THE GENETICS OF *SORDARIA BREVICOLLIS*. I. DETERMINATION OF SEVEN LINKAGE GROUPS¹

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Sordaria brevicollis Olive and Fantini (1961) is the first described heterothallic species of the genus *Sordaria*. Heterothallism is controlled by a single pair of compatibility factors, *A* and *a*. There appears to be no morphological difference between *A* and *a* strains, and both produce numerous protoperithecia and microconidia when grown separately. The microconidia, which are uninucleate, are highly effective in fertilization but show a low percentage of germination when plated out on agar media. Fertile perithecia are formed only when two compatible strains are mated. Mature ascospores are found 7 days after fertilization, and complete maturation of asci generally requires only 12 days from the time mycelial growth begins. The eight ascospores are normally dark in color and linearly arranged in the ascus, thus facilitating genetic analysis. Ascospore color mutants, the chief subjects of this study, offer special advantages for genetic investigation, since their patterns of segregation can be determined by direct ascus analysis, and large numbers of tetrads may be quickly scored.

Fungi where *autonomous* ascospore traits can be studied have recently made fundamental contributions to knowledge of the mechanisms of genetic recombination, e.g., in the case of *Ascobolus immersus* (LISSOUBA, MOUSSEAU, RIZET and ROSSIGNOL 1962) and *Sordaria fimicola* (KITANI, OLIVE and EL-ANI 1962). *S. brevicollis* offers a suitable material for similar studies. A number of ascospore-color and mycelial mutants of *S. brevicollis* have been produced by ultraviolet irradiation (UV). A formal genetic analysis of these mutant loci and the establishment of seven linkage groups are the subject of the present investigation.

MATERIALS AND METHODS

Two single-ascospore cultures of compatible mating types (*A* and *a*) of the original type collection were used, and all mutants were derived from them. The culture medium was Difco cornmeal dextrose agar plus 0.1% yeast extract. Crosses were made in Petri dishes and incubated at 23°C.

For the production of mutants, the microconidial parent was first grown for 5 days on the cornmeal agar supplemented with 0.4% sodium acetate to stimulate abundant microconidial development. Microconidia were harvested by adding 5 to 6 ml of sterile distilled water to the plate and gently loosening them with a bent glass rod. The suspension was subjected to UV in a small petri dish in a dark room. After irradiation, fertilization was accomplished by pouring

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the microconidial suspension onto a 5-day-old culture of the opposite mating type and then pouring off the excess liquid. Fertilized cultures were kept in the dark for 24 hours to prevent photoreversal, then removed to the 23°C incubator for 8 days to allow perithecial development.

The search for ascospore color mutants was made by examining large numbers of mature asci from the fertilized cultures. Such mutants are readily detectable in the hybrid perithecia. Only those mutants which segregated normally in a 1:1 ratio with wild type were selected. Mutant spores were dissected from hybrid asci, allowed to germinate, and the mycelia maintained for crossing tests.

Mycelial mutants were occasionally isolated from mycelia derived from germinating irradiated microconidia, but more often from the ascospores discharged from perithecia that resulted from fertilization by irradiated microconidia. The plates were then examined under a dissecting microscope, and those mutants that could be detected either by their slow rate of germination or unusual growth patterns were isolated.

Crossing was accomplished by placing two compatible cultures on an agar plate. The hybrid perithecia formed along the line of contact between the two cultures and matured in about 12 days after implantation. All genetic data on the mutants studied were obtained from ordered tetrad analysis. With spore color mutants, such an analysis can be easily accomplished by direct observation of the clusters of asci. With mycelial mutants, on the other hand, spore pairs from the hybrid asci were dissected in order. Mature perithecia were first placed on a glass slide in a drop of sterile distilled water and crushed with a cover-slip. Under a dissecting microscope, the walls of the perithecia were removed with a steel needle. Clusters of asci were then lifted out with the needle and placed singly on the agar surface of a Petri dish containing the regular medium with an additional 2% agar to give a firm surface for micromanipulating, and 0.7% sodium acetate was added to stimulate spore germination. The asci were dissected with a deFonbrune micromanipulator. Individual asci were pulled out at random from the clusters, and spore pairs were allowed to commence germination on the original plate. At 30°C most spores germinate in about 6 hours. Germinating spores were then cut out on small blocks of agar and transferred to agar slants to permit mycelial development. Relevant data pertaining to ascospore color and mycelial character were then recorded.

RESULTS

Mutants: The mutants used in this study can be grouped into two main categories: ascospore-color and mycelial mutants. The spore color mutants may be further separated into four groups based upon type of pigmentation: (1) hyaline; (2) yellow; (3) beige; and (4) gray. The great majority of induced spore color mutants failed to germinate. Only those mutants (about 10% of the total) with germinable spores were studied. Of the mycelial mutants, generally five different types could be recognized: dark, orange, corona, colonial and dwarf. All except the spontaneous orange (mycelial) mutant, were UV induced.

Each ascospore-color mutant is symbolized by the first letter of the word describing its particular spore color, while the mycelial mutants are denoted by two or more letters from their descriptive names (Table 1). Mutant cultures having the same designation (e.g., yellow-spored) and symbol (e.g., γ) but representing mutations independently derived are distinguished by different subscript numbers (e.g., γ_1 , γ_2 , γ_3 , etc.).

Positions of mutant loci and their linkage relationships.

(1) *Gene-to-centromere distances:* In *Sordaria*, the eight-spored asci represent ordered tetrads (except for rearrangement by spindle overlap) which are the immediate products of meiosis. By virtue of this linear arrangement, first and second division segregation patterns can be determined directly. The extent of second division segregation is a measure of the amount of crossing

TABLE 1

Mutant cultures of S. brevicollis

Descriptive name	Symbol	Number of mutant strains	Characteristics
hyaline	<i>h</i>	3	Hyaline ascospores. Perithecia produced on mutant mycelium are whitish, without the dark brown pigmentation characteristic of wild type.
yellow	<i>y</i>	7	Yellow ascospores.
beige	<i>b</i>	3	Beige ascospores.
gray	<i>g</i>	7	Gray ascospores.
dark	<i>dk</i>	1	Mycelium with darker than normal pigmentation.
orange	<i>or</i>	1	Substances of orange color accumulating in mycelium; sterility results when mating is homozygous for this factor.
corona	<i>cor</i>	1	Slow growth. Thicker outer ring of mycelium and a thinner inner zone.
colonial	<i>col</i>	1	Slow growth. Mycelium grows out a definite distance and stops, forming a limited colony.
dwarf	<i>df</i>	2	Very slow growth. Like colonial but forming a much smaller colony.

over between centromere and gene locus. One half the percentage of asci showing second division segregation is equivalent to the recombination frequency obtained by random spore selection. Multiple crossovers, which are not detectable by the method used here, have been ignored in this analysis. For an appropriate estimation of this uncorrected gene-to-centromere distance in *S. brevicollis*, the occurrence of partial spindle overlap during the second meiotic division must be taken into account (SHAW 1962; CHEN 1964a, b; CHEN and OLIVE 1965). Partial spindle overlap leads to the transfer of tetrads from the MI (first division segregation) class to the asymmetrical MII (second division segregation) class (2:2:2:2), and from the MII asymmetrical class into the MI class, but leaves the symmetrical MII class (2:4:2) unaffected. The determination of the distance from the centromere to the specific gene locus in this fungus can be calculated from the number of symmetrical MII asci by assuming that the number of legitimate asymmetrical asci is equal to the number of symmetrical asci. Accordingly, the expected number of MII asci is simply twice the number of symmetrical asci observed, and the map distance of the gene in question is one half the percentage of legitimate MII asci.

(2) *Linkage groups*: Linkage relationships are indicated when the number of parental ditype asci significantly exceeds the number of recombinant ditype asci (BARRATT, NEWMAYER, PERKINS and GARNJOBST 1954). The mapping of linkage groups has been greatly facilitated by the fact that most loci have proved to be near the centromere, and none has been further from the centromere than about 32 crossover units. Analysis of the existing data has established seven linkage groups for *S. brevicollis*.

The gene-to-gene interval is measured by taking one half the percentage of tetratype asci as the uncorrected value.

Genetic maps: Maps of seven linkage groups of *S. brevicollis*, based on the data presented in Tables 2 and 3, are shown in Figure 1. Linkage groups are designated by Roman numerals assigned in the chronological order of their discovery,

TABLE 2

Summary of data on segregation of mutants with relation to the centromere

Mutant	MI	Observed MII		Total	Expected MII	Percent legitimate MII	Gene-to-centromere distance	Confidence limits*
		Asym.	Sym.					
<i>a</i>	162	61	4	227	8	3.57	1.8	0.59-2.98
<i>h</i> ₁	744	214	62	1,020	124	12.1	6.0	5.05-7.05
<i>h</i> ₂	801	249	58	1,108	116	10.5	5.2	4.35-6.14
<i>h</i> ₃	896	173	52	1,121	104	9.27	4.6	3.80-5.47
<i>γ</i> ₁	1,593	222	26	1,841	52	2.82	1.4	1.03-2.78
<i>γ</i> ₂	763	23	3	789	6	0.76	0.4	0.08-0.68
<i>γ</i> ₃	680	225	13	918	26	2.85	1.4	0.89-1.96
<i>γ</i> ₄	1,255	157	0	1,412	0	0.0	0.0	0.0
<i>γ</i> ₅	589	155	0	744	0	0.0	0.0	0.0
<i>γ</i> ₆	615	317	9	941	18	1.91	1.0	0.52-1.39
<i>γ</i> ₇	401	74	50	525	100	19.1	9.6	7.83-11.17
<i>b</i> ₁	221	1,019	31	1,271	62	4.88	2.4	1.51-3.35
<i>b</i> ₂	156	121	2	279	4	1.43	0.7	0.02-1.41
<i>b</i> ₃	359	278	45	682	90	13.2	6.6	5.33-7.86
<i>g</i> ₁	1,646	309	156	2,111	312	14.8	7.4	6.64-8.25
<i>g</i> ₂	629	248	25	902	50	5.55	2.8	2.03-3.52
<i>g</i> ₃	1,171	120	32	1,323	64	4.83	2.4	1.84-2.99
<i>g</i> ₄	404	328	332	1,064	664	62.5	31.3	29.80-32.70
<i>g</i> ₅	800	211	145	1,156	290	25.1	12.6	11.30-13.79
<i>g</i> ₆	1,302	305	34	1,641	68	4.14	2.1	1.59-2.55
<i>g</i> ₇	1,432	401	42	1,875	84	4.48	2.2	2.27-2.70
<i>dk</i> ₁	109	55	30	194	60	30.9	15.5	12.21-18.70
<i>or</i> ₂	92	29	4	125	8	6.40	3.2	1.06-5.34
<i>cor</i> ₁	57	35	7	99	14	14.14	7.7	4.23-11.17
<i>col</i> ₁	32	33	1	66	2	3.03	1.5	0.0-3.57
<i>df</i> ₁	35	32	4	71	8	11.2	5.6	1.93-9.27
<i>df</i> ₂	60	36	1	97	2	2.06	1.0	0.0-2.43

* Use the following formula for calculation: $\frac{f}{n} \pm 1.96 \sqrt{\frac{(f/n)[(1-f)/n]}{n}}$.

f/n denotes the proportion of the number of legitimate MII asci in a sample size of *n*.
MI signifies first division segregation; MII, second division segregation.

in accordance with the system adopted by BARRATT and GARNJOBST (1949) for *Neurospora*. In order to facilitate the construction of the genetic map, one well mapped locus is arbitrarily chosen to identify the arm to the right of the centromere in each linkage group (i.e., I-*a*, II-*b*₁, III-*g*₂, IV-*g*₅, V-*γ*₄, VI-*h*₃, and VII-*g*₇). Such markers are chosen because the genes are close to the centromere, and this proximity increases the sensitivity of the linkage tests. Only in linkage group I was a marker (*col*₁) found on the left arm of a chromosome.

Four yellow-spored mutants (*γ*₁, *γ*₂, *γ*₃ and *γ*₆) of linkage group I were found to fall into a cluster. Crosses between these *γ* mutants and the wild type gave only 1.6% and 1.1% recombination with the compatibility locus in the crosses *γ*₂*a* × *γ*₂⁺*A* and *γ*₆*A* × *γ*₆⁺*a*, respectively, and none in crosses involving *γ*₁ and *γ*₃. The centromere distances for both *γ*₂ (0.4 unit) and *γ*₆ (1.0 unit) are less

TABLE 3

Segregation data from crosses involving mutants of seven different linkage groups

Cross [†]	Parental ditypes	Recombi- nant ditypes	Tetratypes	Total	Percent tetratypes‡	Gene-to-gene distances
Linkage group I*						
$\gamma_1 a \times \gamma_1 + A$	269	0	0	269	0.0	?
$\gamma_2 a \times \gamma_2 + A$	59	0	2	61	3.27	1.6
$\gamma_3 a \times \gamma_3 + A$	146	0	0	146	0.0	?
$\gamma_6 A \times \gamma_6 + a$	44	0	1	45	2.22	1.1
$or_2 a \times or_2 + A$	124	0	3	127	2.36	1.2
$\gamma_1 \gamma_6 + (a) \times \gamma_1 + \gamma_6 (A)$	1,839	0	20	1,859	1.07	0.53
$\gamma_2 \gamma_6 + (a) \times \gamma_2 + \gamma_6 (A)$	1,185	0	19	1,204	1.57	0.78
$\gamma_3 \gamma_6 + (a) \times \gamma_3 + \gamma_6 (A)$	1,161	2	15	1,178	1.61	0.80
$dk_1 \gamma_1 + (A) \times dk_1 + \gamma_1 (a)$	80	4	36	120	30.0	15.0
$col_1 \gamma_6 + (a) \times col_1 + \gamma_6 (A)$	64	0	3	67	4.47	2.2
Linkage group II						
$b_1 A \times b_1 + a$	11	14	1	26	...	...
$g_3 b_1 + (a) \times g_3 + b_1 (A)$	765	0	2	767	0.26	0.13
$g_4 b_1 + (A) \times g_4 + b_1 (a)$	133	82	355	570	62.2	31.0
$g_3 g_4 + (a) \times g_3 + g_4 (A)$	162	97	393	652	60.2	30.0
Linkage group III						
$g_2 A \times g_2 + a$	26	21	3	50	...	...
$g_2 b_1 + (A) \times g_2 + b_1 (a)$	115	129	7	251	...	...
$\gamma_7 g_2 + (a) \times \gamma_7 + g_2 (A)$	229	121	51	401	12.7	6.3
Linkage group IV						
$g_5 \gamma_1 + (A) \times g_5 + \gamma_1 (a)$	290	243	67	600	...	...
$g_5 b_1 + (A) \times g_5 + b_1 (a)$	100	99	29	228	...	...
$g_5 g_2 + (a) \times g_5 + g_2 (A)$	110	110	23	243	...	...
$g_5 cor_1 + (a) \times g_5 + cor_1 (A)$	73	0	6	79	7.6	3.8
$cor_1 g_6 + (A) \times cor_1 + g_6 (a)$	61	1	3	65	4.62	2.31
$g_6 g_5 + (a) \times g_6 + g_5 (A)$	792	7	134	933	14.3	7.1
Linkage group V						
$\gamma_4 a \times \gamma_4 + A$	23	24	1	48	...	...
$\gamma_4 b_1 + (a) \times \gamma_4 + b_1 (A)$	211	162	4	377	...	...
$\gamma_4 g_2 + (a) \times \gamma_4 + g_2 (A)$	238	234	26	498	...	...
$\gamma_4 g_5 + (a) \times \gamma_4 + g_5 (A)$	164	168	61	393	...	...
$\gamma_5 \gamma_4 + (a) \times \gamma_5 + \gamma_4 (A)$	2,952	0	3	2,955	0.08	0.04
$df_1 \gamma_4 + (A) \times df_1 + \gamma_4 (a)$	45	0	5	50	10.0	5.0
$df_2 \gamma_4 + (A) \times df_2 + \gamma_4 (a)$	76	0	1	77	1.30	0.65
Linkage group VI						
$h_3 \gamma_1 + (A) \times h_3 + \gamma_1 (a)$	50	52	8	110	...	...
$h_3 b_1 + (a) \times h_3 + b_1 (A)$	40	35	6	81	...	...
$h_3 g_2 + (a) \times h_3 + g_2 (A)$	85	62	34	181	...	...
$h_3 g_5 + (a) \times h_3 + g_5 (A)$	108	98	66	272	...	...
$h_3 \gamma_4 + (a) \times h_3 + \gamma_4 (A)$	61	53	8	122	...	...
$h_1 h_3 + (a) \times h_1 + h_3 (A)$	1,649	2	0	1,651	0.24	0.12
$h_2 h_3 + (a) \times h_2 + h_3 (A)$	8,250	3	4	8,257	0.12	0.060
$h_1 h_2 + (a) \times h_1 + h_2 (A)$	15,900	0	4	15,904	0.025	0.013
$b_3 h_1 + (a) \times b_3 + h_1 (A)$	2,491	0	31	2,522	1.22	0.61
$b_3 h_2 + (A) \times b_3 + h_2 (a)$	1,117	1	23	1,141	2.19	1.1
$b_3 h_3 + (a) \times b_3 + h_3 (A)$	464	1	12	477	2.52	1.3
$g_1 h_1 + (a) \times g_1 + h_1 (A)$	684	0	19	703	2.70	1.4

TABLE 3—Continued

Segregation data from crosses involving mutants of seven different linkage groups

Cross†	Parental ditypes	Recombinant ditypes	Tetratypes	Total	Percent tetratypes‡	Gene-to-gene distances
$g_1h_2+(a) \times g_1+h_2(A)$	954	0	35	989	3.54	1.8
$g_1h_3+(a) \times g_1+h_3(A)$	872	2	36	910	3.95	2.0
$g_1b_3+(a) \times g_1+b_3(A)$	553	0	7	560	1.30	0.65
Linkage group VII						
$g_7\gamma_6+(a) \times g_7+\gamma_6(A)$	68	58	2	128	...	...
$g_7g_3+(a) \times g_7+g_3(A)$	169	133	10	312	...	...
$g_7g_2+(a) \times g_7+g_2(A)$	68	59	11	138	...	...
$g_7g_5+(a) \times g_7+g_5(A)$	75	72	26	173	...	...
$g_7\gamma_4+(a) \times g_7+\gamma_4(A)$	133	126	15	274	...	...
$g_7g_1+(a) \times g_7+g_1(A)$	27	40	1	68	...	...

* Where no linkage is involved the linkage group designation applies only to the first mutant factor given in each cross.

† Analysis for types of asci does not involve compatibility alleles when the letters are in parentheses.

‡ For closely linked genes (less than 1% recombination) recombinant ditypes are included.

FIGURE 1.—Genetic map of the seven linkage groups of *Sordaria brevicollis*.

FIGURE 2.—A rare recombinant (tetratype ascus) detected in the cross between two pseudo-allelic mutants, h_1 and h_2 . (Left: $\times 50$; Right: $\times 400$).

than that of the compatibility locus (1.8 units), and the interval between the compatibility locus and γ_6 (1.1 units) is greater than that between γ_1 and γ_6 (0.53 unit) or between γ_3 and γ_6 (0.80 unit). This indicates that the cluster of γ mutants constitutes a segment about 1.6 map units long between the centromere and the compatibility locus. It should be noted that no direct crosses between γ_1 and γ_3 have been possible, since both mutants are very near the a allele, and no recombinants with A have been obtained.

Another mutant cluster is made up of the three hyaline spore color mutants (h_1 , h_2 and h_3) of linkage group VI. They are located in a segment lying between 4.6 and 6.0 crossover units from the centromere. All possible crossing combinations were made. Only a small amount of recombination (0.013 to 0.12%) was observed among the mutant loci of this cluster (Figure 2).

DISCUSSION AND CONCLUSIONS

These studies indicate that the development of the wild-type spore color is a sequential process. As noted for *S. fimicola* (OLIVE 1956), the pigments are located entirely in the spore wall. The spore starts as a transparent granular structure with its wall gradually changing from hyaline to yellow, beige, gray-brown, and finally dark brown at maturity. Each class of color mutants thus far obtained following UV irradiation probably represents a block in different enzymatic steps concerned with spore pigment formation. Most hyaline mutants yield a great majority of nonviable spores within the ascus, while most of the gray mutants produce germinable spores. It is probable that an enzymatic block takes place at a much earlier stage of spore development in the hyaline mutants than in the gray mutants. However, we have no exact biochemical information on the

sequential steps involved in spore pigmentation, although it is clear that a considerable number of loci are involved.

With the data on linkage relationships of the mutant loci thus far studied, it can be shown that the seven known linkage groups are actually located on separate chromosomes. This is consistent with reports of counts of seven chromosomes for other species of *Sordaria* (HESLOT 1958; CARR and OLIVE 1958). Of 26 mutants studied, all except one (col_1) are confined to a single arm of the particular chromosome involved. col_1 is located on the arm opposite that of the compatibility locus in linkage group I. In the absence of a thorough cytological study, current genetic data are not adequate to provide information concerning the location of centromeres in *S. brevicollis*. If all the centromeres are nonterminal, as they are in *Neurospora* (McCLINTOCK 1945; SINGLETON 1953) and in *S. fimicola* (CARR and OLIVE 1958), then we would expect markers eventually to be found on both arms of all seven linkage groups.

The uncorrected map distances for various mutant loci of *S. brevicollis* derived from direct counts of MII asci from crosses of mutant and wild type are fairly consistent with those obtained from tetrad data of multiple point crosses. This is not surprising in view of the fact that most of the linked loci studied were found to be relatively close to the centromere and to each other, thus precluding a significant number of multiple crossovers between loci. In order to have a uniform treatment of the present data, the uncorrected value has been adopted in both the gene-to-centromere and gene-to-gene intervals.

In the γ region of linkage group I, a small amount of crossing over between mutant locus and compatibility locus was observed in crosses involving γ_2 (3.27%) and γ_8 (2.22%), but none between either γ_1 or γ_3 and the compatibility locus. Therefore, γ_1 and γ_3 are either allelic or closely linked pseudoalleles and are very close to the compatibility locus. The whole γ region, about 1.6 crossover units long, probably represents a single functional unit. The four γ mutants—2, 6, 1 and 3—are located between closely linked bracketing markers col_1 and a (Figure 1) and are thus ideally suited for studies of interallelic recombination. Since the mating type locus is also well marked on both sides, it will also be of interest to examine the possibilities of complexity or transreplication of alleles A and a .

In linkage group VI, the three hyaline mutants (h_1 , h_2 and h_3) occupy a short chromosome segment lying between 4.6 and 6.0 units from the centromere. Since the spore color of these hyaline mutants is similar, and only very rare recombination has been detected among them (Figure 2), it is likely that they are pseudoalleles of another functional unit.

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SUMMARY

Twenty-seven mutants affecting ascospore color and mycelial morphology

were obtained following ultraviolet irradiation of microconidia. These and the mating type alleles have been mapped at not fewer than 21 loci making up seven linkage groups linked to seven independent centromeres. The ascospore color mutants are autonomous in their expression. Four yellow spored mutants belong to a compound locus concerned with a single phase in ascospore pigment development, while three hyaline spore-color mutants at another compound locus involve an earlier stage in pigmentation.

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