ABSENCE OF INTERFERENCE IN ASSOCIATION WITH GENE CONVERSION IN *SORDARIA FIMICOLA*, AND PRESENCE OF INTERFERENCE IN ASSOCIATION WITH ORDINARY RECOMBINATION[1]

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ABSTRACT

From the analysis of large samples of gene conversion asci in the *g* locus of *Sordaria fimicola*, it was found that neither the conversion event itself nor conversion-associated recombination of flanking markers cause either chiasma or chromatid interference with crossing over in a neighboring interval. The presence of more than one kind of crossover event, one causing interference the other not, is considered. The existence of two kinds of gene loci, one of single-cistron composition and the other of multiple-cistron composition, is discussed in relation to reciprocal recombination within a locus.

IN the present study, the nature of gene conversion has been reexamined with regard to the presence or absence of interference in association with conversion, and the well-established observation that a conversion event is accompanied, with high frequency, by flanking marker recombination exhibiting normal segregation ratios.

The presence of conversion-associated recombination, that is recombination of flanking markers on either side of a converted locus, has been noticed since the early period of gene conversion research (MITCHELL 1955; FREESE 1957; KITANI, OLIVE and EL-ANI 1962; STADLER and TOWE 1963; CASE and GILES 1964). The close relationship of gene conversion to recombination of flanking markers has been observed in all cases that permit tetrad analysis in the presence of flanking markers (KITANI and OLIVE 1967, 1969, in *Sordaria fimicola*; FOGEL and HURST 1967 and FOGEL and MORTIMER 1969, in *Saccharomyces cerevisiae*; STADLER and KARIYA 1969, in *Neurospora crassa*; and STADLER, TOWE and ROSIGNOL 1970, in *Ascobolus immersus*; CHOVNICK *et al.*, 1970, CHOVNICK, BALLANTYNE and HOLM 1971, and CHOVNICK 1973, in *Drosophila melanogas-*

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ter). This phenomenon is also conspicuous in the analyses of prototrophs derived from reciprocal recombination even though nonreciprocal and reciprocal recombinants are generally not distinguished from each other (SIDDIQI and PUTRAMENT 1963, in *Aspergillus nidulans*; FINCHAM 1967 and MURRAY 1968, 1969 and 1970, in *Neurospora crassa*). In addition, the phenomenon of localized negative interference (PRITCHARD 1959; PEES 1967) could be considered as conversion-associated recombination, although aberrant segregation was not examined in these studies.

In most of the proposed models, the conversion event itself and its associated recombination of flanking markers are considered to occur by the interaction of two homologous chromatids out of the four in the meiotic bivalent (FREESE 1957; WHITEHOUSE 1963; HOLLIDAY 1964a,b; WHITEHOUSE and HASTINGS 1965; EMERSON 1969; WHITEHOUSE 1970). The involvement of more than two chromatids in the fundamental mechanism of conversion and its associated recombination can be eliminated from consideration, even though more than two chromatids may appear to be involved sporadically as secondary products (EMERSON 1969). This situation is clearly and unambiguously shown in the aberrant 4+ : 4*m* segregation asci described by KITANI and OLIVE (1967), and KITANI (1962), as pointed out by EMERSON (1969).

Chiasma interference is expected in the adjoining short intervals if it is assumed conversion itself and its associated flanking marker recombination take place at the same time and by the same mechanism as ordinary crossing over. On this assumption, the conversion event and associated recombination must require synapsis and chiasma formation at the same time as the ordinary crossovers in nearby intervals. For these reasons, the presence or absence of interference at a suitable interval near the gene conversion locus may indicate an aspect of gene conversion that has fundamental importance in relation to the mechanism of genetic recombination. The present analysis examines these properties in 19 one-point crosses and 11 heteroallelic crosses in *Sordaria fimicola*.

MATERIALS AND METHODS

Many of the asci used in the present analysis are derived from previous studies (KITANI and OLIVE 1967, 1969, 1970). The asci from the crosses in which h_5 or g_6 was used as a parent have not appeared in previous reports. The ascus records (raw data) of the crosses discussed in KITANI and OLIVE (1967, 1969), have been deposited with the Editor of GENETICS. The ascus records of the crosses discussed in KITANI and OLIVE (1970), the crosses introduced in this report, and the crosses of the "zone-analysis" in KITANI and WHITEHOUSE (1974), have been likewise deposited with the Editor.

The linkage relationship of the *g* locus to the adjacent flanking markers *mat* and *cor* and the secondary marker *sp* is shown in Figure 1A. The gene distances in this map are based on EL-ANI, OLIVE and KITANI (1961). Although these distances show slight differences from the ones in the control experiment, the analysis in this report is based on this map. The sequence of the *g* locus alleles is shown in two different orders in Figure 1. Figure 1B is based on the frequency of wild-type spore production (ordinary map sequence) and has some uncertainty in the relative positions of h_4 and h_3, as shown in Figure 11 of KITANI and OLIVE (1969). Figure 1C and 1D are different from 1B in the relative positions of h_5 and h_2, and are based

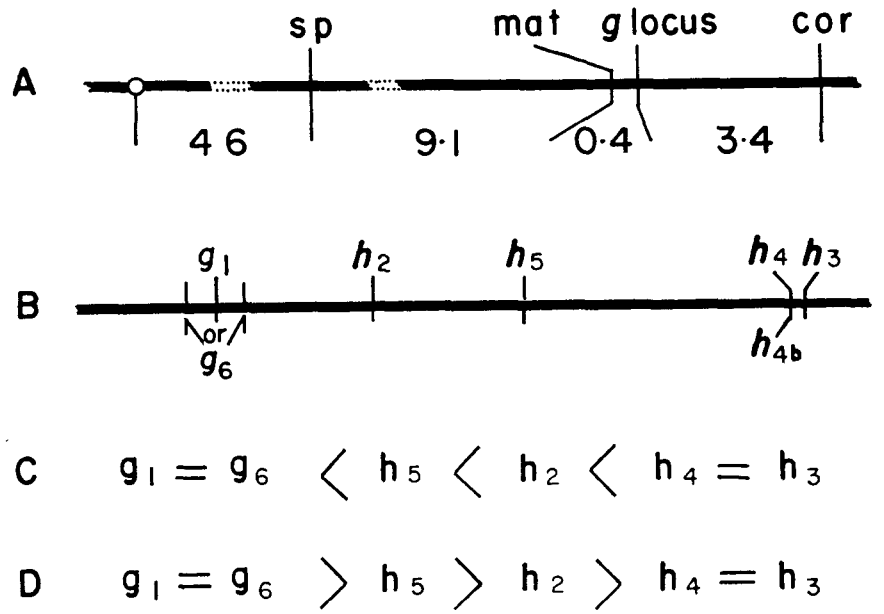

FIGURE 1.—Relation of *g* locus alleles and flanking markers. (A) linkage relation of the *g* locus to the flanking markers; (B) apparent site sequence of the *g* locus based on the frequency of asci with any number of wild-type spores, refer to KITANI and OLIVE (1969); (C) epistatic relation of alleles in the *g* locus; (D) site sequence of alleles according to the tendency to convert to wild type and, also, order in darkness of spore color.

on the epistatic relation (1C), and the degree of the allele's preference to convert to wild type (1D), as well as the darkness of spore-color expression (1D).

Mutant h_5 was obtained at the University of North Carolina by a low dosage UV treatment of a wild-type mycelium grown in cytosine-supplemented cornmeal agar. Another mutant g_6 was obtained at Kyoto University by X irradiation. Both h_5 and g_6 are located in the *g* locus (Figure 1) and their spore colors are light grey and grey, respectively.

The methods of crossing, scoring and determining ascus genotypes have been described in the three previous reports cited above. In order to analyze all of the asci in the perithecia of a crossing plate in fully matured condition with stable spore color distinction and to obtain better germination of dissected spores, a technique called "after-maturation" has been applied to most of the crosses (exceptions are: crosses A, D, F and K in KITANI and OLIVE 1967; and Jd, Jf, Jh, L and Li in KITANI and OLIVE 1969; for the cross records, refer to the APPENDIX). The technique involves transferring the crossing plates from 23° to 5° on the eighth day of cultivation, and keeping the plates in the dark and cold for about two weeks to allow gradual maturation without spore discharge.

The total numbers of asci for the crosses in this report do not always match the ones given in the previous publications and the ones in the APPENDIX of this report. This is primarily due to omission of asci showing conversion at the *sp* locus. These asci were omitted because scoring recombination in the *sp-mat* interval was impossible or ambiguous. The number of omitted asci is negligible and does not affect the conclusions. However, anyone interested in conversion of outside markers may examine the deposited records, the APPENDIX (with an association of the *g* locus conversion) and part II of results (with normal segregation at the *g* locus).

The terminology used in this report is the same as in previous publications and is based upon the unique feature of the *g* locus, which readily permits detection of a variety of conversion

TABLE 1

Analysis of recombination frequencies in the sp-mat *interval in gene conversion asci from one-point crosses**

Part 1

Ascus type	6+ : 2*m*								Aberrant 4+ : 4*m*								2+ : 6*m*							
Recombination class	Ra			Rp					Ra				Rp				Ra			Rp				
sp-mat recombination†	1	2 or 3	3 or 4	1	2	3	4		1	2	3	4	1	2	3	4	1	2 or 3	3 or 4	1	2	3	4	
Number of asci	211	20	26	160	11	23	8		202	12	23	9	210	11	20	14	36	4	6	27	1	2	0	
P-value for 1:2:1 ratio		—			$P > 0.50$					$P > 0.70$				$P > 0.50$				—			—			
Totals for *sp* not recombined and *sp* recombined	211	46		160	42				202	44			210	45			36	10		27	3			
	(82.2)	(17.8)		(79.2)	(20.8)				(82.1)	(17.9)			(82.4)	(17.6)			(78.3)	(21.7)		(90.0)	(10.0)			
P-value for the standard frequency of 18.2%	$P > 0.95$			$P > 0.30$					$P > 0.95$				$P > 0.80$				$P > 0.50$			—				

Part 2

Ascus type	5+ : 3*m*												3+ : 5*m*											
Recombination class	Ra-1			Rp-2				Ra-2				Rp-1				Ra-1			Rp-2				Ra-2				Rp-1			
sp-mat recombination†	1	2or3	3or4	1	2	3	4	1	2	3	4	1	2	3	4	1	2or3	3or4	1	2	3	4	1	2	3	4	1	2	3	4
		2	3	4													2	3	4											
		30	19														21	15												
Number of asci	173			114	8	11	7	88	7	15	6	114	7	15	5	143			86	8	10	4	46	5	2	1	52	2	8	2
P-value for 1:2:1 ratio		—		$P > 0.50$				$P \cong 0.90$				$P > 0.50$					—		$P \cong 0.30$				—				$P > 0.50$			
Totals for classes Ra and Rp	261	30	19	(added on Rp-1)				(added on Ra-1)				228				189	21	15	(added on Rp-1)				(added on Ra-1)				138			
		7	15	6									15	26	12		5	2	1									10	18	6
P-value for 1:2:1 ratio		$P \cong 0.90$										$P > 0.80$					—										$P \cong 0.50$			
Totals for *sp* not recombined and *sp* recombined	261	77										228	53			189	44										138	34		
	(77.2)	(22.8)										(81.1)	(18.9)			(81.1)	(18.9)										(80.2)	(19.5)		

TABLE 1—Continued

P-value for the standard frequency of 18.2%	$P > 0.02$	$P > 0.70$	$P > 0.70$			$P > 0.50$

Part 3

Ascus type	6+ : 2*m*	Aberrant 4+ : 4*m*	2+ : 6*m*	5+ : 3*m*	3+ : 5*m*	All ascus types pooled
Recombination class	Ra and Rp pooled	Ra and Rp pooled	Ra and Rp pooled	Ra and Rp pooled	Ra and Rp pooled	Ra and Rp pooled
sp-mat recombination†	1 2 or 3 3 or 4 2 3 4	1 2 3 4	1 2 or 3 3 or 4 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4
Number of asci	371 20 26 11 23 8	412 23 43 23	63 4 6 1 2 0	489 30 19 22 41 18	327 21 15 15 20 7	1662 75 66 72 129 56
P-value for 1:2:1 ratio	$P > 0.80$	$P = 0.95$	—	$P > 0.70$	$P > 0.20$	$P > 0.30$
Total for *sp* not recombined	371 88	412 89	63 13	489 130	327 78	1662 398
and *sp* recombined	(80.8) (19.2)	(82.2) (17.8)	(82.9) (17.1)	(79.0) (21.0)	(80.7) (19.3)	(20.7) (19.3)
P-value for the standard frequency of 18.2%	$P > 0.50$	$P > 0.70$	$P \cong 0.80$	$P > 0.05$	$P > 0.50$	$P \cong 0.20$

* The complete table is deposited with the Editor of GENETICS.

† The numbers 1 to 4 represent the following: (1) *sp* did not recombine; (2 + 4), *sp* recombined; (3) three chromatids are involved; (4) all four chromatids are involved. The numbers of chromatids involved were determined by three factors: conversion events, flanking marker recombination and recombination of the secondary marker *sp*. In all ascus types except aberrant 4+:4*m*, in which two homologous chromatids involved in the conversion event are phenotypically very obvious, one of the two chromatids involved could not be determined without the aid of flanking marker recombination or the two-strand double crossover of Ra-2. Therefore, when ambiguity is present in the class Ra, numbers of chromatids involved are given in the form of 2 or 3 and 3 or 4.

types. In this report, the six fundamental conversion ascus types (6+:2*m*, 2+:6*m*, 5+:3*m*, 3+:5*m*, normal 4+:4*m* conversion type and aberrant 4+:4*m*) are handled individually, rather than grouping them into "conversion" and "postmeiotic segregation" or "even ratio" and "odd ratio." The recombination classes of flanking markers are represented by Ra (flanking marker *recombination absent*) and Rp (flanking marker *recombination present*), rather than P (*parental*) and R (*recombinant*); Ra-2, one of the two subclasses of class Ra, is not parental in gene alignment with regard to flanking markers and the converted locus, but rather is the double recombinant.

RESULTS

PART I. Gene conversion asci

The results from 19 one-point crosses on the presence or absence of interference in the *sp-mat* interval are shown in Table 1 (Part 1, for the three ascus types, 6+ : 2*m*, aberrant 4+ : 4*m* and 2+ : 6*m*; Part 2, for two ascus types, 5+ : 3*m* and 3+ : 5*m*; Part 3, for all ascus types, but with the samples in which recombination classes Ra and Rp are pooled). The analyzed asci are the ones that showed aberrant segregation at the *g* locus within the interval *mat-cor*. The results described in this table permit examination of three major questions. The first question is whether or not crossing over in the *sp-mat* interval is affected by conversion events at the *g* locus. This can be determined for each ascus type in Part 1 and Part 2 comparing the percentages for the asci showing *sp* recombination with the standard frequency of 18.2% for this interval in nonconversion normal asci. The second question concerns chiasma interference, that is whether recombination classes Ra and Rp (flanking marker recombination absent and present in the interval *mat-cor*; for detail, see KITANI and OLIVE 1967, 1969) differ in the crossover frequency in the *sp-mat* interval. This can be examined along with the first question in Parts 1 and 2 of the table, but with a limitation of sampling within each ascus type. More detailed examination of this second question with larger samples will be done in Table 3, using the pooled data of all ascus types. The third question is whether or not chromatid interference is present. This can be determined for each recombination class of each ascus type by examining the deviation from the expected 1:2:1 ratio (for no interference) of the numbers of chromatids (two, three or four) simultaneously involved in the conversion event and in *sp* recombination.

As can be seen easily in Table 1, the deviation from the standard frequency 18.2% is not significant in any grouping in Parts 1 and 2 of the table, whenever the sample is reasonable in size. Chiasma interference, as well as differences between the recombination classes Ra and Rp, appears to be absent (detailed analysis in Table 3). Since there are no substantial differences in the crossover frequency in the *sp-mat* interval, in any of the classes, the data were pooled (Table 1 Part 3). These larger samples, indicate unambiguously the absence of chiasma interference.

In a previous report (KITANI and OLIVE 1967), the presence of chromatid interference in the *sp-mat* interval was suspected in recombination class Rp of ascus type, aberrant 4+ : 4*m*. However, in the larger sampling of the present report, the possibility of this is diminished. The *p*-values of the χ^2 tests for the

1:2:1 ratio to the numbers of chromatids involved simultaneously in a conversion event, flanking marker recombination, and *sp* recombination, applied on aberrant 4+ : 4*m* asci as well as other ascus types, all show good fit (Ra and Rp separately in Table 1, Part 1, and pooled in Part 3). Therefore, chromatid interference is also absent in gene conversion asci of *S. fimicola*.

The fact that both recombination classes equally lack chiasma interference, as well as chromatid interference, suggests that flanking marker recombination does not have any special effect on recombination in the interval adjacent to that defined by the immediate flanking markers.

The analysis of data from the 11 heteroallelic crosses is shown in Table 2 (Part 1, for the three ascus types, 6+ : 2*m*, aberrant 4+ : 4*m* and 2+ : 6*m*; Part 2, for the other three ascus types, 5+ : 3*m*, normal 4+ : 4*m* conversion type and 3+ : 5*m*; Part 3, for all six ascus types in the samples in which recombination classes Ra and Rp are pooled: the ascus types are classified by the distribution of the epistatic allele in the ascus).

The results of this analysis are similar to those of the one-point crosses. No substantial deviation of crossover frequency in the *sp-mat* interval from the standard frequency of 18.2% occurred in any conversion ascus type, whenever the size of sample is reasonable (as indicated by the *p*-values given in the table). Recombination classes Ra and Rp did not show any difference in the crossover frequency in the *sp-mat* interval, as shown in Table 2, Parts 1 and 2. Also, these classes were not different in the degree of fit to the 1:2:1 ratio for the numbers of chromatids involved in the conversion event and its associated flanking marker recombination or in recombination in the *sp-mat* interval (Table 2, Parts 1 and 2, and also Table 3). Through the examination of Part 3, in which the Ra and Rp classes are pooled, it is clear that the nature of the conversion ascus type at the *g* locus does not affect the frequency of crossing over in the *sp-mat* interval or the chromatids involved in the conversion event.

For convenience in comparing the interference effect in recombination classes Ra and Rp in large samples, Table 3 has been prepared. In this table, all ascus types are pooled within the classes Ra and Rp in one-point crosses and in heteroallelic crosses separately. Then both the samples from both kinds of crosses were put together to apply χ^2 tests on the largest available samples. It is clear from this table that there is no chromatid interference in either the classes Ra or Rp, or in the one-point or the heteroallelic crosses. Also there is no chiasma interference in any grouping.

These observations indicate the following with regard to the relationship of gene conversion events and conversion-associated recombination to crossing over in the short secondary interval (the interval next to the one between the converted locus and its flanking marker) in Sordaria: (1) Chiasma interference is absent. (2) Chromatid interference is absent. (3) There is no difference between the different conversion ascus types, or between one-point and heteroallelic crosses. (4) Both of the recombination classes, Ra and Rp, showed complete absence of interference, even though the former class lacks recombination of the flanking markers, while the latter class exhibits such exchange.

TABLE 2

Analysis of recombination frequencies in the sp-mat *interval in gene conversion asci from heteroallelic crosses**

Part 1

Ascus type	6+ : 2*h*								Aberrant 4+ : 4*h*								2+ : 6*h*							
Recombination class	Ra				Rp				Ra				Rp				Ra				Rp			
sp-mat recombination†	1	2 or 3	3 or 4	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2 or 3	3 or 4	4	1	2	3	4
Number of asci	50	6	2	2	23	7	2	2	100	3	10	3	76	2	3	2	51	3	5	0	29	1	5	2
P-value for 1:2:1 ratio		—				—				—				—				—				—		
Totals for *sp* not recombined and *sp* recombined	50 (80.6)	12 (19.4)			23 (67.6)	11 (32.4)			100 (86.2)	16 (13.8)			76 (91.6)	7 (8.4)			51 (83.6)	10 (16.4)			29 (78.4)	8 (21.6)		
P-value for the standard frequency of 18.2%	$P > 0.80$				$P > 0.02$				$P > 0.20$				$P > 0.02$				$P > 0.70$				$P > 0.50$			

Part 2

Ascus type	5+ : 3*h*								Normal 4+ : 4*h*								3+ : 5*h*							
Recombination class	Ra-1 and Ra 2 pooled				Rp 2 and Rp-1 pooled				Ra-1 and Ra-2 pooled				Rp-2 and Rp-1 pooled				Ra-1 and Ra-2 pooled				Rp-2 and Rp-1 pooled			
sp-mat recombination†	1	2 or 3	3 or 4	4	1	2	3	4	1	2 or 3	3 or 4	4	1	2	3	4	1	2 or 3	3 or 4	4	1	2	3	4
Number of asci	137	10	13	6	103	3	14	7	299	21	27	6	252	16	21	9	133	14	8	2	104	4	7	8
P-value for 1:2:1 ratio	$P \cong 0.80$				$P > 0.30$				$P \cong 0.30$				$P \cong 0.30$				$P > 0.30$				$P \cong 0.30$			
Totals for *sp* not recombined and *sp* recombined	137 (75.7)	44 (24.3)			103 (81.1)	24 (18.9)			299 (82.6)	63 (17.4)			252 (84.6)	46 (15.4)			133 (79.2)	35 (20.8)			104 (84.6)	19 (15.4)		
P-value for the standard frequency of 18.2%	$P > 0.02$				$P > 0.80$				$P > 0.50$				$P > 0.20$				$P > 0.70$				$P > 0.70$			

TABLE 2—Continued

Part 3

Ascus type Recombination class	6+ : 2*h* Ra and Rp pooled	Aberrant 4+ : 4*h* Ra and Rp pooled	2+ : 6*h* Ra and Rp pooled	5+ : 3*h* Ra and Rp pooled	Normal 4+ : 4*h* Ra and Rp pooled	3+ : 5*h* Ra and Rp pooled	All ascus types pooled Ra and Rp pooled
sp-mat recombination†	2 or 3 3 ro 4 1 2 3 4	1 2 3 4	2 or 3 3 or 4 1 2 3 4	2 or 3 3 or 4 1 2 3 4	2 or 3 3 or 4 1 2 3 4	2 or 3 3 or 4 1 2 3 4	2 or 3 3 or 4 1 2 3 4
Number of asci	73 6 2 9 4 2	176 5 13 5	80 3 5 1 7 2	239 10 13 9 23 13	551 21 27 22 26 13	237 14 8 6 13 13	1356 54 55 52 86 48
P-value for 1:2:1 ratio	$P \cong 0.01$	$P > 0.80$	—	$P \cong 0.70$	$P > 0.10$	$P > 0.20$	$P > 0.50$
Totals for *sp* not recombined and *sp* recombined	73 23 (76.0) (24.0)	176 23 (88.4) (11.6)	80 18 (81.6) (18.4)	239 68 (77.9) (22.1)	551 109 (83.5) (16.5)	237 54 (81.4) (18.6)	1356 295 (82.1) (17.9)
P-value for the standard frequency of 18.2%	$P > 0.10$	$P \cong 0.02$	$P \cong 0.95$	$P > 0.50$	$P > 0.20$	$P > 0.80$	$P > 0.70$

* The complete table is deposited with the Editor of GENETICS.
† Refer to Table 1.

TABLE 3

Comparisons between the recombination classes Ra and Rp and between the ascus types in pooled samples

Source of data*	Pooled data from 19 one-point crosses								Pooled data from 11 heteroallelic crosses								Pooled data from both kinds of crosses							
Recombination class	Ra					Rp			Ra					Rp			Ra					Rp		
sp-mat recombination†	1	2 or 3	3 or 4	2	3	4	1	2	3	4	1	2 or 3	3 or 4	2	3	4	1	2 or 3	3 or 4	2	3	4	1	2	3	4
6+ : 2*m*	211		20		26		160	11	23	8	50		6		2		23	7	2	2						
Aberrant														2	2	0										
4+ : 4*m*	202	12	4	23	6	8	210	11	20	14	100	3	3	10	5	3	76	2	3	2						
2+ : 6*m*	36						27	1	2	0	51						29	1	5	2						
														0	2	0										
5+ : 3*m*	261		7	30	15	19	228	15	26	12	137		6	10	9	13	103	3	14	7						
Normal																										
4+ : 4*m*	(not scored)						(not scored)				299		6	21	5	27	252	16	21	9						
3+ : 5*m*	189		5	21	2	15	138	10	18	6	133		2	14	6	8	104	4	7	8						
All ascus types pooled	899		24	75	40	66	763	48	89	40	770		19	54	34	55	587	33	52	30	1669	43	74	129	33	121	1350	81	141	70
P-value for 1:2:1 ratio	$P > 0.30$						$P \cong 0.70$				$P > 0.90$						$P > 0.50$				$P \cong 0.50$					$P > 0.50$			
Totals for *sp* not recombined and *sp* recombined	899		220				763		177		770		180				587		115		1669		400			1350		292	
	(80.3)		(19.7)				(81.2)		(18.8)		(81.1)		(18.9)				(83.6)		(16.4)		(80.7)		(19.3)			(82.2)		(17.8)	
P-value for the standard frequency of 18.2%	$P \cong 0.20$						$P > 0.50$				$P > 0.50$						$P > 0.20$				$P \cong 0.20$					$P > 0.50$			
Contingency χ^2 and *P*-value	$\chi^2 = 0.257$ $P > 0.50$										$\chi^2 = 1.953$ $P > 0.10$										$\chi^2 = 1.487$ $P > 0.20$								

* Refer to Tables 1 and 2 for one-point crosses and heteroallelic crosses, respectively.
† Refer to Table 1.

PART II. Asci of normal segregation

Procedure of the experiment: In this experiment, the *g* locus is represented by h_4 rather than g_1 (commonly used in EL-ANI, OLIVE and KITANI 1961; PERKINS *et al.* 1963; and extensive unpublished observation regarding the gene distances), and the gene alignment of the cross is that of Cross M ($sp + h_4$ $cor/+ \times + mat ++/i$; refer to the APPENDIX).

An average of 14 asci showing the normal segregation ratio at the *g* locus were dissected from each ascus cluster. A technique called "after-maturation" has been applied to all the crossing plates to get homogeneous maturation of nearly all of the asci and to get better germination of spores. The genotypes of outside markers *sp* (secondary marker), *mat* and *cor* (flanking markers), were directly scored through morphological examination of mycelia grown from the dissected spores which had been transferred on CM+ culture plates. Although ascus dissections were carried out keeping in mind the fact that the MI:MII ratio for the *g* locus is 1:2 in the natural population of asci (at 23° cultivation), no attempt was made to maintain this ratio for individual ascus clusters, and the ratio in the pooled data shows some distortion (see Table 4).

The crossover analysis in intervals I, II, III and IV (refer to Table 4) was done on each ascus cluster. The data for each cluster were then pooled, but some clusters that showed a reversed recombination frequency (100% minus the expected percentage) in interval II were omitted from the pooling. These clusters are shown individually in Table 4. This phenomenon is considered to be the result of somatic recombination in ascogonia (KITANI 1962, 1963).

Recombination frequency in each interval: As shown in Table 4, the recombination frequency in the *sp-mat interval* (interval II) is 18.0% (excluding three clusters, #8, #70 and #108). Clusters #8 and #108 showed almost the reverse of the expected frequency in interval II, and are therefore excluded from the pooling. Cluster #70 showed an intermediate frequency in this interval, perhaps due to the structure of this cluster. This cluster was probably composed of two sectors, one containing the asci with the normal recombination frequency and the other containing the asci with the reversed frequency. [For the phenomenon of the sectored cluster of asci, refer to KITANI and WHITEHOUSE (1974); this phenomenon is present also in a heterothallic species *S. brevicollis*, WHITEHOUSE (unpublished observation).]

The recombination frequency in interval III appeared as 0.9% (Table 4), which matches well with 0.84% reported by EL-ANI, OLIVE and KITANI (1961). On the other hand, the recombination frequency in interval IV appeared somewhat lower than that observed by EL-ANI, OLIVE and KITANI (1961); a frequency of 5.9% was recorded in this experiment, while it was 6.83% in the previous one. However, the confidence limits of these data overlap.

Double crossing over and interference: In the absence of interference, the expected frequency of double crossing over in the intervals *sp-mat* (interval II) and *mat-cor* (interval III for *mat-g* and interval IV for *g-cor* are combined) is 18.0%. The observed frequency of double crossing over is 4.4% (5/13 asci have

TABLE 4

*Analysis of crossing over in the g-arm of linkage group I using nonconversion asci**

Ascus cluster	Number of asci dissected	Segregation of *g*		C	Recombination in the interval: I		*sp*	II		*mat*	III	*g*	IV	*cor*	Double crossing over in intervals: II and III or II and IV
		MI	MII		MI	MII		T	NPD		T		T		
Pooled data for clusters #1 to #122 excluding #8, #70 and #108	1,660	518	1,142 (68.9%)		539	1,121 (67.5%)		299 (18.0%)	3		15 (0.9%)		98 (5.9%)		2 asci in II and III (both asci, 3-chromatid event) 3 asci in II and IV (one ascus, 2-chromatid event; two asci, 4-chromatid event) ↘ ↙ 113 (6.8%)
#8	18	5	13		5	13		11 (61%)	0		0		0		0
#70	15	4	11		7	8		6 (40%)	0		0		0		0
#108	15	4	11		8	7		9 (60%)	1		0		0		0

* I, II, III and IV: Intervals examined. MI and MII: First division segregation and second division segregation, respectively. T and NPD: Tetratype ascus and nonparental ditype (recombinant ditype) ascus, respectively.

a crossover in interval III or in interval IV; see Table 4). This 0.75 reduction is statistically significant ($p < 0.01$), indicating that chiasma interference is present in the asci showing normal segregation at the *g* locus.

Three recombinant ditype (NPD; nonparental ditype) asci were obtained in interval II from a total of 1660 asci (Table 4). The expected number of asci of this type is seven if interference is absent and less than this number when interference is in force ($\text{NPD} = \frac{1}{8}\text{T}^2\left(1 + \frac{3}{2}\text{T}\right)$ applied effectively by PERKINS 1962, in utilizing STRICKLAND's (1958) modification of the formula of PAPAZIAN (1952). This data and those previously reported in EL-ANI, OLIVE and KITANI (1961) in which no NPD asci were obtained in the *sp-g* interval among 633 asci from various pooled crosses jointly suggest the presence of relatively weak chiasma interference.

Gene conversion of the outside markers: From a total of 1469 asci in which genotypes were fully scored for all four spore pairs (*e.g.*, at least one member of each spore pair in an ascus germinated), ten asci had gene conversion of an outside marker. The outside markers yielded the following: (1) the *sp* locus (proximal secondary marker): a total of five conversion asci, three with excess of wild type, two with excess of mutant, (2) the *mat* locus (proximal flanking marker): no gene conversion, and (3) *cor* locus (distal flanking marker): total of five conversion asci, all of them with excess of wild type. For the convenience of comparison, the result of the conversion analysis of the outside markers carried out on a total 4350 *g*-locus conversion asci presented in the APPENDIX is shown below: (1) *sp* locus (proximal secondary marker): a total of seven conversion asci, two with excess of wild type, five with excess of mutant, (2) *mat* locus (proximal flanking marker): no gene conversion, (3) *cor* locus (distal flanking marker): a total of 12 conversion asci, ten with excess of wild type, two with excess of mutant.

The chromatid relations of these outside marker conversions to the *g*-locus conversion is ambiguous most of the time because all the outside marker conversions fully analyzed so far are the 6:2 type. The common features evident in the above two sets of data are that the proximal flanking marker *mat* did not show any gene conversion, while the secondary marker *sp*, whose location is further proximal, and the distal marker, *cor*, both showed gene conversion.

DISCUSSION

1. *Expectation of the presence of interference in gene conversion asci and the two different results found in different organisms*

As indicated in the introduction, interference is expected in an interval such as *sp-mat*, close to the locus where gene conversion occurred. This expectation is based on the notion that: (1) The initiation of a gene conversion event involves the intimate interaction between two homologous chromatids (DNA double helices) and one or more of the following processes, "DNA replication," "heteroduplex formation," "DNA base correction," "copy and excision," etc. (2)

Owing to the intimate interaction between chromatids required in all the models of conversion, the state of the chromosome is the same as that which causes chiasmata and, consequently, chiasma interference.

When gene conversion occurs, conversion-associated recombination of flanking markers is observed in high frequency (even the lowest frequency reported so far is 20% in the *me-7* locus conversion in Neurospora; average 40–45% in the *g* locus of *S. fimicola*, some loci in Neurospora, etc.; and as high as 60–65% in two loci of *Aspergillus nidulans*). Conversion-associated recombination appears to be the same as ordinary reciprocal recombination not associated with gene conversion. Since there is no apparent difference between ordinary reciprocal recombination and conversion-associated flanking marker recombination, and since the relationship of reciprocal recombination to interference at near-by regions is an established rule of heredity, interference is expected among conversion tetrads accompanied by flanking marker recombination (recombination class Rp). This situation should apply to the Rp class even if the conversion event itself is separated from the mechanism of reciprocal exchange; the other groups of tetrads that did not show flanking marker recombination (class Ra) may or may not exhibit interference.

In spite of these expectations, the present analysis on the *sp-mat* interval next to the intervals *mat-g-cor* showed no interference at all, neither chiasma interference nor chromatid interference, in all the groupings applied. On the other hand, the present analysis, as well as that of PERKINS *et al.* (1963), of non-conversion tetrads, which represent the relationship between reciprocal recombination and interference, showed the presence of chiasma interference in the *g* arm of linkage group I, including the same *sp-mat* interval.

The lack of interference in *S. fimicola* in the present and previous studies is not the sole example of its kind. As shown in Table 5 (pooling and reorganization were applied by this author to the Tables of SIDDIQI 1962), the recombinant prototrophs in the *paba* locus of *Aspergillus* nidulans did not show chiasma interference in the *y-bi* interval in either recombination classes Ra or Rp (flanking markers *ad-9* and *y*; Ra, recombination absent between these, Rp, recombination present between these). Also in *Sordaria brevicollis*, FIELDS and OLIVE (1967) obtained data indicating the absence of interference induced by gene conversion and associated recombination of flanking markers, although the sample in their experiment was not large. The prototroph spores in *Aspergillus* analyzed in Table 5 and the wild-type spores in *S. brevicollis* may have arisen in three ways: (1) 6+ : 2*m* type conversion occurred at either mutant site of the cross, but the other site segregated normally, (2) both sites were involved in a conversion event, but one site gave rise to normal 4+ : 4*m* segregation (for this process, refer to WHITEHOUSE 1964; the case in which hybrid DNA formation covers only one site but not the other minimizes or excludes the presence of this type) and the other site showed base correction to give either 6+ : 2*m*, 5+ : 3*m* or 4+ : 4*m*, or (3) reciprocal recombination occurred between the sites of alleles employed in the cross. From the first case, there is no double mutant genotype expected among the sister spores of the octads; from the second case,

TABLE 5

Absence of interference in the recombinant prototrophs from paba *heteroallelic crosses**

Interval	A		B		D		E		
Parent p)	+		*ad-9*		*paba* (p)		*y*	+	
Parent (q)	*pro*		+		*paba* (q)		+	*bi*	
Distance (%)	(8.0)		(0.5)		(16.0)		(6.0)		
Genotype in *y* locus			*y*+				*y*		
Recombination class for interval B D	Ra		Rp		Ra		Rp		SIDDIQI (1962)
Gene alignment for interval E	par.†	rec.†	par.	rec.	par.	rec.	par.	rec.	
	493 (89.0)	61 (11.0)	484 (89.8)	55 (10.2)	324 (92.3)	27 (7.7)	884 (91.1)	86 (8.9)	If chiasma interference is present, the observed percentages for recombinant groups must be smaller than the standard 6.0%.
Classes Ra and Rp pooled	977 (89.4)	116 (10.6)			1208 (91.5)	113 (8.5)			
Marker genotypes *y*+ and *y* pooled	2185 (90.5)	229 (9.5)							

* SIDDIQI and PUTRAMENT (1963) obtained mixed data for the presence and absence of interference in the analysis of the same locus, but pooled data complement the differences and show absence of interference.

† Par. = parental; rec. = recombinant.

from none to two double mutant spores will occur; and from the third case, two double mutant spores obligatorily appear in an octad. However, in a majority of recombination analysis, including the data of SIDDIQI, there is no way to determine which of the above three origins was responsible for the recombinants. In the case of SIDDIQI's data, the origin of the recombinants, as judged by the present author, is either the first or second situation but not the third, reciprocal recombination.

Quite unlike the results seen in *S. fimicola*, *S. brevicollis* and *A. nidulans*, there are three loci that indicate the presence of chiasma interference accompanied by the occurrence of recombinant prototrophs or recombinant wild type. These are shown in Table 6 (modified from an unpublished table of WHITEHOUSE). In all three organisms listed, recombination class Ra (Parental) did not show interference, but class Rp (Recombinant) showed significant interference. These results agree with one of the expectations that class Rp (R) should exhibit interference, but disagree with the other expectation that about half of class Ra (P), subclass RA-2, should exhibit interference, as well as class Rp (R). The absence of interference in class Ra (P) and the presence in class Rp (R) has been attributed to secondary crossing over without accounting for the role of subclass Ra-2 (P), (WHITEHOUSE 1967 and 1971). The fact that three loci in Table 6, one each from *Neurospora crassa*, *Saccharomyces cerevisiae* and *Drosophila melanogaster*, did not show any sign of interference in class Ra (P), while showing significant interference in class Rp (R), suggests that in these loci gene conversion and conversion-associated recombination have not caused interference, but ordinary reciprocal recombination classified in Rp (R) exclusively caused the interference. With this interpretation, the above problem with Ra-2 in class Ra (P) can be resolved.

The major conclusion of this study is that conversion-associated recombination behaves differently in some respects from ordinary reciprocal recombination, regardless of their identical genotype. This conclusion necessitates a reexamination of our present understanding of the time at which recombination events occur (Section 2) and of the fine structure of eukaryotic gene loci (Section 3).

2. *Is the origin of recombination confined to one mechanism at one time?*

Since homologous association of chromosomes is considered a necessary prerequisite to genetic recombination, one may ask when this association takes place and does it occur only at one time to gain further insight into the time at which the actual exchange process occurs. Although homologous pairing of chromosomes is well known to occur in meiotic zygotene, there are many studies that suggest it is not a unique feature of the zygotene stage. For example, the initiation of pairing has been traced back to premeiotic telophase and in many cases to syngamy (KITANI 1963; MAGUIRE 1967; BROWN and STACK 1968; WAGENAAR 1969; LA COUR and WELLS 1970; COLOMBERA 1973; RIEGER *et al.* 1973; YOSHIDA and YAMAGUICHI 1973). Moreover, there are now numerous cytological observations of homologous pairing in somatic cells. Similarly, it is clear that genetic recombination and conversion are also not confined to meiotic zygotene (Dro-

TABLE 6

Selected data showing interference by the presence of flanking marker recombination

Reference; author, organism, locus, etc.	"Recombinants" Remark	Number	Recomb. class	Centromere	Proximal Secondary marker	Proximal Adjacent marker	Gene subjected in "recombination" analysis	Distal Adjacent marker	Distal Secondary marker
STADLER (1959)				C	*ade-1*	*yel*	*cys*	*lys-5*	——
	distance (%)			– 1 –	– 11.1 –		– 18.3 –	– 5.5 –	
Neurospora crassa	"recombinant prototrophs"	361 spores	Ra		13.3%				
cystein	"recombinant prototrophs"	282 spores	Rp		($p << 0.01$)	3.9%			
FOGEL and HURST (1967)				C	—	*thr-3*	*his-1*	*arg-6*	*try-2*
	distance (%)				— 68 —		– 4.8 –	– 19.8 –	– 38.6 –
Saccharomyces cerevisiae	conversion	528 asci	Ra						40.2%
	conversion	452 asci	Rp					($p << 0.01$)	25.0%
	recombination	4 asci	Ra						25.0%
	recombination	97 asci	Rp					($p << 0.01$)	23.0%
CARLSON (1971)				C	Bar eyes	forked bristles	rudimentary wings	tiny chaetae	garnet eyes
	distance (%)			– 9 –	– 0.3 –		– 2.2 –	– 2.9 –	– 7.2 –
Drosophila melanogaster	"recombinant wild type"	1189	Ra		0.25%			($p \cong 0.20$)	6.2%
rudimentary wings *X*-chromosome	"recombinant wild type"	1765	Rp		0.00				0.06%

sophila: STERN 1936, 1969; Sordaria: KITANI 1962 and this report; Ustilago; ESPOSITO and HOLLIDAY 1964; Aspergillus: PUTRAMENT 1964, SHANFIELD and KÄFER 1971; Saccharomyces: HOLLIDAY 1964b, HURST and FOGEL 1964, THORNTON and JOHNSTON 1971, CAMPBELL 1973; Glycine: VIG 1973, etc.). Recombination and conversion events are therefore assumed to be associated with homologous pairing of chromosomes regardless of whether the succeeding nuclear division becomes reductional (meiotic) or nonreductional (somatic). Hence, there appears to be no *a priori* reason to expect a cause-and-effect relationship of phenomena characteristic of meiosis (*e.g.*, synaptinemal complex, synapsis, chiasma, and zygotene-pachytene DNA synthesis, HOTTA, ITO and STERN 1966 and HOTTA and STERN 1974) with each other and with genetic recombination, in particular with the two kinds of recombination, one causing interference and the other not, described in this paper.

With regard to the meiotic events noted above, there are other published reports that suggest that the fidelity of one-to-one or cause-and-effect relationships between these phenomena is not satisfactory to confine the origin of recombination to meiotic prophase. In a heterozygous paracentric inversion in Drosophila, for example, a drastic reduction in the recovery of ordinary reciprocal recombination and conversion-associated recombination was observed, while conversion itself was unaltered (CHOVNICK 1973). In a short paracentric inversion in maize, increased synapsis and unaltered frequencies of crossing over has been reported (MAGUIRE 1972). In a genetically asynaptic tomato, MOENS (1969) observed synaptinemal complexes, absence of synapsis, reduced chiasma frequencies, but nevertheless increased recombination frequencies. On achiasmatic chromosomes (PARCHMAN and ROTH 1971) and in the achiasmatic organism, Bolbe (GASSNER 1969), perfect synaptinemal complexes were formed without inducing chiasmata. All of these observations suggest that our present understanding of the relationship between synaptinemal complexes, chiasmata and recombination is incomplete.

At the locus level, recombination frequency is the established metric in measuring gene distances. There are numerous cytological and genetical studies in a wide variety of organisms that support the general validity of this concept. Although there is not yet a comparable body of evidence supporting the extension of this approach to mapping site sequencies within a gene, fine structure maps may be constructed, based upon the frequency of wild-type recombinants in heteroallelic crosses. In prokaryotic systems, this appears to be a justified extension. However, in eukaryotic systems, fine-structure maps based upon recombination frequencies should be viewed with caution, since there is little independent physical evidence, other than the fact that sites can be ordered, that bears on this point.

3. *Possible relation of the Ra:Rp ratio to the structure of the locus*

To expect the accompaniment of chiasma interference exclusively with class Rp (R) may not be valid as explained above (*cf.*, section 1). For this reason the structure of gene loci have been reexamined with regard to the existing diversity

in Ra:Rp (P:R) ratios among species and between loci in a single species. The Ra:Rp ratios of various loci in Neurospora, Aspergillus and Sordaria are compared in Table 7.

In the Neurospora data, the Ra:Rp ratios for the *me-2* locus are roughly 50:50 in the top three rows of the table, but Ra is more frequent than Rp in the rows

TABLE 7-1

Ra:Rp ratios in various loci of various organisms
Part 1; Neurospora

Pooled data from: Author, locus, etc.	Parental (Ra) 1	2	Recombinant (Rp) 3	4	Note
MURRAY 1969 Table 1. *me-2*	375	577	669	220	1, *tryp pan*+ 2, *tryp*+ *pan* 3, *tryp pan* 4, *tryp*+ *pan*+ Crosses between alleles of distant allele-groups.
	952 (51.7%)		889 (48.3%)		
MURRAY 1963 Table 3. *me-2*	36	52	27	61	Alleles used in crosses were obtained from a single original strain. Crosses between α group and γ group.
	88 (50.0%)		88 (50.0%)		
MURRAY 1963 Table 2. *me-2*	222	204	191	186	
	426 (53.1%)		377 (46.9%)		
MURRAY 1963 Table 4. *me-2*	2336	2260	1665	1645	Inter-group crosses.
	4596 (58.1%)		3310 (41.9%)		
MURRAY 1963 Table 6. *me-2*	256	305	159	253	Crosses within each allele-groups.
	561 (57.7%)		412 (42.3%)		
MURRAY 1969 Table 2. *me-7*	599	1329	408	140	The locus *me-7* seems to contain only a single cistron.
	1928 (77.9%)		548 (22.1%)		
MURRAY 1969 Table 4. *mac—me-6—me*					Genes *mac*, *me-6* and *me* are considered by the original author to be in the same locus, but apparently showing difference in functions. Crosses (a) and (b) are done between the alleles functionally different. Crosses were made between alleles seemingly similar in functions.
(a) *mac* × *me-6*	213	60	451	6	
	273 (37.4%)		457 (62.6%)		
(b) *mac* × *me*	86	22	163	3	
	108 (39.4%)		166 (60.6%)		
(c) *me* × *me-6*	75	159	154	20	
	234 (57.7%)		174 (42.6%)		
FINCHAM 1967 Table 1. *am*	1587	1388	937	1040	1, *sp*+ *inos*; 2, *sp inos*+ 3, *sp*+ *inos*+; 4, *sp inos*
	2975 (60.1%)		1977 (39.9%)		

four and five. The explanation for the high frequency of Ra in the fourth row data is not easy to find, but for the data in the fifth row it seems reasonable to consider that this is because all the crosses pooled in this row were made within particular groups of alleles. The *me-2* locus is composed of several clusters of alleles, and the locus itself is large. Contrasting with the general 50:50 distribution of recombination classes in *me-2*, a small compact locus *me-7* showed 77.9% recombinant prototrophs in the Ra class, as shown in the sixth row. A more

TABLE 7-2

Ra:Rp ratios in various loci of various organisms
Part 2; Aspergillus and Sordaria

Pooled data from: Author, locus, etc.	Parental (Ra) 1	2	Recombinant (Rp) 3	4	Note
SIDDIQI 1962 Table 5.	88	520	22	1067	1, *ad y*; 2, *ad*+ *y*+
paba	608		1089		3, *ad y*+; 4, *ad*+ *y*
	(35.8%)		(64.2%)		Proximal *paba* with *ad y*.
SIDDIQI 1962 Table 6.	256	104	508	29	
paba	360		537		Distal *paba* with *ad y*.
	(40.1%)		(59.9%)		
PEES 1967 Table 6.					Actual spore numbers were
lys-51	36.9%		63.1%		not given in the original
PEES 1967 Table 7.					Tables. Therefore, the
lys-51	37.1%		62.9%		mean frequencies were calculated in giving weight of sample size of each class.
Linkage relations of conversion loci to the outside markers. Distances in %.	*Aspergillus nidulans* C — 20 — *pro-1* — 6— *lys-51* — 4.5 — *paba-2* — 16 — *y* — 6 — *bi-1*				
KITANI and OLIVE 1967, 1969 and 1970 6+ : 2*m* type	311 (58.4%)		222 (41.6%)		Pooled data from 19 one-point crosses.
KITANI and OLIVE 1969 and unpublished data Normal 4+ : 4*m* type	298	32	40	230	1, Ra-1; 2, Ra-2; 3, Rp-2; 4, Rp-1. Pooled from 11 interallelic crosses.
	330 (55.0%)		270 (45.0%)		
KITANI and OLIVE 1967, 1969 and 1970 All ascus types pooled	1234 (55.0%)		1010 (45.0%)		Pooled from 19 one-point crosses. (39 asci omitted).
KITANI and OLIVE 1969 and unpublished data All ascus types pooled	892 (56.7%)		680 (43.3%)		Pooled from 11 interallelic crosses. (21 asci omitted).
Linkage relations of conversion locus to the outside markers. Distance in c.u.	*Sordaria fimicola* C — 46 — *sp* — 9.1 — *mat* — 0.4 — *g* locus — 3.4 — *cor* —				

suggestive difference appeared in the *mac-me-6-me* locus. In this compound locus (considered as a single locus, MURRAY 1969), the crosses between mutants differing in function (seventh and eighth rows) showed a 40:60 ratio, while the cross between mutants of similar functions (ninth row) showed the opposite 60:40 ratio. This result suggests that this locus may contain two cistrons, the crosses *between* cistrons showing a high frequency of the Rp class, and the cross *within* a cistron showing the opposite ratio. Another locus in Neurospora, the *am* locus, showed 60% prototrophs in the Ra class, suggesting that this locus contains only one cistron.

The excess of the Rp class in presumably inter-cistronic crosses, that is, between the allele groups, could have resulted from ordinary reciprocal recombination, according to the usual observation that distant alleles produce more "recombinants" than alleles located close to one another. On the other hand, the Rp class progeny that appeared in presumably *intra-cistron* crosses may involve few or no ordinary reciprocal recombinants.

The Ra:Rp ratio for the recombinant prototrophs of the *paba* locus in *Aspergillus nidulans* are shown in the first and the second rows of Table 7, Part 2, which is from the same data used in Table 5 as evidence for the absence of interference. The data from the same organism, but from the neighboring locus *lys-51*, are also shown in the same part (rows third and fourth). A common and almost uniform ratio of 40:60 for the Ra:Rp ratio appeared among these four groups of crosses.

As stated earlier in the discussion, two fundamental ascus types of gene conversion (see KITANI, OLIVE and EL-ANI 1962, KITANI and OLIVE 1967, 1969) and one other type, ordinary reciprocal recombination, are considered to be the main source of recombinant prototrophs. In most analyses of recombinants, it is not possible to separate these three possible sources. However, in the *g* locus of *S. fimicola*, the separation of these three can be done very clearly, almost without ambiguity as regards the epistatic allele. Therefore, the Ra:Rp ratios of 6+ : 2*m* type and normal 4+ : 4*m* conversion type (refer to WHITEHOUSE 1964; KITANI and OLIVE 1967, 1969) are shown in the last half of Table 7, Part 2. In this apparent single cistron locus, ordinary reciprocal recombination is virtually lacking. If present, it occurs with a frequency so low as to make a negligible contribution to the number of double color mutant spores, which are predominantly products of gene conversion events alone (see KITANI and OLIVE 1969). The total conversion frequency is almost uniform from cross to cross, further suggesting the virtual absence of intra-cistron reciprocal recombination; consequently, there is no presentation of this type in Table 7.

Although the 6+ : 2*m* type showed a somewhat higher frequency of the Ra class than the normal 4+ : 4*m* conversion type, or the pool of all ascus types, the general tendency is to show a ratio of 55:45 for Ra:Rp proportion. This Ra:Rp ratio in *S. fimicola* is a firm value for the recombinant prototrophs of conversion origin without accountable contamination of ordinary reciprocal recombination, although apparent reciprocal recombination of conversion origin is involved. This case is the case that did not show interference with flanking marker recom-

bination in the second interval from the conversion locus. The data that do not show interference with flanking marker recombination in addition to the data in *S. fimicola* are the data in *S. brevicollis* by FIELDS and OLIVE (1967) and in Aspergillus by SIDDIQI (1962, tables 5 and 7). The *paba* and *lys-51* loci both show a relatively high frequency of the Rp class, and these two loci did not show any significant difference from each other in the Ra:Rp ratio. This uniformity of Ra:Rp ratio in different, but near-by, loci is quite distinct from the heterogeneous ratios that appeared in the *me-2* locus and the *mac-me-6-me* compound locus of Neurospora, where multi-cistron or distant-multi-group composition is strongly suspected (Table 7, Part 1).

From this comparison of the two groups of data in Table 7, characterizing the presence or absence of interference, the following hypothesis may be considered: (1) There are two kinds of gene loci, one composed of a single cistron, the other composed of multi-cistron or distant-multi-group. (2) Each cistron (or allele group of a large cistron of distant-multi-group composition) has its own characteristics proportion for the Ra:Rp ratio, and this ratio may be unique in each organism, each chromosome arm, location on the arm, etc. (3) As a general rule, it is proposed that no ordinary reciprocal crossovers occur within a single cistron (or allele group), but rather they occur between cistrons (or allele groups), and that only genuine reciprocal recombinations, but neither the apparent ones nor the other kinds of recombinations of conversion origin, are responsible for chiasma interference.

In the data examined, the Ra:Rp (P:R) ratios were uniform in the loci in which wild-type recombinants lacked an association with interference, and the ratios were heterogeneous among Neurospora loci, one of which showed association of interference with its wild-type recombinants. A multicistron locus (*mac-me-6-me* locus) and a large cistron (*me-2*) of Neurospora showed more wild-type recombinants, as well as an Rp class (R) in crosses of intercistron or inter-allele-group, than the crosses of intra-cistron or intra-allele- group of the same loci and the crosses within a small cistron.

The above facts may indicate that gene conversion events and conversion-associated recombination (including the apparent reciprocal recombination; for detail refer to EMERSON 1969, and KITANI and OLIVE 1969), are limited in their origins occurring within noncompound single cistrons or allele groups, while genuine reciprocal recombination occurs at the joints of allele groups in a complex or multi-cistron locus. Therefore, the characteristic Ra:Rp (P:R) ratio of a cistron corresponds to the proportion of prototrophs produced by gene conversion and conversion-associated recombination, as well as genuine reciprocal recombination between allele groups in a locus.

4. *Conclusions*

The assumptions developed in the preceding sections suggest the following. Ordinary (genuine) reciprocal recombination occurs between cistrons, or between allele groups of a locus having compound composition, and causes interference. Gene conversion, regardless of whether aberrant or apparent reciprocal

exchange and associated flanking marker recombination results, occurs within a cistron and does not cause interference. These two kinds of recombination may originate at different times in the cell cycle.

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APPENDIX

Gene conversion asci obtained from both one-point crosses and interallelic crosses in Sordaria fimicola

In this APPENDIX, all the asci analyzed in the main part of the report are presented in abbreviated form. Recombination classes Ra and Rp were separately shown in the presentation of one-point crosses, but due to a very wide diversity of ascus genotypes in interallelic crosses,

this was not applied in the presentation of interallelic crosses. The ascus records of all the crosses included here have been deposited with the Editor of GENETICS. Therefore, it is recommended that the reader refer to those original records to carry out a detailed examination of the crosses.

The linkage relationship of the *g* locus to the flanking markers and some relationships of the alleles in the *g* locus are shown in Figure 1.

1. *One-point crosses*

In one-point crosses, five out of six expected varieties of gene conversion asci are morphologically distinguishable as aberrant ascus types; these are shown in Figure 2. There is no way to distinguish conversion asci of normal 4+:4*m* segregation from the background asci that also show normal 4+:4*m* segregation in any one-point cross (A large proportion of conversion asci of normal 4+:4*m* segregation are recovered in interallelic crosses; the frequency of this type can be estimated for each one-point cross (see KITANI and OLIVE 1967, 1969). Therefore, the data on these five aberrant ascus types are presented in Table 8. In this table, recombination classes Ra and Rp represent the absence and the presence of recombination between the flanking markers *mat* and *cor*, respectively. The recombination subclass Ra-1 represents the lack of apparent two-strand double crossing over in addition to the absence of recombination; while Ra-2 represents the existence of apparent two-strand double crossing over, in spite of the absence of flanking marker recombination. The recombination subclasses Rp-1 and Rp-2 represent the presence of recombination at the proximal and distal sides of the *g* locus, respectively.

The asci shown in individual code numbers at the right-hand side of Table 8 have their own peculiarities (mainly as appears in the captions); their complete genotypes can be found in the deposited ascus records.

2. *Heteroallelic crosses*

Unlike one-point crosses, heteroallelic crosses in the *g* locus of *Sordaria fimicola* show wide diversity in ascus types, like the genotype segregations in the F_2 generation of a multiple-factor cross. This is because the two alleles employed in each cross were different in autonomous color expression in the ascus, and furthermore, the segregation of the six ascus types occurs largely independently for each allele. However, due to the presence of epistatic relations between alleles, the number of distinguishable ascus phenotypes is 21 instead of the 81 expected. These are

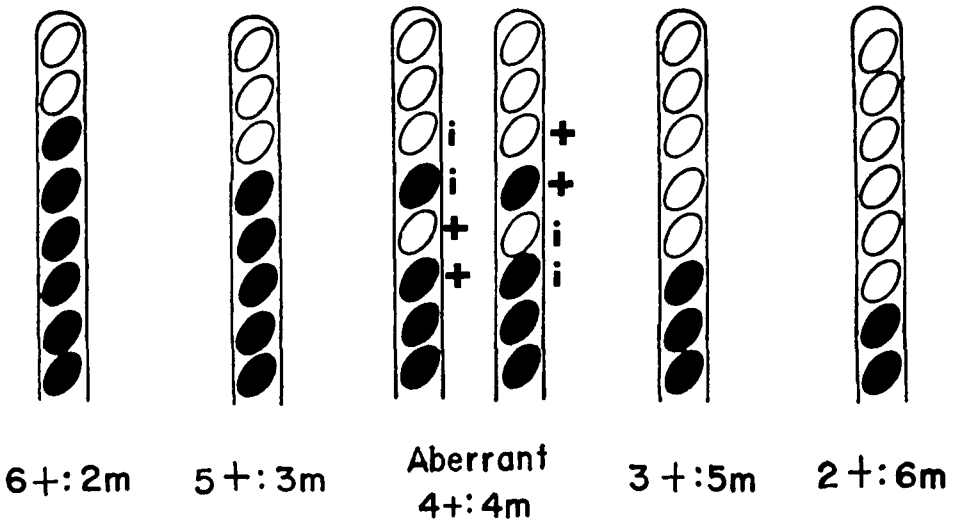

FIGURE 2.—The fundamental ascus types in one-point crosses. Two examples of aberrant 4+:4*m* asci distinguishable from spore-slippage are shown.

TABLE 8

Presentation of gene conversion asci from 20 one-point crosses

One-point cross of:*	Cross code	Gene alignment (i)	Ascus types and recombination classes: 6+:2m Ra	6+:2m Rp	Aberrant 4+:4m Ra	Aberrant 4+:4m Rp	2+:6m Ra	2+:6m Rp	5+:3m Ra −1	5+:3m Ra −2	5+:3m Rp −1	5+:3m Rp −2	3+:5m Ra −1	3+:5m Ra −2	3+:5m Rp −1	3+:5m Rp −2	Total of asci shown left	Individual code numbers of asci omitted from left-half of the table (asci marked with * are not omitted): Conversion at other locus; locus in ( )	Omitted due to ambiguity in recombination class and other reasons (specified)	Grand total	
g_1	A	1	55	21	6	3	4	6	29	21	24	21	13	2	4	3	212	A27*(*sp*)	A79, A110, A111, (A26, A134; 7+ 1*g*)	217	†
h_2	D	2	4	1	17	13	4	0	13	3	3	8	12	6	2	10	96	——	D79	97	†
h_{2a}	F	2	5	2	22	17	0	1	11	1	7	4	7	3	0	3	83	——	F115, F120, F161	86	†
h_3	K	2	1	0	20	28	6	4	9	6	1	5	36	3	8	12	139	——	K45, K70, K72, K86, K91, K146	145	†
h_4	M	1	0	0	10	14	5	0	3	0	4	1	16	5	6	10	74	——	M2, M12	76	†
h_{4b}	Mb	3	0	2	3	9	1	2	5	2	2	1	6	3	3	7	46	Mb15(*cor*)	——	47	‡
$h_4^{(iii)}$	P	3	0	0	2	4	2	0	2	2	0	1	5	2	2	2	24	——	Pa24, Pa28	119	‡
	Pa	2	3	2	11	8	4	5	12	3	3	2	16	5	5	14	93				
h_5	R	2	9	5	12	13	1	0	9	4	7	8	4	3	2	2	79	——	R11, R12, R52	82	‖
$g_6^{(iv)}$	U	2	18	17	2	5	1	0	13	9	10	7	6	1	5	5	99	——	U28, U72	101	¶
$g_6^{(v)}$	V	1	15	10	7	1	2	2	18	8	8	15	3	3	4	4	100	——	V29, V68, (V100* double aberrant 4+ : 4*g*)	102	¶
$g_1^{(A)}$	AA	1	24	20	1	2	4	2	15	13	10	11	3	1	3	2	111	AA37*(*sp*)	——	111	§
$g_1^{(C)}$	AC	1	42	33	1	1	3	2	14	16	12	11	5	0	4	1	145	——	AC2, AC77, (AC102; 7+ : 1*g*)	148	§
$g_1^{(G)}$	AG	1	44	32	3	1	1	2	22	11	15	11	1	0	1	1	145	AG39(*cor*)	AG35, AG143, AG150	149	§
$g_1^{(T)}$	AT	1	39	24	2	2	3	0	11	8	13	7	0	1	2	2	114	——	AT32, AT36, AT47, AT48, AT117	119	§
$g_1^{(g)}$	Ag	1	34	33	1	0	0	2	8	4	8	7	1	0	0	1	99	——	Ag11, Ag12, Ag47, Ag67	103	¶
$h_2^{(A)}$	DA	2	0	4	38	26	1	3	12	4	7	9	14	10	4	7	139	——	DA90	140	§
$h_2^{(C)}$	DC	2	6	7	40	39	2	1	13	5	14	10	6	2	3	8	156	——	DC67, DC102, DC148 (DC44, 4-strand conversion)	160	§

TABLE 8—Continued

Presentation of gene conversion asci from 20 one-point crosses

$h_2^{(G)}$	DG	2	7	2	15	22	6	2	13	2	7	9	28	2	4	10	129	DG45*(*cor*) DT59*(*cor*)	DG72, DG84, DG111 DT17, DT63, (DT12*, DT49*,	132	§
$h_2^{(T)}$	DT	2	5	4	38	38	0	1	17	15	5	15	3	3	6	7	157	DT75*(*cor*)	DT75*; conversion unrelated crossing over involved)	159	§
$h_5^{(w)}$	R(w)	2	8	2	16	12	3	1	10	9	0	5	5	2	0	0	73	——	——	73	‖
$h_5^{(m)}$	R(m)	2	5	2	2	4	3	1	12	4	4	8	7	2	1	2	57	——	——	57	‖
g_7	B	1	24	13	13	10	3	1	23	10	21	13	4	6	8	9	158	B56*(*cor*)	B40, B103	160	‖
$g_7^{(w)}$	B(w)	1	18	11	3	3	0	0	7	4	1	10	1	0	1	2	61	——	B247*	61	‖
$g_7^{(m)}$	B(m)	1	4	1	10	4	3	2	12	1	2	6	2	1	3	1	52	——	——	52	‖

* (i) Gene alignment 1, *sp* + *m cor* × + *mat* + +; Gene alignment 2, + *mat m* + × *sp* + + *cor*; Gene alignment 3, + *mat m cor* × *sp* + + +, *m* represents any mutant in *g* locus; (ii) Refer to Table 1; (iii) Crosses were made in g_1 homozygous condition; (iv) From 44334 asci counted, 101 aberrant asci were obtained; (v) From 42363 asci counted, 94 abberant asci were obtained; (A) Adenine supplemented; (G) Guanine suppleemnted; (g) Deoxyguanilic acid supplemented; (C) Cytosine supplemented; (T) Thymine supplemented.

† KITANI and OLIVE 1967.

‡ KITANI and OLIVE 1969.

§ KITANI and OLIVE 1970.

‖ KITANI and WHITEHOUSE 1974.

¶ Unpublished.

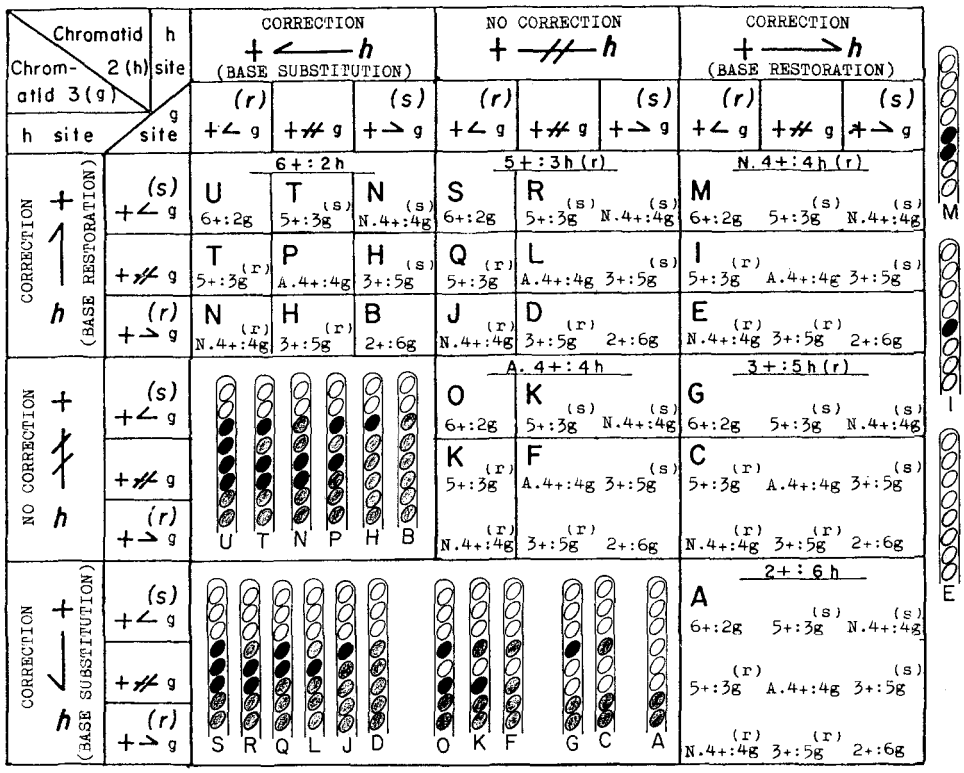

FIGURE 3.—The 21 ascus phenotypes and their 44 genotypes in repulsion heteroallelic crosses. The presentation of lower-left side is omitted as the genotypes here are mirror image of upper-right side (refer to Figure 4b, KITANI and OLIVE 1969).

shown in Figures 3 and 4, respectively representing repulsion and coupling crosses. Since the lighter colored allele is always epistatic against the darker colored one, the epistatic allele in the cross is shown as *h* (hyaline) and the other as *g* (grey), regardless of the actual names of alleles in these figures. These figures do not show all 81 genotypes, but 27 genotypes situated at the lower-left side are omitted as they are mirror images of the ones at the upper-right side. The complete figures for 81 genotypes could be found in Figures 3 and 4 of KITANI and OLIVE (1969). All 81 ascus genotypes have a choice of being in recombination class Ra or Rp. However, for reasons of space, the actual numbers for these classes are not given. For the same reason and owing to further difficulty of handling some asci ambiguous in genotype, the presentation is confined within the visually distinguishable 21 ascus phenotypes, as shown in Table 9.

The asci given in individual code numbers at the right-hand side of the table have individual peculiarities (mainly as given in the captions); their complete genotypes can be found in the deposited records. Two asci, exceptionally unique in some aspects, are shown in detail in Table 10. The double aberrant 4+:4*m* ascus, V100, could be explained as a rare product of a combination of two exactly the same events of conversion on two pairs of homologues (without any base correction) and also with flanking marker recombination occurring simultaneously in these two pairs of chromatids. However, the occurrence of the double color mutant genotype in the hyaline spore of the wild type-hyaline odd spore pair of Snb48 (spores No. 7 and No. 8) is not simple to explain, and requires a step so far not yet applied in the models of gene conversion.

TABLE 9

The distribution of the 21 ascus types in various interallelic crosses

Crossed with g_1	Cross code	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	Total	Individual code number of ascus; ascus type in ( ) Conversion at other locus; locus in (( ))	Recombination class ambiguous
h_2	Jd	20	6	19	9	–	2	12	0	3	13	15	0	7	0	0	0	0	3	0	0	0	109	——	Jd11(I), Jd13(C), Jd103(K), Jd122(R)
h_{2a}	Jf	14	5	20	10	–	1	11	0	1	17	14	0	4	6	1	0	0	1	0	0	0	105	Jf107(A)((*cor*))	Jf28(K), Jf48(C), Jf67(J), Jf109(K)
h_{2b}	Jh	17	1	14	11	–	2	8	0	5	9	5	0	2	1	1	0	0	0	0	0	0	76	——	Jh1(F), Jh31(K)
h_3	L, Li	11	0	28	0	–	2	12	0	58	21	9	3	84	1	8	1	1	1	1	0	0	241	L101(J) & L148(N)((*cor*))	L10(K), L57(I), L76(I), L152(I), L173(I), Li24(I), Li35(C)
h_4	N	8	0	14	0	–	1	7	0	31	9	6	1	60	3	5	1	2	3	2	0	0	153	——	N42(J), N44(J), N47(M)
h_{4b}	Nb	9	0	23	3	–	4	12	0	37	8	4	2	36	1	5	0	4	1	3	1	0	153	Nb99(Q)((*sp*)) Nb103(I)((*cor*))	Nb92(M)
h_5	Sa	3	2	8	2	–	1	24	6	15	19	9	0	30	14	10	1	5	4	7	0	2	162	——	Sa98(J), Sa110(I), Sa156(M)
Crossed with h_5	code	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	Total		
h_2†	Sd	5†	3†	6†	7†	–	4†	10	2	7	19	31	5	11	9	7	1	2	3	2	0	0	134†	——	Sd97(K)
h_4	Sn	3	0	11	16	–	3	15	7	71	29	12	6	35	4	3	0	4	2	0	0	0	211	Sn71(*k*), Sn107(C)((*cor*)) Sn137(I)((*sp*))	Sn101(K), Sn163(I)
h_{4b}	Snb	4	1	10	4	–	5	15	3	76	29	19	4	31	5	3	0	0	0	0	0	0	209	Snb155(I), Snb167(I), Snb206(K) all three asci ((*sp*))	Snb105(I), Snb110(A), "Snb48(K) is exceptional in genotype"
Crossed with +		a	b	c	d	e	f	gc	h	i	jd	fk	l	m	n	ok	p	ql	r	sr	t	u	Total		
h_4	O	5	0	3	0	25	1	7	0	34	4	6	1	2*	4	1	0	0	6	1	1	1	101	——	O81(fk)

* Phenotypically indistinguishable from background asci but encountered in ascus dissection, excluded from total.

† Marked ascus types were not obtained in proper proportions, this distortion could be roughly corrected by multiplying the ascus numbers given for the types A to F by 2.8.

Conversion frequencies of crosses Sa, Sd, Sn and Snb are 23.4×10^{-4}, 21.2×10^{-4}, 24.2×10^{-4} and 24.5×10^{-4}, respectively; for other crosses, refer to KITANI and OLIVE (1969).

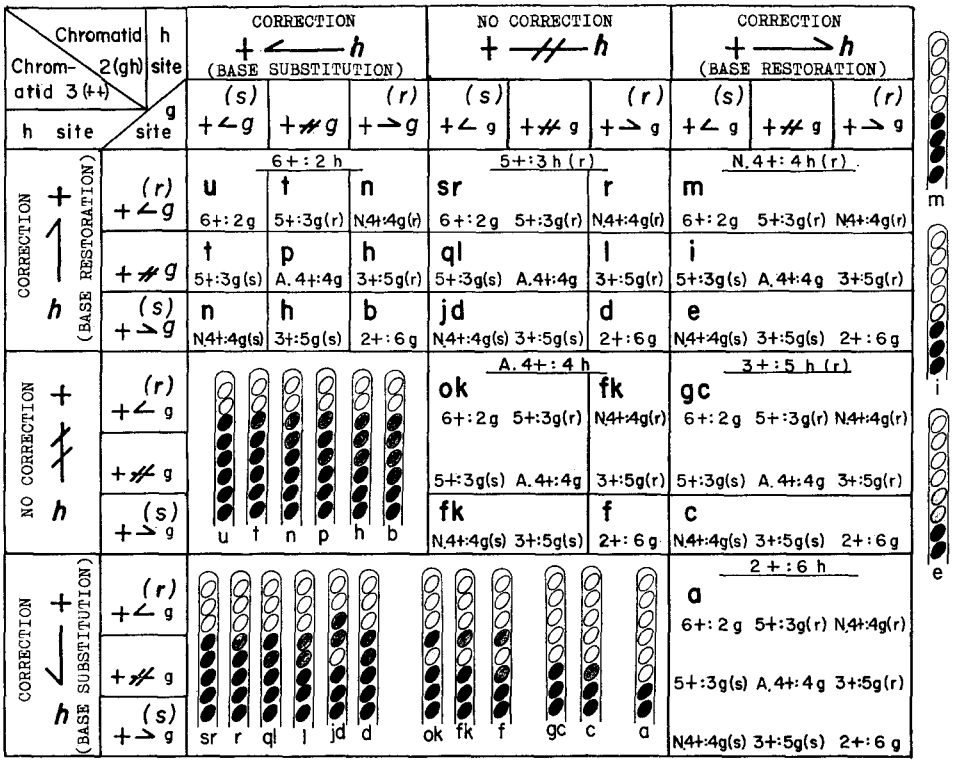

FIGURE 4.—The 21 ascus phenotypes and their 44 genotypes in coupling heteroallelic crosses. Regarding the omitted portion, refer to Figure 3.

TABLE 10

Rare asci of unique genotypes

Double aberrant 4 : 4 ascus V100
(V cross : *sp* + *go cor* / *i* × + *mat* + + / +)

Locus and site	Spore no. 1	2	3*	4	5	6	7	8
sp	+	+	+	+	sp	sp	sp	sp
mat	mat	mat	mat	mat	+	+	+	+
g	+	g	+	g	+	g	+	g
cor	cor	cor	cor	cor	+	+	+	+
i	i	i	+	+	i	i	+	+

Unusual genotype in the odd spore-pair Snb 48
Snb cross: *sp* + h_{4b} *cor* / + × + *mat* h_5 + / *i*)

Locus and site	Spore no. 1†	2	3	4	5	6	7 The odd spore pair	8†
mat	mat	mat	+	+	mat	mat	+	+
g	g*	g	+	+	g	g	+	g†
h	h*	+	h	h	+	+	+	h†
cor	cor	cor	cor	cor	+	+	+	+

* This culture germinated and grew but died later due to bursting of the hyphal tips.
† Double color mutant spore.