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Somatic recombination in the dikaryon of *Coprinus lagopus*

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1. INTRODUCTION

The study of somatic recombination in the Basidiomycetes, *Coprinus lagopus* and *Schizophyllum commune* has been mainly with the use of the technique of di-mon matings (Quintanilha, 1938; Papazian, 1954; Crowe, 1960; Swiezynski, 1962, 1963; Ellingboe & Raper, 1962; Ellingboe, 1964). By this method a monokaryon is dikaryotized by mating it with a dikaryon, and the nuclei of the consequent secondary dikaryon are analysed for somatic recombination. This work has demonstrated that somatic recombination does occur in Basidiomycetes and involves not only reassortment of chromosomes but probably also recombination of linked markers. The complete analysis of recombination by the use of di-mon matings, however, is impossible, because three different nuclear types are involved before the recombinants are isolated and analysed.

Parag (1962) has tried three methods for the isolation of somatic recombinants directly from a dikaryon of *Schizophyllum commune*. He obtained a few recombinants by a non-selective method in which he examined a sample of mycelial fragments. Two selective methods yielded no recombinants at first, although in one slightly different experiment one recombinant was obtained. The recombinants included examples of independent assortment of chromosomes and of crossing-over between the α and β units of the A mating-type locus.

This paper describes somatic recombination in the dikaryon of *Coprinus lagopus* using a technique based upon auxotrophic mutants and recessive suppressor genes.

2. MATERIALS

The following are the symbols used for the different mutant genes: *ad-8* and *ad-9* (adenineless), *adhi-2* (adenineless-histidineless), *chol-1* (cholineless), *me-1* and *me-5* (methionineless) and *su-1* and *su-2* (suppressors that mask the effect of *me-1*). All these mutants are recessive and non-allelic.

Coprinus lagopus is of tetrapolar mating type with two mating-type genes, A and B, each with many alleles. (Each allele is indicated by a subscript, e.g. A_2 or A_6.)

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The minimal and complete media used were those of Fries as adapted by Lewis (1961). Supplemented medium was minimal medium to which the appropriate supplement was added at the following concentrations: adenine sulphate, 100 p.p.m. choline chloride, 2 p.p.m.; L-histidine monohydrochloride, 200 p.p.m. and DL-methionine, 10, 50 or 100 p.p.m. Basidiospores were germinated on medium to which furfuraldehyde had been added giving a final concentration of 0·01% (Emerson, 1954; Day & Anderson, 1961).

3. METHODS

The dikaryon of *Coprinus lagopus* does not produce uninucleate asexual spores, and therefore Roper's technique (1952) cannot be applied as it has been for the selection of diploids from common *A* heterokaryons of *Coprinus lagopus* (Casselton, 1964, 1965). The dikaryon does, however, produce chlamydospores—asexual spores which carry nuclei of both parental types. A method was therefore sought to select somatic recombinant nuclei present in the chlamydospores. It was necessary to devise a system in which the dikaryon and parental monokaryons would be unable to grow while a somatic recombinant would.

Use was made of the complementing methionine suppressor genes described by Lewis (1961). The two monokaryons of genotype *me-1 su-1* + and *me-1* + *su-2* are each prototrophic and methionine-independent, but the dikaryon comprising the two strains requires methionine, since *su-1* and *su-2* are recessive and complementary. If each parental strain is additionally marked with complementing mutants imposing other biochemical requirements then neither the dikaryon nor the two monokaryon components will grow on minimal medium. The dikaryon will not grow because of a requirement for methionine and the monokaryons will not grow because of their recessive auxotrophic mutants, which are expressed in the monokaryon.

Table 1.

Dikaryon to select for:	Parent	Genotype linkage group I	II	III	IV	V
1. Reassortment of	Ms165	*ad*-9 A_2	B_3 +	*me*-1	+	*su*-2
chromosomes	JR6	+ A_6	B_5 *chol*-1	*me*-1	*su*-1	+
2. Mitotic crossing-	JR44	*me*-5 A_2 +	B_6 +	*me*-1	+	*su*-2
over	JR48	+ A_5 *ad*-8	B_5 +	*me*-1	*su*-1	+

Thus chlamydospores from dikaryons whose genotypes were of the types given in Table 1 were sown on minimal medium. (We have found that suppressors 1 and 2 suppress the effect of *me-1* but not that of *me-5*. Lewis (1961) gives *su-1* as linked to *A* but further data have shown this not to be the case.)

Prototrophic colonies arising could only have been derived by somatic recombination or by mutation. Unfortunately the method does not allow the selection of a

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diploid culture since this would be methionine-requiring. A diploid nucleus must lose the wild allele of at least one of the suppressor mutants before the selection works in its favour.

In order to minimise the transfer of nutrients from the dikaryon culture medium to the minimal plates when sowing chlamydospores, the dikaryons were grown on minimal medium supplemented with limiting amounts of methionine, i.e. at 10 and 50 p.p.m., and for a control, 100 p.p.m. which gives normal growth rate. The dikaryons were grown on the methionine medium for 6 to 11 days at 37°C. and chlamydospores were then harvested. A thin layer of the surface agar (about 1mm. thick) with mycelium was taken from the culture and macerated in sterile water using either a test-tube as a mortar with a glass pestle ground to fit exactly inside the test tube, or a Waring Blendor. The suspension of chlamydospores and hyphal fragments was then filtered through glass wool or muslin to remove the larger hyphal fragments. The viability of the chlamydospores was estimated by sowing a suitable dilution of the suspension on complete medium and observing the number of colonies arising.

4. RESULTS

(i) *The efficiency of the selection method*

A test using dikaryon 1 (Table 1) was made to determine whether the method of sowing dikaryotic chlamydospores on selective media would effectively select all the nuclei potentially capable of giving rise to a monokaryon. Dikaryon 1 cannot grow without methionine, and one of its monokaryotic components requires adenine and the other choline. Chlamydospores from this dikaryon cultured on 10 p.p.m. methionine were plated on complete medium, adenine and choline media, and on 100 p.p.m. methionine.

Table 2. *Colonies growing on methionine, adenine and choline media. The density per plate of chlamydospores was the same on all media*

Medium	Number of chlamydospores sown	Dikaryons	Monokaryons requiring adenine	Monokaryons requiring choline	Total
Complete	$13 \cdot 4 \times 10^3$	71	0	1	72
Methionine 100 p.p.m.	$6 \cdot 7 \times 10^3$	34	0	1	35
Adenine	$6 \cdot 7 \times 10^3$	0	1	0	1
Choline	$6 \cdot 7 \times 10^3$	0	0	3*	3

* Choline requirement actually tested in only one of these.

It is concluded from results, given in Table 2, that parental monokaryons can be selected by the method, but that the number of nuclei of either parental strain capable of producing monokaryotic colonies is less than the number of viable nuclei sown. Thirty-four dikaryons developed on methionine medium, and this figure is confirmed by the seventy-four obtained from double the number of spores on

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complete medium. It might be expected therefore that the number of viable nuclei on each of the selective media is thirty-four. The viable nuclei of the parent requiring adenine should give rise to monokaryons on adenine medium; and similarly the nuclei of the other parent, on choline medium. In fact only one colony developed on adenine and three on choline, indicating that only about one-tenth of the potential component monokaryons come to expression.

It is interesting that two other choline-requiring monokaryons developed, one on complete medium and one diffuse colony on methionine medium. One might speculate whether the chlamydospores that gave rise to monokaryons on adenine and on choline might also have developed as monokaryons even if they had been plated on complete medium. It may be that the majority of monokaryons obtained in the selection experiments were derived from nuclei which were already dissociated from other nuclear types at the time the chlamydospores were sown on minimal medium, and that the majority of nuclei still in association with other nuclear types were incapable of individual expression and the production of a monokaryon.

(ii) *Selection for reassortment of chromosomes*

Three separate tests for reassortment of chromosomes were made, using dikaryon 1 in Table 1. In the first test viable chlamydospores and hyphal fragments from the dikaryon grown on 10 p.p.m. methionine were sown on minimal medium. After 5 days' incubation a large number of colonies were present, which were classified into three types:

1. Small dense compact colonies $< 1\cdot5$ mm. radius.
2. Large diffuse colonies > 2 mm. radius.
3. Small diffuse colonies 1–2 mm. radius.

Colonies of each type were isolated to minimal medium to confirm their prototrophy. All those of class 1 were prototrophic dikaryons, class 2 were leaky auxotrophs or prototrophic monokaryons and class 3 were auxotrophic dikaryons and monokaryons. In the second test chlamydospores were taken from the dikaryon growing on 100 p.p.m. methionine and in the third test from the dikaryon growing on 10, 50 and 100 p.p.m. of methionine.

Table 3. *Analysis of colonies isolated from dikaryon 1 on different methionine concentrations*

Chlamydospores from dikaryon grown on methionine	Number of viable chlamydospores and hyphal fragments sown on minimal	Total isolates	Classification		
				Prototrophic	
			Auxotrophic	Dikaryon	Monokaryon
10 p.p.m.	$6\cdot3 \times 10^4$	109	80	23	6
50 p.p.m.	$6\cdot3 \times 10^3$	95	94	1	0
100 p.p.m.	$3\cdot4 \times 10^5$	165	165	0	0

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The results of these tests, summarized in Table 3, show that prototrophic monokaryons were only obtained from dikaryons previously grown on 10 p.p.m. methionine, and that no prototrophs, either monokaryotic or dikaryotic, were obtained on 100 p.p.m. methionine. The prototrophy of the monokaryons was confirmed by comparing their growth on minimal, adenine, choline and complete media. They were also tested for mating type, and for the presence of the wild alleles of the suppressor genes by complementation tests. Each of these prototrophs was mated to four tester strains of mating type A_6B_5, A_2B_3, A_2B_5 and A_6B_3 and the matings were observed for the development of a dikaryon.

Table 4

	Mating type testers			
Prototrophs	A_2B_3	A_6B_5	A_2B_5	A_6B_3
1, 2 and 3	−	−	+	−
4	+	−	+	−
5 and 6	−	+	+	−

Mating type tests of prototrophic monokaryons obtained from dikaryon 1: + indicates dikaryon formation and that both the A and B alleles of the prototroph are different from those of the tester, − indicates no dikaryon formation and that either the A allele or the B allele is common to the tester and prototroph.

The results given in Table 4 show that prototrophs 1, 2 and 3 all have the mating type A_6B_3. The A_6 and B_3 alleles must have originated from the different component nuclei of the dikaryon, and therefore these three prototrophs resulted from reassortment of chromosomes from the two nuclei. The other three prototrophs are compatible with two mating type testers. This work and that of Raper & Oettinger (1962) with disomics of *Schizophyllum commune* and Casselton (1964, 1965) with diploids of *Coprinus lagopus* have demonstrated that disomics or diploids heterozygous for the B mating type gene are compatible with haploid testers carrying either of the B alleles present in the disomic or diploid. The compatibility of prototroph 4 with A_2B_3 and A_2B_5 testers indicates that it is disomic for chromosome II, and its mating type can be represented as A_6B_3/B_5. Prototrophs 5 and 6 are compatible with testers A_6B_5 and A_2B_5, indicating the genotype A_2/A_6B_3.

Prototrophs were further examined by analysis of oidia. The dual mating capacity persisted in 90% of the oidia from prototroph 4 A_6B_3/B_5. The remaining oidia either were compatible only with A_2B_3 and required choline, or were compatible only with A_2B_5 and were prototrophic. Since oidia are uninucleate (Lewis, unpublished) it can be concluded that protroph 4 is disomic for $\underline{B_5\ chol\text{-}1}/\underline{B_3+}$, deriving the $\underline{B_5\ chol\text{-}1}$ chromosome from one nucleus of the original dikaryon and the $\underline{B_3+}$ chromosome from the other, and that oidia with a single mating capacity are haploid segregants. Further work has shown that the loss of one of the two homologous chromosomes in a proportion of the oidia is a general feature of disomics in *Coprinus lagopus*.

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Prototrophs 5 and 6 did not display their dual mating type in the oidial colonies. These were either A_2B_3 and adenine-requiring or A_6B_3 and adenine-independent. A possible explanation of prototrophs 5 and 6 is that they are mixtures of haploid monokaryons, one of which is of the recombinant A_6B_3 mating type; but an extremely unstable disomic for chromosome I cannot be ruled out.

Further confirmation of the disomy of prototroph 4 was obtained from the analysis of basidiospores from the cross of the prototroph to a stock of mating type A_2B_3 in which chromosome II was marked by an adenine-histidine mutant. The basidiospores were analysed for B mating type, adenine-histidine and choline requirement, and the results (given in Table 5) show that the B_3/B_5 disomy was found in nearly one-third of the progeny. Disomics homozygous for B_3 may be expected to occur with about half the frequency of B_3/B_5, and these must contribute to the high number of spores of phenotype $B_5 + +$. The high proportion of disomics in the basidiospore progeny indicates that the extra chromosome was not often lost in meiosis. If the extra chromosome was never lost one would expect half the progeny to be disomic.

Table 5. *Analysis of phenotype of basidiospores from a cross of prototroph 1 with a stock of genotype B_3 adhi-2*

Phenotype	Number of spores
B_3 *adhi-2* +	30
B_3 + +	129
B_5 + *chol-1*	49
B_3 + *chol-1*	18
B_5 + +	15
B_3 *adhi-2 chol-1*	2
B_5 *adhi-2* +	2
B_5 *adhi-2 chol-1*	0
B_3/B_5 + +	112
Total	357

(iii) *Selection for somatic crossing-over*

The dikaryon 2, detailed in Table 1, was used for tests of somatic crossing-over. This has two linked auxotrophic mutants *me-5* and *ad-8* in *trans* position, is homozygous for *me-1* and carries two suppressors of *me-1* in the heterozygous phase. The dikaryon does not grow on minimal medium because of the complementing wild-type alleles of the suppressors, and the component monokaryons are also auxotrophic because of either the *me-5* or the *ad-8* genes. The dikaryon for this experiment was grown on 10 p.p.m. methionine, and although growth was weaker than on 50 p.p.m. methionine, there were patches of more dense growth. Tests of a sample of these patches revealed that at least the larger ones (more than 3 mm. radius) were prototrophic dikaryons. In preparing the chlamydospore suspension, therefore, care was taken to avoid areas of dense growth. Chlamydospores were

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sown on minimal medium, and possible prototrophs were isolated after 2 and 3 days, avoiding any that were obviously dikaryotic. The results, summarized in Table 6, show that only one truly prototrophic monokaryon was obtained, which was derived from the dikaryon previously cultured on 10 p.p.m. methionine.

Table 6. *Analysis of colonies isolated from minimal medium*

Chlamydospores from dikaryon grown on methionine	Number of viable chlamydospores sown on minimal	Days of incubation	Total colonies	Colonies isolated	Auxotrophic	Prototrophic	
						Dikaryon	Monokaryon
10 p.p.m.	$3 \cdot 2 \times 10^6$	2	86	86	61	25	0
		3	many, overgrown	37	17	19	1
50 p.p.m.	$2 \cdot 6 \times 10^6$	3	117	96	91	5	0

The prototrophic monokaryon was further analysed. The first mating type test indicated a mating type A_2B_5/B_6 but all subsequent tests indicated the mating type as A_2B_5 which is, incidentally, a recombinant mating type. All oidial isolates from the prototroph were of mating type A_2B_5, but were auxotrophic, requiring methionine. Complementation tests for the suppressors of *me-1* demonstrated that the prototroph carried *su-2* and the wild allele of *su-1*. The prototroph was mated to a stock of genotype *me-5* A_5B_3 to test for the presence of the wild allele of *me-5*. In the first test the dikaryon obtained was prototrophic, but the dikaryon resulting from a subsequent replica mating was auxotrophic. Therefore the nucleus derived from the prototroph in the first test carried the wild allele of *me-5*, but that in the second test carried *me-5* only.

It is possible to use chlamydospores to resolve the dikaryon into its component monokaryons (Lewis, 1961). This technique was used to resolve the prototrophic dikaryon obtained in the test above. The four monokaryons so obtained which were shown to carry nuclei derived from the original prototrophic monokaryon were themselves prototrophic.

If the original prototroph was grown for 5 days on complete medium, inocula taken from the margin of the colony were methionine-requiring. Similarly, the chlamydospore resolvates, if grown on complete medium, sectored to give methionine-requiring derivatives. A deliberate selection was made to obtain stable prototrophic monokaryons by prolonged growth of the chlamydospore resolvates on minimal medium. Some colonies gave faster growing sectors, but of the eight sectors tested, seven eventually became auxotrophic after growth on complete medium, and only one remained prototrophic. On the other hand the prototrophic dikaryon remained methionine-independent when grown on complete medium for three successive subcultures incubated for 4, 7 and 9 days respectively.

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(iv) *Nature of prototrophic dikaryons obtained in the selection experiments*

The most likely explanation for the prototrophy of these dikaryons is that by some process they had become homozygous for one or other of the suppressor genes for which they were originally heterozygous. Mutation to a dominant suppressor is conceivable but such a mutation has not yet been recorded for *Coprinus lagopus*.

One of the prototrophic dikaryons derived from the second dikaryon in Table 1 was resolved into its component monokaryons using the chlamydospore technique. The twenty-two monokaryons thus isolated were each mated to both of the original parental monokaryons. The dikaryons so obtained were then tested for growth on minimal medium. Seven of the isolates produced auxotrophic dikaryons with one parent (JR44: *me-5* A_2 + B_6 *me-1* + *su-2*) and the remaining fifteen produced prototrophic dikaryons with the other parent (JR48: + A_5 *ad-8* B_5 *me-1* *su-1* +).

The dikaryons with JR48 were prototrophic probably by reason of homozygosity for *su-1*. If this is so, then the original prototrophic dikaryon must also have been homozygous for *su-1*. Homozygosity in the original dikaryon could have arisen by somatic recombination between the two nuclear types or by mutation to *su-1* in a nucleus of JR44 type.

Spontaneous mutation to prototrophy in the oidia of an *me-1* stock has been studied by Lewis (1961), who found the rate of mutation to be $2{\cdot}6 \times 10^{-5}$. Prototrophy was found to be due to mutation to a recessive suppressor in all cases tested. Monokaryotic stocks carrying *me-1* grown on limiting amounts of methionine have been found to develop dense sites of growth where mutation to a suppressor has occurred (Lewis & Cowan, unpublished).

Mutation to *su-1* appears to be the simplest explanation for the prototrophy of the dikaryon analysed. The test employed did not reveal a recombinant mating type such as might have arisen on somatic recombination.

5. DISCUSSION

The experiments described have demonstrated the occurrence of somatic recombination in the dikaryon without recourse to the di-mon mating technique. Of the six recombinants isolated in the selection for reassortment of chromosomes, one was undoubtedly aneuploid and another two may have been aneuploid when first isolated. This is submitted in favour of the theory that somatic recombination in *Coprinus* follows the fusion-haploidization sequence demonstrated in *Aspergillus nidulans* (Pontecorvo & Käfer, 1958; Käfer, 1958), rather than fusion followed by precocious meiosis which is advocated for *Schizophyllum* (Ellingboe & Raper, 1962).

The results of the analysis of the one prototroph obtained in the selection for recombinants involving crossing-over in chromosome I indicates that it carries a duplication of part of that chromosome. Evidence was obtained that both *me-5* and its wild allele were present, and that the prototroph also carried the A_2 mating type gene and the wild allele of *ad-8*, but there was no evidence of the presence of either A_5 or *ad-8* itself. No derivative of the original prototroph was found to be adenine-requiring or was found to carry A_5. If the prototroph was disomic for

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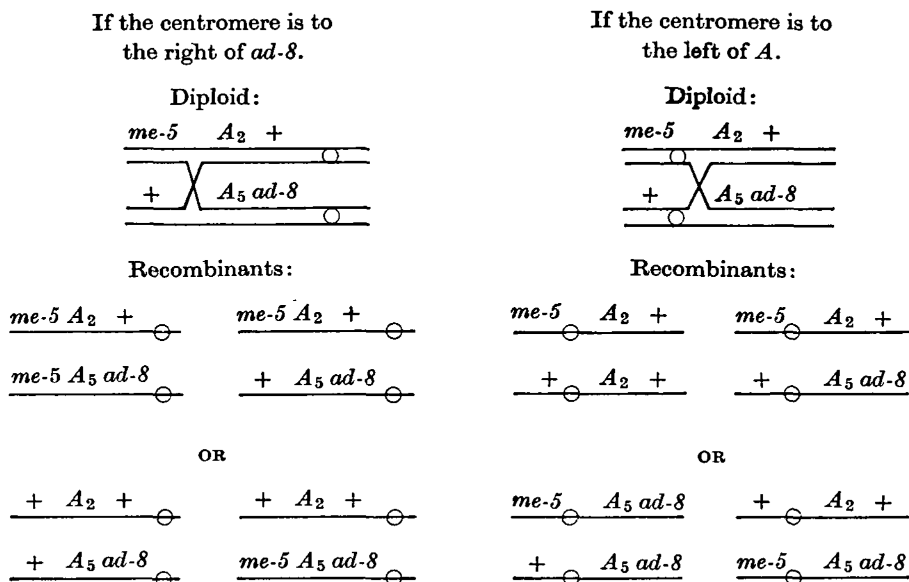
chromosome I carrying the parental chromosome $\underline{me\text{-}5\ A_2+}$ and the recombinant chromosome $\underline{+A_2+}$ the result would be difficult to interpret as the product of mitotic crossing-over. Day & Anderson (1961) have mapped the centromere to the right of $\underline{ad\text{-}8}$. The recombinant $\underline{me\text{-}5\ A_2+}/\underline{+A_2+}$ could only be obtained, assuming only one crossover event, if the centromere was to the left of A. This is illustrated in Table 7.

Table 7



The possible disomic recombinants obtained from a single crossover with two different centromere positions. Note that the disomic $\frac{me\text{-}5\ A_2+}{+\ \ A_2+}$ is only obtained when the centromere is to the left of A.

With one possible exception, no stable methionine-independent monokaryotic derivative of the prototroph was found. It is therefore concluded that the prototroph carried the whole chromosome $\underline{me\text{-}5\ A_2+}$ and a chromosome fragment carrying the wild allele of *me-5* but not the A mating type gene or the *ad-8* gene.

Since the fragment carrying the wild allele of *me-5* does not carry the A_5 or *ad-8* genes it is very unlikely to carry the centromere. If the fragment is acentric it would be unlikely to survive without selective pressure. It is interesting to note that retention of the fragment was very stable in a dikaryon but unstable in a monokaryon.

It would be interesting to estimate the frequency of somatic recombination in the dikaryon from the results of these experiments. However the following factors have to be considered:

1. No recombinants were recovered from dikaryons which had been prepared on 50 p.p.m. and 100 p.p.m. methionine. Only those dikaryons which had

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already been subject to selective pressure by growth on 10 p.p.m. methionine yielded recombinants when chlamydospores were sown on minimal medium.

2. Not all nuclei that were potentially able to give rise to monokaryotic colonies on the selective medium were in fact able to give rise to such colonies.
3. Not all somatic recombinants would be prototrophic.

It is not possible to estimate these three variables and thus to calculate the actual frequency of somatic recombination. From the experimental point of view, however, the frequency of recombinants obtained is one in 10^4 spores.

SUMMARY

A technique based upon auxotrophic mutants and recessive suppressor genes has been used to select for somatic recombinants in the dikaryon of *Coprinus lagopus*. Both haploid and disomic nuclei with a reassortment of chromosomes from the two component nuclei of the dikaryon were found. The presence of the disomics indicates that the recombination process is one of fusion of nuclei with a gradual haploidization by loss of chromosomes at mitotic divisions. An extensive test for crossing-over in the *A* chromosome failed to give an unambiguous crossover recombinant, but it produced a stock with a normal *A* chromosome and a fragment of the chromosome.

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