and observed numbers of 4-strand double exchanges within intervals. The assumption of no chromatid interference has been made.

Cross 1 (pro1 bi1//paba1 y ad8).

Interval	Recombination fraction.	No. of 4-strand doubles Observed	Expected	Probability ++
pro1 - paba1	.07	6	.69	<.005
paba1 - y	.15	7	5.15	N.S.
y - bi1	.05	2	.42	.10 - .05
Total		15	6.26	<.001

Cross 2 (ribo ad14 paba1 y//an pro1 bi1 pyro4)

Interval	Recombination fraction.	No. of 4-strand doubles Observed	Expected	Probability ++
ribo - an	.16	4	4.28	N.S.
an - ad14	.07	2	.34	.05 - .025
ad14 - pro1	.25	13	8.91	N.S.
pro1 - paba1	.06	-	.61	N.S.
paba1 - y	.09	1	1.26	N.S.
y - bi1	.05	1	.28	N.S.
Total		21	15.68	N.S.

Cross 4 (pro3 bi1//pro1 ad15 paba1 y).

Interval	Recombination fraction	No. of 4-strand doubles Observed	Expected	Probability ++
pro1 - paba1	.07	4	1.59	.10 - .05
paba1 - y	.13	6	5.27	N.S.
y - bi1	.04	1	.59	N.S.
Total		11	7.45	N.S.

Table 23 continued.

Total of Crosses 1, 2 and 4. Interval	No. of 4-strand doubles Observed	Expected	Probability ++
Total (excluding exchanges in the interval ad14 - pro1)	34	20.48	<.01
Total (including exchanges in the interval ad14 - pro1)	47	29.39	.001

++ The probabilities of finding 4-strand doubles in each interval in numbers equal to or greater than those observed are calculated by using Stevens' (1942) table of Binomial and Poisson distributions. The probabilities of finding totals of 4-strand doubles in numbers equal to or greater than those observed are calculated by using the table for Normal distributions.

(7) Discussion of chiasma interference. The data bearing on chiasma interference did not give a consistent answer. As seen in Section III - 6, there were no signs of chiasma interference when:-

(a) the distributions of the exchanges among the tetrads were compared to a Poisson distribution;

(b) nor were there any signs of chiasma interference when the numbers of exchanges occurring simultaneously in each of two intervals were considered.

On the other hand the frequency of 4-strand double exchanges within intervals was, in several instances, greater than the frequency expected if the exchanges WITHIN intervals had followed a Poisson distribution. To repeat, these instances were the pro1 to pabal interval of Cross 1, the total data from all the intervals of Cross 1 and the total data from all the intervals of Crosses 1, 2 and 4 together (Table 23).

These excesses of 4-strand double exchanges within intervals could have been the result of positive chromatid interference, negative chiasma interference or of exchange at the two strand stage of meiosis. In view of the fact that the present study had demonstrated the occurrence of negative chromatid interference (subject to the reservations already mentioned on page 59), it seemed probable that the excess was the result of negative chiasma interference (if

exchanges occurred at the 4-strand stage of meiosis). Since the excesses of 4-strand double exchanges within intervals occurred only in Cross 1 and in the pooled data of Crosses 1, 2 and 4, they may have been due to some unexplained peculiarity of Cross 1 which was sufficiently strong to be apparent even in the pooled data. In the absence of uniformity between the three crosses, the evidence from the pooled data on chiasma interference was open to suspicion.

However, it must be remembered that in the estimation of the expected frequency of the 4-strand doubles within intervals, the assumption of no chromatid interference was made. In the present study this assumption has not been upheld, because the proportion of 4-strand doubles between intervals was shown to be less than the .25 expected in the absence of chromatid interference. It thus followed that when one assumed the proportions of 2-, 3- and 4-strand double exchanges to be the same between and within intervals, the estimate of the EXPECTED number of 4-strand doubles within intervals (see Section III - 2 - c) was an overestimate. The limitations of this method for detecting chiasma interference now became apparent. Since the OBSERVED numbers of 4-strand doubles within intervals were, in most cases, already greater than the overestimates

of the expected frequencies (although in most cases not significantly so ---- see Table 23), a failure to demonstrate interference did not rule out the possibility of its occurrence.

The conclusion was that two of the methods available for the detection of chiasma interference showed that none was present whereas the third method gave indications of negative chiasma interference. There was, however, a possible explanation which would have resolved these conflicting results.

On the one hand chiasma interference was studied by comparing the distributions of the chiasmata among the tetrads to a Poisson distribution and by examining the frequency of simultaneous exchange in each of two intervals. No interference was found. The chromosome lengths involved in these calculations ranged from 11.9 units to 69.2 units (as measured by uncorrected recombination frequency)

On the other hand the frequency of exchange within intervals was generally too high (significantly so in some cases but not in others). The chromosome lengths used in these calculations ranged from 4.4 units to 25.4 units (again as measured by uncorrected recombination frequency)

Now Pritchard (1955) has demonstrated the occurrence of strong negative interference in Aspergillus nidulans over recombination lengths of less than one unit. The mean

chromosome length used in the last method of analysis (i.e. using the frequency of 4-strand double exchanges within intervals) was less than the mean chromosome length used in the other two methods of analysis. It was, therefore, just a possibility that the negative interference found by Pritchard was beginning to be detectable over these "within interval" chromosome lengths.

IV. SEGREGATION RATIOS INCONSISTENT WITH THE HYPOTHESIS OF SINGLE GENE INHERITANCE.

1. Some causes of deviation from 1:1 segregation ratios. According to Mendelian laws, in tetrads from a cross heterozygous for a single pair of alleles, each allele should be represented twice among the four products of meiosis. A number of instances have been reported in which the allele ratios of tetrads did not, at first sight, conform to these laws. Closer examination of some of these instances subsequently showed that they could be explained by causes which did not contradict Mendelian laws while others still appeared to do so. Emerson (1956) has already reviewed some of the possible causes of deviation from 1:1 segregation ratios in tetrads of yeasts. Segregation ratios other than 1:1 will be found as the results of the following causes:-

(a) Complementary genes. The expression of a character determined by complementary gene action is dependent on the simultaneous presence of two or more particular alleles at more than one locus. Hawthorne (1956) working with yeast, found that phenotypic ratios of galactose fermentation : non-galactose fermentation other than 1:1 are the result of the interaction of dominant alleles at three separate loci. All three dominant alleles

must be present together for fermentation to proceed. It is therefore immediately obvious that if phenotypic ratios are confused with genotypic or allele ratios, then incorrect conclusions may be reached. (For the purposes of this thesis, an allele ratio is defined as the number of homologous alleles of each type present at the end of a single meiosis; a genotypic ratio by the distribution of these alleles among the nuclei; and a phenotypic ratio by the numbers of each allele expressed).

Magni (1949) studied the accumulator/non-accumulator character in yeast and found that two pairs of complementary genes affected the expression of the character. The non-accumulator form is produced when the two dominant alleles occur together. If complementary gene action is analysed by tetrads, then phenotypic ratios of 2:2, 1:3 and 0:4 (complementary action : non-complementary action) will be recovered. These are analogous to the 9:7 F2 ratios found in single strand analysis of diploid organisms.

Lindegren and Lindegren (1947) found that the dominant allele of methionine dependence/independence plus the recessive allele of adenine dependence/independence must be present together for the production of pink pigment in the cultures. This situation is analogous to that giving 13:3 ratios in single strand analysis of diploid organisms.

(b) Polymeric genes. If a cross is heterozygous

for two or more genes affecting the expression of the same character, phenotypic ratios other than 1:1 will be recovered from the tetrads while the ratios of each pair of alleles are 1:1 as expected. Winge and Roberts (1948, 1950a, 1953 1955) showed that there are four genes affecting the fermentation of maltose in yeast. The presence of the dominant allele of any one of these genes will cause the fermentation of maltose. In the analysis of tetrads these authors obtained 4:0, 3:1 and 2:2 ratios of fermenters: non-fermenters.

(c) Unusual nuclear behaviour. Winge and Roberts (1950b) interpreted asci of yeast with more than four spores to have arisen as the result of an extra mitotic division. If the spores in excess of four degenerated, the allele ratios may not be 1:1. Mundkur (1950) showed that this hypothesis was inadequate to explain the allele ratios obtained by him in one of his tetrads and also in one of Lindegren's tetrads (cited by Mundkur (1950) from Lindegren (1949)) because deduction of the missing spores could not be done without raising the number of genotypes to more than four. However, Lindegren and Lindegren (1953c) concluded that asci with more than four spores usually arose by fusion of neighbouring diploid cells before reduction or by fusion of asci after reduction. This could account for the

number of genotypes in excess of four (Mundkur 1950) if the spores in excess of four degenerated at random. The same explanation could account for the seven different genotypes in a 7-spored ascus of yeast found by Pomper, Daniels and McKee (1954). Winge and Roberts (1954) furthermore showed that an extra mitotic division could be followed by heterokaryosis. Nuclear fusions in these heterokaryons could then give rise to diploids with the result that the phenotypic ratios in the tetrads could differ from 1:1.

(d) Polyploidy and polysomy. Roman and Sands (1953) found that crosses between two strains of yeast obtained from C.C.Lindegren gave, with rare exceptions, 2:2 segregations. Further investigation to account for the rare exceptions showed that diploids had appeared spontaneously in the haploid cultures. It is evident that if crosses of these cultures were to be made by the mass mating method of Lindegren (1949), matings of haploid//diploid, diploid// diploid, etc. might produce phenotypic ratios different from 1:1. Roman, Hawthorne and Douglas (1951), Leupold and H ottinguer (1954) and Roman, Phillip and Sands (1955) have demonstrated tetraploid inheritance in yeast while Pomper, Daniels and McKee (1954) have shown thee results of triploid inheritance in yeast. Winge and Roberts (1949) have also demonstrated the presence of a gene D in Saccharomyces

chevalieri which causes diploidization of the strains in which it occurs. Some of the phenotypic ratios obtained in this thesis (see Section VII) have been shown to be the result of tetraploid segregation of a small piece of the BI chromosome (Pritchard 1956).

(e) Somatic crossing over. This phenomenon has been extensively studied in Aspergillus nidulans by Pontecorvo (1954, 1955a), Pontecorvo, Gloor and Forbes (1954), Pontecorvo and Kafer (1956), Roper and Pritchard (1955) and Pritchard (1955) and in Drosophila by Stern (1936). If somatic crossing over occurred during vegetative growth and the recombinant strands passed to different daughter nuclei, these nuclei would become homozygous for all markers distal to the crossover. If these nuclei subsequently participated in the formation of an ascus, allele ratios of 4:0 and 0:4 would be found.

(f) Mutation. If mutation occurred prior to meiosis, then allele ratios of 4:0 and 0:4 would be recovered. If mutation occurred after the duplication of the chromosomes in meiosis, then 3:1 and 1:3 allele ratios would be recovered.

(g) Double duplication. If a piece of one of a pair of homologous chromosomes is duplicated twice while the same piece of the other homologous chromosome does not duplicate at all, then 3:1 and 1:3 allele ratios will be found.

Mitchell (1955a) suggested that this could be the explanation for the aberrant recombinations of pyridoxine mutants in Neurospora. Later, Mitchell (1956) decided that it was "simpler" to suppose that an unknown property of the heterozygous diploid condition in the ascus increases the frequency of mutations to wild". Some support for the "double duplication" hypothesis has been obtained from an ascus found in the present study (see Section IV - 2. Ascus No. 14.).

(h) Unequal crossing over. If thee two products of unequal crossing over give rise to new genotypes, then genotypic ratios different from 1:1 will be recovered from tetrad analysis. The phenotypic ratios will be decided by the expression of these new genotypes. The classical example of unequal crossing over is the Bar locus of Drosophila (Sturtevant 1925, 1928).

(i) Gene conversion. According to Lindegren (1955) "gene conversion is the interaction, occurring at meiosis, between the dominant and the recessive allele in a heterozygote, resulting in the transformation of one or more dominant alleles into the corresponding recessive allele or vice versa. Gene conversion is essentially a directed mutation occurring at meiosis as a result of the effect of homologous alleles upon each other; it does not

occur (or it is not apparent) at the meiosis of homozygous diploids".

As pointed out by Emerson (1956), the proofs generally offered for gene conversion are that other causes of abnormal allele ratios could not account for the observed results. All possible ratios 4:0, 3:1, 1:3 and 0:4 have been attributed to gene conversion by Lindegren (1949, 1953a, b), Lindegren and Lindegren (1952, 1956) and Lindegren et al (1956). Emerson (1956) criticizes the published accounts of gene conversion in Saccharomyces on the grounds that the range of effects expected from polysomy were not fully evaluated and that also that polysomy is strongly indicated by some of the observations. Lindegren (1953b) showed gene conversion in the pedigree of families inwhich polyploidy had earlier been demonstrated (Lindegren and Lindegren 1951).

Other examples of abnormal allele ratios in tetrads which could perhaps be attributed to gene conversion have been found in Bombardia (Zickler 1934) and Salpiglossis (Reimann-Phillipps 1955).

Hemmons (1952) found eight asci with abnormal allele ratios in 136 crossed asci of Aspergillus nidulans. Hemmons concluded that these abnormalities had two main causes:- "(1) Mutation during the first meiotic division (3/136). (2) Supernumerary divisions in the ascus (2/136), plus a possible 3 more".

2. Discussion of experimental observations. Among the asci dissected, there were a few which did not give the usual allele ratios of 1:1. All these asci could have been caused by contamination but the probability of this explanation varies for each ascus. If the ratios can be rendered normal by the rejection of a single ascospore which has a genotype occurring with a high frequency in the cross, then contamination is more probable. On the other hand, if the ratio cannot be rendered normal by the rejection of a single ascospore which has a genotype occurring with a high frequency, then contamination is less probable. For the purposes of this thesis, if the ascospore has a genotype which occurs with a frequency of 1 in 20 or less, then the explanation of contamination is rejected.

A ripe ascus of Aspergillus nidulans usually broke either on taking it through the surface of the Tween 80 drop or during the transfer to the agar square. On reaching the agar square, the ascospores were usually already separated so if a number other than eight was found, it was impossible to say whether the ascus contained an abnormal number of spores or whether the spores had been accidentally gained or lost. In a few instances asci with other than eight spores were dissected but where this was done, it has been stated in the description of the ascus. IN ALL OTHER CASES IT WAS A STRICTLY OBSERVED RULE THAT ONLY ASCI WITH EIGHT SPORES WERE DISSECTED.

The asci which appeared to have allele ratios other than 1:1 are shown in Table 24 where they are numbered from 1 to 18. These numbers also arrange the asci in chronological order. It will be noted that with the passing of time (i.e. with increasing skill) the incidence of these asci decreased (Table 25). Furthermore, the abnormal asci found in the earlier work were mostly easily explainable by contamination whereas those found later were mostly not explainable by contamination. Possible explanations of how these asci arose are:-

Ascus 1. In this ascus the four genotypes found were consistent with normal Mendelian segregation. However, in an ascus with four genotypes, only one or two spores of each genotype should be found while in this case three spores were of the genotype bi1 sd. The extra spore could have been the result of a second mitotic division accompanied by the degeneration of one of the other ascospores (Winge and Roberts 1950a). Alternatively since the spores of the genotype bi1 sd had a frequency of roughly 1 in 13 in this cross, the extra spore could quite easily have been a contaminant.

Ascus 2. Five genotypes were recovered from this ascus. Although it is possible to obtain more than four genotypes in an ascus as the result of a mutation occurring during ascus development, contamination is the more probable

Table 24.

Asci with segregation ratios other than 1:1 found during ascus dissections.

Cross and ascus number.	Perithecium number.	Genotypes	Number of spores germinating.
y sd//bi1 pyro4 Ascus 1.	3	y + sd +	2
		y + + pyro4	1
		+ bi1 sd +	3
		+ bi1 + pyro4	1
y sd//bi1 pyro4 Ascus 2.	4	y + sd +	11
		y + sd pyro4	1
		y + + pyro4	1
		+ bi1 sd +	1
		+ bi1 sd pyro4	1
ad1//y sd pyro4 Ascus 3.	2	y ad1 + +	1
		y ad1 + pyro4	1
		y ad1 sd pyro4	1
		+ ad1 sd pyro4	1
		+ + + pyro4	1
		+ + sd pyro4	1
ad1//y sd pyro4 Ascus 4.	12	y + sd +	2
		y ad1 + +	1
		+ + + +	1
		+ ad1 sd pyro4	1
wn ad1 pro1 paba1 y//y pyro4 Ascus 5.	5	wn + pro1 paba1 +	2
		wn ad1 + + pyro4	1
		y ad1 pro1 paba1 pyro4	1
		y + + + +	2
		y ad1 + + pyro4	1

Table 24 continued.

Cross and ascus number	Perithecium number	Genotypes	Number of spores germinating.
wn ad14 y//bi1 met1 Ascus 6.	2	wn ad14 met1	2
		wn + met1	1
		wn ad14 +	1
		+ + +	1
		+ ad14 +	1
		+ + met1	1
paba1 y ad8//pro1 bi1 Ascus 7.	2	+ paba1 y ad8 bi1	2
		pro1 + + + bi1	3
paba1 y ad8//pro1 bi1 Ascus 8.	15	+ paba1 y ad8 +	4 ***
		pro1 + + + bi1	2
		pro1 + + + +	2
paba1 y ad8//pro1 bi1 Ascus 9.	17	+ paba1 y ad8 +	2 ***
		pro1 paba1 y ad8 +	1
		pro1 + + + bi1	2
		+ + + + +	1
ribo ad14 paba1 y//an pro1 bi1 pyro4 Ascus 10.	3	ribo + ad14 + paba1 y + pyro4	1 ***
		ribo an + pro1 + + bi1 +	3
ribo ad14 paba1 y//an pro1 bi1 pyro4 Ascus 11.	3	+ an + + paba1 y + +	4 ***
		ribo + ad14 pro1 + + bi1 pyro4	2
		ribo + ad14 pro1 + + + pyro4	2

Table 24 continued.

Cross and ascus number	Perithecium number.	Genotypes								Number of spores germinating.	
ribo ad14 paba1 y//an pro1 bi1 pyro4 Ascus 12.	7	ribo	+	ad14	+	paba1	y	+	+	2	***
		ribo	+	ad14	+	paba1	y	+	pyro4	1	. .
		+	an	+	pro1	+		+	bi1 pyro4	2	
		+	an	+	pro1	+		+	bi1 +	1	
		ribo	+	ad14	+	paba1	y	+	pyro4	1	
		+	an	+	pro1	+		+	bi1 +		
ribo ad14 paba1 y//an pro1 bi1 pyro4 Ascus 13.	10	ribo	+	ad14	+	paba1	+	bi1	+	3	***
		ribo	+	ad14	+	paba1	y	+	+	2	. .
		+	an	+	pro1	+		+	bi1 pyro4	3	
pro1 paba1 y//ad17 bi1 Ascus 14.	1	pro1	+	paba1	+	bi1				1	***
		+	ad17	+	y	+				2	. .
		+	ad17	paba1	y	+				1	
		+	ad17	+	+	bi1				2	
pro1 paba1 y//ad17 bi1 Ascus 15.	4	pro1	+	paba1	y	+				2	***
		pro1	+	paba1	+	bi1				3	. .
		+	ad17	+	y	+				2	
pro1 paba1 y//ad17 bi1 Ascus 16.	4	+	ad17	+	+	+				1	
		pro1	ad17	+	+	bi1				2	
		pro1	+	paba1	+	bi1				1	

Table 24 continued.

Cross and ascus number.	Perithecium number.	Genotypes				Number of spores germinating.
pro3 bi1//pro1 ad15 paba1 y Ascus 17.	6	pro3	+	+	+ bi1	3
		pro3	+	+	y +	2
		+	pro1	ad15	paba1 + bi1	1
		+	pro1	ad15	paba1 y +	1
pro3 bi1//pro1 ad15 paba1 y Ascus 18.	6	pro3	+	+	+ bi1	2
		pro3	+	+	+ +	1
		+	pro1	ad15	paba1 y bi1	1
		+	pro1	ad15	paba1 y +	3

N.B. All the spores carrying the wild genotype and all the spores from asci 10, 11, 13 and 14 were tested for ploidy and were found to be haploid.

*** Indicates those asci where the probability of explaining the deviating ratio by contaminatio is very low.

Table 25.
Classification of the dissected asci.

Number dissected	No germination.	Non-classifiable asci.	Selfed asci.	Classifiable as hybrids.	HYBRID ASCI. Number of genotypes recovered. 4	3	2	1	Abnormal asci.	Abnormal asci as numbered in Table 24.
					y sd//bi1 pyro4.					
78	8	6	14	50	23	14	5	6	2	1 & 2
					ad1//y sd pyro4.					
38	-	3	1	34	22	5	4	1	2	3 & 4
					wn ad1 pro1 paba1 y//y pyro4.					
122	5	-	-	117	97	10	7	2	1	5
					wn ad14 y//y sd.					
24	-	-	-	24	20	4	-	-	-	
					wn ad14 y//bi1 thi2.					
12	1	-	-	11	9	2	-	-	-	
					wn ad14 y//bi1 met1.					
53	-	-	-	53	38	10	4	-	1	6
					pro1 bi1//paba1 y ad8.					
512	11	62 ** (Perithecium No.9).	-	439	256	136	33	11	3	7, 8 & 9.
					ribo ad14 paba1 y//an pro1 bi1 pyro4.					
293	1	-	1	291	216	48	19	5	3	10, 11 & 13.
					pro1 paba1 y//ad17 bi1.					
173	-	6	7	160	120	31	6	-	3	14, 15 & 16
					pro3 bi1//pro1 ad15 paba1 y.					
611	1	5	-	605	453	122	26	2	2	17 & 18
1916	27	82	23	1784	1254	382	104	27	17	

explanation. Mutation is extremely improbable in this ascus as it would require simultaneous mutation of more than one of the markers. It is quite possible that on rare occasions either a single spore, attached to an ascus, passed un-noticed or that a group of spores had stuck together and was mistaken for an ascus.

Another explanation is that two zygotes underwent meiosis normally but were included in the same ascus (Lindegren and Lindegren 1953c). If this had happened, presumably eight of the spores in the "double ascus" had died.

Ascus 3. Six genotypes were recovered from this ascus and the same explanations as given for Ascus 2 above will probably be applicable.

Ascus 4. In this ascus, there were 3 prototrophs : 1 auxotroph with respect to pyro4. There were, however, only five spores growing and either the spore of the genotype y ad1 or the spore of the wild genotype could have been contaminants. The former spores had a frequency of 1 in 28 and the latter spores had a frequency of 1 in 12.

Ascus 5 and Ascus 6. There were more than four genotypes in both these asci and again the explanations given for Ascus 2 above are the most probable ones.

Ascus 7. In this case all of the five germinating spores required biotin for growth. There were three spores

with the genotype pro1 bi1 so there may have been an extra mitotic division or one of the three could have been a contaminant. Spores of the genotype pro1 bi1 had a frequency of 1 in 3 in this cross. An alternative explanation in this ascus is that an unusual event occurred at the locus of the biotin marker either before or during meiosis.

Ascus 8. This ascus had a ratio of 3 prototrophs : 1 auxotroph with respect to the bi1 locus and provided more convincing evidence of abnormalities of meiosis. In this instance all eight spores had grown. The 3:1 ratio could be explained by assuming that the two pro1 spores were contaminants. This is unlikely, however, since the frequency of spores with this genotype was roughly 1 in 60. The other four markers in the cross segregated in a ratio of 1:1.

Ascus 9. Here again a ratio of 3 prototrophs : 1 auxotroph with respect to the bi1 marker was found. Only six of the eight spores germinated but spores of both parental types were present in duplicate and the other two spores carried genotypes which were the products of an exchange with respect to the pro1 - paba1 interval. The 3:1 ratio could be explained if the green prototroph spore was either a contaminant or a diploid. However, since it was a haploid and this type of spore had a frequency of roughly 1 in 660 in the total population of ascospores,

it was probably not a contaminant. The other four markers in the cross segregated in a ratio of 1:1.

Ascus 10. Only four spores germinated in this ascus and they all required riboflavin for growth. There were three spores with the genotype ribo an pro1 bi1 so there may have been an extra mitotic division or one of the three may have been a contaminant. However, as spores carrying this genotype had a frequency of 1 in 40 in the cross, contamination is unlikely. Another possibility is that an unusual event occurred at the locus of the ribo marker either before or during meiosis.

Ascus 11. This is another instance of a ratio of 3 prototrophs : 1 auxotroph with respect to the bi1 marker. The ascus is a 4-strand double exchange within the ad14 - pro1 interval and both products were present in both exchanges. Again the 3:1 ratio could be explained if the two spores with the genotype ribo ad14 pro1 pyro4 were contaminants. However, as the frequency of spores carrying this genotype was about 1 in 350, this is unlikely.

There are various ways in which these 3:1 ratios might be explained. Ascus 8 could have been obtained by extra mitoses of the paba1 y ad8 nuclei accompanied by the degeneration of the paba1 y ad8 bi1 product of an exchange in the y - bi1 interval. Similarly Ascus 11 could have been

obtained by extra mitoses of the an pabal y nuclei accompanied by degeneration of the an pabal y bil nuclei products of an exchange in the y - bil interval. This explanation could not account for the abnormality found in Ascus 9. The probability of obtaining an ascus with eight spores after these two events would be increased if there were some mechanism which made this the optimum number.

An easy explanation is mutation, but the rate would have had to be extremely high to account for all the 3:1 ratios

Further possibilities are gene conversion (Lindegren 1949, 1953a, b, 1955) and exchange within the region determining biotin synthesis. If it were necessary to have a certain number of mutated sites before the synthesis of biotin failed, then an exchange which split this critical number might give 3 prototrophs : 1 auxotroph.

Ascus 12. Hemmons (1952) found that in 6 out of 136 crossed asci, two nuclei, representing two different products of meiosis, were included in the same ascospore. This type of abnormality was not found among the 8-spored asci in the present study. However, Ascus 12 was found to contain seven normal spores and a shrivelled fragment. This fragment did not germinate but among the seven normal spores which did germinate, there was one which contained

two nuclei and gave rise to a mixed green and yellow colony. The two genotypes found in this single colony were the mirror images of the genotypes of two of the other colonies.

Ascus 13. In this ascus there were ratios other than 1:1 for all the markers in the cross and the evidence is therefore in favour of extra mitotic divisions of one of the ribo ad14 paba1 bi1 nuclei and also of one of the an pro1 bi1 pyro4 nuclei. The former genotype had a frequency of 1 in 100 and the latter had a frequency of 1 in 8 in a random sample of ascospores from this cross.

Ascus 14. This ascus was found to have a 3:1 ratio for both the pro1 and ad17 loci. In the case of pro1 there were 3 prototrophs : 1 auxotroph while there were 3 auxotrophs : 1 prototroph of ad17. The paba1, y and bi1 loci segregated 1:1. There was an exchange in the paba1 - y interval from which both products were recovered. The spore with the genotype ad17 paba1 y could have been a contaminant but as the frequency of such spores was roughly 3 in 1000, this is unlikely. The pro1 and ad17 loci were in repulsion and the simplest explanation is that a section of the ad17 bi1 parent chromosome covering at least the interval pro1 - ad17 had been duplicated twice. Double duplication of a small piece of chromosome which is only marked once, is, of course,

another way in which a 3:1 allele ratio of a single locus might arise.

Ascus 15. This is probably an instance of an extra mitotic division of one of the pro1 paba1 bi1 nuclei. Spores of this genotype had a frequency of about 1 in 20 in this cross and would arise as the result of an exchange in the paba1 - y interval. The other product of such an exchange (namely ad17 y) was recovered in duplicate from this ascus.

Ascus 16. This was almost certainly a case of contamination. All the genotypes that were recovered were the result of crossing over and there were no complementary products. It is possible that there was an abnormal ratio at the y locus. However, since only four of the spores germinated, the evidence for an abnormal ratio is un-convincing.

Ascus 17 and Ascus 18. Both these asci can be explained by either the occurrence of an extra mitotic division (the former in one of the pro3 bi1 nuclei and the latter in one of the pro1 ad15 paba1 y nuclei) or by contamination. In Ascus 17 there had been an exchange in the paba1 - y interval and in Ascus 18 there had been an exchange in the y - bi1 interval. In both cases the products of these exchanges were recovered. On the other hand both the pro3 bi1 and the pro1 ad15 paba1 y genotypes had a frequency of

about 1 in 3 among the ascospores of this cross. The extra spore of each of these genotypes could, therefore easily have been contaminants.

It was a curious point that no diploids were found throughout the work although they are known to occur with a variable frequency (from 1 in 1000 ascospores to 1 in 100 ascospores) in Aspergillus nidulans (Pritchard 1953). The most probable explanation is that diploids are found in asci with less than eight spores so the selection of asci with eight spores would have discriminated against them.

During this study 1916 asci were dissected. These asci have been classified into various classes as shown in Table 25. For only 7 of the 17 abnormal asci, contamination is too unlikely to be seriously considered as an explanation. These 7 asci are Asci 8, 9, 10, 11, 13, 14 and 15 of Table 24. Ascus 12 with two nuclei included in one spore is a special case as it arose from an ascus with only seven spores and a fragment.

The frequencies of the various abnormalities described above have been summarized. These frequencies can be calculated by using the fully classifiable asci but this assumes that the fourth product of meiosis was normal in those asci where only three of the four products were recovered. Therefore, a more stringent estimate of the frequencies of the various abnormalities may be obtained by the use of

those asci where the four products of meiosis were actually recovered. Furthermore, the frequencies of the abnormalities can be estimated on the assumption that 10 of the asci were the result of contamination or on the assumption that contamination did not occur. These four alternatives are tabulated in Table 26. Assuming that contamination occurs, the most frequent causes of abnormalities are unusual events at the bil locus and extra mitotic divisions. The frequencies with which abnormalities occurred at each particular locus are given in Table 27. It can be seen that there are large variations in frequency from one locus to another.

Table 26.

The frequencies of the various types of abnormalities when considered:-
(A) Amongst the fully classifiable asci----------)
(B) Amongst the asci from which the four products of meiosis were recovered) Assuming that contamination occurred.

(C) Amongst the fully classifiable asci----------)
(D) Amongst the asci from which the four products of meiosis were recovered) Assuming that NO contamination occurred.

Type of abnormality.	Locus affected.	No. of asci in which heterozygous.	Reference No. in Table 24.	(A)	(B)	Reference No. in Table 24.	(C)	(D).
Contamination	-	-	1 to 7; 16 to 18.	1 in 165	1 in 127	-	-	-
3+:1-	bi1	1556	8, 9, 11.	1 in 477	1 in 359	8, 9, 11.	1 in 477	1 in 359
3+:1-) simultaneous 1+:3-)	pro1 ad17	160	14.	1 in 151	1 in 120	14.	1 in 151	1 in 120
3+:1-	pyro4	492	-	-	-	4	1 in 435	1 in 358
3+:1- or 4+:0-	y	1579	-	-	-	16	1 in 1446	1 in 1090
1+:3- or 0+:4-	bi1	1556	-	-	-	7	1 in 1430	1 in 1077
1+:3- or 0+:4-	ribo	291	10	1 in 264	1 in 216	10	1 in 264	1 in 216
Extra mitotic division	-	-	10, 13, 15.	1 in 551	1 in 424	1, 7, 10, 13, 15, 17, 18.	1 in 236	1 in 182
Fusion of neighbouring cells before reduction or of asci after reduction.	-	-	-	-	-	2, 3, 5, 6.	1 in 413	1 in 318

\+ indicates prototroph or green
\- indicates auxotroph or yellow.

Table 27.

The frequencies of abnormalities with respect to individual loci.

(A) Amongst the fully classifiable asci) Assuming that con-
(B) Amongst the asci from which the four products of meiosis were recovered) tamination occurre
(C) Amongst the fully classifiable asci) Assuming that NO c
(D) Amongst the asci from which the four products of meiosis were recovered) tamination occurre

Locus	Reference number in Table 24.	Total asci in which heterozygous (number)	(A)	(B)	(C)	(D)
ad1		151	0 in 134	0 in 119	0 in 134	0 in 119
ad8		439	0 in 392	0 in 256	0 in 392	0 in 256
ad14		379	0 in 347	0 in 283	0 in 347	0 in 283
ad15		605	0 in 575	0 in 453	0 in 575	0 in 453
ad17	14	160	1 in 151	1 in 120	1 in 151	1 in 120
an		291	0 in 264	0 in 216	0 in 264	0 in 216
bi1	7, 8, 9 & 11	1556	3 in 1431	3 in 1077	4 in 1431	4 in 1077
met1		53	0 in 48	0 in 38	0 in 48	0 in 38
paba1		1612	0 in 1489	0 in 1142	0 in 1489	0 in 1142
pro1	14	1612	1 in 1489	1 in 1142	1 in 1489	1 in 1142
pro3		605	0 in 575	0 in 453	0 in 575	0 in 453
pyro4	4	492	0 in 435	0 in 358	1 in 435	1 in 358
ribo	10	291	1 in 264	1 in 216	1 in 264	1 in 216
sd		108	0 in 88	0 in 65	0 in 88	0 in 65
thi2		11	0 in 11	0 in 9	0 in 11	0 in 9
wn		205	0 in 190	0 in 164	0 in 190	0 in 164
y	16	1579	0 in 1446	0 in 1090	1 in 1446	1 in 1090

V. ABNORMAL AND "TWIN" PERITHECIA.

(1). Abnormal perithecium. Perithecium 9 (Table G) from the cross pro1 bi1//paba1 y ad8 contained a semi-lethal with a viability of 7.8%. This has been named "dwarf" (dw) as the colonies which carried it and survived were very small. Most of the 62 asci dissected did not give germination of more than four spores. Where more than four spores survived, they invariably carried the semi-lethal indicating the segregation of a chromosomal character.

Since it is known that pro1 is 18 units from its centromere, it was possible to test the semi-lethal for centromere linkage. Ditype asci with respect to dwarf (dw) and pro1 are:-

dw pro1 (or absent)
dw pro1 (or absent)
\+ +
\+ +

and

\+ pro1
\+ pro1
dw + (or absent)
dw + (or absent)

It is not possible to distinguish parental ditypes from non-parental ditypes as it is not known in which parental line the dwarf character arose. Tetratype asci are:-

\+ pro1
\+ +
dw pro1 (or absent)
dw + (or absent)

There were 8 ditypes : 33 tetratypes and this has a probability of .10 - .05 when compared with a Null hypothesis of 1 ditype : 2 tetratypes. There is, therefore, no evidence of linkage of the dw character to its centromere.

A cross was then made of paba1 y ad8 dw//an bi1 pyro4 sd wn and the analysis was carried out by random strands. The dw character showed no evidence of linkage to any of these markers and had a viability of 8.0%.

(2) "Twin" perithecia. In a number of perithecia "twins" were found. These are perithecia with a mixture of selfed asci of both parents or selfed asci of one parent and hybrids. Mixed perithecia were previously found by Hemmons (1952). In common with Hemmons, no perithecia were found to contain a triple mixture i.e. hybrid asci with selfed asci from both parents. Examples of twin perithecia were found in the following crosses:-

(a) y sd//bi1 pyro4. (Table A).

Perithecium 27. The asci dissected were 1 crossed and 1 selfed y sd.

Perithecium 38. The asci dissected were 1 crossed, 1 selfed y sd and 1 unclassifiable.

(b) ribo ad14 paba1 y//an pro1 bi1 pyro4 (Table H).

Perithecium 6. The asci dissected were 18 crossed and 1 selfed an pro1 bi1 pyro4.

(c) pro1 paba1 y//ad17 bi1. (Table I).

Perithecium 3. The asci dissected were 26 crossed and 1 selfed pro1 paba1 y.

Perithecium 4. The asci dissected were 21 crossed, 5 selfed pro1 paba1 y and 3 unclassifiable.

Perithecium 6. The asci dissected were 11 crossed, 1 selfed pro1 paba1 y and 2 unclassifiable.

As discussed by Pontecorvo et al (1953) there are three ways in which these twin perithecia may arise. Firstly, two pairs of nuclei may have initiated the formation of one perithecium; one pair being genetically identical and the other pair being genetically different. Secondly, the two initial nuclei may have had different survival values. If one nucleus of a conjugate pair had died, the other nucleus might have then divided and the resulting pair might have continued to multiply by conjugate division. This seems the most probable explanation in view of the fact that Hemmons (1952) found that the percentages of selfed and hybrid asci varied greatly from one perithecium to another. The percentage of selfed asci would depend on the stage at which one nucleus had died and the other nucleus had continued to divide conjugately. In the crosses y sd//bi1 pyro4; ribo ad14 paba1 y //an pro1 bi1 pyro4 and pro1 paba1 y//ad17 bi1 only selfed asci of one parental strain were found but this might have been due to the fact that the strains ribo ad14 paba1 y and ad17 bi1 were completely self-sterile while the strain bi1 pyro4

was only slightly self-fertile. Thirdly, "twin" perithecia might have arisen by fusion of separate perithecia during development.

VI. RECOVERY OF BOTH PRODUCTS OF AN EXCHANGE IN A SHORT REGION. Mitchell (1955a), from a cross heterozygous in repulsion for two closely linked pyridoxine-less mutants of Neurospora found that four asci out of 585 did not carry both products of exchange. It was thought that the same phenomenon might occur in Aspergillus nidulans and so one of the reasons for undertaking the analysis of the cross pro3 bi1// pro1 ad15 paba1 y was that it included two pairs of closely linked markers. These are pro3 - pro1 (recombination fraction .003 ± .0015. Forbes 1956) and ad15 - paba1 (recombination fraction .002 ± .0012 Pritchard, unpublished and Calef 1956). There were two asci with exchanges between ad15 and paba1 (Table J. Perithecia 5 and 6) and in both cases the two products of the exchanges were recovered. There were also three asci with exchanges between pro3 and pro1 (Table J. Perithecia 3 and 6) and again the two products of the exchanges were recovered from all of them. All the double mutants pro3 pro1 were tested by obtaining heterokaryons and also diploids with a known pro3 strain and a known pro1 strain. All the heterokaryons and all the diploids required proline for growth. The double mutant can also be recognized visually. The eight spores obtained from an ascus with an exchange between pro3 and pro1 are shown in Figure 6. These two pairs of mutants apparently do not behave in the same manner as the pyridoxine mutants of Neurospora, a conclusion

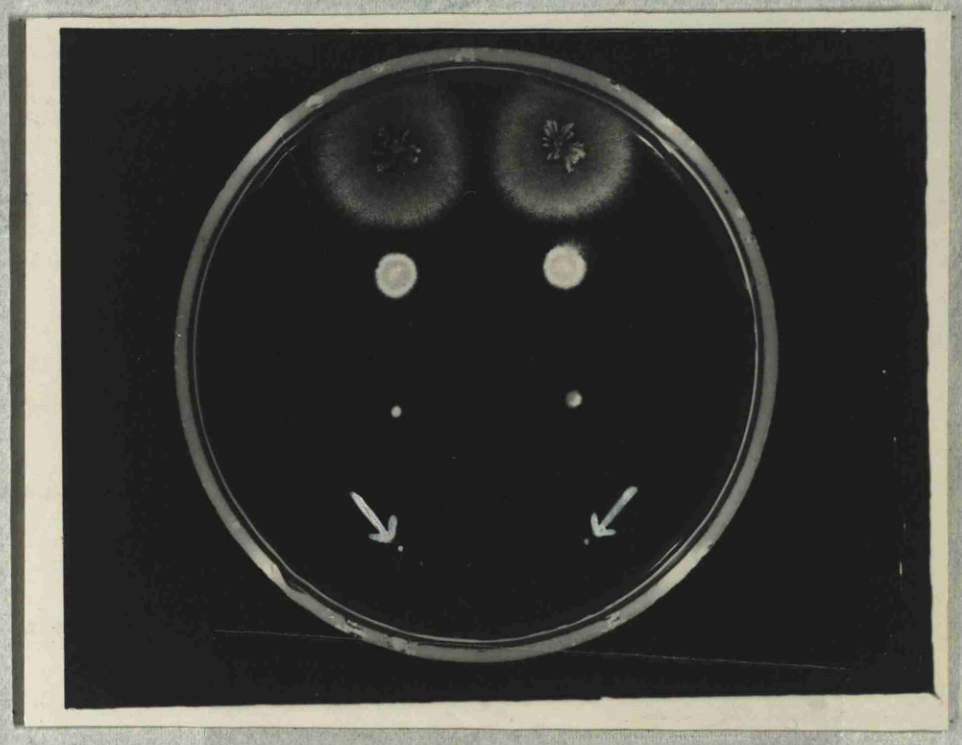

Figure 6. Colonies obtained from a dissected ascus of the cross pro3 bi1//pro1 ad15 paba1 y after incubation for three days at 37° C. on minimal medium + adenine + p-amino benzoic acid + biotin. The colonies are therefore being tested for their proline requirements. The pro1 mutant determines a fair degree of growth; the pro3 mutant determines distinctly less growth; and the double mutant pro1 pro3 determines no growth at all. Therefore the genetic constitutions of the above colonies with respect to proline requirements are:-

Top row	+	+
Second row	+	pro1
Third row	pro3	+
Fourth row	pro3	pro1 (indicated by arrows)

which was expected from the vast amount of work carried out in this Department on Aspergillus (Roper 1950; Pontecorvo 1952a, b; Roper and Pritchard 1955; Pritchard 1955; see also theoretical discussion by Pontecorvo, 1952 to 1955).

VII. ANALYSIS OF A DUPLICATION OF A SEGMENT OF THE BI CHROMOSOME. While investigating reversions of an adenine requiring strain to adenine independence, Pritchard (1956) obtained a duplication of a piece of the BI chromosome involving the y, ad20 (adenine-less-20) and bi1 loci. Subsequently he found that this duplication was attached to the chromosome carrying wn and ad1. A cross paba1 y ad8//y pyro4 dp (dp = duplication carrying ad20 bi1) was analysed by tetrads in order to enquire further into the behaviour of the duplication. Twenty eight asci from six perithecia were dissected and among these eighteen were fully classifiable. All six perithecia were selfed of the strain y pyro4 dp (ad20 bi1). The cross investigated was therefore y pyro4 dp (ad20 bi1)//y pyro4 dp (ad20 bi1). Thus the cross was homozygous pyro4 and the zygote was tetrasomic for the region covered by the duplication. If the duplication pairs with the BI chromosome, the y, ad20 and bi1 loci may segregate in various ways according to where exchanges take place. The segregations observed in the various asci can be most easily explained in the following ways. Asci 2, 24 and 27 (marked in Table K as "single exchange pa - y") could be the result of an exchange between the point of attachment (pa) and the y locus. Asci 7, 11, 18, 21 and 23 (marked in Table K as "single exchange ad20 - bi1") could be the result of an exchange between ad20 and bi1. The remainder

are best explained by multiple exchanges. Ascus 12 could best be described by the following. Each duplication has paired with a BI chromosome and this has been followed by exchanges between pa and y in both pairs. In both Asci 14 and 15 each duplication has paired with a BI chromosome. In Ascus 14 there has then been an exchange between pa and y in one of the pairs and an exchange between ad20 and bi1 in the other pair. In Ascus 15 there has been a 3-strand double exchange in the intervals pa - y; ad20 - bi1 in one pair and an exchange between ad20 and bi1 in the other pair. Ascus 22 has 6 yellow spores and 2 green spores and can best be explained by the loss of one of the duplications. The other duplication has paired with a BI chromosome and there has been an exchange between pa and y.

APPENDIX I. Summary of the available evidence concerning the occurrence or otherwise of sister-strand exchanges. Weinstein (1936) has applied a mathematical treatment to some exchange data of Drosophila which he obtained from various sources and has concluded that no sister strand exchanges occur.

The studies of attached-X chromosomes (Emerson and Beadle 1933; Beadle and Emerson 1935) gave homozygosis values greater than 16.7%. This is the maximum value expected if the markers in question are segregating independently of the centromere, and all four strands participate at random in exchanges. These authors pointed out that their observations only ruled out sister strand exchanges which are equivalent to non-sister strand exchanges. Furthermore, Schwartz (1953) has pointed out that "if the two crossover types" (sister strand and non-sister strand exchanges) "are independent, as has been proposed in this paper, arising by different mechanisms and occurring at different times in the meiotic division, the maximum frequency of homozygosis expected from a combination of sister strand and non-sister strand crossing over would remain at 25%" which is the maximum value of homozygosis expected from non-sister strand exchanges alone.

Morgan (1933) found that the frequencies of the

various classes of progeny obtained from Drosophila females heterozygous for a ring ghromosome were consistent with the assumption of no sister strand exchanges. Schweitzer and Kaliss (1935) used Drosophila females heterozygous for an inversion-X and a ring-X to come to the same conclusion.

The fact that unequal exchanges at the Bar locus of Drosophila, either at its normal position (Sturtevant 1925, 1928) or when translocated to the left end of the chromosome (Muller and Weinstein 1933) are always accompanied by an exchange between the flanking markers is evidence against sister strand exchanges. Sturtevant (1925) did, however, obtain 4 exceptional reversions of Bar which could have been explained equally by sister strand exchanges or by contamination. In a later work (Sturtevant 1928) on Bar, no exceptional flies were found. This evidence from the Bar locus may be misleading as unequal exchanges are unusual. Laughnan (1952) has given some data from the A^b locus of Maize which, among other interpretations, could have been the result of sister strand exchanges.

From the number of single and double bridges occurring in anaphases I and II of a heterozygous inversion involving nearly the whole of chromosome 6 of Maize, Schwartz (1953) concluded that the frequencies observed

were consistent with those expected on the hypothesis that sister strand exchanges occur. In a study of "twin spots" (caused by mitotic exchanges) by the use of attached-X chromosomes, Schwartz (1954) showed whether or not strands which were attached to a common centromere were involved in the same exchange. If exchanges are limited to the new chromatids, no twin spots should be found. Schwartz found that the frequency of twin spots in the attached-X material was very low as compared to the frequency of twin spots in free X chromosomes when the same markers were used. The few spots in the attached-X material could have been caused by exchanges between two strands not attached to a common centromere or by an exchange between two strands attached to the same centromere and accompanied by a sister strand exchange. If these few spots resulted from the latter cause, then any factor causing an increase in sister strand exchanges would be expected to increase the frequency of twin spots. Brown and Hannah (1952) found that there were few or no sister strand exchanges in somatic cells of Drosophila as shown by the stability of the ring chromosomes. However the ring could be induced to become highly unstable in the offspring of females which had been aged as virgins. Schwartz (1954, 1955) suggested that this instability could be explained by an increase of sister strand exchanges. Schwartz (1954) found that females with attached-X chromosomes

which had been aged as virgins gave a nine-fold increase in twin spots among the offspring. Brown and Welshons (1955) repeated the experiment and did not find this increase in their material. They pointed out that their evidence did not disprove the two phase model of exchanges (Belling 1936; Schwartz 1953, 1954, 1955) but suggested that the method chosen to demonstrate sister strand exchanges in Drosophila was not valid.

If dicentric ring formation is used as the criterion, then the evidence is in favour of sister strand exchanges in Maize where McClintock (1938, 1941) has shown that dicentric double sized rings arise from ring chromosomes. The simplest explanation of these dicentric double sized rings is by the occurrence of sister strand exchanges at mitosis.

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Table A./.
Cross y sd//bi1 pyro4. From streak inoculum on minimal medium. Prepared on the 24.11.53. Only the genotypes of the germinated spores are given. If there were only two spores of any one genotype, it was assumed that they were the result of the mitotic division.

Genotypes	Number of asci.	Comments
Perithecium No. 1. Dissected 4.1.54.		
y sd	1	Selfed yellow
y sd		
ysd		
Perithecium No.2. Dissected 4.1.54.		
y	1	
y sd		
bi1 pyro4		
bi1 pyro4 sd		
Perithecium No.3. Dissected 5.1.54.		
y sd (2 spores)	1	ABNORMAL
y pyro4 (1 spore)		
bi1 sd (3 spores)		
bi1 pyro4 (1 spore)		
Perithecium No.4. Dissected 5.1.54.		
y sd (1 spore)	1	ABNORMAL
y sd pyro4 (1 spore)		
y pyro4 (1 spore)		
bi1 sd (1 spore)		
bi1 pyro4 sd (1 spore)		
Perithecium No.5. Dissected 5.1.54.		
y sd	1	Probably selfed yellow
y sd		
Perithecium No.6. Dissected 5.1.54.		
y sd	1	
y pyro4		
bi1		
bi1 pyro4 sd		
Perithecium No.7. Dissected 6.1.54.		
-	1	No growth
Perithecium No.8. Dissected 6.1.54.		
y sd	1	
y pyro4 sd		
bi1		
bi1 pyro4		
Perithecium No.9. Dissected 6.1.54.		
-	1	No growth
Perithecium No.10 Dissected 8.1.54.		
y pyro4	1	
bi1 sd		
bi1 pyro4		
Perithecium No.11. Dissected 8.1.54.		
y sd	1	Selfed yellow
y sd		
y sd		

Table A/. cont[d].

Genotypes	Number of asci	Comments.
Perithecium No.12. Dissected 8.1.54.		
y sd pyro4	1	
bi1		
bi1 pyro4		
Perithecium No.13. Dissected 9.1.54.		
-	1	No growth
Perithecium No.14. Dissected 9.1.54.		
y sd	1	Selfed yellow
y sd		
y sd		
y sd		
Perithecium No.15 Dissected 9.1.54.		
y pyro4	1	
bi1 pyro4 sd		
bi1 sd		
Perithecium No.16. Dissected 10.1.54.		
y sd	1	
y pyro4		
bi1 pyro4 sd		
y pyro4	1	
y sd		
bi1 pyro4 sd		
bi1		
Perithecium No.17. Dissected 11.1.54.		
bi1	1	
y	1	
y sd		
bi1 pyro4		
y pyro4	2	
y pyro4	1	
bi1 pyro4 sd		
Perithecium NO.18. Dissected 12.1.54.		
-	1	No growth
Perithecium No.19. Dissected 13.1.54.		
y pyro4	1	
y bi1 sd	1	Single exchange y - bi
bi1 pyro4 sd		
pyro4		
Perithecium No.20. Dissected 13.1.54.		
y pyro4	1	
y pyro4 sd		
bi1 sd		
bi1		

Table A/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.20. Dissected 13.1.54.		
y sd	1	
y pyro4 sd		
bi1		
bi1 pyro4		
y pyro4 sd	1	
bi1		
bi1		
y sd	1	
bi1		
Perithecium No.21. Dissected 14.1.54.		
y sd	1	
y pyro4 sd		
bi1		
bi1 pyro4		
y	1	
y sd		
bi1 pyro4		
bi1 pyro4 sd		
Perithecium No.22. Dissected 16.1.54.		
y sd	4	Selfed yellow
y sd		
y sd		
y sd		
y sd	1	Probably selfed yellow
y sd		
Perithecium No.23. Dissected 16.1.54.		
y	1	
y sd		
bi1 pyro4		
bi1 pyro4 sd		
Perithecium No.24. Dissected 17.1.54.		
y	1	
y pyro4		
bi1 sd		
bi1 pyro4 sd		
y sd	1	
y sd		
bi1pyro4		
bi1 pyro4		
bi sd	1	
y	1	
y pyro4 sd		
bi1		
bi1 pyro4 sd		

Table A/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.24. Dissected 17.1.54.		
y y pyro4 sd bi1 pyro4 sd	1	
Perithecium No.25. Dissected 18.1.54.		
bi1 sd	1	
y sd y pyro4 bi1 sd bi1 pyro4	1	
y sd bi1 pyro4 bi1 pyro4 sd	1	
y pyro4 bi1 sd	1	
Perithecium No.26. Dissected 19.1.54.		
y y bi1 pyro4 sd bi1 pyro4 sd	1	
-	1	No growth
y sd bi1 bi1 pyro4	1	
y y pyro4 sd bi1 bi1 pyro4 sd	1	
Perithecium No.27. Dissected 21.1.54.		
y sd y sd y sd y sd	1	MIXED PERITHECIUM
y bi1 pyro4 pyro4 sd	1	4-strand double exchange within y - bi
Perithecium No.28. Dissected 21.1.54.		
y sd bi1 pyro4 sd	1	Single exchange y - bi
y y sd bi1 pyro4 bi1 pyro4 sd	1	

Table A/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.29. Dissected 21.1.54.		
y sd	2	Selfed yellow
y sd		
y sd		
y sd		
Perithecium No.30. Dissected 21.1.54.		
y sd	1	
y pyro4 sd		
bi1		
bi1 pyro4		
y pyro4	1	
y pyro4 sd		
bi1		
Perithecium No.31. Dissected 24.1.54.		
y sd	1	Selfed yellow
y sd		
y sd		
y sd		
y sd	1	Probably selfed yellow
-	2	No growth
Perithecium No.32. Dissected 24.1.54.		
y	1	
y sd		
bi1 pyro4		
bi1 pyro4 sd		
Perithecium No.33. Dissected 24.1.54.		
y sd	1	Selfed yellow
y sd		
y sd		
y sd	1	Probably selfed yellow
y sd		
-	1	No growth
Perithecium No.34. Dissected 26.1.54.		
y pyro4 sd	1	
bi1		
Perithecium No.35. Dissected 26.1.54.		
y	1	
y pyro4		
bi1 sd		
bi1 pyro4 sd		
Perithecium No.36. Dissected 27.1.54.		
y sd	1	Selfed yellow
y sd		
y sd		
y sd	1	Probably selfed yellow
y sd		

Table A/. cont[d].

Genotypes	Number of asci	Comments
Perithecium No.37. Dissected 27.1.54.		
y sd y pyro4 bi1 bi1 pyro4 sd	1	
y bi1 sd	1	
y pyro4 bi1 bi1 sd	1	
y pyro4 sd bi1 bi1	1	
y pyro4 y pyro4 sd bi1 bi1 sd	1	
Perithecium No.38. Dissected 27.1.54.		
y sd y sd	1	Probably selfed yellow
y sd y bi1 pyro4 bi1 pyro4 sd	1	Single exchange y - bi
y sd y sd y sd	1	Selfed yellow MIXED PERITHECIUM

SUMMARY

Types of asci	Number of ascospores germinating. 0	1	2	3	4	5	6	7	8
Classifiable									
Selfed yellow	-	-	-	-	-	4	4	4	2/14
Selfed green	-	-	-	-	-	-	-	-	-
Hybrid	-	5	5	5	6	5	6	10	6/48
Non-classifiable									
Yellow	-	1	-	3	2	-	-	-	-/ 6
Green	-	-	-	-	-	-	-	-	-
No germination	8	-	-	-	-	-	-	-	-/8
Abnormal	-	-	-	-	-	1	-	1	-/ 2
Grand total	8	6	5	8	8	10	10	15	8/78

Table B/.
Cross ad1//y sd pyro4. From streak inoculum on minimal medium. Prepared on the 5.2.54. Only the genotypes of the germinated spores are given. If there were only two spores of any one genotype, it was assumed that they were the result of the mitotic division.

Genotypes	Number of asci	Comments.
Perithecium No.1. Dissected 2.3.54.		
y sd ad1 sd	1	
y ad1 sd y pyro4 ad1 sd pyro4	1	
Perithecium No.2. Dissected 3.3.54.		
y pyro4 sd y ad1 pyro4 ad1	1	
pyro4	1	
y pyro4 y pyro4 sd ad1 sd ad1	1	
y pyro4 sd	2	
y ad1 pyro4 (1 spore) y ad1 (1 spore) y ad1 pyro4 sd (1 spore) ad1 pyro4 sd (1 spore) pyro4 (1 spore) pyro4 sd (1 spore)	1	ABNORMAL
Perithecium No. 3. Dissected 4.3.54.		
y pyro4 sd y pyro4 sd	1	Possibly a mixed perithecium
y pyro4 y ad1 sd ad1 pyro4 sd	1	
Perithecium No.4. Dissected 4.3.54.		
y pyro4 y ad1 pyro4 sd ad1 sd + + + +	1	
Perithecium No.5. Dissected 6.3.54.		
y ad1 pyro4 y ad1 sd + + + + pyro4 sd	1	

Table B/. cont^{d}.

Genotypes	Number of asci	Comments.
Perithecium No.5. Dissected 6.3.54.		
y sd	1	
y pyro4		
ad1 sd		
ad1 pyro4		
y ad1	1	
y pyro4 sd		
ad1 pyro4		
sd		
y pyro4 sd	1	
y sd		
ad1		
ad1 pyro4		
Perithecium No.6. Dissected 7.3.54.		
y	1	
ad1 pyro4 sd		
Perithecium No.7. Dissected 8.3.54.		
y	1	
y ad1 pyro4		
ad1 sd		
pyro4 sd		
Perithecium No.8. Dissected 9.3.54.		
y ad1 sd	1	
y ad1 pyro4		
+ + + +		
pyro4 sd		
Perithecium No.9. Dissected 9.3.54.		
y ad1 sd	1	
y ad1		
pyro4		
pyro4 sd		
Perithecium No.10 Dissected 9.3.54.		
y pyro4	1	
y pyro4 sd		
ad1		
ad1 sd		
y sd	1	
ad1 pyro4		
ad1 sd		
Perithecium No.11. Dissected 10.3.54.		
y ad1 (1 spore)	1	ABNORMAL
y sd (2 spores)		
+ + + + (Haploid) (1 spore)		
ad1 pyro4 sd (1 spore)		

Table B/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.12. Dissected 10.3.54.		
y pyro4 sd y ad1 sd + + + + ad1 pyro4	1	
Perithecium No.13 Dissected 10.3.54.		
y y ad1 pyro4 sd ad1 pyro4 sd	1	
Perithecium No.14. Dissected 10.3.54.		
y ad1 pyro4 sd sd	1	
Perithecium No.15. Dissected 11.3.54.		
y pyro4 sd y pyro4 sd y pyro4 sd	1	Selfed yellow
Perithecium No.16. Dissected 12.3.54.		
y sd y ad1 pyro4 sd + + + + ad1 pyro4	1	
y y ad1 pyro4 sd sd ad1 pyro4	1	
Perithecium No.17. Dissected 15.3.54.		
y y ad1 pyro4 sd + + + + ad1 pyro4 sd	1	
y ad1 pyro4 sd ad1 + + + + (Haploid)	1	
y y ad1 pyro4 pyro4 sd ad1 sd	1	
y sd y ad1 sd pyro4 ad1 pyro4	1	
y ad1 pyro4 pyro4 sd ad1 sd	1	

Table B/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.17. Dissected 15.3.54.		
y ad1 pyro4 + + + + (Haploid)	1	
y pyro4 y pyro4 ad1 sd ad1 sd	1	
Perithecium No.18. Dissected 17.3.54.		
y sd y ad1 pyro4 sd pyro4	1	
y ad1 sd y ad1 pyro4 pyro4 sd	1	
y pyro4 y ad1 sd pyro4 sd ad1	1	

SUMMARY

Types of asci	Number of ascospores germinating. 0	1	2	3	4	5	6	7	8
Classifiable									
Selfed yellow	-	-	-	-	-	-	1	-	-/1
Selfed green	-	-	-	-	-	-	-	-	-
Hybrid	-	1	3	1	3	4	6	8	6/32
Non-classifiable									
Yellow	-	2	-	-	1	-	-	-	-/ 3
Green	-	-	-	-	-	-	-	-	-
No germination	-	-	-	-	-	-	-	-	-
Abnormal	-	-	-	-	-	1	1	-	-/ 2
Grand Total	-	3	3	1	4	5	8	8	6/38

Table C/.
Cross wn ad1 pro1 paba1 y//y pyro4. From streak inoculum on minimal medium. Prepared on the 13.2.54. Only the genotypes of the germinated spores are given. If there were only two spores of any one genotype, it was assumed that they were the result of the mitotic division.

Genotypes	Number of asci	Comments
Perithecium No.1. Dissected 23.3.54.		
wn ad1 pyro4 wn pro1 paba1 y pro1 paba1 y ad1 pyro4	1	
wn ad1 pro1 paba1 pyro4 wn pro1 paba1 y y ad1 pyro4	1	
wn ad1 pyro4 wn ad1 pro1 paba1 y pro1 paba1 pyro4 y	1	
wn ad1 pyro4 wn ad1 pyro4 y pro1 paba1 y pro1 paba1	1	
wn pyro4 wn ad1 pro1 paba1 y pyro4	2	
wn ad1 pro1 paba1 wn pro1 paba1 y pyro4 y ad1 pyro4	1	
wn ad1 wn ad1 pro1 paba1 pyro4 y pro1 paba1 y pyro4	1	
wn wn ad1 pro1 paba1 y ad1 pro1 paba1 pyro4 y pyro4	1	
wn pro1 paba1 y ad1 y ad1 pyro4	1	
y ad1 pro1 paba1pyro4	1	

Table C/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.2. Dissected 31.3.54.		
wn pro1 paba1	1	
wn pro1 paba1 pyro4		
y ad1 pyro4		
y ad1		
wn ad1 pro1 paba1 pyro4	2	
wn		
y pro1 paba1 pyro4		
y ad1		
Perithecium No.3. Dissected 1.4.54.		
wn ad1 pro1 paba1	1	
wn pyro4		
y ad1 pyro4		
y pro1 paba1		
wn pro1 paba1	1	
wn ad1 pro1 paba1 pyro4		
y ad1 pyro4		
y		
-	2	No growth
Perithecium No.4. Dissected 3.4.54.		
wn ad1 pyro4	1	
wn pro1 paba1		
y ad1 pro1 paba1 pyro4		
y		
wn ad1 pro1 paba1	2	
wn pyro4		
y ad1		
y pro1 paba1 pyro4		
wn ad1 pro1 paba1 pyro4	1	
wn pro1 paba1		
y ad1 pyro4		
y		
wn ad1 pro1 paba1	1	Single exchange pro1 - paba1
wn pro1 pyro4		
y paba1 pyro4		
y ad1		
wn ad1 pyro4	1	
wn		
y ad1 pro1 paba1		
y pro1 paba1 pyro4		
wn pro1 paba1 pyro4	1	
wn ad1 pro1 paba1		
y ad1		
y pyro4		

Table C/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.4. Dissected 3.4.54.		
wn pyro4 wn ad1 y pro1 paba1 y ad1 pro1 paba1 pyro4	1	
wn pro1 wn pro1 paba1 pyro4 y ad1 paba1 y ad1 pyro4	1	Single exchange pro1 - paba1
wn ad1 pro1 paba1 wn ad1 pyro4 y pro1 paba1 pyro4 y	1	
wn ad1 pro1 paba1 pyro4 wn y pyro4 y ad1 pro1 paba1	1	
Perithecium No.5. Dissected 6.4.54.		
wn ad1 pyro4 wn paba1 pyro4 y pro1 y ad1 pro1 paba1	1	Single exchange pro1 - paba1
wn ad1 wn ad1 pro1 paba1 y pro1 paba1x pyro4 y pyro4	1	
wn ad1 pyro4 wn y ad1 pro1 paba1 pyro4 y pro1 paba1	1	
wn ad1 wn pro1 paba1 pyro4 y ad1 pyro4	1	
wn pro1 paba1 pyro4 wn ad1 pro1 paba1 y pyro4 y ad1	1	
wn ad1 pro1 paba1 pyro4 wn y pro1 paba1 y ad1 pyro4	1	

Table C/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.5. Dissected 6.4.54.		
wn ad1 wn pro1 pyro4 y paba1 y ad1 pro1 paba1 pyro4	1	Single exchange pro1 - paba1
wn pro1 paba1 (2 spores) wn ad1 pyro4 (1 spore) y ad1 pro1 paba1 pyro4 (1 spore) y ad1 pyro4 (1 spore) y (2 spores)	1	ABNORMAL
wn ad1 pro1 paba1 wn ad1 pro1 pyro4 y paba1 y pyro4	1	Single exchange pro1 - paba1
wn pyro4 wn ad1 pro1 paba1 y pro1 paba1 y ad1 pyro4	1	
wn wn pro1 paba1 pyro4 y ad1 y ad1 pro1 paba1 pyro4	1	
wn ad1 pyro4 wn ad1 pro1 paba1 pyro4 y pro1 paba1 y	1	
wn pyro4 wn ad1 pro1 paba1 y pro1 paba1 pyro4 y ad1	1	
wn pro1 paba1 pyro4 wn pro1 paba1 y ad1 y ad1 pyro4	1	
Perithecium No.6. Dissected 10.4.54.		
y ad1 y	1	
wn pyro4 wn ad1 pyro4 y pro1 paba1 y ad1 pro1 paba1	2	

Table C/. cont[d].

Genotypes	Number of asci	Comments
Perithecium No.6. Dissected 10.4.54.		
wn ad1 pro1 paba1 wn y pro1 paba1 pyro4 y ad1 pyro4	1	
wn pyro4 wn ad1 y pro1 paba1 pyro4 y ad1 pro1 paba1	1	
wn ad1 pyro4 wn y pro1 paba1 y ad1 pro1 paba1 pyro4	1	
wn pyro4 wn ad1 y pro1 paba1 y ad1 pro1 paba1 pyro4	1	
wn pro1 paba1 wn ad1 pro1 paba1 pyro4 y ad1 pyro4 y	1	
Perithecium No.7. Dissected 10.4.54.		
wn pro1 paba1 pyro4 wn pro1 paba1 y ad1 pyro4 y ad1	1	
wn ad1 pro1 paba1 wn pyro4 y ad1 pro1 paba1 pyro4 y	1	
wn pyro4 wn ad1 pyro4 y ad1 pro1 paba1 y pro1 paba1	1	
wn ad1 pro1 paba1 wn pro1 pyro4 y paba1 pyro4 y ad1	1	Single exchange pro1 - paba1
Perithecium No.8. Dissected 14.4.54.		
wn pro1 pyro4 wn pro1 paba1 y ad1 y ad1 paba1 pyro4	1	Single exchange pro1 - paba1

Table C/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.8. Dissected 14.4.54.		
wn ad1 pro1 paba1 wn ad1 pro1 y paba1 pyro4 y pyro4	1	Single exchange pro1 - paba1
wn pro1 paba1 pyro4 wn ad1 pro1 paba1 y ad1 pyro4 y	1	
wn pro1 paba1 pyro4 wn ad1 y pro1 paba1 pyro4 y ad1	1	
wn pro1 paba1 pyro4 wn pro1 paba1 y ad1 pyro4 y ad1	1	
wn ad1 wn pyro4 y ad1 pro1 paba1 pyro4	1	
wn pro1 paba1 wn ad1 pro1 paba1 pyro4 y	1	
wn pyro4 wn ad1 pro1 y ad1 paba1 y pro1 paba1 pyro4	1	Single exchange pro1 - paba1
wn ad1 wn pyro4 y pro1 paba1 y ad1 pro1 paba1 pyro4	1	
wn ad1 pro1 paba1 pyro4 y y ad1 pyro4	1	
wn ad1 pro1 paba1 wn ad1 pyro4 y y pro1 paba1 pyro4	1	
wn wn ad1 pyro4 y ad1 pro1 paba1 pyro4 y pro1 paba1	1	

Table C/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.8. Dissected 14.4.54.		
wn ad1 pro1 paba1 wn y ad1 pyro4 y pro1 paba1 pyro4	1	
Perithecium No.9. Dissected 17.4.54.		
wn ad1 pro1 paba1 wn ad1 pyro4 y pro1 paba1 pyro4 y	1	
-	3	No growth
wn ad1 pyro4 y	1	
wn pro1 paba1 pyro4 wn ad1 pyro4 y ad1 y pro1 paba1	1	
wn pro1 paba1 pyro4 wn ad1 y ad1 pro1 paba1 y pyro4	1	
wn pro1 paba1 pyro4 wn ad1 pro1 y y ad1 paba1 pyro4	1	Single exchange pro1 - paba1
wn pro1 paba1 wn ad1 pro1 pyro4 y ad1 pyro4 y paba1	1	Single exchange pro1 - paba1
wn ad1 wn y ad1 pro1 paba1 pyro4 y pro1 paba1 pyro4	1	
wn ad1 y pro1 paba1 pyro4	1	
y ad1 pro1 paba1 pyro4	1	
wn pyro4 y ad1 pyro4	1	

Table C/. cont[d].

Genotypes	Number of asci	Comments
Perithecium No.10. Dissected 26.4.54.		
wn pyro4 wn ad1 pro1 paba1 pyro4 y pro1 paba1 y ad1	1	
wn pro1 paba1 pyro4 wn ad1 y pro1 paba1 pyro4 y ad1	2	
wn pro1 paba1 wn ad1 pro1 paba1 y ad1 pyro4 y pyro4	1	
wn ad1 pro1 paba1 pyro4 wn y ad1 y pro1 paba1 pyro4	1	
wn ad1 paba1 wn pro1 paba1 pyro4 y ad1 y pro1 pyro4	1	Single exchange pro1 - paba1
wn pro1 paba1 pyro4 wn ad1 pyro4 y ad1 pro1 y paba1	1	Single exchange pro1 - paba1
wn pro1 paba1 pyro4 wn pro1 paba1 y ad1 y ad1 pyro4	1	
wn pro1 paba1 wn ad1 pyro4 y ad1 pro1 paba1 y pyro4	1	
wn ad1 pro1 paba1 wn ad1 pyro4 y pro1 paba1 y pyro4	1	
wn pro1 paba1 y ad1 pyro4	1	

Table C/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.11. Dissected 29.4.54.		
wn ad1 pro1 paba1 pyro4 wn pro1 paba1 y ad1 y pyro4	1	
wn pyro4 wn ad1 pyro4 y ad1 pro1 paba1 y pro1 paba1	1	
wn pro1 paba1 pyro4 wn ad1 y pro1 paba1 pyro4 y ad1	1	
Perithecium No.12. Dissected 29.4.54.		
wn pro1 paba1 pyro4 wn pyro4 y ad1	1	
wn pro1 paba1 pyro4 y ad1 y	1	
wn pro1 paba1 pyro4 wn ad1 pro1 y y ad1 paba1 pyro4	1	Single exchange pro1 - paba1
wn ad1 pyro4 wn ad1 pro1 paba1 pyro4 y pro1 paba1 y	1	
wn pro1 paba1 pyro4 y ad1 pro1 paba1 pyro4 y	1	
wn ad1 pro1 paba1 pyro4 y ad1	1	
wn pyro4 y ad1 pro1 paba1	1	
Perithecium No.13. Dissected 6.5.54.		
wn ad1 pro1 paba1 pyro4 wn ad1 y pro1 paba1 y pyro4	1	

Table C/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.13. Dissected 6.5.54.		
wn ad1 pro1 paba1 pyro4 wn ad1 pro1 paba1 y pyro4 y	1	
wn pyro4 wn y ad1 pro1 paba1 pyro4 y ad1 pro1 paba1	1	
wn pyro4 wn ad1 pro1 paba1 y pro1 paba1 pyro4 y ad1	1	
wn pro1 paba1 wn y ad1 pro1 pyro4 y ad1 paba1 pyro4	1	Single exchange pro1 - paba1
wn ad1 pro1 paba1 pyro4 wn y ad1 paba1 y pro1 pyro4	1	Single exchange pro1 - paba1
wn pro1 paba1 pyro4 wn y ad1 pyro4 y ad1 pro1 paba1	1	
wn ad1 pro1 paba1 pyro4 wn pyro4 y ad1 pro1 paba1 y	1	
wn ad1 pyro4 wn y ad1 pro1 paba1 pyro4 y pro1 paba1	1	
wn pro1 paba1 wn ad1 pyro4 y pro1 paba1 pyro4 y ad1	1	
Perithecium No.14. Dissected 13.5.54.		
wn ad1 pro1 paba1 pyro4 wn ad1 y pro1 paba1 y pyro4	1	

Table C/. cont[d].

Genotypes	Number of asci	Comments
wn pyro4 wn ad1 y pro1 paba1 pyro4 y ad1 pro1 paba1	1	
wn pro1 paba1 pyro4 wn pro1 pyro4 y ad1 paba1 y ad1	1	Single exchange pro1 - paba1
wn pro1 paba1 wn pro1 paba1 pyro4 y ad1 y ad1 pyro4	1	
wn paba 1 pyro4 wn y ad1 pro1 y ad1 pro1 paba1 pyro4	1	Single exchange pro1 - paba1
wn pyro4 y ad1 pro1 paba1 y pro1 paba1	1	
wn pro1 paba1 wn ad1 pyro4 y ad1 pro1 paba1 pyro4 y	1	
wn pro1 paba1 wn ad1 y ad1 pro1 paba1 pyro4 y pyro4	1	
wn pro1 paba1 pyro4 wn y ad1 pro1 paba1 pyro4 y ad1	1	
wn ad1 pro1 paba1 pyro4 wn y ad1 pro1 paba1 y pyro4	1	

Table C/. cont[d].

SUMMARY.

Types of asci	Number of ascospores germinating. 0	1	2	3	4	5	6	7	8
Classifiable									
Selfed white	-	-	-	-	-	-	-	-	-
Selfed yellow	-	-	-	-	-	-	-	-	-
Hybrid	-	2	6	2	3	5	20	34	44/116
Non-classifiable									
White	-	-	-	-	-	-	-	-	-
Yellow	-	-	-	-	-	-	-	-	-
No germination	5	-	-	-	-	-	-	-	-/ 5
Abnormal	-	-	-	-	--	-	-	1	-/ 1
Grand Total	5	2	6	2	3	5	20	35	44/122

Table D/.

Cross wn ad14//y sd. From streak inoculum on minimal medium. Prepared on the 25.5.54. Only the genotypes of the germinated spores are given. If there were only two spores of any one genotype, it was assumed that they were the result of the mitotic division.

Genotypes	Number of asci	Comments
Perithecium No.1. Dissected 26.7.54.		
wn y y ad14 sd	1	
wn wn sd y ad14 sd y ad14	1	
wn ad14 y ad14 sd y sd	1	
wn sd wn ad14 y ad14 y sd	1	
wn sd y ad14 sd y ad14	1	
wn ad14 wn ad14 sd y y sd	2	
wn ad14 wn sd y ad14 sd y	2	
wn ad14 wn ad14 y sd y sd	1	
wn ad14 sd wn y ad14 y sd	1	
wn wn ad14 sd y ad14 sd y	1	

Table D./. cont.

Genotypes	Number of asci.	Comments.
Perithecium no.1. Dissected 26.7.54.		
wn ad14 sd wn sd y	1	
Perithecium no.2. Dissected 30.7.54.		
wn sd wn y ad14 sd y ad14	2	
wn wn ad14 sd y sd y ad14	2	
wn ad14 wn sd y y ad14 sd	1	
wn ad14 sd wn ad14 y sd y	3	
wn wn ad14 sd y y ad14 sd	1	
wn ad14 wn y ad14 sd y sd	1	
wn ad14 sd wn ad14 sd y y	1	

SUMMARY

Types of asci	Number of ascospores germinating. 0.	1.	2.	3.	4.	5.	6.	7.	8.
Classifiable									
Selfed white	-	-	-	-	-	-	-	-	-
Selfed yellow	-	-	-	-	-	-	-	-	-
Hybrid	-	-	-	-	3	-	4	3	14/24
Non-classifiable	None.								
Grand Total	-	-	-	-	3	-	4	3	14/24

Table E/.
Cross wn ad14 y//bi1 thi2. From streak inoculum on minimal medium. Prepared on the 15.7.54. Only the genotypes of the germinated spores are given. If there were only two spores of any one genotype, it was assumed that they were the result of the mitotic division.

Genotypes	Number of asci	Comments
Perithecium No.1. Dissected 16.9.54.		
wn wn bi1 thi2 y ad14 ad14 bi1 thi2	2	
wn thi2 wn ad14 thi2 ad14 bi1 bi1	2	
wn wn ad14 bi1 thi2 + + + + ad14 bi1 thi2	1	
wn ad14 bi1 thi2 wn ad14 bi1 thi2 + + + +	1	
-	1	No growth
Perithecium No.2. Dissected 17.9.54.		
wn thi2 wn bi1 y ad14 ad14 bi1 thi2	1	
wn ad14 thi2 wn thi2 y ad14 bi1	1	
wn ad14 wn bi1 y ad14 thi2 bi1 thi2	1	
wn bi1 wn ad14 thi2 y ad14 bi1 thi2	1	
wn thi2 y ad14 bi1 y ad14	1	

Table E./. cont.

SUMMARY.

Types of asci	Number of ascospores germinating. 0.	1.	2.	3.	4.	5.	6.	7.	8.
Classifiable									
Selfed white	-	-	-	-	-	-	-	-	-
Selfed green	-	-	-	-	-	-	-	-	-
Hybrid	-	-	-	-	-	1	3	4	3/11
Non-classifiable									
White	-	-	-	-	-	-	-	-	-
Green	-	-	-	-	-	-	-	-	-
No germination	1	-	-	-	-	-	-	-	-/1
Grand Total	1	-	-	-	-	1	3	4	3/12

Table F/.
Cross wn ad14 y// bi1 met1. From streak inoculum on minimal medium. Prepared on the 20.8.54. Only the genotypes of the germinated spores are given. If there were only two spores of any one genotype, it was assumed that they were the result of the mitotic division. The bi1marker was not used.

Genotypes	Number of asci	Comments.
Perithecium No.1. Dissected 25.10.54.		
wn ad14 wn ad14 met1 met1	1	
wn wn ad14 y ad14 met1 y met1	1	
wn ad14 met1 wn ad14 met1 + + + +	1	
wn ad14 met1 wn ad14 y y met1	1	
wn ad14 wn met1 y y ad14 met1	1	
wn wn y ad14 met1 y ad14 met1	1	
wn wn met1 y ad14 y ad14 met1	1	
wn wn ad14 y ad14 met1	1	
wn met1 wn met1 y ad14 y ad14	1	

Table F./. cont.

Genotypes	Number of asci.	Comments.
Perithecium no.1.	Dissected 25.10.54.	
wn met1 wn ad14 y ad14 met1	1	
wn wn ad14 met1 ad14 met1 + + +	2	
wn wn ad14 met1 ad14 met1	1	
wn ad14 met1 wn ad14 met1 + + + + + +	2	
wn met1 wn y ad14 met1 ad14	1	
wn ad14 met1 wn met1 + + +	1	
wn ad14 met1 y ad14 met1	1	
Perithecium no.2.	Dissected 28.10.54.	
wn wn met1 y ad14 met1 ad14	1	
wn ad14 wn ad14 met1 met1	1	
wn ad14 wn met1 y ad14 met1	1	
wn ad14 met1 wn ad14 + + + met1	1	

Table F./. cont.

Genotypes	Number of asci.	Comments.
Perithecium no.2. Dissected 28.10.54.		
wn wn ad14 met1 y met1 y ad14	1	
wn ad14 wn met1 y ad14 met1 + + +	1	
wn ad14 wn ad14 met1 y	1	
wn wn met1 ad14 ad14 met1	1	
wn wn ad14 y ad14 met1 met1	2	
wn met1 wn ad14 y met1 ad14	1	
wn ad14 wn ad14 met1 y met1 + + +	1	
wn ad14 wn ad14 y met1 y met1	1	
wn ad14 met1 (2 spores) wn met1 (1 spore) wn ad14 (1 spore) + + + (1 spore) (Haploid) ad14 (1 spore) met1 (1 spore)	1	ABNORMAL
wn ad14 met1 ad14 met1	1	

Table F./. cont.

Genotypes	Number of asci.	Comments.
Perithecium no.3. Dissected 1.11.54.		
wn met1 wn ad14 y ad14 met1	1	
wn ad14 met1 wn + + + ad14 met1	1	
wn ad14 met1 wn y ad14 met1	2	
wn ad14 wn met1 y ad14 met1	1	
wn wn ad14 met1 y met1 ad14	1	
wn ad14 met1 wn ad14 met1 + + + + + +	1	
wn wn ad14 y ad14 met1 met1	1	
wn ad14 met1 wn ad14 met1 y	1	
wn wn ad14 y met1 ad14 met1	1	
wn wn ad14 y met1 y ad14 met1	1	
wn met1 wn ad14 met1 y ad14 + + +	1	

Table F./. cont.

Genotypes	Number of asci.	Comments.
Perithecium no.3. Dissected 1.11.54.		
wm ad14 met1 y + + +	2	
wm ad14 met1 ad14	1	
wm met1 wm ad14 met1 ad14 + + +	1	
wm met1 y ad14 ad14	1	
wm ad14 wm met1	1	
y ad14 met1	1	
wm y ad14	1	

SUMMARY.

Types of asci	Number of ascospores germinating. 0.	1.	2.	3.	4.	5.	6.	7.	8.
Classifiable									
Selfed white	-	-	-	-	-	-	-	-	-
Selfed green	-	-	-	-	-	-	-	-	-
Hybrid	-	1	1	1	3	2	11	16	17/52
Non-classifiable	None								
Abnormal	-	-	-	-	-	-	-	1	-/1
Grand Total	-	1	1	1	3	2	11	17	17/53

Table G/.
Cross pro1 bi1//paba1 y ad8. From streak inoculum on minimal medium. Prepared on the 23.12.54. Only the genotypes of the germinated spores are given. If there were only two spores of any one genotype, it was assumed that they were the result of the mitotic division.

Genotypes	Number of asci	Comments
Perithecium No.1. Dissected 10.1.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	11	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	5	No exchanges
paba1 y ad8 pro1 bi1 pro1 bi1	3	No exchanges
paba1 y ad8 pro1 paba1 y ad8 bi1 pro1 bi1	3	Single exchanges pro1 - paba1
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	3	Single exchanges paba1 - y
paba1 y ad8 pro1 y ad8 pro1 bi1	1	Single exchange paba1 - y
paba1 y ad8 paba1 y ad8 bi1 pro1 pro1 bi1	2	Single exchanges y - bi1
paba 1 y ad8 paba1 y ad8 bi1 pro1	1	Single exchange y - bi1
y ad8 pro1 paba1 y ad8 paba1 bi1 pro1 bi1	1	Double exchange pro1 - paba1; paba1 - y
paba1 y ad8 bi1 y ad8 pro1 bi1	1	Double exchange pro1 - paba1; y - bi1

Table G/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.2. Dissected 17.1.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	12	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	2	No exchanges
paba1 y ad8 pro1 bi1 pro1 bi1	3	No exchanges
paba1 y ad8 pro1 paba1 y ad8 bi1 pro1 bi1	3	Single exchanges pro1 - paba1
paba1 y ad8 pro1 paba1 y ad8 pro1 bi1	1	Single exchange pro1 - paba1
paba1y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	2	Single exchanges paba1 - y
pro1 y ad8 paba1 bi1 pro1 bi1	1	Single exchange paba1- y
paba1y ad8 pro1 y ad8 paba1 bi1	1	Single exchange paba1- y
paba1y ad8 paba1 y ad8 bi1 pro1 pro1 bi1	2	Single exchanges y - bi1
pro1 y ad8 pro1 y ad8 bi1 paba1 paba1 bi1	1	4-strand double exchange within paba1 - y; single exchange y - bi1
paba1y ad8 pro1 bi1	3	Incomplete
paba1 y ad8	1	Incomplete

Table G/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.2. Dissected 17.1.55.		
paba1 y ad8 bi1 (2 spores) pro1 bi1 (3 spores)	1	ABNORMAL
Perithecium No.3. Dissected 21.1.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	8	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	5	No exchanges
paba1 y ad8 pro1 paba1 y ad8 bi1 pro1 bi1	1	Single exchange pro1 - paba1
paba1 y ad8 pro1 y ad8 paba1 bi1	4	Single exchanges paba1 - y
paba1 y ad8 pro1 y ad8 pro1 bi1	2	Single exchanges paba1 - y
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	2	Single exchanges paba1 - y
paba1 y ad8 paba1 y ad8 bi1 pro1	1	Single exchange y - bi1
pro1 paba1 y ad8 y ad8 bi1	1	4-strand double exchange within pro1 - paba1; single exchange paba1 - y
pro1 paba1 y ad8 paba1 y ad8 bi1 pro1 bi1	1	4-strand double exchange pro1 - paba1; y - bi1
paba1 y ad8 pro1 bi1	2	Incomplete
-	1	No growth

Table G/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.4. Dissected 14.2.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	9	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	2	No exchanges
paba1 y ad8 pro1 bi1 pro1 bi1	2	No exchanges
paba1 y ad8 pro1 paba1 y ad8 bi1 pro1 bi1	1	Single exchange pro1 - paba1
paba1 y ad8 bi1 pro1 bi1	1	Single exchange pro1 - paba1
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	1	Single exchange paba - y
paba1 y ad8 paba1 bi1 pro1 bi1	1	Single exchange paba1 - y
paba1 y ad8 paba1 y ad8 bi1 pro1 pro1 bi1	1	Single exchange y - bi1
Perithecium No.5. Dissected 18.2.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	5	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	1	No exchange
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	2	Single exchanges paba1 - y

Table G/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.5. Dissected 18.2.55.		
paba1 y ad8 pro1 y ad8 pro1 bi1	1	Single exchange paba1 - y
paba1 y ad8 paba1 y ad8 bi1 pro1 pro1 bi1	2	Single exchanges y - bi1
paba1 y ad8 pro1 pro1 bi1	1	Single exchange y - bi1
paba1 y ad8 bi1 paba1 y ad8 bi1 pro1 pro1	1	4-strand double exchange within y - bi1
paba1 y ad8 pro1 bi1	4	Incomplete
pro1 bi1 pro1 bi1	1	Incomplete
Perithecium No.6. Dissected 24.2.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	7	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	4	No exchanges
paba1 y ad8 pro1 bi1 pro1 bi1	5	No exchanges
paba1 y ad8 pro1 paba1 y ad8 bi1 pro1 bi1	1	Single exchange pro1 - paba1
paba1 y ad8 pro1 y ad8 paba1 bi1	1	Single exchange paba1 - y
paba1 y ad8 paba1 bi1 pro1 bi1	1	Single exchange paba1 - y

Table G/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.6. Dissected 24.2.55.		
pro1 y ad8 paba1 bi1 pro1 bi1	1	Single exchange paba1 - y
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	1	Single exchange paba1 - y
pro1 y ad8 pro1 paba1 y ad8 bi1 paba1 bi1	1	4-strand double exchange pro1 - paba1; paba1 - y
paba1 y ad8 pro1 y ad8 pro1 paba1 bi1	1	3-strand double exchange pro1 - paba1; paba1 - y
paba1 y ad8 pro1 y ad8 bi1 pro1 bi1	1	2-strand double exchange paba1 - y; y - bi1
paba1y ad8 pro1 bi1	4	Incomplete
paba1 y ad8	1	Incomplete
pro1 bi1	1	Incomplete
-	1	No growth
Perithecium No.7. Dissected 28.2.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	5	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	4	No exchanges
paba1 y ad8 pro1 bi1 pro1 bi1	3	No exchanges
paba1 y ad8 pro1 paba1 y ad8 pro1 bi1	1	Single exchange pro1 - paba1

Table G/T cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.7. Dissected 28.2.55.		
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	7	Single exchanges paba1 - y
paba1 y ad8 pro1 y ad8 paba1 bi1	2	Single exchanges paba1 - y
pro1 y ad8 pro1 y ad8 paba1 bi1 paba1 bi1	2	4-strand double exchanges within paba1 - y
paba1 y ad8 paba1 y ad8 bi1 pro1	1	Single exchange y - bi1
paba1 y ad8 paba1 y ad8 bi1 pro1 bi1	1	Single exchange y - bi1
paba1 y ad8 pro1 y ad8 bi1 paba1 bi1 pro1	1	3-strand double exchange paba1 - y; y - bi1
pro1 paba1 y ad8 pro1 paba1 y ad8 bi1 bi1	1	4-strand double exchange within pro1 - paba1; single exchange y - bi1
paba1 y ad8 pro1 bi1	3	Incomplete
paba1 y ad8 paba1 y ad8	1	Incomplete
Perithecium No.8. Dissected 2.3.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	5	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	5	No exchanges
paba1 y ad8 pro1 bi1 pro1 bi1	4	No exchanges

Table G/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.8. Dissected 2.3.55.		
paba1 y ad8 pro1 paba1 y ad8 bi1 pro1 bi1	2	Single exchanges pro1 - paba1
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	7	Single exchanges paba1 - y
paba1 y ad8 pro1 y ad8 pro1 bi1	2	Single exchanges paba1 - y
paba1 y ad8 paba1 y ad8 bi1 pro1 pro1 bi1	1	Single exchange y - bi1
pro1 y ad8 pro1 paba1 y ad8 bi1 paba1 bi1	1	4-strand double exchange pro1 - paba1; paba1 - y
pro1 bi1 paba1 bi1	1	Incomplete
paba1 y ad8 pro1 bi1	2	Incomplete
-	1	No growth
Perithecium No.9. Dissected 4.3.55.		
N.B. This perithecium carried a semi-lethal factor (Dwarf = dw)		
paba1 y ad8 pro1 bi1	20	
paba1 y ad8 pro1 y ad8	4	
paba1 bi1 pro1 bi1	1	
paba1 bi1	1	
pro1 bi1	5	
paba1 y ad8	4	
paba1 y ad8 paba1 y ad8	1	

Table G/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.9. Dissected 4.3.55.		
paba1 y ad8 bi1	2	
pro1 y ad8	1	
pro1 bi1 bi1	1	
paba1 y ad8 pro1 paba1 y ad8 bi1	1	
pro1	1	
pro1 paba1ad8 bi1	1	
pro1 y ad8 paba1 bi1	2	
pro1 paba1 y paba1 y ad8	1	
paba1 y ad8 pro1 bi1 pro1 bi1 dw	2	dw = semi-lethal dwarf.
paba1 y ad8 paba1 y ad8 pro1 bi1 dw	2	
paba1 y ad8 pro1 y ad8 dw paba1 bi1	1	
paba1 y ad8 dw pro1 y ad8 pro1 bi1 paba1 bi1 dw	1	
paba1 y ad8 paba1 y ad8 dw	1	
paba1 y ad8 dw pro1 y ad8 bi1 paba1 dw pro1 bi1	1	
paba1 y ad8 pro1 y ad8 bi1 paba1 dw	1	
paba1 bi1 dw	1	

Table G/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.9. Dissected 4.3.55.		
-	6	No growth
Perithecium No.10. Dissected 14.3.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	15	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	1	No exchange
paba1 y ad8 pro1 bi1 pro1 bi1	2	No exchanges
paba1 y ad8 pro1 paba1 y ad8 bi1 pro1 bi1	2	Single exchanges pro1 - paba1
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	2	Single exchanges paba1 - y
pro1 y ad8 pro1 y ad8 paba1 bi1	1	4-strand double exchange within paba1 - y
paba1 y ad8 paba1 y ad8 bi1 pro1 pro1 bi1	1	Single exchange y - bi1
paba1 y ad8 pro1 y ad8 bi1 paba1 pro1 bi1	1	2-strand double exchange paba1 - y; y - bi1
paba1 y ad8 pro1 paba1 y ad8 bi1 + + + + + pro1 bi1	1	2-strand double exchange pro1 - paba1; y - bi1
paba1 y ad8 y ad8 pro1 paba1 bi1 pro1 bi1	1	2-strand double exchange pro1 - paba1; paba1 - y

Table G/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.10. Dissected 14.3.55.		
paba1 y ad8 pro1 bi1	1	Incomplete
Perithecium No.11. Dissected 15.3.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	7	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	4	No exchanges
paba1 y ad8 pro1 bi1 pro1 bi1	2	No exchanges
paba1 y ad8 pro1 paba1 y ad8 bi1 pro1 bi1	2	Single exchanges pro1 - paba1
paba1 y ad8 pro1 paba1 y ad8 pro1 bi1	1	Single exchange pro1 - paba1
paba1 y ad8 paba1 bi1 pro1 bi1	1	Single exchange paba1 - y
paba1 y ad8 pro1 y ad8 paba1 bi1	1	Single exchange paba1 - y
paba1 y ad8 pro1 y ad8 pro1 bi1	1	Single exchange paba1 - y
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	3	Single exchanges paba1 - y
pro1 y ad8 paba1 bi1 paba1 bi1	1	4-strand double exchange within paba1 - y
pro1 paba1 y ad8 y ad8 pro1 paba1 bi1	1	4-strand double exchange within pro1 - paba1; single exchange paba1 - y

Table G/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.11. Dissected 15.3.55.		
pro1 paba1 y ad8 y ad8 paba1 bi1 pro1 bi1	1	3-strand double exchange pro1 - paba1; paba1 - y
paba1 y ad8 y ad8 pro1 bi1	1	2-strand double exchange pro1 - paba1; paba1 - y
paba1 y ad8 pro1 bi1	2	Incomplete
paba1 y ad8 paba1 y ad8	1	Incomplete
-	2	No growth
Perithecium No.12. Dissected 16.3.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	14	No exchanges
paba1 y ad8 pro1 bi1 pro1 bi1	1	No exchange
paba1 y ad8 pro1 paba1 y ad8 bi1 pro1 bi1	2	Single exchanges pro1 - paba1
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	6	Single exchanges paba1 - y
paba1 y ad8 paba1 bi1 pro1 bi1	1	Single exchange paba1 - y
pro1 y ad8 pro1 y ad8 paba1 bi1 paba1 bi1	1	4-strand double exchange within paba1 - y
pro1 paba1 y ad8 pro1 paba1 y ad8 bi1 bi1	1	4-strand double exchange within pro1 - paba1

Table G/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.12. Dissected 16.3.55.		
pro1 paba1 y ad8 pro1 paba1 bi1 y ad8 bi1	1	4-strand double exchange within pro1 - paba1; single exchange paba1 - y
paba1 y ad8 y ad8 pro1 paba1 bi1 pro1 bi1	1	2-strand double exchange pro1 - paba1; paba1 - y
paba1 y ad8 pro1 bi1	2	Incomplete
Perithecium No.13. Dissected 17.3.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	8	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	4	No exchanges
paba1 y ad8 pro1 bi1 pro1 bi1	1	No exchange
paba1 y ad8 pro1 paba1 y ad8 bi1 pro1 bi1	4	Single exchanges pro1 - paba1
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	7	Single exchanges paba1 - y
paba1 y ad8 pro1 y ad8 pro1 bi1	1	Single exchange paba1 - y
pro1 y ad8 pro1 y ad8 paba1 bi1 paba1 bi1	1	4-strand double exchange within paba1 - y
paba1 y ad8 pro1 paba1 y ad8 bi1 pro1 bi1	1	3-strand double exchange pro1 - paba1; y - bi1

Table G/. cont[d].

Genotypes	Number of asci	Comments
Perithecium No.13. Dissected 17.3.55.		
pro1 y ad8 bi1 paba1 y ad8 pro1 paba1 bi1	1	3-strand double exchange paba1 - y; y - bi1
pro1 paba1 y ad8 y ad8 bi1 pro1 paba1 bi1	1	3-strand double exchanges pro1 - paba1; paba1 - y and paba1 - y; y - bi1. 4-strand double exchange pro1 - paba1; y - bi1
paba1 y ad8 pro1 bi1	1	Incomplete
-	1	No growth
Perithecium No.14. Dissected 18.3.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	6	Nox exchanges
paba1 y ad8 pro1 bi1 pro1 bi1	2	No exchanges
paba1 y ad8 paba1 y ad8 bi1 pro1 pro1 bi1	1	Single exchange y - bi1
paba1 y ad8 bi1 pro1 y ad8 pro1 paba1 bi1	1	4-strand double exchange paba1 - y; y - bi1
paba1 y ad8	1	Incomplete
Perithecium No.15. Dissected 18.3.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	6	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	1	No exchange
paba1 y ad8 pro1 bi1 pro1 bi1	3	No exchanges

Table G/. cont[d].

Genotypes	Number of asci	Comments
Perithecium No.15. Dissected 183.55.		
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	3	Single exchanges paba1 - y
paba1 y ad8 paba1 y pro1 bi1	1	2-strand double exchange y - ad8; ad8 - bi1
paba1 y ad8 pro1 bi1	2	Incomplete
paba1 y ad8	1	Incomplete
paba1 y ad8 (4 spores) pro1 bi1 (2 spores) pro1 (2 spores)	1	ABNORMAL
Perithecium No.16. Dissected 28.3.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	7	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	3	No exchanges
paba1 y ad8 pro1 bi1 pro1 bi1	6	No exchanges
paba1 y ad8 pro1 paba1 y ad8 bi1 pro1 bi1	2	Single exchanges pro1 - paba1
paba1 y ad8 pro1 y ad8 paba1 bi1	2	Single exchanges paba1 - y
paba1 y ad8 paba1 bi1 pro1 bi1	1	Single exchange paba1 - y
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	7	Single exchanges paba1 - y

Table G/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.16. Dissected 28.3.55.		
paba1 y ad8 pro1 pro1 bi1	1	Single exchange y - bi1
pro1 paba1 y ad8 y ad8 paba1 bi1 pro1 bi1	1	3-strand double exchange pro1 - paba1; paba1 - y
-	3	No growth
Perithecium No.17. 29.3.55. Dissected		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	6	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	6	No exchanges
paba1 y ad8 paba1 bi1 pro1 bi1	1	Single exchange paba1 - y
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	5	Single exchanges paba1 - y
paba1 y ad8 paba1 y ad8 bi1 pro1 pro1 bi1	1	Single exchange y - bi1
paba1 y ad8 pro1 y ad8 bi1 paba1 bi1	1	3-strand double exchange paba1 - y; y - bi1
pro1 paba1 y ad8 pro1 paba1 y ad8 bi1 bi1 + + + + +	1	4-strand double exchange within pro1 - paba1; single exchange y - bi1
paba1 y ad8 pro1 paba1 y ad8 bi1 + + + + + pro1 bi1	1	2-strand double exchange pro1 - paba1; y - bi1
paba1 y ad8 pro1 bi1	2	Incomplete

Table G/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.17. Dissected 29.3.55.		
paba1 y ad8	4	Incomplete
pro1 y ad8	1	Incomplete
pro1 paba1 y ad8 paba1 y ad8	1	Incomplete
-	2	No growth
paba1 y ad8 (2 spores) pro1 paba1 y ad8 (1 spore) pro1 bi1 (2 spores) + + + + + (1 haploid spore)	1	ABNORMAL
Perithecium No.18. Dissected 31.3.55.		
paba1 y ad8 paba1 y ad8 pro1 bi1 pro1 bi1	5	No exchanges
paba1 y ad8 pro1 bi1 pro1 bi1	2	No exchanges
paba1 y ad8 paba1 y ad8 pro1 bi1	1	No exchange
paba1 y ad8 pro1 paba1 y ad8 bi1 pro1 bi1	1	Single exchange pro1 - paba1
paba1 y ad8 pro1 y ad8 paba1 bi1 pro1 bi1	1	Single exchange paba1 - y
paba1 y ad8 paba1 y ad8 bi1 pro1 pro1 bi1	1	Single exchange y - bi1
pro1 y ad8 bi1 paba1 y ad8 bi1 pro1	1	4-strand double exchange within y - bi1; single exchange paba1 - y
pro1 bi1	1	Incomplete

Table G/. cont^{d}.

SUMMARY.

Types of asci	Number of ascospores germinating. 0	1	2	3	4	5	6	7	8
Selfed green	-	-	-	-	-	-	-	-	-
Selfed yellow	-	-	-	-	-	-	-	-	-
Hybrid	-	2	6	10	31	84	91	112	87/436
Non-classifiable									
Green	-	-	2	-	1	-	-	-	-/ 3
Yellow	-	3	5	2	-	-	-	-	-/ 10
No germination	11	-	-	-	-	-	-	-	-/ 11
Abnormal	-	-	-	-	-	1	1	-	1/ 3
Perithecium No. 9 (semi-lethal)	6	5	17	14	15	3	2	-	-/ 62
Grand Total	17	10	30	26	47	88	94	112	88/512

Table H/.
Cross ribo ad14 paba1 y//an pro1 bi1 pyro4. From streak inoculum on minimal medium. Prepared on the 9.7.55. Only the genotypes of the germinated spores are given. If there were only two spores of any one genotype, it was assumed that they were the result of the mitotic division.

Genotypes	Number of asci	Comments
Perithecium No.1. Dissected 9.9.55.		
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1	2	No exchanges
ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1 pyro4	1	No exchange
ribo ad14 paba1 y ribo an pro1 bi1 pyro4 ad14 paba1 y an pro1 bi1 pyro4	1	Single exchange ribo - an
ribo ad14 paba1 y an paba1 y pyro4 ribo ad14 pro1 bi1 pyro4 an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 paba1 y ribo ad14 pro1 bi1 pyro4 an paba1 y an pro1 bi1 pyro4	1	Single exchange ad14 - pro1
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 pyro4 an paba1 y an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an paba1 y an pro1 bi1 pyro4	1	Single exchange ad14 - pro1
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 pyro4 an paba1 y	1	Single exchange ad14 - pro1
ribo ad14 pro1 bi1 pyro4 an paba1 y an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 pro1 bi1 pyro4 ribo ad14 pro1 bi1 pyro4 an paba1 y	1	4-strand double exchange within ad14 - pro1

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.1. Dissected 9.9.55.		
ribo ad14 paba1 y ribo ad14 bi1 pyro4 an pro1 paba1 y an pro1 bi1 pyro4	1	Single exchange pro1 - paba1
ribo ad14 paba1 bi1 pyro4 an pro1 y an pro1 bi1	1	Single exchange paba1 - y
ribo pro1 bi1 pyro4 ribo ad14 pro1 bi1 pyro4 an paba1 y an ad14 paba1 y	1	4-strand double exchange an - ad14; ad14 - pro1
ribo pro1 bi1 pyro4 ribo ad14 pro1 bi1 an paba1 y pyro4 an ad14 paba1 y	1	4-strand double exchange an - ad14; ad14 - pro1
ribo an pro1 y ad14 paba1 y pyro4 an pro1 bi1 pyro4	1	3-strand double exchange ribo - an; paba1 - y
ribo ad 14 paba1 y ribo pro1 bi1 an ad14 bi1 pyro4 an pro1 paba1 y pyro4	1	3-strand double exchange an - ad14; pro1 - paba1
ribo ad14 y pyro4 ribo ad14 paba1 bi1 pyro4 an pro1 bi1	1	3-strand double exchange pro1 - paba1; paba1 - y
ribo ad14 pro1 y pyro4 an paba1 bi1 an pro1 bi1 pyro4	1	2-strand double exchange ad14 - pro1; paba1 - y
ribo ad14 paba1 y pyro4 an paba1 bi1 pyro4 an pro1 bi1	1	2-strand double exchange ad14 - pro1; paba1 - y
ribo ad14 paba1 y an pro1 y bi1 pyro4 an pro1 bi1	1	2-strand double exchange paba1 - y; y - bi1
ribo ad14 y pyro4 ribo ad14 paba1 bi1 an pro1 y an pro1 paba1 bi1 pyro4	1	4-strand double exchange within paba1 - y; single exchange pro1 - paba1

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.1. Dissected 9.9.55.		
ribo pro1 bi1 ribo an ad14 paba1 y pyro4 an paba1 y pyro4 ad14 pro1 bi1	1	3-strand double exchanges ribo - an; an - ad14 and ribo - an; ad14 - pro1. 4-strand double exchange an - ad14; ad14 - pro1
ribo an paba1 y an paba1 y pyro4 ad14 pro1 bi1 pyro4	1	4-strand double exchange within ad14 - pro1; single exchange ribo - an
ribo ad14 paba1 y pyro4 an ad14 paba1 y	1	Incomplete
ribo ad14 paba1 y pyro4 an pro1 bi1	3	Incomplete
an paba1 y pyro4 an pro1 bi1	2	Incomplete
Perithecium No.2. Dissected 11.9.55.		
ribo ad14 paba1 y ribo ad14 paba1 y pyro4 an pro1 bi1 an pro1 bi1 pyro4	2	No exchanges
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y pyro4 an pro1 bi1 an pro1 bi1	1	No exchange
ribo ad14 paba1 y pyro4 an pro1 bi1 pyro4 an pro1 bi1	2	No exchanges
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 ad14 paba1 y pyro4 an pro1 bi1	1	Single exchange ribo - an
ribo ad14 paba1 y ribo pro1 bi1 pyro4 an pro1 bi1 pyro4	1	Single exchange an - ad14
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 pyro4 an paba1 y an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 paba1 y pyro4 an paba1 y an pro1 bi1 pyro4	1	Single exchange ad14 - pro1

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.2. Dissected 11.9.55.		
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an paba1 y pyro4 an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 paba1 y ribo ad14 pro1 bi1 an paba1 y pyro4 an pro1 bi1 pyro4	1	Single exchange ad14 - pro1
ribo ad14 paba1 y pyro4 ribo ad14 paba1 bi1 an pro1 y an pro1 bi1 pyro4	1	Single exchange paba1 - y
ribo ad14 paba1 y pyro4 ribo ad14 paba1 bi1 pyro4 an pro1 y an pro1 bi1	1	Single exchange paba1 - y
ribo ad14 paba1 y ribo an paba1 y ad14 pro1 bi1 pyro4 an pro1 bi1 pyro4	1	2-strand double exchange ribo - an; ad14 - pro1
ribo ad14 pro1 bi1 pyro4 ribo an pro1 bi1 pyro4 ad14 paba1 y an paba1 y	1	4-strand double exchange ribo - an; ad14 - pro1
ribo ad14 bi1 ribo an pro1 paba1 y ad14 paba1 y pyro4 an pro1 bi1 pyro4	1	3-strand double exchange ribo - an; pro1 - paba1
ribo ad14 paba1 y bi1 pyro4 ribo an pro1 pyro4 ad14 paba1 y an pro1 bi1	1	3-strand double exchange ribo - an; y - bi1
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an bi1 pyro4 an pro1 paba1 y	1	3-strand double exchange ad14 - pro1; pro1 - paba1
ribo ad14 paba1 y pyro4 ribo ad14 pro1 y an paba1 bi1 pyro4 an pro1 bi1	1	2-strand double exchange ad14 - pro1; paba1 - y

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.2. Dissected 11.9.55.		
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 pyro4 paba1 y an ad14 pro1 bi1	1	3-strand double exchanges ribo - an; an - ad14 and ribo - an; ad14 - pro1. 2-strand double exchange an - ad14; ad14 - pro1
ribo an pro1 y ribo ad14 pro1 bi1 an paba1 bi1 pyro4	1	3-strand double exchanges ribo - an; paba1 - y and ad14 - pro1; paba1 - y. 4-strand double exchange ribo - an; ad14 - pro1.
ribo ad14 pro1 y pyro4 ribo an bi1 ad14 paba1 y an pro1 paba1 bi1 pyro4	1	3-strand double exchanges ribo- an; ad14 - pro1 and ribo - an; paba1 - y and ad14 - pro1; pro1 - paba1 and pro1 - paba1; paba1 - y. 4-strand double exchange ribo - an; pro1 - paba1. 2-strand double exchange ad14 - pro1; paba1 - y.
ribo an ad14 pro1 bi1 pyro4 ribo an pro1 y paba1 y	1	4-strand double exchange within ribo - an. 2-strand double exchange an - ad14; ad14 - pro1. 4-strand double exchanges an - ad14; paba1 - y and ad14 - pro1; paba1 - y.
ribo ad14 pro1 paba1 y pyro4 ribo an y pyro4	1	Incomplete
ad14 paba1 y an pro1 bi1	1	Incomplete
an paba1 y an pro1 bi1 pyro4	1	Incomplete
an ad14 pro1 bi1 an paba1 y pyro4	1	Incomplete
ribo ad14 pro1 bi1 an paba1 y pyro4	1	Incomplete
ribo ad14 y an pro1 paba1 y	1	Incomplete

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.3. Dissected 13.9.55.		
ribo ad14 paba1 y ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1 pyro4	1	No exchanges
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y pyro4 an pro1 bi1 an pro1 bi1	1	No exchange
ribo ad14 paba1 y ribo ad14 paba1 y pyro4 an pro1 bi1 an pro1 bi1 pyro4	2	No exchanges
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y an pro1 bi1	1	No exchange
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y an pro1 bi1 pyro4	2	No exchanges
ribo ad14 paba1 y pyro4 an pro1 bi1 an pro1 bi1	1	No exchange
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 pyro4 ad14 paba1 y an pro1 bi1	1	Single exchange ribo - an
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 ad14 paba1 y an pro1 bi1 pyro4	1	Single exchange ribo - an
ribo ad14 paba1 y ribo an pro1 bi1 pyro4 ad14 paba1 y an pro1 bi1 pyro4	1	Single exchange ribo - an
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 pyro4 an paba1 y an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 paba1 y an paba1 y pyro4 an pro1 bi1	1	Single exchange ad14 - pro1

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.3. Dissected 13.9.55.		
ribo ad14 paba1 y pyro4 an paba1 y pyro4 an pro1 bi1	1	Single exch ange ad14 - pro1
ribo ad14 paba1 y ribo ad14 paba1 bi1 pyro4 an pro1 y pyro4 an pro1 bi1	1	Single exchange paba1 - y
ribo ad14 pro1 bi1 pyro4 ribo an paba1 y pyro4 ad14 paba1 y	1	3-strand double exchange ribo - an; ad14 - pro1
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 ad14 pro1 bi1 pyro4 an paba1 y	1	3-strand double exchange ribo - an; ad14 - pro1
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 pyro4 ad14 bi1 an pro1 paba1 y	1	3-strand double exchange ribo - an; pro1 - paba1
ribo ad14 paba1 y pyro4 ribo pro1 bi1 pyro4 an ad14 paba1 bi1 an pro1 y	1	3-strand double exchange an - ad14; paba1 - y
ribo ad14 pro1 bi1 ribo an paba1 y ad14 pro1 bi1 pyro4 an paba1 y pyro4	1	4-strand double exchange within ad14 - pro1; single exchange ribo - an.
ribo ad14 pro1 bi1 pyro4 ribo an paba1 y ad14 pro1 bi1 an paba1 y pyro4	1	4-strand double exchange within ad14 - pro1; single exchange ribo - an
ribo ad14 paba1 y pyro4 ribo ad14 pro1 y an paba1 bi1 pyro4 an pro1 bi1	1	2-strand double exchange ad14 - pro1; paba1 - y
ribo ad14 bi1 pyro4 ribo an pro1 bi1 ad14 pro1 paba1 y an paba1 y pyro4	1	3-strand double exchanges ribo - an; ad14 - pro1 and ad14 - pro1; pro1 - paba1. 4-strand double exchange ribo - an; pro1 - paba1

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.3. Dissected 13.9.55.		
ribo paba1 y pyro4 ribo an pro1 bi1 ad14 paba1 y	1	2-strand double exchange an - ad14; ad14 - pro1. 4-strand double exchanges ribo - an; an - ad14 and ribo - an; ad14 - pro1.
ribo ad14 y pyro4 ribo ad14 pro1 paba1 bi1 an paba1 y pyro4 an pro1 bi1	1	2-strand double exchange pro1 - paba1; paba1 - y. 3-strand double exchanges ad14 - pro1; pro1 - paba1 and ad14 - pro1; paba1 - y.
ribo ad14 bi1 ribo ad14 pro1 paba1 y bi1 an paba1 y pyro4 an pro1 pyro4	1	3-strand double exchanges ad14 - pro1; pro1 - paba1 and pro1 - paba1; y - bi1. 4-strand double exchange ad14 - pro1; y - bi1.
ribo an paba1 y ad14 pro1 bi1 pyro4	1	Incomplete
ribo ad14 paba1 y pyro4 an pro1 bi1	1	Incomplete
-	1	No growth
ribo ad14 paba1 y pyro4 (1 spore) ribo an pro1 bi1 (3 spores)	1	ABNORMAL
an paba1 y (4 spores) ribo ad14 pro1 bi1 pyro4 (2 spores) ribo ad14 pro1 pyro4 (2 spores)	1	ABNORMAL
Perithecium No.4. Dissected 15.9.55.		
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1	5	No exchanges
ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1	1	No exchange
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 pyro4 ad14 paba1 y an pro1 bi1	2	Single exchanges ribo - an
ribo ad14 paba1 y ribo an pro1 bi1 pyro4 ad14 paba1 y an pro1 bi1 pyro4	1	Single exchange ribo - an

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.4. Dissected 15.9.55.		
ribo ad14 paba1 y ribo an pro1 bi1 ad14 paba1 y pyro4 an pro1 bi1 pyro4	1	Single exchange ribo - an
ribo ad14 paba1 y ribo an pro1 bi1 an pro1 bi1 pyro4	1	Single exchange ribo - an
ribo ad14 paba1 y pyro4 ribo pro1 bi1 pyro4 an ad14 paba1 y an pro1 bi1	1	Single exchange an - ad14
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an paba1 y pyro4 an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 paba1 y ribo ad14 pro1 bi1 pyro4 an paba1 y pyro4 an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an paba1 y an pro1 bi1 pyro4	1	Single exchange ad14 - pro1
ribo ad14 paba1 y pyro4 ribo ad14 bi1 an pro1 paba1 y pyro4 an pro1 bi1	1	Single exchange pro1 - paba1
ribo ad14 paba1 y ribo ad14 paba1 bi1 pyro4 an pro1 y an pro1 bi1 pyro4	1	Single exchange paba1 - y
ribo ad14 paba1 y bi1 pyro4 ribo ad14 pro1 an paba1 y an pro1 bi1 pyro4	1	3-strand double exchange ad14 - pro1; y - bi1
ribo ad14 paba1 ribo ad14 paba1 y bi1 pyro4 an pro1 y pyro4 an pro1 bi1	1	3-strand double exchange paba1 - y; y - bi1

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.4. Dissected 15.9.55.		
ribo ad14 paba1 y pyro4 ribo an paba1 y ad14 pro1 bi1 pyro4 an pro1 bi1	1	2-strand double exchange ribo - an; ad14 - pro1
ribo ad14 pro1 bi1 ribo ad14 pro1 bi1 pyro4 an paba1 y an paba1 y pyro4	1	4-strand double exchange within ad14 - pro1
ribo ad14 pro1 paba1 y pyro4 ribo an paba1 y ad14 bi1 an pro1 bi1 pyro4	1	2-strand double exchange ribo - an; pro1 - paba1. 3-strand double exchanges ribo - an; ad14 - pro1 and ad14 - pro1; pro1 - paba1.
ribo ad14 pro1 y pyro4 ribo an pro1 bi1 an paba1 y pyro4	1	3-strand double exchanges ribo - an; paba1 - y and ad14 - pro1; paba1 - y. 4-strand double exchange ribo - an; ad14 - pro1.
ribo pro1 y ribo an pro1 bi1 ad14 paba1 y pyro4 an ad14 paba1 bi1 pyro4	1	2-strand double exchange an - ad14; paba1 - y. 4-strand double exchanges ribo - an; an - ad14 and ribo - an; paba1 - y.
ribo ad14 paba1 y ribo an paba1 bi1 ad14 pro1 bi1 pyro4 an pro1 y pyro4	1	2-strand double exchange ribo - an; ad14 - pro1. 3-strand double exchanges ribo - an; paba1 - y and ad14 - pro1; paba1 - y.
ribo ad14 paba1 y ribo pro1 bi1 pyro4 an ad14 pro1 pyro4 an paba1 y bi1	1	2-strand double exchange ad14 - pro1; y - bi1. 3-strand double exchanges an - ad14; ad14 - pro1 and an - ad14; y - bi1.
ribo ad14 pro1 y ribo ad14 pro1 bi1 an paba1 y pyro4 an paba1 bi1 pyro4	1	4-strand double exchange within ad14 - pro1; single exchange paba1 - y.
ribo ad14 pro1 pyro4 ribo an paba1 y ad14 paba1 y bi1 an pro1 bi1 pyro4	1	2-strand double exchange ribo - an; y - bi1. 3-strand double exchanges ribo - an; ad14 - pro1 and ad14 - pro1; y - bi1.

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.4. Dissected 15.9.55.		
ribo ad14 paba1 bi1 ribo pro1 y an ad14 pro1 bi1 pyro4	1	3-strand double exchanges an - ad14; ad14 - pro1 and an - ad14; paba1 - y. 4-strand double exchange ad14 - pro1; paba1 - y
ribo ad14 paba1 y pyro4 an pro1 bi1	2	Incomplete
an pro1 bi1	1	Incomplete
an paba1 y pyro4 an pro1 bi1	1	Incomplete
Perithecium No.5. Dissected 17.9.55.		
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y an pro1 bi1 pyro4	1	No exchange
ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1 pyro4	1	No exchange
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y an pro1 bi1 an pro1 bi1 pyro4	1	No exchange
ribo ad14 paba1 y ribo an pro1 bi1 ad14 paba1 y pyro4 an pro1 bi1 pyro4	2	Single exchanges ribo - an
ribo ad14 paba1 y ribo ad14 pro1 bi1 pyro4 an paba1 y pyro4 an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 paba1 y an paba1 y an pro1 bi1 pyro4	1	Single exchange ad14 - pro1
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an paba1 y an pro1 bi1 pyro4	1	Single exchange ad14 - pro1
ribo ad14 paba1 y ribo ad14 pro1 bi1 pyro4 an paba1 y pyro4	1	Single exchange ad14 - pro1

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.5. Dissected 17.9.55.		
ribo ad14 paba1 y ribo ad14 pro1 bi1 pyro4 an paba1 y an pro1 bi1 pyro4	1	Single exchange ad14 - pro1
ribo ad14 paba1 y ribo ad14 bi1 an pro1 paba1 y pyro4 an pro1 bi1 pyro4	1	Single exchange pro1 - paba1
ribo ad14 paba1 y ribo ad14 paba1 bi1 pyro4 an pro1 y pyro4 an pro1 bi1	1	Single exchange paba1 - y
ribo ad14 paba1 y pyro4 ribo ad14 paba1 bi1 pyro4 an pro1 y an pro1 bi1	1	Single exchange paba1 - y
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an pro1 y an paba1 bi1 pyro4	1	3-strand double exchange ad14 - pro1; paba1 - y
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 an pro1 ad14 paba1 y bi1 pyro4	1	3-strand double exchange ribo - an; y - bi1
ribo ad14 paba1 y ribo an pro1 bi1 pyro4 ad14 pro1 bi1 pyro4 an paba1 y	1	3-strand double exchange ribo - an; ad14 - pro1
ribo ad14 pro1 paba1 y pyro4 an paba1 y an pro1 bi1	1	3-strand double exchange ad14 - pro1; pro1 - paba1
ribo ad14 pro1 bi1 pyro4 ribo an pro1 bi1 ad14 paba1 y pyro4 an paba1 y	1	4-strand double exchange ribo - an; ad14 - pro1.
ribo ad14 paba1 bi1 pyro4 ribo an pro1 y pyro4 ad14 paba1 y an pro1 bi1	1	3-strand double exchange ribo - an; paba1 - y.

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.5. Dissected 17.9.55.		
ribo an pro1 pyro4 ribo an pro1 bi1 pyro4 ad14 paba1 y bi1 ad14 paba1 y	1	4-strand double exchange within ribo - an. Single exchange y - bi1
ribo ad14 pro1 y pyro4 ribo ad14 paba1 y bi1 pyro4 an pro1 an paba1 bi1	1	2-strand double exchange ad14 - pro1; paba1 - y. 4-strand double exchanges ad14 - pro1; y - bi1 and paba1 - y; y - bi1.
ribo ad14 paba1 bi1 ribo an pro1 bi1 pyro4 an paba1 y	1	3-strand double exchanges ribo - an; ad14 - pro1 and ad14 - pro1; paba1 - y. 4-strand double exchange ribo - an; paba1 - y.
ribo an pro1 bi1 ad14 bi1 pyro4 an paba1 y	1	3-strand double exchanges ribo - an; pro1 - paba1 and ad14 - pro1; pro1 - paba1. 4-strand double exchange ribo - an; ad14 - pro1.
ribo ad14 pro1 paba1 y ribo an pro1 bi1 pyro4 an y	1	2-strand double exchange ad14 - pro1; pro1 - paba1. 3-strand double exchanges ribo - an; paba1 - y and ad14 - pro1; paba1 - y and pro1 - paba1; paba1 - y. 4-strand double exchanges ribo - an; ad14 - pro1 and ribo - an; pro1 - paba1.
an pro1 bi1 pyro4	1	Incomplete
an pro1 bi1	2	Incomplete
Perithecium No.6. Dissected 15.11.55.		
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y pyro4 an pro1 bi1 an pro1 bi1	2	No exchanges
ribo ad14 paba1 y ribo ad14 paba1 y an pro1 bi1 pyro4	1	No exchange
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y an pro1 bi1 an pro1 bi1 pyro4	2	No exchanges

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.6. Dissected 15.11.55.		
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 ad14 paba1 y pyro4 an pro1 bi1	1	Single exchange ribo - an
ribo ad14 paba1 y ribo an pro1 bi1 ad14 paba1 y pyro4 an pro1 bi1 pyro4	1	Single exchange ribo - an
ribo ad14 paba1 y ribo pro1 bi1 pyro4 an ad14 paba1 y an pro1 bi1 pyro4	1	Single exchange an - ad14
ribo ad14 paba1 y ribo ad14 pro1 bi1 pyro4 an paba1 y an pro1 bi1 pyro4	1	Single exchange ad14 - pro1
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an paba1 y an pro1 bi1 pyro4	1	Single exchange ad14 - pro1
ribo ad14 paba1 y ribo ad14 paba1 y bi1 pyro4 an pro1 an pro1 bi1 pyro4	1	Single exchange y - bi1
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y bi1 an pro1 pyro4 an pro1 bi1	1	Single exchange y - bi1
ribo ad14 paba1 y pyro4 ribo an paba1 y ad14 pro1 bi1 pyro4 an pro1 bi1	1	2-strand double exchange ribo - an; ad14 - pro1
ribo ad14 paba1 bi1 ribo ad14 pro1 y pyro4 an paba1 y an pro1 bi1 pyro4	1	3-strand double exchange ad14 - pro1; paba1 - y
ribo ad14 paba1 bi1 pyro4 ribo ad14 y an pro1 paba1 y pyro4 an pro1 bi1	1	3-strand double exchange pro1 - paba1; paba1 - y

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.6. Dissected 15.11.55.		
ribo an pro1 bi1 pyro4 ribo an paba1 y ad14 pro1 bi1 pyro4 ad14 paba1 y	1	4-strand double exchange within ribo - an; single exchange ad14 - pro1.
ribo pro1 paba1 y pyro4 ribo ad14 pro1 bi1 pyro4 an paba1 y an ad14 bi1	1	2-strand double exchange an - ad14; pro1 - paba1. 4-strand double exchanges an - ad14; ad14 - pro1 and ad14 - pro1; pro1 - paba1.
ribo ad14 pro1 bi1 pyro4 ad14 paba1 y	1	Incomplete
an pro1 bi1 pyro4 (8 spores)	1	Selfed green ascus
Perithecium No.7. Dissected 16.11.55.		
ribo ad14 paba1 y ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1 pyro4	1	No exchange
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1	3	No exchanges
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y pyro4 an pro1 bi1 an pro1 bi1	1	No exchange
ribo ad14 paba1 y (2 spores) ribo ad14 paba1 y pyro4 (1 spore) an pro1 bi1 pyro4 (2 spores) an pro1 bi1 (1 spore) an pro1 bi1 ribo ad14 paba1 y pyro4 (1 spore)	1	Ascus contained 7 normal spores and a fragment. No exchanges
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 ad14 paba1 y pyro4 an pro1 bi1	1	Single exchange ribo - an
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an paba1 y pyro4 an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 paba1 y ribo ad14 paba1 bi1 an pro1 y pyro4 an pro1 bi1 pyro4	1	Single exchange paba1 - y

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.7. Dissected 16.11.55.		
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 an paba1 y ad14 pro1 bi1 pyro4	1	3-strand double exchange ribo - an; ad14 - pro1
ribo ad14 pro1 paba1 pyro4 ribo ad14 bi1 an paba1 y an pro1 bi1 pyro4	1	3-strand double exchange ad14 - pro1; pro1 - paba1
ribo ad14 pro1 bi1 pyro4 ribo an paba1 y pyro4 an paba1 y ad14 pro1 bi1	1	4-strand double exchange within ad14 - pro1; single exchange ribo - an.
ribo ad14 paba1 y ribo an pro1 bi1 ad14 pro1 paba1 y pyro4 an bi1 pyro4	1	2-strand double exchange ad14 - pro1; pro1 - paba1. 3-strand double exchanges ribo - an; ad14 - pro1 and ribo - an; pro1 - paba1.
Perithecium No.8. Dissected 17.11.55.		
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1	2	No exchanges
ribo ad14 paba1 y ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1 pyro4	1	No exchange
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 ad14 paba1 y pyro4 an pro1 bi1	1	Single exchange ribo - an
ribo ad14 paba1 y ribo ad14 pro1 bi1 an paba1 y pyro4 an pro1 bi1 pyro4	1	Single exchange ad14 - pro1
ribo pro1 bi1 ribo pro1 bi1 an ad14 paba1 y pyro4 an ad14 paba1 y pyro4	1	4-strand double exchange within an-ad14
ribo ad14 paba1 y pyro4 ribo ad14 pyro4 an pro1 paba1 y bi1 an pro1 bi1	1	2-strand double exchange pro1 - paba1; y - bi1

Table H/. cont^{d}.

Genotypes	Numbers of asci	Comments.
Perithecium No.8. Dissected 17.11.55.		
ribo ad14 paba1 y ribo pro1 bi1 pyro4 an ad14 paba1 y bi1 pyro4 an pro1	1	3-strand double exchange an - ad14; y - bi1
ribo ad14 paba1 y bi1 an paba1 y bi1 an pro1 pyro4	1	4-strand double exchange within y - bi1; single exchange ad14 - pro1.
ribo ad14 paba1 bi1 ribo an pro1 bi1 pyro4 ad14 pro1 y an paba1 y pyro4	1	3-strand double exchanges ribo - an; ad14 - pro1 and ad14 - pro1; paba1 - y. 4-strand double exchange ribo - an; paba1 - y.
Perithecium No.9. Dissected 18.11.55.		
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1	3	No exchanges
ribo ad14 paba1 y ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1 pyro4	3	No exchanges
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 ad14 paba1 y an pro1 bi1 pyro4	1	Single exchange ribo - an
ribo ad14 paba1 y ribo an pro1 bi1 pyro4 ad14 paba1 y an pro1 bi1 pyro4	1	Single exchange ribo - an
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 pyro4 ad14 paba1 y an pro1 bi1	2	Single exchanges ribo - an
ribo ad14 paba1 y ribo an pro1 bi1 pyro4 ad14 paba1 y pyro4 an pro1 bi1	2	Single exchanges ribo - an
ribo ad14 paba1 y ribo an pro1 bi1 pyro4 an pro1 bi1 pyro4	1	Single exchange ribo - an

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.9. Dissected 18.11.55.		
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an paba1 y pyro4 an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 pyro4 an paba1 y an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an paba1 y an pro1 bi1 pyro4	1	Single exchange ad14 - pro1
ribo ad14 paba1 y ribo ad14 pro1 paba1 y pyro4 an bi1 an pro1 bi1 pyro4	1	2-strand double exchange ad14 - pro1; pro1 - paba1
ribo pro1 bi1 pyro4 an ad14 pro1 bi1 an paba1 y	1	3-strand double exchange an - ad14; ad14 - pro1
ribo ad14 paba1 y pyro4 ribo an paba1 y ad14 pro1 bi1 an pro1 bi1 pyro4	1	2-strand double exchange ribo - an; ad14 - pro1
ribo ad14 pro1 bi1 pyro4 ribo ad14 pro1 bi1 an paba1 y an paba1 y pyro4	1	4-strand double exchange within ad14 - pro1
ribo ad14 pro1 bi1 ribo an paba1 y pyro4 ad14 pro1 bi1 an paba1 y pyro4	1	4-strand double exchange within ad14 - pro1; single exchange ribo - an
ribo ad14 pro1 pyro4 ribo pro1 bi1 pyro4 an paba1 y bi1	1	2-strand double exchange ad14 - pro1; y - bi1. 4-strand double exchanges an - ad14; ad14 - pro1 and an - ad14; y - bi1.
ribo ad14 pro1 bi1 pyro4 ribo an bi1 pyro4 ad14 paba1 y an pro1 paba1 y	1	3-strand double exchanges ribo - an; ad14 - pro1 and ad14 - pro1; pro1 - paba1. 4-strand double exchange ribo - an; pro1 - paba1.

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.9. Dissected 18.11.55.		
ribo pro1 bi1 pyro4 ribo paba1 y bi1 an ad14 pro1 an ad14 paba1 y pyro4	1	4-strand double exchange within an - ad14. 2-strand double exchange ad14 - pro1; y - bi1.
Perithecium No.10. Dissected 19.11.55. to 20.11.55.		
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y pyro4 an pro1 bi1 an pro1 bi1	3	No exchanges
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1	11	No exchanges
ribo ad14 paba1 y ribo ad14 paba1 y an pro1 bi1 pyro4 an pro1 bi1 pyro4	5	No exchanges
ribo ad14 paba1 y pyro4 an pro1 bi1 an pro1 bi1 pyro4	1	No exchange
ribo ad14 paba1 y ribo ad14 paba1 y an pro1 bi1 pyro4	1	No exchange
ribo ad14 paba1 y pyro4 ribo ad14 paba1 y an pro1 bi1	1	No exchange
ribo ad14 paba1 y ribo an pro1 bi1 pyro4 ad14 paba1 y an pro1 bi1 pyro4	2	Single exchanges ribo - an
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 ad14 paba1 y pyro4 an pro1 bi1	1	Single exchange ribo - an
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 ad14 paba1 y an pro1 bi1 pyro4	1	Single exchange ribo - an
ribo ad14 paba1 y ribo pro1 bi1 an ad14 paba1 y pyro4 an pro1 bi1 pyro4	1	Single exchange an -ad14

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.10. Dissected 19.11.55. to 20.11.55.		
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 pyro4 an paba1 y an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 paba1 y ribo ad14 pro1 bi1 pyro4 an paba1 y an pro1 bi1 pyro4	3	Single exchanges ad14 - pro1
ribo ad14 paba1 y ribo ad14 pro1 bi1 an paba1 y pyro4 an pro1 bi1 pyro4	2	Single exchanges ad14 - pro1
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an paba1 y an pro1 bi1 pyro4	2	Single exchanges ad14 - pro1
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an paba1 y pyro4 an pro1 bi1	1	Single exchange ad14 - pro1
ribo ad14 paba1 y ribo ad14 pro1 bi1 pyro4 an paba1 y pyro4 an pro1 bi1	2	Single exchanges ad14 - pro1
ribo ad14 paba1 y pyro4 ribo ad14 bi1 pyro4 an pro1 paba1 y an pro1 bi1	1	Single exchange pro1 - paba1
ribo ad14 bi1 an pro1 paba1 y pyro4 an pro1 bi1 pyro4	1	Single exchange pro1 - paba1
ribo ad14 paba1 y pyro4 ribo ad14 paba1 bi1 an pro1 y an pro1 bi1 pyro4	1	Single exchange paba1 - y
ribo ad14 paba1 y ribo ad14 paba1 bi1 pyro4 an pro1 y an pro1 bi1 pyro4	1	Single exchange paba1 - y

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.10. Dissected 19.11.55. to 20.11.55.		
ribo ad14 paba1 y pyro4 ribo ad14 paba1 bi1 an pro1 y pyro4 an pro1 bi1	1	Single exchange paba1 - y
ribo ad14 paba1 y an pro1 an pro1 bi1 pyro4	1	Single exchange y - bi1
ribo ad14 paba1 y pyro4 ribo ad14 pro1 y an paba1 bi1 pyro4 an pro1 bi1	1	2-strand double exchange ad14 - pro1; paba1 - y
ribo ad14 pro1 bi1 pyro4 ribo ad14 bi1 pyro4 an paba1 y	1	4-strand double exchange ad14 - pro1; pro1 - paba1
ribo ad14 paba1 y ribo pro1 bi1 pyro4 an pro1 y an ad14 paba1 bi1 pyro4	1	3-strand double exchange an - ad14; paba1 - y
ribo ad14 pro1 paba1 y ribo ad14 bi1 an paba1 pyro4 y an pro1 bi1 pyro4	1	3-strand double exchange ad14 - pro1; pro1 - paba1
ribo an pro1 bi1 pyro4 ribo ad14 pro1 bi1 an paba1 y pyro4 ad14 paba1 y	1	4-strand double exchange ribo - an; ad14 - pro1.
ribo an pro1 bi1 ribo ad14 paba1 bi1 pyro4 an pro1 y pyro4 ad14 paba1 y	1	4-strand double exchange ribo - an; paba1 - y
ribo ad14 paba1 bi1 ribo pro1 bi1 an ad14 paba1 y pyro4 an pro1 bi1 pyro4	1	3-strand double exchange an - ad14; paba1 - y.
ribo ad14 paba1 y ribo ad14 paba1 pyro4 an pro1 y bi1 an pro1 bi1 pyro4	1	2-strand double exchange paba1 - y; y - bi1
ribo ad14 paba1 y bi1 ribo ad14 pro1 pyro4 an paba1 y an pro1 bi1 pyro4	1	3-strand double exchange ad14 - pro1; y - bi1

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.10. Dissected 19.11.55. to 20.11.55.		
ribo ad14 paba1 y pyro4 ribo ad14 pro1 bi1 an pro1 y an paba1 bi1 pyro4	1	3-strand double exchange ad14 - pro1; paba1 - y
ribo ad14 paba1 y ribo an paba1 y ad14 pro1 bi1 pyro4 an pro1 bi1 pyro4	1	2-strand double exchange ribo - an; ad14 - pro1
ribo ad14 paba1 y ribo ad14 pro1 paba1 y an bi1 pyro4 an pro1 bi1 pyro4	1	2-strand double exchange ad14 - pro1; pro1 - paba1
ribo ad14 paba1 y pyro4 ribo an pro1 bi1 an paba1 y ad14 pro1 bi1 pyro4	1	3-strand double exchange ribo - an; ad14 - pro1
ribo paba1 y pyro4 ribo ad14 pro1 bi1 pyro4 an ad14 paba1 y an pro1 bi1	1	3-strand double exchange an - ad14; ad14 - pro1
ribo ad14 paba1 y ribo an pro1 bi1 pyro4 an paba1 y ad14 pro1 bi1 pyro4	1	3-strand double exchange ribo - an; ad14 - pro1
ribo an paba1 y ad14 pro1 bi1 pyro4 an pro1 bi1 pyro4	1	2-strand double exchange ribo - an; ad14 - pro1
ribo ad14 paba1 y ribo an pro1 y ad14 paba1 bi1 pyro4 an pro1 bi1 pyro4	1	2-strand double exchange ribo - an; paba1 - y
ribo an pro1 bi1 pyro4 ribo ad14 bi1 ad14 paba1 y an pro1 paba1 y pyro4	1	4-strand double exchange ribo - an; pro1 - paba1
ribo ad14 pro1 bi1 ribo an paba1 y pyro4 ad14 paba1 y pyro4 an pro1 bi1	1	3-strand double exchange ribo - an; ad14 - pro1

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.10. Dissected 19.11.55. to 20.11.55.		
ribo ad14 pro1 bi1 pyro4 ribo ad14 pro1 bi1 an paba1 y pyro4 an paba1 y	1	4-strand double exchange within ad14 - pro1
ribo an pro1 bi1 pyro4 ribo an pro1 bi1 ad14 paba1 y pyro4 ad14 paba1 y	1	4-strand double exchange within ribo - an.
ribo ad14 paba1 bi1 pyro4 ribo ad14 an pro1 paba1 y an pro1 y bi1 pyro4	1	3-strand double exchanges pro1 - paba1; y - bi1 and paba1 - y; y - bi1. 4-strand double exchange pro1 - paba1; paba1 - y.
ribo ad14 pro1 bi1 pyro4 ribo an paba1 y an paba1 y pyro4 ad14 pro1 bi1	1	4-strand double exchange within ad14 - pro1; single exchange ribo - an.
ribo ad14 pro1 bi1 ribo an paba1 y pyro4 an paba1 y pyro4 ad14 pro1 bi1	1	4-strand double exchange within ad14 - pro1; single exchange ribo - an
ribo ad14 pro1 bi1 pyro4 ribo an pro1 bi1 pyro4 paba1 y an ad14 paba1 y	1	3-strand double exchanges ribo - an; an - ad14 and an - ad14; ad14 - pro1. 4-strand double exchange ribo - an; ad14 - pro1.
ribo ad14 pro1 y pyro4 ribo ad14 bi1 an pro1 paba1 bi1 pyro4 an paba1 y	1	3-strand double exchanges ad14 - pro1; paba1 - y and pro1 - paba1; paba1 - y. 4-strand double exchange ad14 - pro1; pro1 - paba1.
ribo ad14 paba1 y ribo paba1 y bi1 pyro4 an ad14 pro1 an pro1 bi1 pyro4	1	2-strand double exchanges an - ad14; ad14 - pro1 and ad14 - pro1; y - bi1 and an - ad14; y - bi1.
ribo ad14 paba1 y ribo an pro1 bi1 pyro4 paba1 y pyro4 an ad14 pro1 bi1	1	2-strand double exchange an - ad14; ad14 - pro1. 3-strand double exchanges ribo - an; an - ad14 and ribo - an; ad14 - pro1.

Table H/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.10 Dissected 19.11.55. to 20.11.55.		
ribo ad14 paba1 bi1 ribo an paba1 y an pro1 y bi1 pyro4 ad14 pro1 pyro4	1	2-strand double exchange ribo - an; ad14 - pro1. 3-strand double exchanges ribo - an; y - bi1 and ad14 - pro1; y - bi1 and paba1 - y; y - bi1. 4-strand double exchanges ribo - an; paba1 - y and ad14 - pro1; paba1 - y
ribo ad14 pro1 paba1 y bi1 ribo ad14 pro1 bi1 an paba1 y pyro4 an pyro4	1	4-strand double exchange within ad14 - pro1. 2-strand double exchange pro1 - paba1; y - bi1.
ribo an ad14 pro1 bi1 ad14 pro1 bi1	1	Incomplete
ribo an pro1 paba1 y	1	Incomplete
ribo ad14 paba1 bi1 (3 spores) ribo ad14 paba1 y (2 spores) an pro1 bi1 pyro4 (3 spores)	1	ABNORMAL

SUMMARY.

Types of asci.	Number of ascospores germinating.								
	0	1	2	3	4	5	6	7	8
Classifiable									
Selfed green	-	-	-	-	-	-	-	-	1/ 1
Selfed yellow	-	-	-	-	-	-	-	-	-
Hybrid	-	3	8	12	32	40	51	77	64/289
Non-classifiable									
Green	-	-	1	-	-	-	-	-	-/ 1
Yellow	-	-	-	-	-	-	-	-	-
No germination	1	-	-	-	-	-	-	-	-/ 1
Abnormal	-	-	-	-	1	-	-	1	1/ 3
Grand Total	1	3	9	12	33	40	51	78	66/293

Table I/.
Cross pro1 paba1 y//ad17 bi1. From streak inoculum on minimal medium. Prepared on the 1.11.55. Only the genotypes of the germinated spores are given. If there were only two spores of any one genotype, it was assumed that they were the result of the mitotic division.

Genotypes	Number of asci	Comments
Perithecium No1. Dissected 3.1.56.		
pro1 paba1 y pro1 paba1 y ad17 bi1 ad17 bi1	34	No exchanges
pro1 paba1 y pro1 paba1 y ad17 bi1	4	No exchanges
pro1 paba1 y ad17 bi1 ad17 bi1	3	No exchanges
pro1 paba1 y pro1 ad17 bi1 paba1 y ad17 bi1	5	Single exchanges pro1 - ad17
pro1 ad17 bi1 pro1 ad17 bi1 paba1 y paba1 y	1	4-strand double exchange within pro1 - ad17.
pro1 paba1 y pro1 paba1 bi1 ad17 y ad17 bi1	4	Single exchanges paba1 - y
pro1 ad17 bi1 pro1 paba1 bi1 ad17 y paba1 y	1	4-strand double exchange pro1 - ad17; paba1 - y.
pro1 paba1 y bi1 ad17 y ad17 bi1	1	3-strand double exchange paba1 - y; y - bi1.
pro1 paba1 bi1 ad17 paba1 y	1	3-strand double exchanges pro1 - ad17; paba1 - y and paba1 - y; y - bi1. 4-strand double exchange pro1 - ad17; y - bi1.
pro1 paba1 y pro1 paba1 y	1	Incomplete

Table I/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.1. Dissected 3.1.56.		
paba1 y ad17 bi1	2	Incomplete
pro1 paba1 bi1 (1 spore) ad17 y (2 spores) ad17 paba1 y (1 spore) ad17 bi1 (2 spores)	1	ABNORMAL Single exchange paba1 - y
Perithecium No.2. Dissected 5.1.56.		
pro1 paba1 y pro1 paba1 y ad17 bi1 ad17 bi1	1	No exchanges
pro1 paba1 y ad17 bi1 ad17 bi1	1	No exchanges
pro1 paba1 bi1 pro1 paba1 bi1 ad17 y ad17 y	2	4-strand double exchange within paba1 - y.
Perithecium No.3. Dissected 7.1.56.		
pro1 paba1 y pro1 paba1 y ad17 bi1 ad17 bi1	12	No exchanges
pro1 paba1 y ad17 bi1 ad17 bi1	3	No exchanges
pro1 paba1 y pro1 ad17 bi1 paba1 y ad17 bi1	4	Single exchanges pro1 - ad17
pro1 paba1 y pro1 ad17 bi1 ad17 bi1	1	Single exchange pro1 - ad17
pro1 paba1 y pro1 paba1 bi1 ad17 y ad17 bi1	1	Single exchange paba1 - y
pro1 paba1 y pro1 paba1 y bi1 ad17 ad17 bi1	1	Single exchange y - bi1

Table I/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.3. Dissected 7.1.56.		
pro1 paba1 y pro1 ad17 y paba1 bi1 ad17 bi1	1	2-strand double exchange pro1 - ad17; paba1 - y
pro1 paba1 y pro1 ad17 paba1 y bi1 ad17 bi1	1	2-strand double exchange pro1 - ad17; y - bi1
pro1 ad17 bi1 pro1 paba1 bi1 ad17 y paba1 y	1	4-strand double exchange pro1 - ad17; paba1 ~~y~~ y.
pro1 paba1 y pro1 paba1 ad17 y bi1 ad17 bi1	1	2-strand double exchange paba1 - y; y - bi1
pro1 paba1 y (8 spores)	1	Selfed yellow ascus MIXED PERITHECIUM.
Perithecium No.4. Dissected 8.1.56.		
pro1 paba1 y pro1 paba1 y ad17 bi1 ad17 bi1	5	No exchanges
pro1 paba1 y ad17 bi1 ad17 bi1	1	No exch ange.
pro1 paba1 y pro1 paba1 y ad17 bi1	1	No exchange
pro1 paba1 y pro1 ad17 bi1 paba1 y ad17 bi1	2	Single exchanges pro1 - ad17
pro1 paba1 y pro1 paba1 bi1 ad17 y ad17 bi1	5	Single exchanges paba1 - y
pro1 paba1 y pro1 paba1 y bi1 ad17 bi1	2	Single exchanges y - bi1

Table I/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.4. Dissected 8.1.56.		
pro1 ad17 y pro1 paba1 bi1 paba1 y ad17 bi1	1	3-strand double exchange pro1 - ad17; paba1 - y.
pro1 paba1 bi1 paba1 y ad17 y	1	4-strand double exchange pro1 - ad17; paba1 - y.
pro1 ad17 bi1 paba1 bi1 paba1 y	1	4-strand double exchange within pro1 - ad17; single exchange paba1 - y.
ad17 bi1	1	Incomplete
pro1 paba1 y	2	Incomplete
pro1 paba1 y (7 spores)	3	Selfed yellow asci. MIXED PERITHECIUM
pro1 paba1 y (6 spores)	2	Selfed yellow asci. MIXED PERITHECIUM.
pro1 paba1 y (2 spores) pro1 paba1 bi1 (3 spores) ad17 y (2 spores)	1	ABNORMAL. Single exchange paba1 - y.
ad17 (1 spore) pro1 ad17 bi1 (2 spores) pro1 paba1 bi1 (1 spore)	1	ABNORMAL
Perithecium No.5. Dissected 9.1.56.		
pro1 paba1 y pro1 paba1 y ad17 bi1 ad17 bi1	9	No exchanges
pro1 paba1 y ad17 bi1 ad17 bi1	1	No exchange
pro1 paba1 y pro1 ad17 bi1 paba1 y	1	Single exchange pro1 - ad17
pro1 paba1 y pro1 paba1 bi1 ad17 y ad17 bi1	2	Single exchanges paba1 - y

Table I/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.5. Dissected 9.1.56.		
pro1 paba1 y ad17 y ad17 bi1	1	Single exchange paba1 - y
pro1 paba1 y pro1 paba1 y bi1 ad17 ad17 bi1	1	Single exchange y - bi1
pro1 paba1 y bi1 pro1 ad17 bi1 ad17 paba1 y	1	4-strand double exchange pro1 - ad17; y - bi1
pro1 paba1 y pro1 paba1 bi1 ad17 ad17 y bi1	1	3-strand double exchange paba1 - y; y - bi1
pro1 paba1 y pro1 ad17 bi1 ad17 y paba1 bi1	1	3-strand double exchange pro1 - ad17; paba1 - y.
pro1 paba1 y pro1 ad17 y paba1 bi1 ad17 bi1	1	2-strand double exchange pro1 - ad17; paba1 - y.
pro1 paba1 bi1 pro1 paba1 bi1 ad17 y ad17 y	1	4-strand double exchange within paba1 - y.
pro1 paba1 y	1	Incomplete
pro1 paba1 y ad17 bi1	1	Incomplete
Perithecium No.6. Dissected 12.1.56.		
pro1 paba1 y pro1 paba1 y ad17 bi1 ad17 bi1	6	No exchanges
pro1 paba1 y ad17 bi1 ad17 bi1	3	No exchanges
pro1 paba1 y pro1 paba1 y ad17 bi1	1	No exchange

Table I/ cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.6. Dissected 12.1.56 .		
pro1 paba1 y ad17 y ad17 bi1	1	Single exchange paba1 - y
pro1 paba1 y ad17 bi1	1	Incomplete
ad17 bi1	1	Incomplete
pro1 paba1 y (8 spores)	1	Selfed yellow ascus. MIXED PERITHECIUM
Perithecium No.7. Dissected 12.1.56.		
pro1 paba1 y pro1 paba1 bi1 ad17 y ad17 bi1	2	Single exchanges paba1 - y
pro1 paba1 y ad17 bi1	1	Incomplete
Perithecium No.8. Dissected 14.1.56.		
pro1 paba1 y pro1 paba1 y ad17 bi1 ad17 bi1	3	No exchanges
Perithecium No.9. Dissected 14.1.56.		
pro1 paba1 y pro1 paba1 y ad17 bi1 ad17 bi1	4	No exchanges
pro1 paba1 y pro1 paba1 y ad17 bi1	1	No exchange.
pro1 paba1 y pro1 ad17 bi1 paba1 y ad17 bi1	2	Single exchanges pro1 - ad17
pro1 paba1 y pro1 paba1 y bi1 ad17 ad17 bi1	1	Single exchange y - bi1
pro1 paba1 y bi1 pro1 ad17 ad17 bi1	1	3-strand double exchange pro1 - ad17; y - bi1.
pro1 paba1 y pro1 paba1 bi1 ad17	1	3-strand double exchange paba1 - y; y - bi1

Table I/. cont[d].

Genotypes	Number of asci	Comments
Perithecium No.9. Dissected 14.1.56.		
pro1 paba1 y pro1 ad17 paba1 y bi1 ad17 bi1	1	2-strand double exchange pro1 - ad17; y - bi1.
pro1 paba1 bi1 pro1 paba1 bi1 ad17 y ad17 y	1	4-strand double exchange within paba1 - y.
pro1 paba1 y ad17 bi1	1	Incomplete

SUMMARY.

Types of asci	Number of ascospores germinating. 0	1	2	3	4	5	6	7	8
Classifiable									
Selfed green	-	-	-	-	-	-	-	-	-
Selfed yellow	-	-	-	-	-	-	2	3	2/ 7
Hybrid	-	-	3	2	4	16	32	43	57/157
Non-classifiable									
Green	-	2	-	-	-	-	-	-	-/ 2
Yellow	-	3	-	1	-	-	-	-	-/ 4
No germination	-	-	-	-	-	-	-	-	-
Abnormal	-	-	-	-	1	-	1	1	-/ 3
Grand Total	-	5	3	3	5	16	35	47	59/173

Table J/.
Cross pro3 bi1//pro1 ad15 paba1 y. From streak inoculum on minimal medium. Prepared on the 17.1.56. Only the genotypes of the germinated spores are given. If there were only two spores of any one genotype, it was assumed that they were the result of the mitotic division.

Genotypes	Number of asci	Comments
Perithecium No.1. Dissected 2.4.56.		
pro3 bi1 pro3 bi1 pro1 ad15 paba1 y pro1 ad15 paba1 y	10	No exchanges
pro3 bi1 pro3 bi1 pro1 ad15 paba1 y	4	No exchanges
pro3 bi1 pro1 ad15 paba1 y pro1 ad15 paba1 y	1	No exch ange
pro3 bi1 pro3 ad15 paba1 y pro1 bi1 pro1 ad15 paba1 y	1	Single exchange pro1 - ad15
pro3 bi1 pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	3	Single exchanges paba1 - y
pro3 bi1 pro1 ad15 paba1 y bi1 pro1 ad15 paba1 y	1	Single exchange y - bi1
pro3 bi1 pro1 ad15 paba1 y	3	Incomplete
pro1 ad15 paba1 y pro1 ad15 paba1 y	1	Incomplete
pro1 ad15 paba1 y	1	Incomplete
Perithecium No.2. Dissected 3.4.56.		
pro3 bi1 pro3 bi1 pro1 ad15 paba1 y pro1 ad15 paba1 y	5	No exchanges
pro3 bi1 pro3 bi1 pro1 ad15 paba1 y	4	No exchanges

Table J/. cont[d].

Genotypes	Number of asci	Comments
Perithecium No.2. Dissected 3.4.56.		
pro3 bi1 pro3 ad15 paba1 y pro1 bi1 pro1 ad15 paba1 y	1	Single exchange pro1 - ad15
pro3 bi1 pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	3	Single exchanges paba1 - y
pro3 bi1 pro3 y pro1 ad15 paba1 y	1	Single exchange paba1 - y
pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	2	Single exchanges paba1 - y
pro3 bi1	1	Incomplete
pro3 bi1 pro1 ad15 paba1 y	1	Incomplete
Perithecium No.3. Dissected 4.4.56. to 6.4.56.		
pro3 bi1 pro3 bi1 pro1 ad15 paba1 y pro1 ad15 paba1 y	32 MØ	No exchanges
pro3 bi1 pro3 bi1 pro1 ad15 paba1 y	13	No exchanges
pro3 bi1 pro1 ad15 paba1 y pro1 ad15 paba1 y	9	No exchanges
pro3 bi1 pro3 pro1 ad15 paba1 bi1 bi1 pro1 ad15 paba1 y	1	Single exchange pro3 - pro1
pro3 bi1 pro3 ad15 paba1 y pro1 bi1 pro1 ad15 paba1 y	6	Single exchanges pro1 - ad15
pro3 bi1 pro1 bi1 pro1 ad15 paba1 y	2	Single exchanges pro1 - ad15

Table J/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.3. Dissected 4.4.56. to 6.4.56.		
pro3 ad15 paba1 y pro1 bi1 pro1 ad15 paba1 y	1	Single exchange pro1 - ad15
pro3 bi1 pro3 ad15 paba1 y pro1 bi1	1	Single exchange pro1 - ad15
pro3 bi1 pro3 ad15 paba1 y pro1 ad15 paba1 y	1	Single exchange pro1 - ad15
pro3 bi1 pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	10	Single exchanges paba1 - y
pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	2	Single exchanges paba1 - y
pro3 bi1 pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	1	Single exchange paba1 - y
pro3 bi1 pro3 y pro1 ad15 paba1 y	1	Single exchange paba1 - y
pro3 bi1 pro3 pro1 ad15 paba1 y bi1 pro1 ad15 paba1 y	3	Single exchanges y - bi1
pro3 bi1 pro1 ad15 paba1 y bi1 pro1 ad15 paba1 y	1	Single exchange y - bi1
pro3 ad15 paba1 y pro1 ad15 paba1 bi1 pro1 y	1	3-strand double exchange pro1 - ad15; paba1 - y.
pro3 y pro3 ad15 paba1 bi1 pro1 bi1 pro1 ad15 paba1 y	1	3-strand double exchange pro1 - ad15; paba1 - y
pro3 bi1 pro3 ad15 paba1 y pro1 ad15 paba1 bi1	1	3-strand double exchange pro1 - ad15; paba1 - y

Table J/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.3. Dissected 4.4.56. to 6.4.56.		
pro3 ad15 paba1 y pro3 y pro1 bi1 pro1 ad15 paba1 bi1	3	4-strand double exchanges pro1 - ad15; paba1 - y.
pro3 bi1 pro3 y bi1 pro1 ad15 paba1 pro1 ad15 paba1 y	1	2-strand double exchange paba1 - y; y - bi1
pro3 bi1 pro3 ad15 paba1 y bi1 pro1 ad15 paba1 y	1	2-strand double exchange pro1 - ad15; y - bi1.
pro3 y pro3 ad15 paba1 y bi1 pro1 bi1	1	4-strand double exchange pro1 - ad15; paba1 - y. 3-strand double exchanges paba1 - y; y - bi1 and pro1 - ad15; y - bi1.
pro3 ad15 paba1 bi1 pro1 y pro1 ad15 paba1	1	4-strand double exchange within paba1 - y; single exchanges pro1 - ad15 and y - bi1.
pro1 ad15 paba1 y pro1 ad15 paba1 y	1	Incomplete
pro1 ad15 paba1 y	1	Incomplete
pro3 bi1 pro1 ad15 paba1 y	5	Incomplete
pro1 bi1 pro3 ad15 paba1 y	2	Incomplete
pro3 bi1 pro1 ad15 paba1 y bi1	1	Incomplete
pro3 y pro1 ad15 paba1 y	1	Incomplete
Perithecium No.4. Dissected 9.4.56. to 13.4.56.		
pro3 bi1 pro3 bi1 pro1 ad15 paba1 y pro1 ad15 paba1 y	36	No exchanges
pro3 bi1 pro1 ad15 paba1 y pro1 ad15 paba1 y	3	No exchanges

Table J/. cont^{d}.

Genotypes	Number of asci	Comments.
Perithecium No.4. Dissected 9.4.56. to 13.4.56.		
pro3 bi1 pro3 ad15 paba1 y pro1 bi1 pro1 ad15 paba1 y	6	Single exchanges pro1 - ad15.
pro3 bi1 pro3 ad15 paba1 y pro1 bi1	1	Single exchange pro1 - ad15
pro3 bi1 pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	18	Single exchanges paba1 - y
pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	1	Single exchange paba1 - y
pro3 y pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 bi1	1	4-strand double exchange within paba1 - y
pro3 y pro3 y pro1 ad15 paba1 bi1	1	4-strand double exchange within paba1 - y
pro3 bi1 pro3 pro1 ad15 paba1 y bi1 pro1 ad15 paba1 y	6	Single exchanges y - bi1
pro3 bi pro1 ad15 paba1 y bi1 pro1 ad15 paba1 y	1	Single exchange y - bi1
pro3 y pro3 ad15 paba1 bi1 pro1 bi1 pro1 ad15 paba1 y	1	3-strand double exchange pro1 - ad15; paba1 - y
pro3 y pro3 ad15 paba1 y pro1 bi1 pro1 ad15 paba1 bi1	2	4-strand double exchanges pro1 - ad15; paba1 - y
pro3 pro3 ad15 paba1 y pro1 bi1 pro1 ad15 paba1 y bi1	1	4-strand double exchange pro1 - ad15; y - bi1

Table J/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.4. Dissected 9.4.56. to 13.4.56.		
pro3 pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	1	3-strand double exchange paba1 - y; y - bi1.
pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	1	Incomplete
Perithecium No.5. Dissected 16.4.56. to 20.4.56.		
pro3 bi1 pro3 bi1 pro1 ad15 paba1 y pro1 ad15 paba1 y	20	No exchanges
pro3 bi1 pro3 bi1 pro1 ad15 paba1 y	6	No exchanges
pro3 bi1 pro1 ad15 paba1 y pro1 ad15 paba1 y	4	No exchanges
pro3 bi1 pro3 ad15 paba1 y pro1 bi1 pro1 ad15 paba1 y	3	Single exchanges pro1 - ad15.
pro3 bi1 pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	5	Single exchanges paba1 - y
pro3 bi1 pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	1	Single exchange paba1 - y
pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	1	Single exchange paba1 - y
pro3 y pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 bi1	1	4-strand double exchange within paba1 - y
pro3 bi1 pro3 paba1 y pro1 ad15 bi1 pro1 ad15 paba1 y	1	Single exchange ad15 - paba1

Table J/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.5. Dissected 16.4.56. to 20.4.56.		
pro3 bi1 pro3 pro1 ad15 paba1 y bi1 pro1 ad15 paba1 y	1	Single exchange y - bi1
pro3 bi1 pro3 ad15 paba1 y pro1 ad15 paba1 bi1 pro1 y	1	3-strand double exchange pro1 - ad15; paba1 - y
pro3 y pro3 ad15 paba1 y pro1 bi1 pro1 ad15 paba1 bi1	1	4-strand double exchange pro1 - ad15; paba1 - y
pro3 pro1 bi1 pro1 ad15 paba1 y	1	3-strand double exchange pro1 - ad15; y - bi1
pro3 bi1 pro3 y bi1 pro1 ad15 paba1 pro1 ad15 paba1 y	1	2-strand double exchange paba1 - y; y - bi1
pro3 ad15 paba1 bi1 pro3 pro1 y pro1 ad15 paba1 y bi1	1	2-strand double exchange pro1 - ad15; paba1 - y. 4-strand double exchanges pro1 - ad15; y - bi1 and paba1 - y; y - bi1.
pro3 ad15 paba1 pro3 y pro1 bi1 pro1 ad15 paba1 y bi1	1	3-strand double exchanges pro1 - ad15; paba1 - y and paba1 - y; y - bi1. 4-strand double exchange pro1 - ad15; y - bi1.
pro3 bi1 pro1 ad15 paba1 y	3	Incomplete
Perithecium No.6. Dissected 23.4.56. to 27.4.56.		
pro3 bi1 pro3 bi1 pro1 ad15 paba1 y pro1 ad15 paba1 y	93	No exchanges
pro3 bi1 pro3 bi1 pro1 ad15 paba1 y	4	No exchanges
pro3 bi1 pro1 ad15 paba1 y pro1 ad15 paba1 y	10	No exchanges

Table J/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.6. Dissected 23.4.56. to 27.4.56.		
pro3 bi1 pro3 pro1 ad15 paba1 y bi1 pro1 ad15 paba1 y	1	Single exchange pro3 - pro1
pro3 pro1 ad15 paba1 y bi1 pro1 ad15 paba1 y	1	Single exchange pro3 - pro1
pro3 bi1 pro3 ad15 paba1 y pro1 bi1 pro1 ad15 paba1 y	14	Single exchanges pro1 - ad15.
pro3 ad15 paba1 y pro3 ad15 paba1 y pro1 bi1 pro1 bi1	1	4-strand double exchange within pro1 - ad15
pro3 bi1 pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	23	Single exchanges paba1 - y
pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	1	Single exchange paba1 - y
pro3 bi1 pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	1	Single exchange paba1 - y
pro3 y pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 bi1	2	4-strand double exchanges within paba1 - y
pro3 bi1 pro3 paba1 y pro1 ad15 bi1 pro1 ad15 paba1 y	1	Single exchange ad15 - paba1
pro3 bi1 pro3 pro1 ad15 paba1 y bi1 pro1 ad15 paba1 y	9	Single exchanges y - bi1
pro3 bi1 pro3 ad15 paba1 bi1 pro1 y pro1 ad15 paba1 y	2	2-strand double exchanges pro1 - ad15; paba1 - y.

Table J/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.6. Dissected 23.4.56. to 27.4.56.		
pro3 bi1 pro3 ad15 paba1 y pro1 ad15 paba1 bi1 pro1 y	1	3-strand double exchange pro1 - ad15; paba1 - y
pro3 y pro1 bi1 pro1 ad15 paba1 y	1	3-strand double exchange pro1 - ad15; paba1 - y
pro3 bi1 pro1 ad15 paba1 pro1 ad15 paba1 y	1	2-strand double exchange paba1 - y; y - bi1
pro3 bi1 pro3 y bi1 pro1 ad15 paba1 pro1 ad15 paba1 y	2	2-strand double exchanges paba1 - y; y - bi1
pro3 ad15 paba y bi1 pro3 ad15 paba1 y pro1 pro1 bi1	1	4-strand double exchange within pro1 - ad15; single exchange y - bi1.
pro3 bi1 (3 spores) pro3 y (2 spores) pro1 ad15 paba1 bi1 (1 spore) pro1 ad15 paba1 y (1 spore)	1	ABNORMAL. Single exchange paba1 - y
pro3 bi1 (2 spores) pro3 (1 spore) pro1 ad15 paba1 y bi1 (1 spore) pro1 ad15 paba1 y (3 spores)	1	ABNORMAL. Single exchange y - bi1.
pro3 bi1 pro1 ad15 paba1 y	1	Incomplete
pro3 bi pro3 ad15 paba1 y	1	Incomplete
pro3 y pro3 ad15 paba1 y	1	Incomplete
pro3	1	Incomplete
-	1	No growth
Perithecium No.7. Dissected 30.4.56. to 4.5.56.		
pro3 bi1 pro3 bi1 pro1 ad15 paba1 y pro1 ad15 paba1 y	60	No exchanges

Table J/. cont^{d}.

Genotypes	Number of asci	Comments
Perithecium No.7. Dissected 30.4.56. to 4.5.56.		
pro3 bi1 pro3 bi1 pro1 ad15 paba1 y	16	No exchanges
pro3 bi1 pro1 ad15 paba1 y pro1 ad15 paba1 y	10	No exchanges
pro3 bi1 pro3 ad15 paba1 y pro1 bi1 pro1 ad15 paba1 y	9	Single exchanges pro1 - ad15.
pro3 bi1 pro3 ad15 paba1 y pro1 ad15 paba1 y	1	Single exchange pro1 - ad15
pro3 bi1 pro3 ad15 paba1 y pro1 bi1	2	Single exchanges pro1 - ad15.
pro3 ad15 paba1 y pro3 ad15 paba1 y pro1 bi1 pro1 bi1	1	4-strand double exchange within pro1 - ad15.
pro3 ad15 paba1 y pro3 ad15 paba1 y pro1 bi1	1	4-strand double exchange within pro1 - ad15.
pro3 bi1 pro3 y pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	30	Single exchanges paba1 - y
pro3 bi1 pro3 y pro1 ad15 paba1 y	1	Single exchange paba1 - y
pro3 bi1 pro3 pro1 ad15 paba1 y bi1 pro1 ad15 paba1 y	9	Single exchanges y - bi1
pro3 pro1 ad15 paba1 y bi1 pro1 ad15 paba1 y	1	Single exchange y - bi1
pro3 bi1 pro3 ad15 paba1 bi1 pro1 y pro1 ad15 paba1 y	2	2-strand double exchanges pro1 - ad15; paba1 - y

Table J/. cont[d].

Genotypes	Number of asci	Comments
Perithecium No.7. Dissected 30.4.56 to 4.5.56.		
pro3 bi1 pro3 ad15 paba1 y pro1 y pro1 ad15 paba1 bi1	1	3-strand double exchange pro1 - ad15; paba1 - y
pro3 bi1 pro3 ad15 paba1 y pro1 ad15 paba1 y bi1 pro1	1	3-strand double exchange pro1 - ad15; y - bi1
pro3 bi1 pro3 y pro1 ad15 paba1 pro1 ad15 paba1 y bi1	1	3-strand double exchange paba1 - y; y - bi1
pro3 y bi1 pro3 pro1 ad15 paba1 bi1 pro1 ad15 paba1 y	1	3-strand double exchange paba1 - y; y - bi1
pro3 pro3 ad15 paba1 y bi1 pro1 ad15 paba1 y bi1 pro1	1	4-strand double exchange within y - bi1. Single exchange pro1 - ad15.
pro3 bi1 pro1 ad15 paba1 y	4	Incomplete
pro1 ad15 paba1 bi1 pro3 ad15 paba1 y	1	Incomplete
pro3 y pro1 ad15 paba1 bi1	1	Incomplete
pro3 ad15 paba1 bi1	1	Incomplete

SUMMARY.

Types of asci	Number of ascospores germinating. 0	1	2	3	4	5	6	7	8
Classifiable									
Selfed green	-	-	-	-	-	-	-	-	-
Selfed yellow	-	-	-	-	-	-	-	-	-
Hybrid	-	2	9	12	33	71	136	164	176/603
Non-classifiable									
Green	-	1	-	-	-	-	-	-	-/ 1
Yellow	-	-	2	2	-	-	-	-	-/ 4
No germination	1	-	-	-	-	-	-	-	-/ 1
Abnormal	-	-	-	-	-	-	-	2	-/ 2
Grand Total	1	3	11	14	33	71	136	166	176/611

Table K./.
Cross paba1 y ad8//y pyro4 dp (dp = duplication carrying ad20 bi1). From streak inoculum on minimal medium. Prepared on the 15.3.54. pa = point of attachment of the duplication to the "white " chromosome. ad20x2 indicates that two ad20 mutants are present.

Genotypes	Ascus number	Comments
Perithecium No.1. Dissected 25.5.54.		
pyro4 (5 spores)	1	No exchanges
pyro4 (2 spores) ad20x2 bi1 pyro4 (2 spores) y pyro4 (2 spores)	2	Single exchange pa - y
Perithecium No.2. Dissected 25.5.54.		
pyro4 (4 spores)	3	Incomplete
y pyro4 (1 spore)	4	Incomplete
bi1 pyro4 (2 spores) y pyro4 (1 spore)	5	Incomplete
pyro4 (2 spores) ad20x2 bi1 pyro4 (1 spore)	6	Incomplete
pyro4 (6 spores) bi1 pyro4 (2 spores)	7	Single exchange ad20 - bi1
-	8	No growth
-	9	Ascus with 2 small shrivelled spores and 6 normal spores.
-	10	Ascus with 1 small shrivelled spore and 8 normal spores.
Perithecium No.3. Dissected 27.5.54.		
pyro4 (6 spores) bi1 pyro4 (2 spores)	11	Single exchange ad20 - bi1
pyro4 (4 spores) y pyro4 (3 spores)	12	Single exchange pa - y in both pairs. 7 -spored ascus.
pyro4 (7 spores)	13	No exchanges. 7-spored ascus.
ad20x2 pyro4 (2 spores) bi1 pyro4 (2 spores) pyro4 (2 spores) y pyro4 (2 spores)	14	Single exchange pa - y; single exchange ad20 - bi1

Table K/. cont^{d}.

Genotypes	Ascus number	Comments.
Perithecium No. 4. Dissected 30.5.54.		
bi1 pyro4 (4 spores) ad20x2 pyro4 (2 spores) y pyro4 (2 spores)	15	3-strand double exchange pa - y; ad20 - bi1. Single exchange ad20 - bi1 in the other pair
pyro4 (8 spores)	16	No exchanges
pyro4 (5 spores)	17	No exchanges
pyro4 (4 spores) bi1 pyro4 (1 spore)	18	Single exchange ad20 - bi1.
pyro4 (7 spores)	19	No exchanges
Perithecium No.5. Dissected 2.6.54.		
pyro4 (7 spores)	20	No exchanges
pyro4 (6 spores) bi1 pyro4 (1 spore)	21	Single exchange ad20 - bi1.
y pyro4 (6 spores) ad20x2 bi1 pyro4 (2 spores)	22	Loss of one duplication. Single exchange pa - y
Perithecium No.6. Dissected 3.6.54.		
pyro4 (6 spores) bi1 pyro4 (2 spores)	23	Single exchange ad20 - bi1.
pyro4 (2 spores) ad20x2 bi1 pyro4 (2 spores) y pyro4 (1 spore)	24	Single exchange pa - y
-	25	No growth
-	26	No growth
pyro4 (4 spores) ad20x2 bi1 pyro4 (2 spores) y pyro4 (1 spore)	27	Single exchange pa - y.
pyro4 (8 spores)	28	No exchanges.