A STABLE ANEUPLOID OF *SACCHAROMYCES CEREVISIAE*

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ANEUPLOIDS of the (n + 1) type have been described in several fungi. In *Aspergillus nidulans* (KÄFER 1960; POLLARD, KÄFER and JOHNSON 1968), a number of aneuploids produced by mitotic and meiotic nondisjunction have been studied. These disomics were distinguished by a characteristic colony morphology. In *Neurospora crassa,* disomics for five of the seven linkage groups were studied by PITTENGER (1954, 1958). These were readily recognized as pseudowild types in progeny from crosses between strains with complementary auxotrophic markers. In both these fungi aneuploids are typically unstable even under conditions where the contribution of both homologues is necessary for growth.

Spontaneously arising aneuploids have been studied in yeast. Cox and BEVAN (1962) reported data on strains aneuploid for chromosome I. In another spontaneously arising trisomic, MORTIMER and HAWTHORNE (1966) found evidence for linkage between two groups of genes even though these genes were unlinked by standard recombination measurements. These studies indicated that yeast aneuploids were stable enough to be useful in genetic investigations. However, to facilitate genetic and biochemical studies in yeast, many more disomics than are presently known would have to be available.

The present report describes the construction and characterization of a stable disomic (n + 1) strain of *Saccharomyces cerevisiae.* The technique used here for the isolation of strains disomic for chromosome III should be applicable as a general method for other chromosomes. The aneuploids recovered from the selection are very stable and thus suitable for many kinds of genetic and biochemical analyses. Segregation analysis performed on the trisomic constructed from this strain provides evidence for the kinds of pairing arrangements during meiosis.

MATERIALS AND METHODS

Yeast strains: The strains used to test the segregation of specific markers in aneuploid strains are listed in Table 1. Strains beginning 66A28- or 66A4- were sent by Dr. R. SNOW.

Media: All media were prepared as described by HAWTHORNE and MORTIMER (1960). To satisfy nutritional requirements, supplements were added to minimal media to a final concentration of 0.1 mM, except for threonine, which was added to give a final concentration of 1.7 mM.

Sporulation and dissection: Diploids were induced to sporulate and the cultures treated with snail digestive juice as described by HAWTHORNE and MORTIMER (1960). The cultures were then either plated on solid medium for random spore analysis or dissected by micromanipulation for

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TABLE 1

Description of Strains

STRAIN	GENOTYPE
A4429A	α his1
A4660B	α his1 HOL8
333/7	α his1-123 his4-481
152/3	α his2-1
66A28-35	α his4-35
66A4-675	α his4-675
66A4-176	α his4-176
66A28-47	α his4-47
27/5	a his4C-864 leu2-1
A5969A	α his4-331 thr4 leu2-3 trp1 MAL2
A2380B	α his4-280 trp1
A2379C	σ his4-280 trp1
59/2	α his5
59/1	σ his6
ICR1229	α his7
EMS4	σ ade1
XT300-3A	σ ade2-1
A6001A	α arg4-17 thr1
EMS27	σ leu2-27 his1-123
EJ13	α trp3
FB35	σ trp5

tetrad analysis. In the following tetrad analyses, the data represent only those asci in which all four spores germinated. All crosses for which data are presented had at least 80% germination.

Induction of mitotic recombinants: The following procedure was used to confirm the aneuploidy of suspected disomic strains. Mitotic recombinants between noncomplementing *leu2* alleles were induced by ultraviolet irradiation. A large mass of aneuploid cells heterozygous for two *leu2* mutations was grown on solid YEP medium overnight and then replica-plated to two YEPD plates. The cells on one of these were then irradiated for 2 min, 40 cm from two 15 watt germicidal bulbs (Sylvania #G15T8). After incubation at 30°C for 3–5 hr, the irradiated and unirradiated colonies were replica-plated to supplemented minimal medium without leucine. A 10–20-fold increase in the number of leu+ colonies in response to UV treatment (as compared with controls) indicated the induction of mitotic recombinants.

Test for mating ability: Strains were analyzed for their mating response by crossing them to *a* and α tester strains, carrying complementary auxotrophic markers. After the strains were mixed, they were grown on YEP medium at 30°C for 24 hr, and then replica-plated to minimal medium. Confluent growth on minimal medium was scored as a positive mating response. Colonies giving a negative response with tester strains of both mating types were scored as presumptive *a*/α aneuploids.

Complementation analysis: Complementation tests were used to analyze histidine-requiring haploids derived from diploids carrying multiple histidine mutations. This test permits the identification of unlinked histidine mutations, as well as the different classes of mutations within the *his4* region (FINK 1966).

Biochemical methods: Sedimentation properties of the *his4* complex were studied using the technique of MARTIN and AMES (1961). For analysis by sucrose gradient ultracentrifugation, 0.1 ml of a crude French Pressure Cell extract was layered on a 5–20% sucrose gradient (4.6 ml) buffered with Tris-HCl, pH 7.5, and centrifuged for 15 hr at 45,000 rpm in the Spinco SW65 rotor (SHAFFER, RYTKA and FINK 1969). Alkaline phosphatase (MW 80,000) was used as the standard and it was assayed by the method of GAREN and LEVINTHAL (1960). After centrifugation, a hole was punched in the bottom of the tube and fractions of 6 drops each were collected. Fractions were assayed for the three *his4* enzymes as described previously (SHAFFER, RYTKA and FINK 1969).

Construction and lineage of aneuploid strains: A strain disomic (n + 1) for chromosome III (Figure 1) was isolated as a meiotic product of the following diploid:

$$\frac{his4C\text{-}864\ leu2\text{-}1\ a}{his4A\text{-}481\ +\ \alpha}\quad\frac{ade2}{+}\quad\frac{CAN^s}{can^r}$$

A culture of this diploid strain was sporulated and plated on minimal medium supplemented with canavanine (60 μg/ml) and adenine. Only red colonies were picked from this medium.

This selection procedure takes advantage of three factors: the complementation between the *his4* alleles *his4C-864* and *his4A-481* (FINK 1966), the recessive nature of the canavanine resistance mutation, and the red color of haploid strains carrying the *ade2* mutation. Since the sporulated culture was plated on medium without histidine, colonies growing on these plates must be phenotypically his+. Colonies not requiring histidine could arise from (1) diploids, (2) recombinants, (3) revertants, (4) aneuploids for chromosome III. The majority of the diploids will have the CAN^s/can^r genotype and will not grow on this medium. Canavanine resistant diploid colonies which arise by mitotic recombination will usually be heterozygous for *ade2* and therefore white. This procedure cannot differentiate between revertants (including suppressors), recombinants, and aneuploids. Chromosome III aneuploids of the genotype a/α may arise by meiotic nondisjunction but are not useful for further genetic analysis because they do not mate. In order to eliminate this class, the potential aneuploid strains from the diploid described above were crossed by genetically his+ haploid strains of each mating type: strains A941B (a) and EJ13 (α). Of the 48 strains selected for the phenotype ade$^-$ can^r his+, 14 did not mate with either mating-type tester. Aneuploids of the type a/a or α/α are rarer, presumably arising from a meiotic crossover and subsequent nondisjunction. Thirty-four strains mated with one or the other of the two testers, but twelve of the resulting diploids could not be induced to sporulate. Analysis of the nonsporulating cultures was not continued. Progeny from the 22 diploids which sporulated were analyzed by random spore analysis to determine whether they required histidine. Among the progeny of one of these diploids, the original *his4* alleles, *his4A-481* and *his4C-864* were identified. The ade$^-$ can^r his+ parent which gave this result was assumed to be *his4A-481/his4C-864*. This strain gave low percent sporulation and extremely low viability in crosses, so it was crossed in an attempt to obtain a strain more suitable for genetic analysis. The diploid resulting from a cross to 27/1 (*α leu2 his4C-864*) was sporulated and ascospores were dissected by micromanipulation. Strain A1517B was isolated from one of the few four-spored asci and was shown to have the genotype $\frac{ade2}{\quad}\ \frac{his4C\text{-}864\ leu2\text{-}1\ a}{his4C\text{-}864\ leu2\text{-}1\ a}$.

The lineage of strains derived from A1517B and used for further study is shown in Table 2. In crosses, the strains show abnormal segregation for genes mapping on chromosome III and normal segregation for markers not on this linkage group. Strains 896/1 and A5236A give good sporulation and the viability of the spores is greater than 80%. These two strains were used to obtain most of the data presented here.

TABLE 2

Lineage of strains disomic for chromosome III

	A1517B ade2 his4C-864 leu2-1 a / his4C-864 leu2-1 a
crossed by 333/7 his1 his4A-481	
	A1995A ade2 his1 his4A-481 + a / his4C-864 leu2-1 a
crossed by EMS27 leu2-27 his1	
	843/32A his1 his4C-864 leu2-1 a / + leu2-27 a
crossed by XT300-3A ade2	
	896/1 ade2 + leu2-1 a / + leu2-27 a
crossed by A2380B his4C-280 trp1	
	A5236A trp1 + + a / his4C-280 leu2 a

RESULTS

The arrangement of genes on chromosome III is diagramed in Figure 1 (HAWTHORNE and MORTIMER 1968).

Confirmation of aneuploidy: The strains listed in Table 2 were designated as disomic for chromosome III because they met the following three criteria:

1. The segregation of genes on chromosome III was aberrant. The putative disomics were crossed to strains carrying alleles on chromosome III such that the resulting diploids had the +/+/− genotype, for example +/+/*leu2*. Such diploids give rise to asci which show aberrant (3:1 or 4:0) segregation for the auxotrophic requirement. In addition, the fact that the mating-type locus is located on chromo-

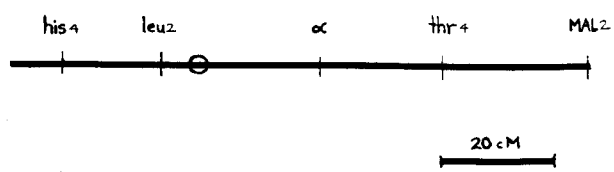


FIGURE 1.—A map of chromosome III of yeast. Map distances are discussed in the text.

some III made aneuploids for this chromosome easy to recognize. The disomics investigated were a/a, and when crossed to an α tester, resulted in tetrads containing large numbers of a/α spores. These spores are easily recognized because they give negative responses with both mating-type testers. Table 3 summarizes analyses of tetrads from $+/+/-$ and $a/a/\alpha$ diploids. Data were compiled from crosses between various disomics listed in Table 2 and the tester strains listed in Table 1.

2. The segregation of genes not located on chromosome III was normal. When crossed to an appropriate tester stock, strains which are disomic for chromosome III and haploid for all other linkage groups will show normal ($2^+:2^-$) segregation for genes not located on chromosome III. Table 4 summarizes the data from crosses between the presumptive disomics and haploid strains carrying auxotrophic markers on various linkage groups. Unless otherwise indicated, strain 896/1 $\left(\frac{ade2\ \ leu2\text{–}1\ \ a}{leu2\text{–}27\ \ a}\right)$ was the putative aneuploid parent; the haploid parents are listed in Table 1. The data clearly show that the aneuploids are haploid for chromosomes I, II, IV, V, VI, VII, VIII, and IX and for fragments 1, 4, and 5. The few aberrant tetrads probably resulted from gene conversion; their frequency is too low to have resulted from aneuploidy.

3. The protein products from both *his4* alleles on the homologous chromosomes could be detected in crude extracts. The *his4* locus consists of three cistrons coding for an enzyme complex which catalyzes three enzymatic reactions in the pathway of histidine biosynthesis: PR-AMP cyclohydrolase (*his4A*), PR-ATP pyrophosphohydrolase (*his4B*) and histidinol dehydrogenase (*his4C*). In sucrose gradients the trifunctional enzyme complex has a molecular weight of 80–90,000 (Figure 2a). Analysis of haploid strains carrying the missense mutation *his4A-588* shows that they produce a *his4* complex of normal molecular weight with the pyrophosphohydrolase (*his4B*) and dehydrogenase (*his4C*) activities (Figure 2c). Haploid strains carrying the nonsense mutation *his4C-864* produce a *his4* protein of reduced molecular weight 40–50,000 (Figure 2b), which has the cyclohydrolase (*his4A*) and pyrophosphohydrolase (*his4B*) activities (SHAFFER, RYTKA and FINK 1969).

A strain carrying these two particular mutations on separate homologues could yield two different molecular species of *his4* protein. Genetic analysis indicated that A1995A is a disomic strain having the genotype $\frac{his4A\text{-}481\ \ +\ \ a}{his4C\text{-}864\ \ leu2\ \ a}$. A crude extract prepared from A1995A was analyzed by sucrose gradient ultracentrifugation (Figure 2d). Cyclohydrolase (*his4A*) activity was found at a position in the gradient corresponding to a molecular weight of 45,000; histidinol dehydrogenase (*his4C*) was found at 95,000. As expected, two peaks of pyrophosphohydrolase (*his4B*) activity were detected, at positions in the gradient corresponding to molecular weights of 45,000 and 95,000. These data show that strain A1995A produces the gene products of two independently functioning *his4* regions, as expected if the strain is disomic for chromosome III.

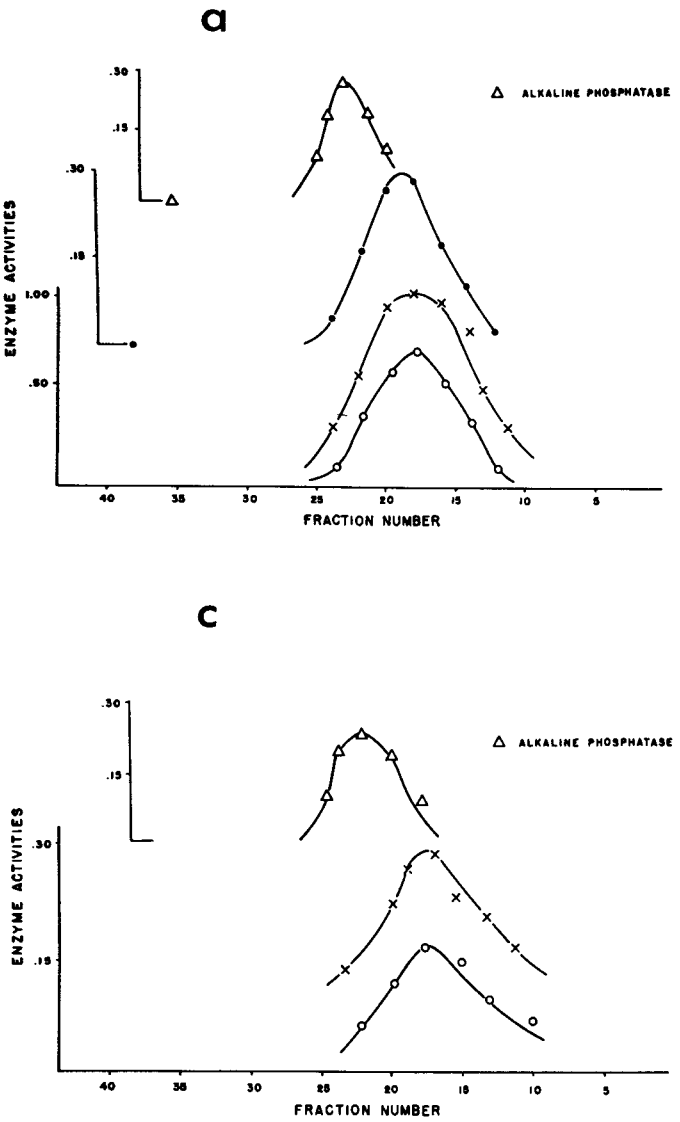
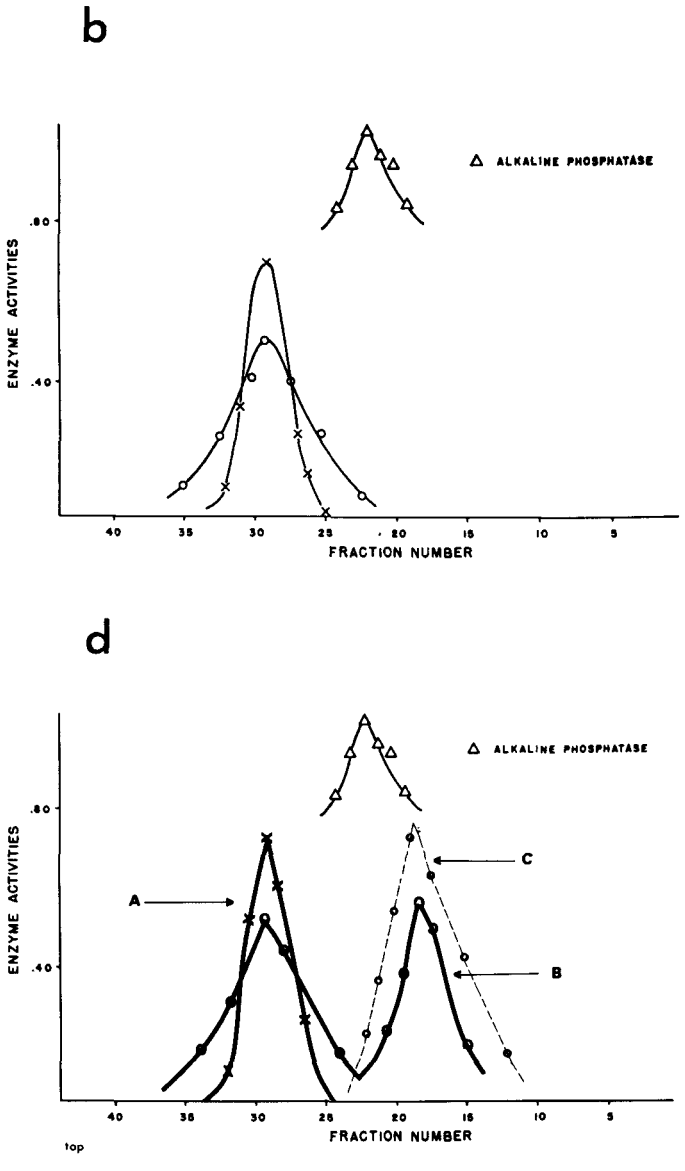


FIGURE 2.—Sucrose gradient analysis of the *his4* activities in haploid and disomic strains. Strains: a) wild type; b) *his4C-864*; c) *his4A-588*; d) *A1995A* (*his4C-864/his4A-588*). -●--●--- histidinol dehydrogenase (*his4C*); -×-×- PR-AMP cyclohydrolase (*his4A*); -O-O- PRATP pyrophosphohydrolase (*his4B*). The X's in Figure 2c should be replaced by closed circles representing *his4C* activity.

Stability of strains: The disomics for chromosome III are relatively stable. Their stability during vegetative growth was demonstrated using strain 896/1 which carries two recombining but noncomplementing *leu2* alleles, and gives rise



to leu+ mitotic recombinants when irradiated with ultraviolet light. Strains which have become haploid for chromosome III are no longer able to produce leu+ recombinants after UV irradiation. Strain 896/1 was grown from a small inoculum to stationary phase in liquid YEP and the cells plated out on solid YEP medium. Of the resulting colonies, 294 were picked and tested for their ability to give rise to leu+ recombinants. Recombinants were detected in all but three of

294 irradiated colonies. These three may have lost the extra chromosome. Thus, even in the absence of conditions favoring retention of the chromosome, strain 896/1 remained disomic 99% of the time.

Diploids which are trisomic for chromosome III are very stable. Evidence for this comes from crosses in which the diploid produced was of the +/−/− genotype, either +/*leu2*/*leu2* or +/*his4*/*his4*. The asci from such diploids will always show $2^+:2^-$ segregation for the auxotrophic marker, except in the case where the chromosome carrying the wild-type allele has been lost. The data from tetrad analysis of +/−/− diploids are shown in Table 5. The segregation of the auxotrophic requirement was $2^+:2^-$ in 206 of 211 tetrads. Regardless of whether the wild-type allele came from the disomic or haploid parent, no tetrad in which all four spores showed the auxotrophic requirement has ever been observed. Chromosome loss cannot account for the five aberrant tetrads listed; they are more likely the result of gene conversion or, in the case of $1^+ : 3^-$ tetrads, trivalent formation and meiotic recombination (see below). Similarly (Table 3), when *a*/*a* disomics were crossed to α haploids, no tetrads were seen in which mating type segregated 4*a*:0α. Clearly, diploids which are trisomic for chromosome III are extremely stable during meiosis, an obligate requirement for the recombination analysis described below.

Recombination in trisomic diploids: The fact that the disomic strains derived here are very stable in crosses (Tables 3 and 5) made it possible to examine the data obtained from tetrad analysis in terms of the type and extent of recombination that occurs during meiosis in trisomic diploids.

During the first meiotic division, there are two possible arrangements of the three homologous chromosomes on the metaphase plate which must be considered. In the bivalent–univalent arrangement, two of the chromosomes pair, crossing over can occur, and these two chromosomes move to opposite poles; the third homologue is completely unpaired at metaphase I and has an equal probability of migrating to either pole. In the trivalent arrangement, all three homo-

TABLE 3

*The meiotic segregations of genes on chromosome III from a trisomic**

Genotype of diploid	Number of tetrads	Segregation of auxotrophic requirement in tetrads				
		$4^+:0^-$	$3^+:1^-$	$2^+:2^-$	$1^+:3^-$	$0^+:4^-$
+/+/*leu2*	51	29	5	17	0	0
+/+/*his4*	123	52	39	32	0	0
+/+/*thr4*	58	17	38	3	0	0
+/+/*MAL2*	48	0	1	45	2	0

		Segregation of mating type				
		2*a*:2*a*/α	2*a*/*a*:2α	*a*:*a*/*a*:*a*/α:α	2*a*:*a*/*a*:α/α	2*a*:*a*/α:α/α
a/*a*/α	264	81	38	108	24	13†

* The trisomics had the composition +/+/— or *a*/*a*/α.

† The segregation of the mating-type alleles in these tetrads can be explained only by gene conversion or chromosome loss. They were not counted in the total number of tetrads when the frequencies of each class were calculated (Table 6).

TABLE 4

Analysis of crosses between putative aneuploids and haploid strains carrying auxotrophic markers not located on chromosome III

Linkage group*	Auxotrophic marker	Analysis of tetrads		
		Number of tetrads	Number showing 2+:2- segregation	Number aberrant tetrads
Chrom I	*ade1*	18	17	1
Chrom II	*his7*	15	15	0
Chrom IV	*trp1*	57	57	0
Chrom V	*his1*†	35	35	0
Chrom VI	*his2*	11	11	0
Chrom VII	*trp5*	12	11	1
Chrom VIII	*arg4, thr1*	13	13	0
Chrom IX	*his6*	12	12	0
Frag 1	*ade2*†	84	83	1
Frag 4	*his5*	14	13	1
Frag 5	*trp3*	15	15	0

* The genetic map of *Saccharomyces cerevisiae* reported by HAWTHORNE and MORTIMER (1968) was used to assign markers to linkage groups.
† Data are taken from a cross between XT3003A and 843/32A (see Table 2).

logous chromosomes are associated together during metaphase I. Crossing over can occur between any two chromosomes with subsequent migration to the poles at random, two to one pole and one to the opposite pole. Only the trivalent model allows both chromosomes involved in the crossover event to migrate to the same pole during the first meiotic division. The two models predict different frequencies of the possible tetrad arrangements derived from $A/A/B$ diploids.

Using the formulas below, we have calculated the frequencies of the possible tetrad arrangements expected under the two models. In deriving these formulas it was assumed that only two of the three homologous chromosomes take part in recombination regardless of the chromosome arrangement at the metaphase plate during meiosis I, and that the frequency of recombination is unaffected by the chromosome arrangement. The formulas derived are:

Segregation of alleles in tetrads	Frequency of tetrad arrangement
$1A/A$: $1A/B$: $1A$: $1B$	$2/3\ s - 2/9\ sz$
$2A/B$: $2A$	$2/3 - 1/3\ s$
$1A/A$: $1B/B$: $2A$	$1/9\ sz$
$2A/A$: $2B$	$1/3 - 1/3\ s + 1/9\ sz$

In these formulas, z is the frequency of trivalent formation during the first meiotic division. Considering only the two chromosomes which take part in crossing over in an AAB trisomic, s is the probability that the two alleles attached to a given centromere will be unlike due to a recombinational event. The quantity s is related to map distance, and was calculated from the formula

$$s = 2r - (4/3)\ r^2$$

TABLE 5

Tetrads from +/ — / — trisomic diploids

Genotype of diploid	Number of tetrads	Analysis of tetrads: Number showing $3^+:1^-$ segregation	Number showing $2^+:2^-$ segregation	Number showing $1^+:3^-$ segregation
+/ *leu2* / *leu2*	173	3	168	2
+/ *his4* / *his4*	38	0	38	0

where r is the frequency of effective single strand recombination, taken from the empirical mapping function of KOSAMBI (BARRATT *et al.* 1954). The term $(4/3)r^2$ is used to correct for undetectable double crossovers between the centromere and the gene in question.

Table 6 shows the expected frequencies of the possible tetrad arrangements from *A/A/B* diploids. Under each tetrad arrangement, the first column shows the expected frequencies of possible tetrads assuming that only the bivalent–univalent arrangement is possible during meiosis I, i.e., the case where $z = 0$. The second column gives the expected frequencies assuming that only trivalent formation occurs, i.e., the case where $z = 1$. In the calculations of expected frequencies, the gene–centromere map distances computed from our own data were: *his4*, 20 cM; *leu2*, 5 cM; α, 40 cM. Table 6 also lists the observed frequencies of the possible tetrad arrangements, calculated from the data in Tables 3 and 5. No datum is given for a tetrad showing $0^+:4^-$ segregation; such tetrads are not predicted by either model, and none was ever observed.

Although some data are available from +/+/*thr4* diploids, they were not ex-

TABLE 6

Expected and observed percentages of possible tetrad arrangements derived from A/A/B *diploids trisomic for chromosome III*

Genotype of diploid	Segregation of auxotrophic marker: $4^+:0^-$ exp_b^*	exp_t^{**}	obs	$3^+:1^-$ exp_b	exp_t	obs	$2^+:2^-$ exp_b	exp_t	obs	$1^+:3^-$ exp_b	exp_t	obs
+/ leu2/ leu2	0	0	0	0	0	1.7	100	98.9	98	0	1.1	1.3
+/ +/ leu2	64	64	56.8	6	5	9.8	30	32	33	0	0	0
+/ his4/ his4	0	0	0	0	0	0	100	96.5	100	0	4	0
+/ +/ his4	55	55	42.3	22	19	31.7	22	25	26	0	0	0
	Segregation of mating type alleles: 2a/α: 2a			1a:1a/a:1a/α:1α			2a/a: 2α			2a: 1a/a: 1α/α		
a/ a/ α	48	48	32.3	36	24	43	15	21	15.2	0	6	9.5

* Expected under bivalent–univalent assumption, $z = 0$.
** Expected under trivalent assumption, $z = 1$.

amined here because relatively few tetrads were analyzed and because it is difficult to assign an exact gene–centromere distance to a locus so far from the centromere (about 60 cM).

The data on the mating-type alleles show that trivalent formation occurs during meiosis I in trisomic diploids. Calculations including the assumption of complete trivalent formation predict that 6% of the tetrads from $a/a/\alpha$ diploids should have the $2a{:}1a/a{:}1\alpha/\alpha$ mating-type arrangement; if the bivalent–univalent arrangement is assumed, the expected frequency of this tetrad type is zero. Since 9% of the observed tetrads from $a/a/\alpha$ diploids were of the $2a{:}1a/a{:}1\alpha/\alpha$ arrangement, trivalents must be formed during meiosis I at a frequency approaching one. It should be mentioned that a single gene conversion event would not produce such tetrads; only a rare double conversion would produce such arrangements. The expected frequencies of the other tetrad arrangements do not differentiate between the bivalent–univalent and trivalent models and the observed data agree equally well with either assumption.

For all three markers studied, the observed frequencies of the possible tetrad arrangements differed from the expected frequencies in the same manner: the observed frequencies of the $A/A{:}\ 1A/B{:}\ 1A{:}\ 1B$ ($3^+{:}1^-$) class was higher than the expected and the observed frequencies of the $2A/B{:}\ 2A$ ($4^+{:}0^-$) class were lower than the expected. Assuming intermediate values for z did not bring the expected and observed frequencies closer together. In attempting to account for this systematic deviation, an observed value of s, s_{obs}, was calculated by using the observed frequencies of each tetrad arrangement in the trivalent formulas. In all but one case, the s_{obs} was higher than that calculated from the formula, $s_{exp} = 2r - (4/3)r^2$, suggesting that some type of crossover interference is operating. The value of s_{exp} would be increased if the derivation of the formula had included assumptions of higher levels of chromatid interference or positive chromosome interference. The value of s_{exp} would increase if there were increased chromatid interference, i.e., if r increased, or if some chromosome interference were assumed, i.e., if the term $(4/3)r^2$ were diminished. However, from our data it is impossible to determine which type of interference should have been included in the derivation of the formula for s_{exp}.

DISCUSSION

Most of the aneuploid strains of *Saccharomyces cerevisiae* currently available arose spontaneously in laboratory stocks, as was the case for the chromosome I aneuploids described by Cox and BEVAN (1962). The present report describes a general method for selecting aneuploid strains. The procedure should be applicable to the construction of disomics for any linkage group; all that is required is the presence of complementing alleles on the chromosome.

The aneuploids for chromosome III are extremely stable. We have found no evidence for significant chromosome loss during either mitosis or meiosis. The trisomic diploids sporulate well and the viability of the spores is excellent. Consequently, these aneuploids can be used for a variety of genetic purposes. For ex-

ample, the disomics have been used to map a number of temperature-sensitive mutations to chromosome III.

Studies on the segregation of markers during meiosis in trisomics lead to a number of interesting findings. First of all, the data indicate that trivalents are formed at a very high frequency at meiosis I (almost 100%). The level of crossover interference in these trivalents is much higher than that computed in studies on the same markers in bivalent arrangements.

The disomic strains should be useful in both biochemical and genetic studies. First of all, strains aneuploid for chromosome III should be particularly useful for the study of the control of meiosis by the mating-type locus. Disomics which are a/α appear to go through some of the cytological events associated with meiosis even though most of the genome is haploid. For example, on sporulation medium the a/α disomic forms what appears to be a single spore. So far such spores have not been viable. It will be interesting to compare meiosis in a/α disomics with meiosis in diploids. Second, the disomic can be used in the isolation of a (mitotic) recombinationless mutant (*rec*$^-$). We have isolated a *rec*$^-$ strain from 896/1 $\frac{ade2}{} \frac{leu2\text{-}1 \quad a}{leu2\text{-}27 \quad a}$ after EMS treatment. The *rec*$^-$ mutant segregates both parental *leu2* alleles, but does not itself give rise to leu$^+$ mitotic recombinants after ultraviolet irradiation. Third, aneuploid strains should also be valuable in investigations of dosage effects and allelic interactions, such as complementation. In some cases, the disomics may contain higher levels of certain enzymes than the isogenic monosomic strain, thus facilitating the isolation of proteins normally found at low levels in the cells.

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SUMMARY

A stable disomic for the linkage group III of *Saccharomyces cerevisiae* has been characterized. Both biochemical and genetic evidence indicate that in this strain chromosome III is present in duplicate, whereas eleven others are haploid. Meiotic segregation and recombination patterns from trisomics derived from this strain are best explained if pairing occurs in trivalents and if interference in trivalents is greater than in bivalents.

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