THE STRUCTURE OF THE A MATING TYPE LOCUS IN COPRINUS LAGOPUS

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IN basidiomycetes with a tetrapolar mating system, compatibility between haploid monocaryons is controlled by the action of alleles at two independent loci *A* and *B*. If two monocaryons possess different alleles at both loci they may, by exchanging nuclei, form stable binucleate dicaryons. If they possess common alleles at either or both loci, they are incompatible but may form a heterocaryon. In many species the dicaryon is easily recognized by the presence of clamp connexions between adjacent cells. In the Hymenomycetes each mating type locus has a large number of alleles which has been calculated to be in the order of magnitude of 100 per locus in natural populations (WHITEHOUSE 1949). Ninety-six *A* alleles and 56 *B* alleles were found in a recent survey of *Schizophyllum commune* (RAPER, KRONGELB, and BAXTER 1958a). KNIEP (1930) was the first to find that nonparental alleles may occur at both loci in single fruit bodies of *S. commune*. Two such nonparental *A* factors, when intercrossed, gave rise to a small proportion of the original *A* factors (six in 33 or 18.2 percent). PAPAZIAN (1951) also found nonparental *A* alleles in tetrads and random spores of *S. commune* and attributed their origin to crossing over between subunits of the *A* locus. KNIEP's earlier data can also be explained in this way. RAPER, BAXTER, and MIDDLETON (1958b) have shown that both loci of *S. commune* are each made up of at least two subunits. The frequency of recombination between subunits at the *A* locus varied between 0.9 and 15.9 percent according to which stocks were intercrossed. Recombinant mating type factors have also been described in the tetrapolar species *Collybia velutipes* (TAKEMARU 1957) and *Pleurotus ostreatus* (TERAKAWA 1957; RAPER *et al.* 1958b).

This paper reports studies of recombination within the *A* mating type locus of *Coprinus lagopus* using linked markers. A preliminary report has already appeared (DAY 1959b).

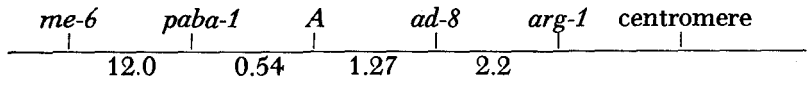
MATERIALS AND METHODS

Wild type stocks H1 (A_5B_5) and H9 (A_6B_6) were isolated from a single fruit body growing on a manure heap at Bayford in June 1956. Mutants 2242 (*ad-8*), 2246 (*arg-1*), 2214 (*me-6*), 2519 (*paba-1*), with requirements for adenine, arginine, methionine and para-aminobenzoic acid respectively, were induced in stock H9 by ANDERSON (1959). Recombinant stocks were obtained from crosses with H1. In addition tester stocks of the following mating types—A_5B_1, A_6B_1, A_2B_5 and A_2B_6—were obtainted by crossing H1 and H9 with stock 68 (A_2B_1). The

origin of stock 68 and the culture media used were given by DAY (1959a). Basidiospores were germinated on dung decoction (100 gm horse dung boiled in one L water) cleared by filtration through diatomaceous silica and solidified with two percent agar. Tetrads were isolated with a glass microneedle held in a Singer micromanipulator. The spores were separated and transferred to dung agar by hand using a glass needle with a small bead at the tip.

Mating types were determined by pairing unknown and tester stocks on complete medium in Petri dishes, 16 matings per dish. Clamp formation was scored after three days' incubation at 28°C.

The approximate linkage values and order of the *A* linked markers used are shown below (DAY and ANDERSON, unpublished).



RESULTS

Analysis of random spores: Several crosses were made between stocks bearing markers linked with the *A* locus before the order of the markers had been established. Cultures produced from basidiospores from these crosses were tested for *A* factors compatible with both parental *A* factors, A_5 and A_6, in matings with A_5B_1 and A_6B_1 tester stocks. From a total of 1213 cultures tested, two (A_xB_5 and $A_{x'}B_5$) with stable nonparental *A* reactions were found. Their genotypes and the crosses from which they came are given in Table 1.

The A_xB_5 culture was crossed with an A_6B_6 stock and the dicaryon was fruited. The alleles A_x and A_6 segregated normally among 130 random basidiospore cultures tested for mating type. A recombinant culture, A_xB_6, was selected and mated with $A_{x'}B_5$. The mating was incompatible, and it was concluded that A_x and $A_{x'}$ are identical. The genotypes of the two cultures with nonparental *A* reactions are consistent with their each having arisen as the result of a single cross-

TABLE 1

Crosses which gave nonparental A *alleles*

Cross	Nonparental *A* stock	Progeny tested
me-6$^+$ A_6 *arg-1* B_6		36 prototrophs
×	*me-6*$^+$ A_x *arg-1*$^+$ B_5	
me-6 A_5 *arg-1*$^+$ B_5		100 auxotrophs
A_6 *ad-8 arg-1*$^+$ B_5		83 prototrophs
×	$A_{x'}$ *ad-8*$^+$ *arg-1* B_5	
A_5 *ad-8*$^+$ *arg-1* B_6		613 auxotrophs

over between subunits of the *A* locus, but the reciprocal recombinants were not recovered.

Analysis of tetrads: In a study of the effects of temperature and marker combinations on patterns of crossing over within a region of the *A* chromosome (DAY and SWIEZYNSKI, unpublished) some 688 tetrads were available from three crosses and these were examined for nonparental *A* and *B* factors. Four tetrads with nonparental *A* factors were found, but in one of the tetrads only three spores germinated. The constitution of the tetrads and the crosses from which they were produced are given in Table 2. No cultures with nonparental *B* reactions and no tetrads showing 3:1 segregations of the *A* or *B* loci were found.

Two cultures with nonparental *A* reactions were found in each of the tetrads 2397–2400 and 2689–2692. These cultures were mated with each other and with cultures carrying the A_x factor already recovered. The results of these matings are given in Table 3.

The test matings show that two new *A* specificities were present in each tetrad, one of which was identical with that of A_x. The other was different from A_x and was designated A_y. A recombinant stock, A_yB_1, was produced by crossing culture 2398 (A_yB_5) with stock 68(A_2B_1). The results of crosses with the A_yB_1 stock are also shown in Table 3.

TABLE 2

Tetrads with nonparental A *reactions recovered from crosses*

(1.) *me-6 A_6 ad-8 arg-1$^+$* B_5 × *me-6$^+$ A_5 ad-8$^+$ arg-1* B_6 (203 tetrads)

(2.) *me-6$^+$ A_5 ad-8 arg-1$^+$* B_6 × *me-6 A_6 ad-8$^+$ arg-1* B_5 (220 tetrads)

Cross	Spore no.	Genotype	A_5B_1	A_6B_1†
(1.)	2397	*me-6$^+$ A_5 ad-8$^+$ arg-1* B_5	—	+
	2398	*me-6$^+$ A_y ad-8 arg-1$^+$* B_5	+	+
	2399	*me-6 A_x ad-8$^+$ arg-1* B_6	+	+
	2400	*me-6 A_6 ad-8 arg-1$^+$* B_6	+	—
(1.)	2413	* *me-6$^+$ A? ad-8$^+$ arg-1$^+$* B_6	+	+
	2414	*me-6 A_6 ad-8 arg-1$^+$* B_5	+	—
	2415	*me-6$^+$ A_5 ad-8$^+$ arg-1* B_5	—	+
	2416	*me-6 A_6 ad-8 arg-1$^+$* B_6	+	—
(2.)	2689	*me-6 A_x ad-8 arg-1$^+$* B_6	+	+
	2690	*me-6$^+$ A_y ad-8$^+$ arg-1* B_5	+	+
	2691	*me-6$^+$ A_5 ad-8 arg-1$^+$* B_6	—	+
	2692	*me-6 A_6 ad-8$^+$ arg-1* B_5	+	—
(2.)	1957	* *me-6$^+$ A? ad-8$^+$ arg-1$^+$* B_5	+	+
	1958	*me-6$^+$ A_5 ad-8 arg-1$^+$* B_6	—	+
	1959	*me-6 A_6 ad-8$^+$ arg-1* B_6	+	—
	1960	*(me-6 A? ad-8 arg-1* B_5)		

* Phenotypes, genotypes discussed in text.
† + = compatible; — = incompatible.

TABLE 3

Results of intercrossing cultures with nonparental A *factors*

		2398 A_yB_5	2399 A_xB_6	2689 A_xB_6	2690 A_yB_5	A_xB_5	A_xB_6	A_yB_1
2398	A_yB_5	..	+	+	(—)*	(—)	+	—
2399	A_xB_6	..	..	(—)	+	—	(—)	+
2689	A_xB_6	..	..	..	+	—	(—)	+
2690	A_yB_5	..	..	..	..	(—)	+	—
	A_xB_5	..	..	..	..	..	—	+
	A_xB_6	..	..	..	..	..		+
2413	$A?B_6$	..	..	..	..	+	(—)	+
1957	$A?B_5$	..	..	..	..	(—)	+	+

* (—) = Incompatibility due wholly or in part to common *B* factors.

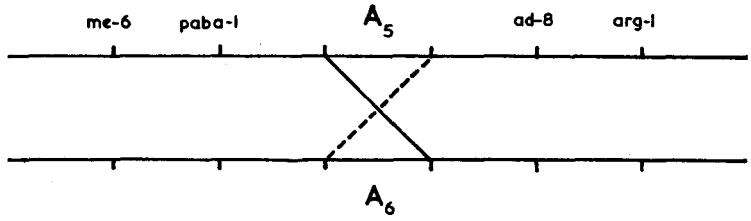


FIGURE 1.—Position of crossover recombining subunits of the *A* locus. A_x recombinant shown by broken line. A_y recombinant shown by unbroken line.

Both tetrads show the recombination of adjacent markers that would be expected if the only crossover within the region *me-6–arg-1* was between subunits of the *A* locus. Two recombinants (2398 and 2690) reacted as A_y, whereas the reciprocal recombinants (2399 and 2689) reacted as A_x (in Figure 1, the unbroken line and the broken line, respectively).

Tetrad 2413–16 gave one culture (2413) with a nonparental *A* reaction and also showed a 3:1 segregation for arginine independence. Culture 2413 was compatible with A_5B_1, A_6B_1, A_xB_5 and A_yB_1. The dicaryons produced by crossing 2413 with A_5B_1 and A_6B_1 were fruited, and basidiospore cultures from each cross were tested. The markers *me-6*, A_6 and *ad-8* segregated in the cross with A_5B_1 and markers A_5 and *arg-1* segregated in the cross with A_6B_1. The original culture showed occasional clamp connexions which failed to fuse with their neighboring cells (false clamps). Such clamps are produced by common *B* heterocaryons (SWIEZYNSKI and DAY 1960). It seems likely that the culture was originally disomic with two *A* chromosomes, *me-6* A_6 *ad-8 arg-1*$^+$/*me-6*$^+$ A_5 *ad-8*$^+$ *arg-1* and subsequently broke down to form a common *B* heterocaryon. The component

nuclei of the heterocaryon were sampled in the testcrosses which were fruited. PITTENGER (1954) has reported similar examples of disomics forming heterocaryons in *Neurospora crassa.*

Culture 1957 from the incomplete tetrad bore false clamps and was also compatible with the tester stocks A_5B_1, A_6B_1, A_xB_6 and A_yB_1. This culture produced oidia, which are uninucleate, and these, when sown, yielded 11 subcultures which were all *me-6*$^+$ A_5 *ad-8 arg-1*$^+$ B_5. It is possible that the missing culture, (spore 1960) was *me-6* A_6 *ad-8*$^+$ *arg-1* B_5 and was accidentally placed on the same slant as spore 1957 during the transfer of the tetrad to dung agar.

Analysis of prototrophs selected from crosses of linked auxotrophs in repulsion: The data from the tetrads established that the factors A_5 and A_6 were composed of two subunits each and that crossing over between them gave rise to the expected reciprocal products. An attempt was then made to recover more than two crossover products from crosses of $A_5 \times A_6$. There is no direct means of selecting nonparental *A* factors. This difficulty was overcome by crossing stocks with two linked auxotrophic markers, one on either side of the *A* locus, in repulsion. If crossing over occurred between or within the subunits of the *A* locus, this would, provided it was the only crossover within the interval bounded by the auxotrophic markers, bring about their recombination and give rise to a prototrophic recombinant and the reciprocal double mutant. Hence, half of the products of all single crossovers within the *A* locus would be recovered among the prototrophs. Since the distance of each marker from the *A* locus is known, the relative frequencies of prototrophs with parental and nonparental *A* reactions would give some indication of the distance between the subunits. If crossing over within the subunits occurred, more than two specificities would be found among the nonparental *A* factors.

The markers *paba-1* and *ad-8*, respectively 0.54 and 1.27 crossover units from *A*, were intercrossed in both repulsion crosses. Prototrophs were selected from random basidiospores spread on minimal medium and were mated with A_5B_1 and A_6B_1 to select cultures with nonparental *A* factors. The nonparental *A* cultures were either monocaryons or had clamp connexions. Both types were again mated with A_5B_1 and A_6B_1, and with A_xB_1 and A_yB_1. A summary of the results is shown in Table 4.

The monocaryon stocks with nonparental *A* reactions from each cross were only of one kind, A_x or A_y. This shows that either crossing over within subunits did not take place sufficiently frequently for the products to be recovered in this experiment or that the crossover products were not detected by the tests employed. Estimates of the frequency of crossing over between the markers, obtained by doubling the frequency of prototrophs, were 1.85 percent for the first cross and 1.04 percent for the second cross. The expected frequency was $0.54 + 1.27 = 1.81$ percent. The lower frequency (1.04 percent) in the second cross could have been due to differences in genetic background between the two crosses. This is supported by the lower frequency of nonparental *A* factors recovered, namely 3.61 percent in the second cross against 4.11 percent in the first cross. However, if we

TABLE 4

Summary of prototrophs isolated with the aid of linked selective markers

	(1) *paba-1* A_5 *ad-8*$^+$ B_5 × *paba-1*$^+$ A_6 *ad-8* B_6	(2) *paba-1*$^+$ A_5 *ad-8* B_5 × *paba-1* A_6 *ad-8*$^+$ B_6	(3) *paba-1* A_x *ad-8*$^+$ B_5 × *paba-1*$^+$ A_y *ad-8* B_1
Percent prototrophs (×2)	1.85	1.04	1.18
Monocaryons			
A_5	246	655	30
A_6	739	267	0
A_x	43	0	208
A_y	0	36	380
Parental *A* ratios	1:3.00	1:2.45	1:1.81
Stocks with clamps	19	38	24
Total	1047	996	642

accept the interval between *paba-1* and *ad-8* as 1.81 units, then we may calculate the distance between the subunits of the *A* locus from each cross as

$$\frac{43}{1028} \times 1.81 = 0.076 \text{ and } \frac{36}{958} \times 1.81 = 0.068$$

(average = 0.072 units).

The relative frequency of crossing over expected in the two intervals, one on each side of the *A* locus, was 0.54:1.27 or 1:2.35. As shown in Table 4 the frequencies obtained were 1:3 and 1:2.45 in the two crosses.

All 19 stocks with clamps from the first cross in Table 4 were subcultured to sterile dung to test their ability to fruit. All except one fruited readily. A_5 and A_6 segregated in the progeny of four of these fruited cultures selected at random, no other factors being found in the samples (32 colonies) tested. Adenine and PABA requirements segregated in two progenies while only one requirement segregated in the other two progenies. These results show that the four dicaryons which were progeny tested most likely arose by crossing between complementary compatible strains in the original platings of basidiospores to minimal medium.

Other stocks bearing clamps, produced in the second cross, were tested with similar results. Of 11 stocks tested six failed to fruit. These latter stocks produced many false clamps and appeared to be common *B* heterocaryons.

Reconstitution of parental A *factors:* An additional proof that crossing over was the mechanism by which the nonparental *A* factors arose was obtained by crossing the two stocks *paba-1* A_x *ad-8*$^+$ B_5 × *paba-1*$^+$ A_y *ad-8* B_1. The results are summarized in the last column of Table 4. Of the 618 monocaryon prototrophs tested 30 had nonparental *A* factors and were all incompatible with A_5. Thus, one of the original parental *A* factors was recovered by crossing the recombinant factors A_x and A_y. The distance between the subunits calculated from this cross was 0.088 units and is in fair agreement with the results presented above.

DISCUSSION

The structure of genes concerned with incompatibility has now been investigated in several different organisms. In some self incompatible flowering plants the *S* gene controlling incompatibility has been shown to have a two subunit structure in which one subunit controls stylar specificity and the other pollen specificity. LEWIS and CROWE (1953) working with *Prunus avium* and PANDEY (1956) working with *Trifolium pratense* and *T. repens* have shown that mutations to self-fertility (S.F.) may be induced at either subunit by X-ray treatment. S.F. mutations of the pollen subunit are easier to screen than S.F. mutations of the style subunit. BREWBAKER and SHAPIRO (1958) found that nonparental alleles may arise in *Petunia inflata* as a result of crossing over between the subunits so that an *S* allele is produced which has, say, S_1 pollen specificity but S_2 style specificity and is consequently self-fertile.

LEUPOLD (1958) has shown that the mating type gene of the yeast *Schizosaccharomyces pombe* has two subunits which are thought to have arisen by duplication of a locus with two alleles, + and −, controlling heterothallism. One subunit, however, only has one functional allele +, the other allele 0, is nonfunctional. The genotypes associated with the '+' phenotype are ++ or +0, while the genotype for the '−' phenotype is −0 and that for the homothallic phenotype is −+. Thus when a homothallic recombinant (−+) is produced by crossing ++ × −0 a reciprocal '+' strain is formed, +0 which can be distinguished from ++ by genetic tests. The homothallic recombinant is analogous to the self-fertile recombinant of Petunia.

RAPER *et al.* (1958b) and DAY and HOLLIDAY (1959) have discussed the relationship between the subunits of the *A* and *B* loci of *Schizophyllum commune*. Here the subunits of each locus appear to be functionally indistinguishable and if a monocaryon has different alleles at both pairs of subunits (A_{1-2}, B_{1-2}) it is not self-fertile. If both subunits do have the same function, the simplest hypothesis is that a mating is compatible if at least three of the four subunits of each locus, brought together in a common cytoplasm, are different. These considerations also apply to the *A* locus of Coprinus (e.g., A_{1-2} is incompatible with A_{1-2}, A_{2-1}, A_{1-1} and A_{2-2} but is compatible with A_{1-4}, A_{4-1}, A_{3-4} and A_{3-3}).

If the subunits of the *A* locus of Coprinus or Schizophyllum have evolved by duplication of a pre-existing unit then it would be reasonable to expect that both subunits of a single locus might sometimes be identical. The reactions of three such loci (A_{1-1}, A_{2-2} and A_{3-3}) are shown above. With n different subunit specificities, which can be imagined as an allelic series, there are n^2 possible pairs, n of which will be identical pairs, $n^2 - n$ will be nonidentical pairs. With n^2 *A* factors the total number of possible different matings is n^4, and if we accept the restriction that at least three different subunits must be present for a mating between any two *A* factors to be fertile, the number of fertile matings can be calculated as follows:

(1) n identical pairs are each compatible with $(n-1)(n-2)$ nonidentical pairs

(2) $n(n-1)$ nonidentical pairs are each compatible with n^2-4 pairs.

The total fraction of compatible matings $=$

$$\frac{n(n-1)(n-2)+n(n-1)(n-2)(n+2)}{n^4}=\frac{n(n-1)(n-2)(n+3)}{n^4}=\frac{n^3-7n+6}{n^3}$$

Curve (a) in Figure 2 shows the percentage of fertile matings plotted against values of n between three and 30.

It can be seen that even for low values of n, between 10 and 20, the maximal frequency of compatible matings is already high, 93.6 to 98.3 percent.

In a collection of 114 strains of *S. commune* 97.05 percent of random matings between A factors were fertile (RAPER *et al.* 1958a), a condition which could be satisfied by either subunit occurring in one of 15 different alternate states.

If this model is correct, there are some further implications. If the subunits of a pair may have identical specificities, then A_{1-1} is incompatible with A_{1-1}, A_{1-2}, A_{2-1} and A_{2-2} for reasons given above. All four A factors, when intercrossed, would appear to have the same specificity since they are cross incompatible. If these four A factors were present in a population with A_{3-4}, A_{5-6}, A_{7-8}, etc., and if they are equally fertile with the other factors, and the population is large enough, it might be expected that all four would be retained. If, however, the population contains other factors with identical subunits, then all such factors will be at a selective disadvantage compared with the others since they are unable to mate with each other and can mate with fewer nonidentical pairs than the nonidentical pairs themselves. Thus, A_{1-2} or A_{2-1} could mate with A_{9-9} while A_{1-1} and A_{2-2} could not; also A_{1-2} can mate with A_{1-3} but A_{1-1} cannot.

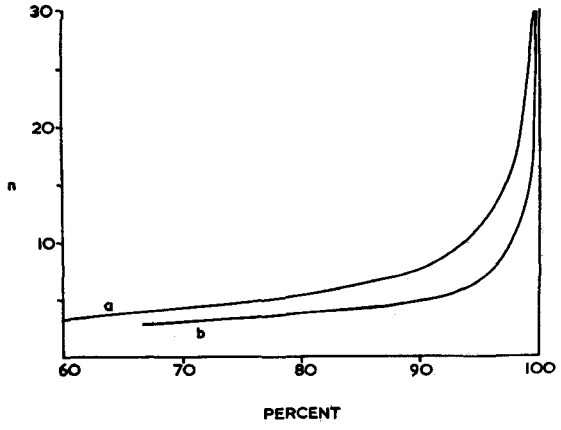


FIGURE 2.—The percentage (P) of random matings, which are fertile, plotted against n, the number of specificities at the two subunits of the A mating type locus. Curve a, including identical pairs, $P=\frac{n^3-7n+6}{n^3}\times 100$.

Curve b, excluding identical pairs, $P=\frac{(n+1)(n-2)}{n(n-1)}\times 100$.

These considerations imply that identical subunits will almost certainly be rare in nature and may, in fact, only be found in the laboratory—through recognizing that two cross incompatible factors, A_{1-2} and A_{2-1}, may have different structures.

Curve b in Figure 2 shows that the frequency of cross compatible matings is increased by removing A factors with identical subunits. A minimum of nine different subunits are needed to account for RAPER's finding that 97.05 percent of random matings between A factors were fertile. RAPER has already identified nine specificities at one A subunit and 19 at the other in his collections of Schizophyllum (J. R. RAPER, personal communication).

PAPAZIAN (1958) and RAPER *et al.* (1958b) have both speculated on models for the structure of the A locus and have arrived at estimates of the numbers of specificities at each subunit to account for the numbers of A and B alleles found in nature. In both Schizophyllum and Coprinus the evidence so far indicates only two subunits. No clear example of recombination within subunits has been found. From our current knowledge of the structure of the gene (PONTECORVO 1959), it seems most likely that the subunits are made up of smaller recombination units. It is also very likely that crossing over within the subunits would lead to nonparental subunit specificities detectable by the mating reaction. To obtain 32 different subunit specificities would require only five different sites each with two alternate states. The five percent upper fiducial limit on the total length of the two subunits was calculated from the data in Table 4 as the recombination fraction 2.08×10^{-5}. Recombination of this frequency or greater would have been detected unless both pairs of subunits in the cross $A_5 \times A_6$ and, hence, $A_x \times A_y$ were heterozygous at only one site. Since this is unlikely, we may conclude that the sites within the subunits are very tightly linked.

SUMMARY

(1) Crosses between monocaryotic stocks of *Coprinus lagopus* bearing markers linked with the A mating type locus yield a low frequency of nonparental A factors in tetrads and random spores. The marker arrangements in these nonparental cultures show that the new A factors arise as a result of crossing over between subunits of the A locus. Less extensive tests of the B locus have not revealed nonparental recombinants.

(2) Seventy-nine nonparental A factors, isolated with the aid of linked selective markers, from crosses between A_5 and A_6 were of two types only, suggesting that only two subunits were able to recombine and give nonparental A factors. The original parental factor A_5 was recovered by intercrossing the two recombinant factors. The frequency of recombination between the subunits was 0.068 to 0.088 percent.

(3) It is suggested that the two subunits of the A locus arose by duplication of a pre-existing unit. The possible structure of the subunits and the gentical basis of their specificity are briefly considered.

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