THE GENETICS OF *SORDARIA BREVICOLLIS*. III. GENE CONVERSION INVOLVING A SERIES OF HYALINE ASCOSPORE COLOR MUTANTS¹

WILLIAM G. FIELDS² AND LINDSAY S. OLIVE

Department of Biological Sciences, Columbia University, New York, N. Y. 10027

Received July 10, 1967

NONRECIPROCAL genetic exchange in ascomycetes has been the subject of several investigations (MITCHELL 1955; LISSOUBA and RIZET 1960; KITANI, OLIVE and EL-ANI 1962; LISSOUBA, MOUSSEAU, RIZET and ROSSIGNOL 1962; MURRAY 1963; ROMAN 1963; STADLER and TOWE 1963; CASE and GILES 1964). This phenomenon, previously called transreplication by KITANI *et al.* (1962), is here referred to by the more commonly used term, gene conversion.

The work reported here concerns gene conversion in the heterothallic *Sordaria brevicollis* Olive and Fantini, for which many ascospore color mutants have been obtained and established in seven linkage groups (CHEN 1965). A series of closely linked hyaline ascospore color mutants in linkage group VI was chosen for investigation. Of the 22 independently derived mutants with sites in this region, designated the 6A region, five which exhibited good development and germination were chosen for investigation.

MATERIALS AND METHODS

Derivation of strains: Wild-type strains *A* and *a* were reisolated from those of CHEN (1965). Mutant *h*₃ of CHEN was redesignated C17 in this investigation. Additional ascospore color mutants and morphological mutants were isolated by the method of CHEN (1965), with 2 or 3 minutes ultraviolet treatment of microconidia. Each mutant was passed through two or three crosses with wild type before being used in the present study.

Media: CM+ agar (Difco cornmeal agar, 17.0 g; dextrose, 2.0 g; yeast extract, 1.0 g; 1000 ml distilled water); B agar (Difco cornmeal agar, 17.0 g; sucrose, 5.0 g; dextrose, 2.0 g; yeast extract, 1.0 g; KH₂PO₄ 0.5 g; 1000 ml distilled water); Ac agar (CM+ agar supplemented with 0.7% sodium acetate); Dissecting agar (Difco cornmeal agar, 10.0 g; Difco agar, 26.0 g; sucrose, 30.0 g; dextrose, 20.0 g; sodium acetate, 7.0 g; yeast extract, 1.0 g; 1000 ml distilled water).

Mutant strains: Hyaline ascospore color mutants—designated C17, C22, C27, C28, C29—were used in this investigation. These exhibited some slight differences in color, but in crosses of pairs of mutants, they were usually indistinguishable from one another. In crosses designed to detect back mutations, no such reversions were found among several million asci surveyed. Two distinct morphological mutants were also employed: R83 (restricted growth) and R155 (restricted growth for a period of about 15 hr following germination, but not later).

Crossing techniques: For mapping studies, compatible cultures were paired on B agar. For conversion studies in each cross, the strain carrying restricted growth marker R83 was used as

¹ Supported by Public Health Service Training Grant 5 T1 GM216-7 and National Science Foundation Research Grant GB-4998.

² Present address: Department of Botany and Plant Pathology, Michigan State University, East Lansing, Michigan 48823.

protoperithecial parent and inoculated onto B agar. The microconidial strain, marked with R155, was simultaneously inoculated onto Ac agar. After 4 days growth, sterile distilled water was poured on the microconidial parent, microconidia were dislodged with a glass rod, and 2 or 3 ml of the suspension were spread on the protoperithecial parent. Crosses were incubated at 25°C until mature (usually 6 days), then placed at 4°C until used. Mature hybrid perithecia at 4°C remained in good condition for approximately 4 days.

Isolation of ascospores: Ascospores were isolated in linear order on dissecting agar with the aid of a deFonbrune micromanipulator.

Scoring of mutants: After dissection, single ascospores were allowed to germinate and grow on the dissecting agar for approximately 12 to 15 hours. Restricted growth mutants were scored by visual observation at this time. Germlings were then transferred to CM+ tubes and maintained at room temperature until tested. The hyaline ascospore progeny were crossed on B agar or CM+ agar with the parental color mutants. If no recombination in the 6A region (detectable only in asci with wild-type spores) was observed in crosses with either parent after a survey of 10 to 35 thousand asci in each cross, the culture was considered to be doubly mutant for the hyaline sites. If any doubt arose in scoring the morphological mutants, tetrads from crosses with wild type were dissected for confirmation. The germination rate of the ascospore color mutants was approximately 85%. Members of a hyaline spore pair were considered to be genetically identical in instances where only one spore germinated.

Recombination analysis of ascospore color mutants: The number of asci in each cross involving two ascospore color mutants was estimated by averaging the counts of numbers of asci per perithecium for 10 to 20 perithecia in each plate and multiplying this figure by the total number of perithecia examined. The protoperithecial parent was the same for all replicates of each cross. Perithecial size and number of asci per perithecium did not vary greatly.

RESULTS

Genetic map: *Sordaria brevicollis* is characterized by frequent partial spindle-overlap in the second meiotic division, which leads to an excess of asymmetrical (2:2:2:2) MII (second-division segregation) asci (SHAW 1962; CHEN 1965; CHEN and OLIVE 1965). Symmetrical (2:4:2) MII asci are unaffected and centromere-gene distances may be calculated on the basis of this class. Centromere-gene distances thus obtained for the mutants employed in this investigation are shown in Table 1. Both morphological mutants, R83 and R155, lie distal to the 6A region,

TABLE 1

Summary of data on segregation of mutants with relation to centromere

Mutant	MI	Observed MII		Total	Expected MII*	Percent legitimate MII	Gene-to-centromere distance
		Asymmetrical	Symmetrical				
C17	1200	735	159	2094	318	15.2	7.6
C22	1664	1217	278	3159	556	17.6	8.8
†C27 (1)	925	261	76	1262	152	12.0	6.0
(2)	732	438	27	1197	54	4.5	2.8
†C28 (1)	3746	1495	267	5508	534	9.7	4.9
(2)	398	96	87	1092	174	15.9	8.0
C29	619	400	65	1084	130	12.0	6.0
R83	56	42	12	104	24	23.0	11.5
R155	95	28	12	129	24	18.6	9.3

MI: First-division segregation; MII: Second-division segregation.

* Computed as 2 × symmetrical MII class.

† Two different single-spore isolates of these mutants were used.

TABLE 2

Segregation data from cross involving three loci: $\frac{\text{C28 R155} +}{+ + \text{R83}}$

Cross	PD	NPD	T	Total	Percent T	Gene-gene- distance
R83 and C28	207	0	6	213	2.9	1.5
R155 and C28	212	0	1	213	0.5	0.25
R83 and R155	208	0	5	213	2.4	1.2

PD: parental ditype; NPD: nonparental ditype; T: tetratype.

while the centromere is a short distance to the left of it. Segregation data are given for two different monosporous cultures of both C27 and C28 to indicate the variability that may be observed. The cause of this variation has not been resolved, although factors may be present which influence crossing over. The method indicates the close linkage of the color mutants, but centromere distances established in this way are of little value in ordering these closely linked sites. We have arbitrarily chosen the largest value of 8.8 units (Table 1) as the distance between the centromere and the 6A region. This may not reflect the true value, but in view of the variation observed, it will prevent an overestimation of crossing over in this region.

A single 3-point cross was made to establish the order and positions of the morphological mutants relative to the color mutants. The results are presented in Table 2. R155 is approximately 0.25 units distal to the color mutants (6A) and R83 lies about 1.2 units distal to R155. The genetic map is presented in Figure 1.

The order of mutants based on percent of total wild-type spores in each cross involving pairs of hyaline mutants appears in Figure 2. The calculations are based on the recombination data presented in Table 3. The method of ordering mutants shown in Figure 2 is similar to the construction of fine structure maps based on the recovery of prototrophs by random analysis from crosses of two auxotrophic mutants. However, the present data, derived from observations of whole asci, give more information on how the wild-type spores arise. Later crosses using mutants R155 and R83 indicated that C17 is proximal and C28 distal within the 6A region.

Complementation: Occasionally, in each cross of a pair of hyaline color mutants, asci containing 4 colored spores and 4 aborted spores were produced. The colored spores were slightly larger than normal spores. The occurrence of these 4:4 asc varied in each cross. In the crosses C17 $\times$ C28, C22 $\times$ C28 and C27 $\times$ C28, the colored spores were wild-type in appearance. In the crosses

FIGURE 1.—Genetic map of mutants based on tetrad analysis.

FIGURE 2.—Genetic map of five ascospore color mutants based on the frequency of wild-type spores obtained in mutant $\times$ mutant crosses ($\times 10^{-4}$).

C17 $\times$ C29, C17 $\times$ C22, C17 $\times$ C27, C22 $\times$ C27, C22 $\times$ C29, C27 $\times$ C29 and C28 $\times$ C29, the colored spores were light green. Most of the colored spores of both types germinated, but usually no mycelial growth followed. These asci appear similar to those in which pseudo-wild types occur in *Neurospora crassa* (COYLE and PITTINGER 1965). However, failure of such spores from our crosses to produce mycelial growth is unresolved.

In three crosses—C17 $\times$ C28, C22 $\times$ C28 and C27 $\times$ C28—very rare asci were produced containing eight wild-type spores (8:0 asci), which like those described above, germinated but usually did not produce mycelia. In one cross, C17 $\times$ C28, all of the spores from a single 8:0 ascus germinated and produced mycelia, of which four were *A* and 4 *a*. Mycelia from four of the spores proved to be heterokaryotic for the two parental color factors. The other four spores produced mycelia containing only one of the parental color factors. These asci containing eight wild-type spores may have had some kind of polyploid origin.

The occurrence of the 4:4 and the very rare 8:0 asci is interpreted as evidence of complete complementation between mutant sites (in pseudo-wild spores) when dark spores are produced, and partial complementation when lightly colored spores are produced. On this basis, a complementation map can be constructed as shown in Figure 3.

TABLE 3

Recombination data from crosses involving pairs of the five ascospore color mutants

Crosses	Total no. asci	No. asci with two wild-type spores	No. asci with one wild-type spore	Total no. wild-type spores	Total no. spores	Frequency of wild-type spores $\times 10^{-4}$
C17 $\times$ C22	960,360	101	0	101	7,682,880	.263
C17 $\times$ C27	1,374,750	28	6	62	10,998,000	.056
C17 $\times$ C28	1,010,500	236	35	507	8,084,000	.627
C22 $\times$ C27	1,037,740	61	0	122	8,301,910	.147
C17 $\times$ C29	365,000	54	0	108	2,920,000	.370
C22 $\times$ C28	1,045,170	213	0	426	8,201,360	.519
C22 $\times$ C29	461,500	109	5	223	3,592,000	.623
C27 $\times$ C28	1,161,840	248	54	550	9,294,720	.592
C27 $\times$ C29	541,000	143	4	290	4,328,000	.670
C28 $\times$ C29	705,000	21	2	44	5,640,000	.078

FIGURE 3.—Complementation map of five ascospore color mutants in the 6A region based on the presence or absence of complete complementation. The order of C17, C22 and C27 may not be as shown.

Gene conversion at single ascospore-color mutant sites: Each of the five color mutants was crossed with wild type to determine the frequency and pattern of gene conversion. Significant numbers to establish these objectives were not obtained because of the low frequency with which gene conversion occurred. The data are shown in Table 4. Visually observable frequencies varied considerably. The predominant direction of conversion was from wild type to mutant allele for all sites except C29. Aberrant 4:4 asci, which contain 4 wild-type and 4 mutant spores but with two heterogeneous spore pairs, were not detected.

Gene conversion in crosses involving pairs of hyaline mutants: The system chosen here for analysis is based on the selection of asci containing wild-type spores. The 398 asci derived from crosses of the hyaline mutant alleles are described in Table 5. The arrangement in each class reflects the position of the spores without regard to which is the top or bottom half of the ascus. The 29 classes are grouped to include: (1) 6 mutant:2 wild type ($6m:2m^+$) asci containing reciprocal recombinants (Classes 1–7); (2) $6m:2m^+$ asci with conversion of the proximal allele (Classes 8–12); (3) $6m:2m^+$ asci with conversion of the distal allele (Classes 13–17); (4) $7m:1m^+$ asci with postmeiotic segregation of the proximal allele (Classes 18–21); (5) $7m:1m^+$ asci with postmeiotic segregation of the distal allele (Classes 22–23); (6) very unusual arrangements of alleles (Classes 24–29).

The most frequently occurring class was not consistent for all crosses. Asci containing reciprocal recombinants exceeded the proximal and distal convertants only in the crosses $C17 \times C29$, while in the other crosses the frequency of the reciprocal recombinant class varied considerably. Based on the hypothesis of crossing over between hyaline mutant sites, the data in Table 5 indicate the order of alleles to be: Centromere–C17–C27–C22–C29–C28.

Table 6 presents an analysis of crossing over in asci showing conversion of proximal and distal alleles and asci showing postmeiotic segregation. Excessive crossing over occurs predominantly in Region I and to a lesser extent in Region II.

TABLE 4

Patterns of aberrant ascus production for single mutant sites in crosses with wild type

Mutant	No. asci examined	No. asci $6m:2m^+$	No. asci $5m:3m^+$	No. asci $6m^+:2m$	No. asci $5m^+:3m$	Total aberrant asci	Frequency aberrant asci
C17	13,000	8	4	2	0	14	1/929
C22	13,600	6	4	2	0	12	1/1333
C27	11,928	3	4	2	2	11	1/1004
C28	23,980	9	1	0	2	12	1/2000
C29	16,857	5	0	5	1	11	1/1532

TABLE 5

Description of 398 asci containing wild-type spores from crosses of alleles within the 6A region with respect to flanking markers. All crosses were of the general form: shown below, where 1 and 2 are the proximal and distal alleles respectively within the 6A region

1 + R155 + + 2 + R83																	
Ascus class	First spore-pair	Second spore-pair	Third spore-pair	Fourth spore-pair	Asci analyzed from:												Total
					C17 X C22	C17 X C27	C17 X C28	C17 X C29	C22 X C27	C22 X C28	C22 X C29	C27 X C28	C27 X C29	C28 X C29			
6m:2m + asci containing reciprocal recombinants:																	
1	+	+	+	+	+	2	+	—	1	2	+	—	1	+	+	0	109
2	+	+	+	+	+	1	2	+	—	+	2	+	—	1	+	+	23
3	+	+	+	+	+	+	2	+	—	1	2	+	+	1	+	+	5
4	+	+	+	+	+	+	2	+	—	1	2	+	+	1	+	+	1
5	+	+	+	+	+	+	2	+	—	1	2	+	+	1	+	+	1
6	+	+	+	+	+	+	2	+	—	1	2	+	+	1	+	+	3
7	+	+	+	+	+	+	2	+	—	1	2	+	+	1	+	+	1
Totals																	
6m:2m + nonreciprocal asci containing conversions of proximal allele:																	
8	+	+	+	+	+	1	+	—	+	2	+	—	+	2	+	—	93
9	+	+	+	+	+	+	2	+	—	1	+	—	+	2	+	—	51
10	+	+	+	+	+	1	+	—	+	2	+	—	+	2	+	—	4
11	+	+	+	+	+	1	+	—	+	2	+	—	+	2	+	—	3
12	+	+	+	+	+	1	+	—	+	2	+	—	+	2	+	—	1
Totals																	
6m:2m + nonreciprocal asci containing conversion of distal allele:																	
13	+	+	+	+	+	+	2	+	—	1	+	—	+	1	+	—	40
14	+	+	+	+	+	1	+	—	+	2	+	—	1	+	—	+	15
15	+	+	+	+	+	+	2	+	—	1	+	—	+	1	+	—	9
16	+	+	+	+	+	+	2	+	—	1	+	—	+	1	+	—	3
17	+	+	+	+	+	+	2	+	—	1	+	—	+	1	+	—	1
Totals																	

TABLE 6

Analysis of crossing over in aberrant asci

		6A				
		Mutants			R155	R83
Centromere		Region				
		I	II	III		
Crosses	Site of conversion	Region of crossing over			No crossing over detected	Total asci
		I	II	III		
<i>6m:2m⁺ asci</i>						
C17 × C22	C17	2	0	0	4	6
	C22	2	0	0	3	5
C17 × C27	C17	1	0	0	5	6
	C27	1	0	0	4	5
C17 × C28	C17	11	0	0	22	33
	C28	2	1*	0	7	10
C17 × C29	C17	1	0	0	1	2
	C29	0	0	0	3	3
C22 × C27	C22	2	0	1	7	10
	C27	1	0	0	7	8
C22 × C28	C22	6	2*	1	10	19
	C28	2	3*	0	7	12
C22 × C29	C22	6	1*	0	10	17
	C29	4	1*	2*	3	10
C27 × C28	C27	16	0	2*	26	44
	C28	1	4*	0	1	6
C27 × C29	C27	7	0	0	5	12
	C29	1	0	1	4	6
C28 × C29	C28	0	0	0	1	1
	C29	0	1*	1*	3	5
<i>7m:1m⁺ asci</i>						
C17 × C28	C17	1	0	0	4	5
	C28	0	0	0	1	1
C17 × C27	C17	0	0	0	1	1
	C27	0	0	0	1	1
C22 × C29	C29	0	0	0	1	1
C27 × C28	C27	3	1*	1*	8	13
	C28	3	0	0	3	6
Totals		73	14	9	152	248
Expected		43.6	1.2	6.0		
P		0.01	0.01	0.10		

* The chromatid involved in conversion or postmeiotic segregation also participated in the crossover.

In crosses involving distantly spaced mutants, crossing over in Region I is more often associated with conversion of the proximal allele. However, crosses involving C29 are not consistent in this respect. Crossing over in Region II occurs only in crosses involving C28 and C29 and appears most often to be associated with conversion of these distal alleles. The chromatid involved in the conversion event participated in all of the crossovers in Region II, and in 6 of the 9 crossovers in Region III.

DISCUSSION

Two interesting models have recently been proposed to explain recombination at the intragenic level (HOLLIDAY 1964; WHITEHOUSE and HASTINGS 1965; WHITEHOUSE 1966). Both models propose genetic recombination by a process of hybrid DNA formation, followed by correction of both sites of heterogeneity or by correction of only one or neither of such sites in the two participating chromatids, the later leading to postmeiotic segregation. Data presented here lend themselves to interpretation in terms of models of this type, but no commitment to a specific model can be made on the basis of our data. If such models prove correct, then the relative scarcity of asci showing postmeiotic segregation in our investigation would indicate a high rate of correction of heterogeneous sites.

ROSSEN and WESTERGAARD (1966) have shown that the major round of DNA replication in the discomycete *Neottiella rutilans* (Fr.) Dennis occurs prior to nuclear fusion in the crozier. If further DNA synthesis failed to occur after chromosome pairing, mechanisms which involve copy choice at the last premeiotic DNA replication would be untenable. However, HOTTA, ITO and STERN (1966) have clearly shown that a small but distinct amount of DNA synthesis (0.3% of the total DNA) occurs at zygotene-pachytene in *Trillium* and *Lilium*, which they think may be associated with crossing over. This evidence might favor a mechanism of gene conversion such as that proposed by WHITEHOUSE and HASTINGS (1965), but it could also accommodate a copy choice-base repair model.

In our data from crosses of more distantly spaced mutants, C17 $\times$ C28, C22 $\times$ C28, C27 $\times$ C28 and C27 $\times$ C29 (Tables 5 and 6) there are two noteworthy features: (1) prominent polarity in conversion in nonreciprocal 6m:2m⁺ ascus types, with the mutant to the left in the genetic map always showing more conversion to wild type, and (2) a greater amount of apparent crossing over in the proximal region in the majority class of conversion asci. The cross C17 $\times$ C29 is an exception, although the sample size is small. Crosses between mutants at the proximal end of the genetic map also do not show the above features.

Excess apparent crossing over in the region immediately distal to the hyaline sites (Region II) is strongly correlated with the conversion event only when the distal mutants C28 and C29 are involved in a cross. The chromatid identifiable as being involved in the conversion event also participated in all of the crossovers in this region.

All these results suggest that the event which initiates conversion also initiates associated crossing over in adjacent regions. They also suggest that the conversion event may generally be initiated proximally within the 6A region, resulting in polarity of conversion to wild type. However, the correlation between involvement of distal sites and crossing over in the adjacent distal region indicates that the conversion event may occasionally originate distally.

The largest class of asci showing conversion was not associated with crossing over in adjacent regions, suggesting that related crossing over is not a necessary feature of gene conversion in the 6A region. It should be pointed out that double crossing over involving both Regions I and II was not detectable in these asci.

The patterns of segregation of flanking markers in asci showing reciprocal recombination (Table 5) suggest that crossing over occurred between the hyaline sites. An analysis of double crossing over in these asci was limited since we could not distinguish among all the kinds of double crossovers which might occur. Reciprocal recombination could also arise from gene conversion. Many of the reciprocal recombinant asci in our data might have arisen in this way, but, if so, different arrangements of flanking markers would have been expected for some of the asci.

The unusual aberrant asci (Table 5, Classes 24–29) clearly indicate that more than one chromatid may be involved in the conversion event. All of these asci could be interpreted in this way, although Class 29 may have resulted from a reverse mutation to wild type prior to karyogamy.

Caution must be used in the assessment of gene conversion from data such as these where there is selection for certain types of aberrant asci. Conversion from wild type to mutant in crosses of mutant $\times$ wild type is predominant for three of our hyaline mutants. It is evident that in all of the crosses analyzed here, a large proportion of asci with aberrant segregations could not be detected, since double-mutant progeny are not visually distinguishable from parental mutants. An ideal system using intra-cistron ascospore-color mutants would be one in which the color mutants were distinguishable from one another and from the double mutant and where there is a high rate of conversion at the mutant sites. A system possessing most of these properties is under investigation in *S. brevicollis*.

The authors are very grateful to Miss MAJORIE CHRISTIANSEN for her skillful technical assistance, and to Drs. S. FOGEL and D. D. HURST for a prepublication copy of their manuscript on gene conversion in yeast.

SUMMARY

Five hyaline ascospore color mutants of the 6A region were crossed in all possible pairwise combinations, and samples of complete asci showing visually detectable recombination were isolated and analyzed. Of 398 asci analyzed, 143 6m:2m⁺ asci exhibited reciprocal recombination, 152 nonreciprocal 6m:2m⁺ asci contained conversions of the proximal allele, 68 nonreciprocal 6m:2m⁺ asci contained conversion of the distal allele, 19 7m:1m⁺ asci showed postmeiotic segregation of the proximal allele, 9 7m:1m⁺ asci showed postmeiotic segregation of the distal allele, and 7 asci contained even more unusual progeny. A total of 248 aberrant asci were analyzed for crossing over in regions adjacent to 6A. Crossing over in excess of the expected was observed in the proximal and distal regions adjacent to the hyaline sites. Five of the crosses between hyaline alleles showed prominent conversion polarity, with the mutant site to the left in the genetic map showing a higher frequency of conversion to wild type.

LITERATURE CITED

- CASE, M. E., and N. H. GILES, 1964 Allelic recombination in *Neurospora*. Tetrad analysis of a three-point cross within the *pan-2* locus. *Genetics* **49**: 529-540.
- CHEN, K. C., 1965 The genetics of *Sordaria brevicollis*. I. Determination of seven linkage groups. *Genetics* **51**: 509-517.
- CHEN, K. C., and L. S. OLIVE, 1965 The genetics of *Sordaria brevicollis*. II. Biased segregation due to spindle overlap. *Genetics* **51**: 761-766.
- COYLE, M. B., and T. H. PITTINGER, 1965 Mitotic recombination in pseudo-wild types of *Neurospora*. *Genetics* **52**: 609-625.
- HOTTA, Y., M. ITO, and H. STERN, 1966 Synthesis of DNA during meiosis. *Proc. Natl. Acad. Sci. U. S.* **56**: 1184-1191.
- HOLLIDAY, R., 1964 A mechanism for gene conversion in fungi. *Genet. Res.* **5**: 282-303.
- KITANI, Y., L. S. OLIVE, and A. S. EL-ANI, 1962 Genetics of *Sordaria fimicola*. V. Aberrant segregation at the *g* locus. *Am. J. Botany* **49**: 697-706.
- LISSOUBA, P., and G. RIZET, 1960 Sur l'existence d'une unité génétique polarisée ne subissant que des échanges non réciproques. *Comp. Rend.* **250**: 3408-3410.
- LISSOUBA, P., J. MOUSSEAU, G. RIZET, and J. L. ROSSIGNOL, 1962 Fine structure of genes in the ascomycete *Ascobolus immersus*. *Advan. Genet.* **11**: 343-380.
- MITCHELL, M. A., 1955 Aberrant recombination of pyridoxine mutants of *Neurospora*. *Proc. Nat. Acad. Sci. U. S.* **41**: 215-220.
- MURRAY, N. E., 1963 Polarized recombination and fine structure within the *me-2* gene of *Neurospora crassa*. *Genetics* **48**: 1163-1183.
- ROMAN, H., 1963 Gene conversion in fungi. pp. 209-227. *Methodology in Basic Genetics*. Edited by W. J. BURDETTE. Holden-Day, San Francisco.
- ROSSEN, J. M., and M. WESTERGAARD, 1966 Studies on the mechanism of crossing over. II. Meiosis and the time of meiotic chromosome replication in the ascomycete. *Neottiella rutilans* (Fr.) Dennis. *Compt. Rend. Trav. Lab. Carlsberg* **35**: 233-260.
- SHAW, J., 1962 Asymmetrical segregation of mating type and two morphological mutant loci in *Sordaria brevicollis*. *Bull. Torrey Bot. Club* **89**: 83-91.
- STADLER, D. R., and A. M. TOWE, 1963 Recombination of allelic cysteine mutants in *Neurospora*. *Genetics* **48**: 1323-1344.
- WHITEHOUSE, H. L. K., 1966 An operator model of crossing-over. *Nature* **211**: 708-713.
- WHITEHOUSE, H. L. K., and P. J. HASTINGS, 1965 The analysis of genetic recombination on the polaron hybrid DNA model. *Genet. Res.* **6**: 27-92.