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Polarity of gene conversion and post-meiotic segregation at the *buff* locus in *Sordaria brevicollis*

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SUMMARY

The flanking markers of wild-type recombinant spores originating from crosses of spore colour mutants in *Sordaria brevicollis* were analysed. Recombinant asci were of two main types – either with one or with two wild-type spores. In most crosses the behaviour of flanking markers was significantly different for these two types of recombinant asci. The main differences were in the polarity of gene conversion (as inferred from parental outside marker combinations) and in the frequency of recombinant outside markers. These differences were interpreted in terms of hybrid DNA models of recombination and correction of heteroduplex DNA.

1. INTRODUCTION

Models of recombination which are currently under active consideration as affording the best account of the mechanism of recombination (e.g. Holliday, 1962, 1964; Whitehouse, 1963) do not encounter any great difficulty in accommodating any single observation. Rather it is a combination of experiments on polarity of gene conversion, reciprocal recombination, and correction of heteroduplex DNA which are not easily reconciled.

Polarity was first described by Lissouba *et al.* (1962) in *Ascobolus immersus* and, using a different method of detection, by Murray (1963) in *Neurospora crassa*. It is recognized as a position-dependent preferential conversion of one of the two alleles in an intragenic cross. Operationally polarity is detected either from complete analysis of the products of meiosis (for example, in *Ascobolus*) or from analysis of the behaviour of outside markers (for example, in *Neurospora* and *Drosophila*). Analysis of tetrads with flanking markers present has shown that the two criteria are equivalent (Stadler & Towe, 1963; Fogel & Hurst, 1967).

Polarity is accounted for by postulating a discontinuous distribution of recombination events, and an analysis of a large body of data by Whitehouse & Hastings (1965) in terms of hybrid DNA models led them to conclude that the discontinuities (or opening points) were located between cistrons. Convincing experimental evidence to support this view has been obtained by Murray (1970) working on *N. crassa*. She analysed recombination in two contiguous genes (*me-7* and *me-9*). The results revealed a discontinuity to the left of the *me-9* alleles and to the right of the *me-7* alleles, i.e. between the two cistrons.

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Different patterns of polarity exist for different genes dependent (according to hybrid DNA models) upon the relationship of the region studied to the nearest opening point. For example, if a gene shows preferential conversion of proximal alleles then this is taken to show that the nearest opening point for hybrid DNA formation is on the proximal side of that gene.

Recent studies have revealed several features which do not accord with this simple interpretation. There is now good evidence that, whilst gene conversion events are discontinuously distributed, events that result in reciprocal recombination are not. Fogel & Hurst (1967) showed for a *his* gene in *Saccharomyces cerevisiae* that reciprocal recombination resulted, almost invariably, in the coincident crossing over of the flanking markers. This would not be expected if they arose through a process of gene conversion, but it is consistent with the event giving rise to them having been initiated between the two alleles involved in the cross. Gene conversion events showed distal polarity, however, consistent with an opening point at the distal end of the gene. Clearly it is difficult to reconcile, into a single unitary hypothesis of recombination, the findings that gene conversion events are discontinuously distributed whilst reciprocal events are not. Attempts to do so have been made by Whitehouse (1967) and Sobell (1972).

The investigations by Rossignol (1969) of recombination in a series of ascospore colour mutants of *Ascobolus* reveal another factor which complicates the simple interpretation of polarity. He showed that the mutants he used had a characteristic gene conversion spectrum which could be defined in terms of a coefficient of dissymmetry. The dissymmetry coefficient was defined as:

$$\frac{\text{frequency of conversion to mutant}}{\text{frequency of conversion to wild type}}.$$

Mutants classified in this manner fell into four groups with characteristic dissymmetry coefficients. The differences between the conversion spectra of the mutants were sufficiently great to mask polarity of gene conversion. The latter could only be detected after classification of the mutants using the dissymmetry coefficient. Rossignol accounted for the differences in conversion spectra by postulating that they were a reflexion of the different mutational changes in the DNA. Leblon (1972) obtained some experimental support for this postulate by inducing mutations with different mutagens. He showed that each mutation had a characteristic conversion spectrum depending upon its mutational origin.

There is a great need to extend recombination studies in order to determine how far the above results are peculiar to particular organisms or loci and how far they are of general applicability. Therefore studies of recombination at the *buff* locus in *Sordaria brevicollis* were initiated. In the course of this work another, hitherto unsuspected, factor which can modify the pattern and intensity of polarity was revealed. Polarity, as determined by parental configurations of flanking markers, was significantly different in asci with only one wild-type spore (i.e. post-meitotic segregants) compared to those with two wild-type spores.

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2. MATERIALS AND METHODS

(a) *Mutants and media*

All the spore colour mutants used in this study are members of the *buff* locus, which has been shown to be equivalent to the *beige* and *grey-3* complex of Chen (1965). This locus was reported by Chen to be two map units from the centromere of linkage group II. All the mutants were u.v.-induced, some by M. H. V. Cooray. Those prefixed by the letter c were kindly supplied by Professor L. S. Olive. Mutants isolated in this laboratory were backcrossed several times to wild-type prior to mapping experiments.

The outside markers used were, proximally, a morphological mutant (*mo-1*) characterized by a sharper colony outline and slower growth than wild-type when grown on corn-meal agar, and distally a nicotinamide requiring mutant (*nic-1*). These markers are 1·5 and 1·1 map units respectively from the *buff* gene.

Crosses were made on corn-meal agar of the following composition: corn-meal agar (Difco), 17 g; glucose, 2 g; sucrose, 3 g; yeast extract, 1 g; distilled water up to 1000 ml. Asci were dissected on 4 % agar and the ascospores germinated in tubes of suitably supplemented Vogel's N medium (1956) to which 0·7 % sodium acetate was added to stimulate germination.

(b) *Crossing methods*

The *buff* mutants were crossed in pairwise combinations, in most cases one *buff* mutant carried the *mo-1* mutation and the other the *nic-1* marker. The parent strains were grown separately in Petri dishes at 25 °C for 4 days. The microconidia from one of the parents were harvested in a small quantity of sterile distilled water and the resulting suspension was poured over the ♀ parent of compatible mating type. The crosses were then incubated for a further 6 days until they were mature and ascospore discharge commenced.

(c) *Scoring methods*

In the initial experiments the recombinants were detected in the following way. A slab of 4 % agar was placed in the lid of the Petri dish containing the maturing cross. When ascospore discharge commenced the asci adhered to the surface of the agar and the recombinants could be detected under a dissecting microscope. The lids over the crosses were changed periodically in order to prevent them becoming overcrowded. This method provided a rapid means of scanning a cross for recombinants but in many cases the spores were not discharged in groups of eight. In these cases it was impossible to obtain accurate counts of the number of asci examined. In later crosses therefore the asci were harvested before discharge by scraping perithecia from the surface of the cross as soon as the first few asci were discharged. The perithecia were crushed in 10 % sucrose solution on a slide and the sugar allowed to dry out. In this condition the asci can be stored for a considerable period and examined when convenient.

Examination of perithecial clumps was carried out as follows. The clumps were

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transferred to the surface of a 4 % agar slab, a coverslip was placed over them, and the asci were examined for recombinant spores. When a recombinant was detected the coverslip was removed, the clump of asci containing the recombinant almost always stuck to the agar surface from which it could be removed. The recombinant ascus was dissected, the spores grown up separately and subsequently tested for outside markers. The genotype of the black spores was confirmed by backcrossing.

Table 1. *Numbers and frequencies of recombinant asci in* buff × buff *crosses*

Alleles crossed	Frequency of recombinant asci (× 10^4)	Ascus count on which frequency based	No. of recombinant asci with 1+	2+	3+	4+	Frequency of post-meiotic segregation (± standard error)
c47 × *c79*	1·86	29/155 528	5	24	—	—	0·172
c47 × *S156*	(1·89)	1/5282	1	—	—	—	—
c47 × *S180*	3·79	29/76 551	59	73	1	2	0·438 ± 0·042
c47 × *S6*	2·89	26/90 022	39	58	0	1	0·394 ± 0·049
c79 × *S41*	0	0/9540	—	—	—	—	—
c79 × *S156*	0	0/51 637	—	—	—	—	—
c79 × *S180*	5·00	65/129 976	76	40	—	—	0·649 ± 0·045
c79 × *S6*	2·46	17/69 045	16	53	—	—	0·232 ± 0·052
c79 × *c70*	—	Not counted	42	39	2	—	0·518 ± 0·054
S41 × *S156*	0	0/250 000*	—	—	—	—	—
S41 × *S180*	{ 4·24 3·38	5/11 800* 11/33 566 }	24	43	—	—	0·358 ± 0·058
S41 × *S6*	—	Not counted	5	23	—	—	0·179
S156 × *S180*	1·10	4/36 500*	17	27	—	—	0·386 ± 0·073
S156 × *S6*	—	Not counted	8	47	—	—	0·145 ± 0·048
S180 × *S6*	(0·28)	1/35 600*	3	15	—	—	0·167

* Numbers estimated (to the nearest hundred) by observation on shot ascopsores on Petri dish lids.

3. RESULTS

The recombination frequencies which were estimated in one of the two ways described in the Materials and Methods are presented in Table 1. These figures are intended only as a rough guide, and were not used in compiling the map of the *buff* locus since there were experimental factors which affected the accuracy of the estimates. This applied particularly to the crosses from which discharged ascospores were counted. In some crosses asci were discharged on to the Petri dish lid as scattered groups and not as units of eight spores representing one ascus. This made estimates of ascus numbers very difficult. Also, in some wild-type crosses, ascospore discharge can occur before spores are fully pigmented (Bond & MacDonald, unpublished). This premature discharge, if it occurred in *buff* × *buff* crosses, would go undetected. It would result in an underestimate of the recombination frequency because some recombinants would be unpigmented and therefore undetectable.

Table 1 also contains estimates of the frequency of post-meiotic segregation asci

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amongst recombinants for the various *buff* × *buff* crosses. These figures were calculated from the total asci detected including those in which the wild-type spores subsequently did not germinate. The frequency of non-germinated wild-type spores was very low. In the case of the germinated spores, backcrossing revealed no instance where the genotype of a spore did not conform to its phenotype.

Table 2. *Classification of outside markers in wild-type recombinant spores from* buff × buff *crosses*

Map order: *c47* — *S156*, *S41*, *c79* — *c70* (?) → *S180* — *S6*

Genotype of parents *mo-1 Buff*^{P} *nic* × *mo-1 Buff*^{D} *nic*			No. and frequency of spores with outside marker combination P$_1$	P$_2$	R$_1$	R$_2$
− *c47* +	×	+ *c79* −	12 (25%)	8 (17%)	24 (50%)	4 (8%)
− *c47* +	×	+ *S180* −	29 (30%)	25 (26%)	26 (27%)	16 (17%)
+ *c47* −	×	− *S180* +	19 (29%)	10 (15%)	28 (43%)	8 (12%)
− *c47* +	×	+ *S6* −	48 (36%)	32 (24%)	32 (24%)	20 (15%)
+ *c79* +	×	− *S180* −	8 (6%)	81 (56%)	36 (21%)	19 (13%)
+ *c79* −	×	− *S6* +	30 (27%)	40 (36%)	37 (33%)	4 (4%)
+ *c79* −	×	− *c70* +	12 (10%)	56 (45%)	42 (34%)	15 (12%)
+ *S41* −	×	− *S180* +	16 (15%)	49 (45%)	39 (36%)	4 (4%)
− *S41* +	×	+ *S6* −	18 (49%)	9 (24%)	10 (27%)	0 (−)
+ *S156* −	×	− *S180* +	15 (23%)	20 (30%)	30 (45%)	1 (2%)
− *S156* +	×	+ *S6* −	17 (19%)	27 (30%)	44 (49%)	2 (2%)
− *S180* +	×	+ *S6* −	7 (21%)	8 (24%)	16 (48%)	2 (6%)

P$_1$ = Parental flanking marker combination which entered the cross with the proximal allele.

P$_2$ = Parental flanking marker combination which entered the cross with the distal allele.

R$_1$ = Majority recombinant flanking marker combination which defines the order of the alleles.

R$_2$ = Minority recombinant flanking marker combination. Origin consistent with an apparent triple exchange one in each of the three marked intervals.

The post-meiotic segregation frequencies exhibited in the various crosses were often significantly different from each other and appeared to be a specific feature of any particular cross. In most cases the data came from replicate crosses. In these crosses there were no instances of significant heterogeneity between repeats and therefore the post-meiotic segregation frequencies were based on the pooled data.

The recombinant asci were dissected and the outside markers of the wild-type spores determined. The results are presented in Table 2. The order of any two alleles was inferred from the combination of recombinant outside markers which was in the majority. This class (R$_1$) can be considered to arise simply from a single crossover between the alleles. Analysis of the results in this manner gave a map in which there were no contradictions (Fig. 1). It can be seen that several of the mutants mapped in a cluster; alleles within this cluster did not yield any recombinants when intercrossed. The position of *c70* was not determined accurately. It

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is distal to the cluster of mutants but its position with respect to *S180* and *S6* is not known.

Subdivision of the recombinant asci into the two main categories (those with 2+ spores and those with 1+ spores) revealed hitherto unsuspected differences between them with respect to the outside marker pattern. The results of this subdivision are presented in Table 3.

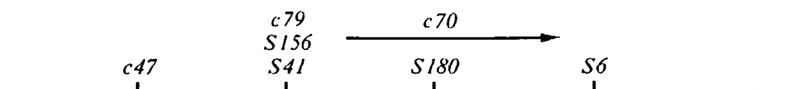

Fig. 1. Fine structure map of the *buff* locus.

Table 3. *Comparison of outside marker behaviour in 1+ spored and 2+ spored asci*

Alleles crossed	Number of asci with outside marker combination in: 1+ spored asci				2+ spored asci				Contingency χ^2 test		
	P_1	P_2	R_1	R_2	P_1	P_2	R_1	R_2	1	2	3
c47 × *c79*	2	0	2	2	5	4	11	0	—	—	—
c47 × *S180*	17	11	10	6	14	11	20	9	0·12	2·94	3·24
c47 × *S6*	16	8	6	4	16	12	12	7	0·50	1·04	1·57
c79 × *S180*	0	51	8	7	4	15	14	6	7·81**	9·00**	19·71**
c79 × *S6*	0	8	1	2	15	16	18	1	4·41*	0·11	14·00**
c79 × *c70*	1	30	6	5	5	12	17	5	4·70*	7·65**	15·55**
S41 × *S180*	0	19	5	0	8	15	17	2	6·06*	3·93*	13·08**
S41 × *S6*	0	3	0	0	9	6	5	0	—	—	—
S156 × *S180*	1	8	6	1	7	6	12	0	—	—	—
S156 × *S6*	1	7	2	0	8	10	21	1	1·28	2·65	7·30
S180 × *S6*	1	2	0	0	3	3	8	1	—	—	—

Test 1: χ^2_1 = parental markers compared in 1+ and 2+ spored asci.
Test 2: χ^2_1 = parental *v.* recombinant markers compared in 1+ and 2+ spored asci.
Test 3: χ^2_3 = 1+ and 2+ spored asci compared.
* $P = < 0·05$.
** $P = < 0·01$.

In many of the crosses the outside marker patterns of recombinants from asci with 2+ spores were significantly different from the pattern in those from asci with only 1+ spore. Contingency χ^2 tests were carried out on those crosses where the data were extensive enough to justify a test. The values obtained can be seen in Table 3. The crosses involving the allele *c47* were different from all the others. For *c47* crosses there were no significant differences between the 2+ spored asci and the 1+ spored asci. In other crosses where the samples were large enough (total asci > 50) there were significant differences between the two classes. There was one exception, the cross *S156* × *S6* gave χ^2 values which were not significant. In this cross the low frequency of 1+ spored asci meant that the numbers obtained were small. The remaining crosses where individual χ^2 tests were not justified also showed a similar trend.

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Furthermore, the crosses in which the two classes differed all showed differences of a similar nature:

(1) In those asci showing post-meiotic segregation, the parental combination of flanking markers in the wild-type spores was virtually always the combination that entered with the distal allele. In 2+ spored asci both parental combinations occurred. This difference could be seen in all crosses (except those involving *c47*) and was statistically significant in the cases of *c79* × *S6*, *c79* × *S180*, *S180* × *S41* and *c79* × *c70*.

(2) The proportion of recombinant asci with the outside markers recombined ($R_1 + R_2$) was higher in the 2+ spored asci. This was true for all crosses for which large samples were available, including the *c47* crosses. The trend was significant in the case of the crosses *c79* × *S180*, *c79* × *c70* and *S180* × *S41*.

(3) The proportion of R_2 amongst the recombinant classes was greater in the 1+ spored asci. The data, even for the largest samples, were not large enough to justify individual χ^2 tests but the trend could be seen in nearly every case.

Table 4. *Classification of Kitani & Olive's (1969)* data for the* g *locus in* S. fimicola

Cross	Classification of outside markers in recombinant asci with: 1+ spore				2+ spores			
	P_1	P_2	R_1	R_2	P_1	P_2	R_1	R_2
$g_1 \times h_2$	27	42	26	22	7	9	8	1
$g_1 \times h_5$	34	24	30	17	24	14	9	10
$g_1 \times h_4$	25	16	22	9	28	5	33	2
$g_1 \times h_{4b}$	25	20	27	12	19	3	18	2
$g_1 \times h_3$	48	31	29	14	32	7	41	6

* Data extracted from an ascus classification by Whitehouse (unpublished).

4. DISCUSSION

(*a*) *Post-meiotic segregation at the* buff *locus*

A characteristic feature of recombination in *Sordaria brevicollis* is the relatively high proportion of recombination events which exhibit post-meiotic segregation. In such an organism one test of models of recombination such as those proposed by Stahl (1969), Boon & Zinder (1969) and Paszewski (1970) is possible. These models exclude the possibility of heterozygosity in DNA being 'cured' by enzymic correction. Post-meiotic segregation is seen as a consequence of staggered breaks in DNA chains. Non-correction models all make a similar prediction about the proportion of post-meiotic segregation amongst gene conversion events. The proportion will be smallest for large intervals and will increase as the interval size decreases. In models postulating the existence of enzymic correction on the other hand, post-meiotic segregation is a reflexion of the inefficiency of the enzyme in

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recognizing mispaired regions. These models make no specific predictions concerning post-meiotic segregation frequency.

From the results it can be seen that the prediction of the non-correction models was not borne out. The proportion of post-meiotic events did not show any simple relationship to interval distance. The post-meiotic segregation frequency appeared to be a characteristic feature of any particular combination of alleles.

(*b*) *Polarity at the* buff *locus*

From the behaviour of the flanking markers it can be inferred that recombination at the *buff* locus is polarized. The parental combinations of flanking markers serve to identify which of the alleles has undergone gene conversion. In the case of the *buff* locus there was a definite tendency to recover the parental combination which marked the distal allele. Thus the *buff* locus exhibits distal polarity. According to hybrid DNA models this is explained by postulating that an opening point for initiation of hybrid DNA is located near the distal end of the *buff* locus.

c47 mapped as the most proximal mutant. In crosses involving *c47* the outside marker combination identifying this allele was recovered most often. This implies the preferential conversion of *c47*, i.e. proximal polarity. Thus for these crosses there was a reversal of polarity. Such a reversal of polarity has been reported previously by Murray (1969). She detected polarity reversal in several genes in *N. crassa*. The *me-2* gene exhibits distal polarity, but there was a preferential conversion of the two most proximal alleles when these were crossed to alleles in mid cistron. It would be interesting to see if the polarity reversal is still detected when *c47* is crossed to alleles more distal than those used in this study

An intriguing finding in this report is the difference in polarity shown between 1+ and 2+ spored asci. This is not predicted by any of the current recombination models. In terms of hybrid DNA models postulating the correction of mispairing, it would appear that the hybrid DNA of proximal origin was always corrected, i.e. there were virtually no P_1 flanking marker genotypes for the wild-type spores in the post-meiotic segregation asci. Hybrid DNA of distal origin remained uncorrected in a large proportion of the cases. A similar difference is shown in Kitani & Olive's (1969) data for the *g* locus in *S. fimicola*. Table 4 contains an analysis of their results. It has been based on an unpublished classification of recombinant asci by Dr H. L. K. Whitehouse. Only those asci containing wild-type spores were considered and these were classified for outside markers. It can be seen that three of these crosses ($g_1 \times h_4$; $g_1 \times h_{4b}$ and $g_1 \times h_3$) show differences of a similar kind to those shown in this paper. As judged from the frequency of the P_2 combination of flanking markers, distal events are found predominantly in the 1+ spored class (67 times out of a total of 82 events), whereas proximal events, though more frequent, show no such preponderance.

The simplest explanation for this difference in both cases is that it is the outcome of the post-meiotic segregation characteristics of the mutants used. That is, if the distal mutants were of the sort which exhibited more post-meiotic segregation than proximal ones, then recombination events at the distal end would yield

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1+ spored asci whilst proximal events would be corrected and end up as 2+ spored recombinants. This is a probable explanation in the case of Kitani & Olive's data but it is less likely to apply at the *buff* locus. In *S. fimicola* the distal mutants (h_3 and h_4) showed a higher frequency of post-meiotic segregation than g_1 (Kitani & Olive, 1967) in single-point crosses, and this is consequently reflected in the two-point results. At the *buff* locus those mutants which have been studied in single point crosses all show post-meiotic segregation about equally often (Ahmad, 1970). The implication is, therefore, that factors other than the mispairing itself can affect the correction process.

One such factor could be the proximity of the mispaired bases to the fixed opening point. The nearer the mutant site to the opening point the greater the likelihood of correction. This is not borne out by the results. The occurrence of distal polarity implies that the distal alleles are nearer the distal opening point than the proximal alleles are to the proximal opening point, yet it is the distal mispairing which often remains uncorrected. Another possibility is that the correction process is influenced by the length of the hybrid DNA in which the mispairing is contained. The longer the hybrid DNA the greater the chance of correction. This is formally the converse of the first suggestion above. This then would explain the situation at the *buff* locus since the proximal convertants arise from hybrid DNA which is on average longer than that giving rise to the distal convertants. It is interesting to note that where the proximal hybrid DNA is inferred to be shorter, i.e. in the case of conversion of *c47*, then post-meiotic segregation of the proximal allele is found.

(*c*) *Crossing over at the* buff *locus*

A second feature of the recombination at the *buff* locus was the excess of the R_1 recombinant outside marker class in the 2+ spored asci. This could reflect a difference in overall crossover frequency between hybrid DNA of proximal and distal origin, since the two sorts of DNA are asymmetrically distributed between the two classes. Such a difference has been found previously. Fogel & Hurst (1967) showed that in recombinant asci at the *his-1* locus there was more crossing over associated with distal convertants. From their data, 368 or 847 asci with proximal conversion were recombinant for outside markers whilst for distal convertants 84 out of 133 showed crossing-over. This difference is highly significant ($\chi^2_1 = 17{\cdot}96$, $P < 0{\cdot}001$).

The excess of crossovers in the 2+ spored asci can also be accounted for by postulating the existence of reciprocal recombinant events initiated in mid cistron. A proportion of the 2+ spored asci would then be formed through recombination between alleles and these could not be represented amongst post-meiotic segregants. This possibility is open to test by determining the frequency of reciprocal recombination at the *buff* locus. Such a test has been hampered to date by poor germination of the mutant spores. If this difficulty can be overcome and it can be shown that reciprocal recombination does occur with appreciable frequency and with obligatory recombination of flanking markers, then such a confirmation of the

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important finding of Fogel & Hurst (1967) would strengthen the case for suggesting that reciprocal recombinants are formed through a process other than reciprocal gene conversion.

(*d*) *Conclusion*

The major inference from the results reported in this work is that the correction process resulting in gene conversion is influenced by factors other than the mispaired bases themselves. This discovery opens the way for an explanation of an intriguing difference that exists between gene conversion in *Ascobolus* and either *Neurospora* or yeast. From the work of Rossignol and Leblon it would appear that in *Ascobolus* the type of mispairing is of primary importance in determining the conversion characteristics of any mutation (Leblon, 1972; Leblon & Rossignol, 1973). In this organism therefore mispair-specific correction occurs. In *Neurospora* or yeast, on the other hand, there is no evidence that the type of mispair has any influence on the correction process. For example, polarity of gene conversion in these organisms is never masked or modified by the type of mutation used as has been shown to be the case in *Ascobolus* (Rossignol, 1969). Research is being continued in this laboratory in an attempt to determine whether mispair-specific correction is a feature of *Sordaria brevicollis*.

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