MICROBIOLOGICAL REVIEWS, Dec. 1980, p. 519-571 Vol. 44, No. 4
0146-0749/80/04-0519/53$02.00/0

# Genetic Map of *Saccharomyces cerevisiae*

ROBERT K. MORTIMER* AND DAVID SCHILD

*Department of Biophysics and Medical Physics and Donner Laboratory, University of California, Berkeley, California 94720*



## INTRODUCTION

The yeast *Saccharomyces cerevisiae* has been studied genetically for over 40 years and has been used in biochemical studies for an even longer time. The genetics of this organism is very well developed, a fact that has made this yeast suitable for a wide range of studies (70a). Many of these studies are dependent on the availability of detailed genetic maps, and current research involving recombinant deoxyribonucleic acid (DNA) techniques has provoked a renewed interest in the yeast map. The first genetic map of *S. cerevisiae* was published in 1949 by Lindegren (56a), and several revisions have been published subsequently (35, 36, 40, 41, 57, 70, 71, 72).

In this review, we present a compilation of most of the published yeast mapping data, as well as a large amount of unpublished data, according to chromosomes and intervals; the numbers of independent sets of data for the different intervals ranged from 1 to 12. These data have been analyzed and a new genetic map has been constructed. Although all of the data presented in this article are from tetrad analyses, many other techniques have been used to assign genes to chromosomes or to specific chromosome arms. These techniques include aneuploid analysis, mitotic recombination analysis, mitotic chromosome loss or nondisjunction, and random spore analysis (70a–72, 108).

Tetrad analysis involves examination of the four meiotic products (spore clones) of individual meioses. A diploid that is heterozygous at two or more genetic loci will yield, for each pairwise gene combination (e.g., A/a and B/b) three types of asci: parental ditypes (PD) (AB, AB, ab, ab), nonparental ditypes (NPD) (Ab, Ab, aB, aB), and tetratypes (T) (AB, Ab, aB, ab). The relative frequencies of PD, NPD, and T asci depends on the distance between the two genes if they are on the same chromosome or on the distances between both genes and their respective centromeres if they are on different chromosomes (70a).

## GENETIC MAP, GLOSSARY, AND LIST OF MAPPED GENES

The current genetic map of *S. cerevisiae* is presented in Fig. 1. This map is based primarily on the tetrad analysis data included in Tables 1 through 18. Some genes have been located only by aneuploid analysis combined with mitotic crossover analysis; these genes will be discussed in a following section. In cases in which a gene

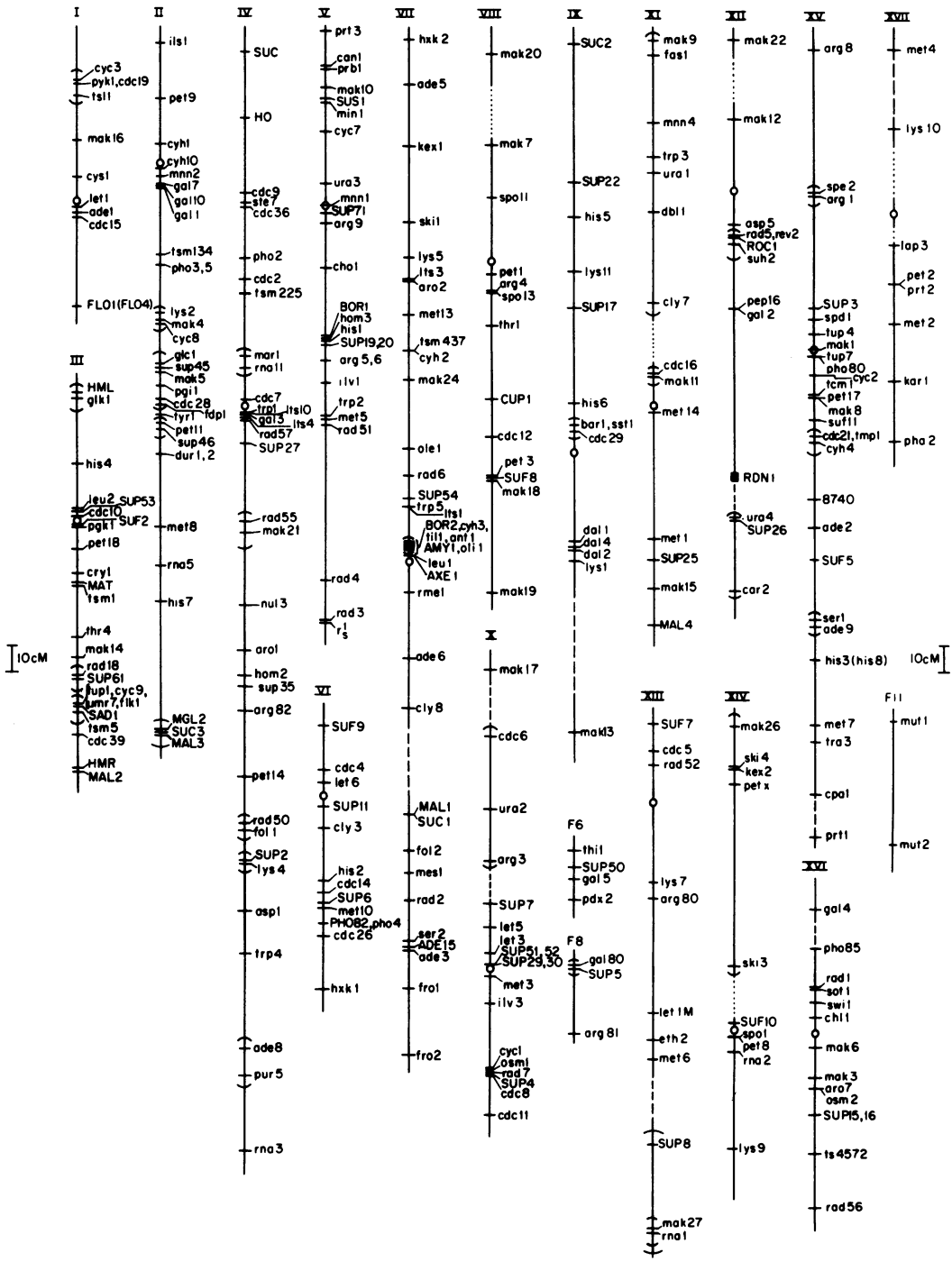


FIG. 1. *The genetic map of S. cerevisiae, based on the data presented in Tables 1 through 18 and in the text. Centromeres are represented as circles, and the left arm of each chromosome has arbitrarily been drawn above the centromere. Solid lines are drawn to scale and represent linkage distances established by tetrad analysis. The dashed and dotted lines represent linkages established by mitotic and aneuploid analysis, respectively. They have arbitrarily been assigned a minimum distance of 100 cM (see text); these intervals are not drawn to scale. When the orientation of two or more genes relative to outside markers has not been determined, these genes are enclosed within parentheses.*

TABLE 1. *Tetrad analysis data for chromosome I*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *tsl1-mak16* | | | 23 | 0 | 13 | 18.9 | 4.4 | J. McCusker and J. Haber, pers. comm. |
| *tsl1-ade1* | | | 7 | 2 | 26 | 58.6 | 17.4 | J. McCusker and J. Haber, pers. comm. |
| *tsl1-ade1* | | | 23 | 6 | 73 | 58.3 | 19.7 | 47 |
| Total | | | 30 | 8 | 99 | 58.4 | 9.1 | |
| *cyc3-pyk1* | | | 111 | 0 | 5 | 2.2 | 1.0 | 85 |
| *cyc3-cys1* | | | 55 | 1 | 59 | 28.4 | 3.5 | 85 |
| *pyk1-cys1* | | | 22 | 4 | 38 | 55.6 | 16.8 | 85 |
| *pyk1-cys1* | | | 19 | 0 | 13 | 21.4 | 4.9 | G. Sprague, pers. comm. |
| (*cdc19*)-*cys1* | | | 52 | 2 | 63 | 32.5 | 4.5 | 48; G. Kawasaki, pers. comm. |
| Total | | | 93 | 6 | 114 | 36.6 | 4.6 | |
| *mak16-cys1* | | | 42 | 1 | 8 | 16.6 | 13.0 | 111 |
| *mak16-ade1* | | | 11 | 1 | 23 | 42.5 | 10.5 | J. McCusker and J. Haber, pers. comm. |
| *mak16-ade1* | | | 46 | 1 | 21 | 20.5 | 6.1 | 111 |
| Total | | | 57 | 2 | 44 | 28.0 | 5.5 | |
| *pyk1-ade1* | | | 135 | 19 | 205 | 49.5 | 6.0 | 63 |
| *pyk1-ade1* | | | 9 | 0 | 23 | 40.7 | 5.6 | 85 |
| *pyk1-ade1* | | | 11 | 0 | 15 | 31.4 | 6.0 | 97 |
| *pyk1-ade1* | | | 17 | 0 | 19 | 28.4 | 5.0 | G. Sprague, pers. comm. |
| Total | | | 172 | 19 | 262 | 44.5 | 4.2 | |
| *cys1-cen1* | 170 | 41 | | | | 10.0 | 1.5 | 85 |
| *cys1-ade1* | | | 201 | 6 | 79 | 21.7 | 4.0 | 30 |
| *cys1-ade1* | | | 60 | 0 | 11 | 7.9 | 2.2 | 48; G. Kawasaki, pers. comm. |
| *cys1-ade1* | | | 44 | 0 | 7 | 6.9 | 2.5 | 111 |
| *cys1-ade1* | | | 25 | 0 | 9 | 13.7 | 4.0 | G. Sprague, pers. comm. |
| Total | | | 330 | 6 | 106 | 16.8 | 2.4 | |
| *cen1-ade1* | 1,177 | 131 | | | | 5.1 | 0.4 | 70 |
| *cen1-ade1* | 300 | 31 | | | | 4.8 | 0.8 | 85 |
| *cen1-ade1* | 3,722 | 286 | | | | 3.6 | 0.1 | T. Takahaski, pers. comm. |
| *cen1-ade1* | 56 | 5 | | | | 4.2 | 1.8 | J. McCusker and J. Haber, pers. comm. |
| Total | 5,255 | 453 | | | | 4.0 | 0.2 | |
| *cen1-cdc15* | 53 | 9 | | | | 7.4 | 2.4 | J. McCusker and J. Haber, pers. comm. |
| *let1-ade1* | | | 11 | 0 | 1 | 4.3 | 4.1 | 71 |
| *ade1-cdc15* | | | 30 | 0 | 0 | 0 | | 71 |
| *ade1-cdc15* | | | 59 | 0 | 4 | 3.2 | 1.6 | J. McCusker and J. Haber, pers. comm. |
| Total | | | 89 | 0 | 4 | 2.2 | 1.1 | |
| *ade1-FLO1* | | | 7 | 1 | 21 | 48.0 | 12.6 | 38 |
| *ade1-FLO1* | | | 104 | 6 | 185 | 38.0 | 3.0 | 85 |
| *ade1-FLO1* | | | 29 | 2 | 43 | 38.3 | 7.3 | 98 |
| *ade1-FLO1* | | | 22 | 1 | 51 | 38.7 | 4.8 | J. Johnston, pers. comm. |
| *ade1-FLO1* | | | 12 | 1 | 22 | 41.2 | 10.7 | G. Stewart and I. Russell, pers. comm. |
| Total | | | 174 | 11 | 322 | 38.9 | 2.4 | |

[a] FD, First-division segregation; SD, second-division segregation. These segregations are determined by examination of the segregation of a marker relative to that of a known centromere-linked marker (72). PD, NPD, T, and $x'$ are defined in the text. SE, Standard error; pers. comm., personal communication.

TABLE 2. *Tetrad analysis data for chromosome II*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | x' (cM) | SE | |
| *ils1-pet9* | | | 30 | 0 | 23 | 23.0 | 3.9 | 68 |
| *ils1-gal1* | | | 15 | 2 | 36 | 47.2 | 10.3 | 68 |
| *ils1-gal1* | | | 19 | 0 | 23 | 29.6 | 4.7 | 68 |
| Total | | | 34 | 2 | 59 | 38.0 | 5.4 | |
| *pet9-cyh1* | | | 32 | 0 | 19 | 19.5 | 3.8 | 70 |
| *pet9-cen2* | 108 | 62 | | | | 19.5 | 2.2 | 70 |
| *pet9-gal1* | | | 28 | 0 | 25 | 25.1 | 4.0 | 68 |
| *pet9-gal1* | | | 29 | 0 | 27 | 25.7 | 3.9 | 18 |
| *pet9-gal1* | | | 72 | 0 | 70 | 26.4 | 2.5 | 70 |
| Total | | | 129 | 0 | 122 | 26.0 | 1.8 | |
| *cyh1-cen2* | 123 | 30 | | | | 10.1 | 1.7 | 70 |
| *cyh1-gal1* | | | 93 | 1 | 52 | 20.0 | 2.9 | 70 |
| *cyh?-gal1* | | | 269 | 11 | 149 | 26.9 | 3.5 | 57 |
| Total | | | 362 | 12 | 201 | 24.9 | 2.6 | |
| *cen2-cyh10* | 68 | 2 | | | | 1.4 | 1.0 | 91 |
| *cen2-mnn2* | 23 | 4 | | | | 7.6 | 3.6 | 4 |
| *cen2-gal7* | 548 | 72 | | | | 5.9 | 0.7 | 70 |
| *cen2-gal10* | 159 | 20 | | | | 5.7 | 1.3 | 70 |
| *cen2-gal1* | 454 | 82 | | | | 7.8 | 0.8 | 35 |
| *cen2-gal1* | 981 | 150 | | | | 6.8 | 0.5 | 70 |
| *cen2-gal1* | 225 | 31 | | | | 6.2 | 1.1 | T. Takahashi, pers. comm. |
| *cen2-gal1* | 22 | 5 | | | | 9.5 | 4.0 | 4 |
| Total | 1,682 | 268 | | | | 7.0 | 0.4 | |
| *cen2-tsm134* | 30 | 97 | | | | 49.2 | 4.5 | R. Contopoulou, pers. comm. |
| *cen2-lys2* | 180 | 381 | | | | 40.9 | 1.8 | 70 |
| *cen2-lys2* | 34 | 93 | | | | 45.8 | 4.0 | R. Contopoulou, pers. comm. |
| *cen2-lys2* | 334 | 763 | | | | 42.3 | 1.3 | T. Takahashi, pers. comm. |
| Total | 548 | 1,237 | | | | 42.1 | 1.1 | |
| *mnn2-gal1* | | | 24 | 0 | 3 | 5.7 | 3.1 | 4 |
| *gal7-gal10* | | | 993 | 0 | 0 | 0 | | 6 |
| *gal7-gal10* | | | 72 | 0 | 0 | 0 | | 18 |
| Total | | | 1,065 | 0 | 0 | 0 | | |
| *gal7-gal1* | | | 313 | 0 | 0 | 0 | | 18 |
| *gal7-gal1* | | | 993 | 0 | 0 | 0 | | 6 |
| Total | | | 1,306 | 0 | 0 | 0 | | |
| *gal10-gal1* | | | 992 | 0 | 1 | 0.06 | 0.06 | 6 |
| *gal10-gal1* | | | 59 | 0 | 0 | 0 | | 18 |
| Total | | | 1,051 | 0 | 1 | 0.05 | | |

TABLE 2—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *gal1-tsm134* | | | 8 | 0 | 11 | 31.6 | 7.0 | 71 |
| *gal1-lys2* | | | 101 | 23 | 259 | 57.3 | 5.9 | 70 |
| *gal1-lys2* | | | 43 | 6 | 95 | 48.0 | 6.9 | 35 |
| *gal1-lys2* | | | 73 | 15 | 170 | 55.6 | 7.1 | 18 |
| Total | | | 217 | 44 | 524 | 54.9 | 3.9 | |
| *tsm134-pho5* | | | 21 | 0 | 2 | 4.4 | 3.0 | 31 |
| *tsm134-lys2* | | | 15 | 0 | 8 | 18.2 | 5.5 | 31 |
| *tsm134-lys2* | | | 11 | 0 | 8 | 22.3 | 6.4 | 71 |
| *tsm134-lys2* | | | 81 | 1 | 44 | 20.0 | 3.3 | R. Contopoulou, pers. comm. |
| *tsm134-lys2* | | | 27 | 1 | 20 | 28.0 | 8.5 | 64 |
| Total | | | 134 | 2 | 80 | 21.5 | 2.7 | |
| *tsm134-pgi1* | | | 11 | 5 | 40 | 75.6 | 24.9 | 64 |
| *pho5-pho3* | | | 20 | 0 | 0 | 0 | | 104 |
| *pho3-lys2* | | | 47 | 0 | 9 | 8.2 | 2.5 | 104 |
| *pho3-lys2* | | | 64 | 0 | 26 | 15.0 | 2.6 | 31 |
| *pho3-lys2* | | | 219 | 0 | 56 | 10.4 | 1.3 | 100 |
| *pho3-lys2* | | | 26 | 0 | 4 | 6.8 | 3.2 | 94 |
| Total | | | 356 | 0 | 95 | 10.7 | 1.1 | |
| *pho1-sup1* | | | 14 | 1 | 15 | 37.1 | 14.2 | 94 |
| *pho5-tyr1* | | | 18 | 1 | 48 | 40.6 | 5.2 | 31 |
| *lys2-mak4* | | | 94 | 0 | 7 | 3.5 | 1.3 | 109 |
| *lys2-pgi1* | | | 39 | 1 | 49 | 31.1 | 4.3 | 64 |
| *lys2-glc1* | | | 22 | 0 | 14 | 20.4 | 4.5 | J. Pringle, pers. comm. |
| *lys2-sup1* | | | 19 | 0 | 11 | 19.2 | 4.9 | 94 |
| *lys2-sup45* | | | 55 | 1 | 48 | 26.1 | 3.8 | 36 |
| Total | | | 74 | 1 | 59 | 24.4 | 3.1 | |
| *lys2-mak5* | | | 77 | 1 | 43 | 20.4 | 3.4 | 109 |
| *lys2-cdc28* | | | 31 | 1 | 30 | 29.5 | 6.2 | 109 |
| *lys2-cdc28* | | | 228 | 3 | 266 | 28.6 | 1.5 | 12 |
| Total | | | 259 | 4 | 296 | 28.7 | 1.5 | |
| *lys2-fdp1* | | | 27 | 2 | 16 | 37.6 | 20.4 | 105 |
| *lys2-tyr1* | | | 476 | 33 | 802 | 39.1 | 1.6 | 80 |
| *lys2-tyr1* | | | 5 | 1 | 13 | 54.0 | 22.9 | G. Kawasaki, pers. comm. |
| *lys2-tyr1* | | | 148 | 17 | 268 | 45.1 | 3.9 | T. Takahashi, pers. comm. |
| *lys2-tyr1* | | | 129 | 6 | 200 | 35.7 | 2.7 | 70 |
| *lys2-tyr1* | | | 227 | 8 | 336 | 33.9 | 1.8 | 109 |
| *lys2-tyr1* | | | 504 | 26 | 1,020 | 38.3 | 1.2 | 12 |
| *lys2-tyr1* | | | 28 | 0 | 39 | 31.7 | 3.7 | 31 |
| *lys2-tyr1* | | | 12 | 0 | 18 | 32.9 | 5.6 | 85 |
| *lys2-tyr1* | | | 31 | 0 | 8 | 10.5 | 3.4 | B. Ono, J. Stewart, and F. Sherman, pers. comm. |
| Total | | | 1,560 | 91 | 2,704 | 37.9 | 0.8 | |

TABLE 2—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *cyc8-lys2* | | | 60 | 0 | 6 | 4.6 | 1.8 | 85 |
| *cyc8-tyr1* | | | 9 | 0 | 21 | 39.4 | 5.8 | 85 |
| *lys2-pet11* | | | 277 | 25 | 751 | 43.5 | 1.7 | 12 |
| *lys2-dur1* | | | 280 | 71 | 944 | 56.9 | 2.8 | 12 |
| *lys2-dur2* | | | 258 | 51 | 807 | 52.6 | 2.5 | 12 |
| *lys2-met8* | | | 219 | 82 | 752 | 68.4 | 4.7 | 12 |
| *lys2-his7* | | | 275 | 153 | 852 | 102.7 | 11.3 | 80 |
| *mak4-cdc28* | | | 21 | 1 | 15 | 30.1 | 11.8 | 109 |
| *mak4-tyr1* | | | 19 | 2 | 21 | 44.0 | 17.1 | 109 |
| *pgi1-tyr1* | | | 33 | 0 | 14 | 15.4 | 3.6 | 64 |
| *glc1-tyr1* | | | 28 | 0 | 8 | 11.4 | 3.7 | J. Pringle, pers. comm. |
| *sup45-tyr1* | | | 76 | 2 | 27 | 20.0 | 6.3 | 36 |
| *mak5-tyr1* | | | 85 | 0 | 41 | 16.9 | 2.3 | 109 |
| *cdc28-tyr1* | | | 37 | 0 | 0 | 0 | | 33 |
| *cdc28-tyr1* | | | 440 | 0 | 57 | 5.8 | 0.7 | 12 |
| *cdc28-tyr1* | | | 57 | 0 | 11 | 8.2 | 2.3 | 109 |
| Total | | | 534 | 0 | 68 | 5.7 | 0.7 | |
| *cdc28-dur1* | | | 146 | 1 | 95 | 20.9 | 2.0 | 12 |
| *cdc28-dur2* | | | 148 | 1 | 106 | 22.0 | 1.9 | 12 |
| *tyr1-pet11* | | | 17 | 0 | 0 | 0 | | 70 |
| *tyr1-pet11* | | | 989 | 0 | 64 | 3.1 | 0.4 | 12 |
| *tyr1-pet11* | | | 52 | 0 | 12 | 9.6 | 2.6 | 36 |
| Total | | | 1,058 | 0 | 76 | 3.4 | 0.4 | |
| *tyr1-SUP46* | | | 47 | 0 | 6 | 5.7 | 2.2 | B. Ono, J. Stewart, and F. Sherman, pers. comm. |
| *tyr1-dur1* | | | 922 | 5 | 368 | 15.4 | 0.8 | 12 |
| *tyr1-dur2* | | | 786 | 6 | 334 | 16.5 | 1.0 | 12 |
| *tyr1-met8* | | | 87 | 0 | 42 | 16.9 | 2.2 | 70 |
| *tyr1-met8* | | | 634 | 8 | 411 | 21.9 | 1.1 | 12 |
| *tyr1-met8* | | | 36 | 1 | 33 | 28.2 | 5.5 | 36 |
| Total | | | 757 | 9 | 486 | 21.7 | 1.0 | |
| *tyr1-rna5* | | | 13 | 0 | 5 | 14.0 | 5.5 | G. Kawasaki, pers. comm. |
| *tyr1-his7* | | | 34 | 3 | 90 | 43.2 | 4.8 | 70 |
| *tyr1-his7* | | | 428 | 58 | 792 | 47.8 | 2.6 | 80 |
| *tyr1-his7* | | | 7 | 0 | 12 | 34.9 | 7.1 | G. Kawasaki, pers. comm. |
| Total | | | 469 | 61 | 894 | 47.0 | 2.3 | |

TABLE 2—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *pet11-dur1* | | | 806 | 4 | 243 | 12.7 | 0.9 | 12 |
| *pet11-dur2* | | | 657 | 4 | 210 | 13.5 | 1.0 | 12 |
| *pet11-met8* | | | 689 | 7 | 357 | 19.1 | 1.1 | 12 |
| *pet11-met8* | | | 41 | 0 | 17 | 15.2 | 3.2 | 36 |
| Total | | | 730 | 7 | 374 | 18.8 | 1.0 | |
| *SUP46-met8* | | | 32 | 0 | 21 | 20.8 | 3.8 | B. Ono, J. Stewart, and F. Sherman, pers. comm. |
| *dur1-dur2* | | | 852 | 0 | 19 | 1.1 | 0.2 | 12 |
| *dur1-met8* | | | 917 | 1 | 135 | 6.7 | 0.6 | 12 |
| *dur2-met8* | | | 785 | 0 | 86 | 5.0 | 0.5 | 12 |
| *met8-his7* | | | 21 | 1 | 35 | 36.4 | 6.4 | 66 |
| *met8-his7* | | | 53 | 0 | 35 | 20.9 | 2.9 | 70 |
| *met8-his7* | | | 15 | 1 | 23 | 38.2 | 9.7 | B. Ono, J. Stewart, and F. Sherman, pers. comm. |
| Total | | | 89 | 2 | 93 | 28.7 | 3.0 | |
| *lys2-rna5* | | | 4 | 0 | 14 | 45.1 | 7.6 | G. Kawasaki, pers. comm. |
| *rna5-his7* | | | 15 | 0 | 5 | 12.9 | 5.2 | 71 |
| *rna5-his7* | | | 24 | 0 | 5 | 8.8 | 3.7 | B. Ono, J. Stewart, and F. Sherman, pers. comm. |
| *rna5-his7* | | | 9 | 0 | 9 | 26.8 | 6.9 | G. Kawasaki, pers. comm. |
| Total | | | 48 | 0 | 19 | 14.8 | 3.0 | |
| *his7-MAL3* | | | 6 | 1 | 22 | 49.7 | 12.4 | 48 |
| *MAL3-MGL2* | | | 377 | 0 | 4 | 0.5 | 0.3 | B. Rockmill, pers. comm. |
| *MAL3-MGL2* | | | 123 | 0 | 0 | 0 | 0 | 70 |
| Total | | | 500 | 0 | 4 | 0.4 | 0.2 | |
| *MAL3-SUC3* | | | 248 | 0 | 2 | 0.4 | 0.3 | B. Rockmill, pers. comm. |
| *MAL3-SUC3* | | | 124 | 0 | 0 | 0 | | 70 |
| Total | | | 372 | 0 | 2 | 0.3 | 0.2 | |
| *SUC3-MGL2* | | | 204 | 0 | 3 | 0.7 | 0.4 | B. Rockmill, pers. comm. |
| *SUC3-MGL2* | | | 61 | 0 | 1 | 3.1 | 1.5 | 70 |
| Total | | | 265 | 0 | 4 | 0.75 | 0.38 | |

[a] See footnote *a* of Table 1.

or groups of genes has been assigned to a chromosome arm by mitotic crossover analysis only, i.e., there is no evidence of meiotic linkage, we have arbitrarily assigned a minimum distance of 100 centimorgans (cM) to the relevant intervals. For example, *SUC1* shows clear mitotic linkage to *cly8* on the right arm of chromosome VII. Extensive tetrad analysis, however, has failed to reveal any evidence for meiotic linkage between these genes (H. Roman, personal communication; Table 7). Accordingly, we have assigned a minimum distance of 100 cM for the *cly8-SUC1* interval.

The map in Fig. 1 describes the location of 317 genes on 17 chromosomes and three fragments. The total minimum length of this map is 4,600 cM (using 100 cM for intervals defined only by mitotic crossing over).

In addition to the map, we have compiled a glossary of gene symbols (Table 19) and a list of mapped genes (Table 20). A list of gene products has been published by Plischke et al. (79).

TABLE 3. *Tetrad analysis data for chromosome III*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *HML-his4* | | | 55 | 1 | 52 | 27.0 | 3.7 | A. Klar, pers. comm. |
| *HML-leu2* | | | 31 | 2 | 77 | 40.9 | 4.5 | A. Klar, pers. comm. |
| *HML-MAT* | | | 116 | 54 | 272 | 111.2 | 27.1 | 32 |
| *glk1-his4* | | | 43 | 1 | 29 | 24.4 | 5.4 | P. Maitra and Z. Lobo, pers. comm. |
| *glk1-leu2* | | | 20 | 2 | 48 | 43.9 | 7.3 | P. Maitra and Z. Lobo, pers. comm. |
| *his4-leu2* | | | 102 | 0 | 35 | 13.2 | 2.0 | R. Mortimer, pers. comm. |
| *his4-leu2* | | | 281 | 4 | 157 | 20.7 | 1.9 | J. McCusker and J. Haber, pers. comm. |
| *his4-leu2* | | | 80 | 0 | 28 | 13.4 | 2.3 | A. Klar, pers. comm. |
| *his4-leu2* | | | 44 | 0 | 30 | 21.3 | 3.2 | P. Maitra and Z. Lobo, pers. comm. |
| *his4-leu2* | | | 340 | 1 | 114 | 13.2 | 1.2 | S. Fogel, pers. comm. |
| *his4-leu2* | | | 1,156 | 9 | 566 | 18.0 | 0.8 | T. Takahashi, pers. comm. |
| *his4-leu2* | | | 53 | 0 | 35 | 20.9 | 2.9 | 106 |
| *his4-leu2* | | | 677 | 9 | 304 | 18.3 | 1.2 | G. Sprague and J. Rine, pers. comm. |
| *his4-leu2* | | | 85 | 0 | 21 | 10.1 | 2.0 | 13 |
| Total | | | 2,818 | 23 | 1,290 | 17.4 | 0.5 | |
| *his4-cen3* | 1,528 | 859 | | | | 19.3 | 0.6 | T. Takahashi, pers. comm. |
| *his4-SUF2* | | | 113 | 0 | 72 | 20.4 | 2.0 | 13 |
| *his4-MAT* | | | 28 | 4 | 59 | 48.5 | 9.1 | 106 |
| *his4-MAT* | | | 310 | 54 | 558 | 53.8 | 4.0 | J. McCusker and J. Haber, pers. comm. |
| *his4-MAT* | | | 343 | 58 | 827 | 51.0 | 2.6 | F. Tavares and R. Mortimer, pers. comm. |
| *his4-MAT* | | | 335 | 65 | 798 | 54.0 | 3.0 | S. Fogel and R. Mortimer, pers. comm. |
| *his4-MAT* | | | 643 | 97 | 1,277 | 49.7 | 2.1 | T. Takahashi, pers. comm. |
| Total | | | 1,659 | 278 | 3,519 | 51.5 | 1.4 | |
| *leu2-cdc10* | | | 106 | 0 | 38 | 13.6 | 1.9 | R. Mortimer, pers. comm. |
| *leu2-cdc10* | | | 103 | 0 | 9 | 4.1 | 1.3 | J. McCusker and J. Haber, pers. comm. |
| Total | | | 209 | 0 | 47 | 9.4 | 1.3 | |
| *leu2-SUP53* | | | 84 | 0 | 2 | 1.2 | 0.9 | 81; C. Reed and S. Liebman, pers. comm. |
| *leu2-cen3* | 244 | 36 | | | | 6.6 | 1.0 | 70 |
| *leu2-cen3* | 134 | 18 | | | | 6.0 | 1.4 | 13 |
| *leu2-cen3* | 222 | 60 | | | | 11.0 | 1.3 | R. Mortimer, pers. comm. |
| *leu2-cen3* | 441 | 31 | | | | 3.3 | 0.6 | S. Fogel and R. Mortimer, pers. comm. |
| *leu2-cen3* | 2,751 | 259 | | | | 4.4 | 0.3 | T. Takahashi, pers. comm. |
| Total | 3,792 | 404 | | | | 4.9 | 0.2 | |
| *leu2-SUF2* | | | 327 | 0 | 50 | 6.7 | 0.9 | 13 |

TABLE 3—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *leu2-pgk1* | | | 110 | 0 | 28 | 10.4 | 1.8 | R. Mortimer, pers. comm. |
| *leu2-MAT* | | | 186 | 9 | 277 | 35.6 | 2.3 | S. Fogel and R. Mortimer, pers. comm. |
| *leu2-MAT* | | | 42 | 3 | 46 | 37.2 | 8.1 | 106 |
| *leu2-MAT* | | | 132 | 3 | 104 | 25.8 | 2.8 | 57 |
| *leu2-MAT* | | | 231 | 2 | 142 | 20.6 | 1.7 | 99 |
| *leu2-MAT* | | | 333 | 6 | 249 | 24.4 | 1.7 | 99 |
| *leu2-MAT* | | | 419 | 41 | 555 | 42.4 | 2.8 | G. Sprague and J. Rine, pers. comm. |
| *leu2-MAT* | | | 199 | 14 | 319 | 38.9 | 2.6 | J. McCusker and J. Haber, pers. comm. |
| *leu2-MAT* | | | 1,144 | 72 | 1,349 | 36.1 | 1.3 | T. Takahashi, pers. comm. |
| Total | | | 2,686 | 150 | 3,041 | 34.7 | 0.8 | |
| *leu2-thr4* | | | 29 | 6 | 54 | 58.9 | 15.5 | 106 |
| *leu2-thr4* | | | 124 | 8 | 167 | 37.1 | 3.7 | 99 |
| *leu2-thr4* | | | 211 | 23 | 282 | 44.3 | 4.3 | 99 |
| *leu2-thr4* | | | 55 | 13 | 146 | 57.9 | 7.9 | J. McCusker and J. Haber, pers. comm. |
| Total | | | 419 | 50 | 649 | 45.8 | 2.8 | |
| *cdc10-cen3* | 24 | 0 | | | | 0 | | 71 |
| *cdc10-cen3* | 152 | 0 | | | | 0 | | 13 |
| *cdc10-cen3* | 131 | 2 | | | | 0.7 | 0.5 | R. Mortimer, pers. comm. |
| Total | 307 | 2 | | | | 0.3 | 0.2 | |
| *cdc10-SUF2* | | | 252 | 0 | 5 | 1.0 | 0.4 | 13 |
| *cdc10-pgk1* | | | 96 | 0 | 2 | 1.0 | 0.7 | R. Mortimer, pers. comm. |
| *cen3-SUF2* | 135 | 5 | | | | 1.8 | 0.8 | 13 |
| *cen3-pgk1* | 237 | 10 | | | | 2.0 | 0.6 | R. Mortimer, pers. comm. |
| *cen3-cly9* | 16 | 3 | | | | 8.1 | 4.4 | 71 |
| *cen3-pet18* | 58 | 12 | | | | 8.8 | 2.4 | 109 |
| *cen3-pet18* | 23 | 10 | | | | 16.0 | 4.5 | 71 |
| Total | 81 | 22 | | | | 11.1 | 2.2 | |
| *cen3-MAT* | 650 | 432 | | | | 21.6 | 0.9 | 35 |
| *cen3-MAT* | 1,463 | 1,015 | | | | 22.2 | 0.6 | 70 |
| *cen3-MAT* | 184 | 158 | | | | 25.4 | 1.7 | 109 |
| *cen3-MAT* | 3,874 | 3,667 | | | | 26.9 | 0.4 | T. Takahashi, pers. comm. |
| Total | 6,171 | 5,272 | | | | 25.3 | 0.3 | |
| *SUF2-pgk1* | | | 60 | 0 | 6 | 4.6 | 1.8 | G. Fink and C. Styles, pers. comm. |
| *pgk1-pet18* | | | 53 | 0 | 13 | 10.1 | 2.6 | G. Fink and C. Styles, pers. comm. |
| *pgk1-MAT* | | | 71 | 0 | 55 | 23.1 | 2.5 | 50 |
| *pgk1-MAT* | | | 140 | 1 | 95 | 21.4 | 2.0 | R. Mortimer, pers. comm. |
| *pgk1-MAT* | | | 40 | 0 | 26 | 20.7 | 3.4 | G. Fink and C. Styles, pers. comm. |
| Total | | | 251 | 1 | 176 | 21.3 | 1.4 | |

TABLE 3—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *pgk1-thr4* | | | 29 | 4 | 66 | 47.8 | 8.0 | 50 |
| *pet18-MAT* | | | 42 | 0 | 6 | 6.4 | 2.5 | 71 |
| *pet18-MAT* | | | 84 | 1 | 23 | 13.8 | 3.9 | 109 |
| *pet18-MAT* | | | 42 | 0 | 18 | 15.6 | 3.2 | 109 |
| *pet18-MAT* | | | 49 | 0 | 17 | 13.2 | 2.9 | G. Fink and C. Styles, pers. comm. |
| Total | | | 217 | 1 | 64 | 12.5 | 1.7 | |
| *cly9-MAT* | | | 14 | 0 | 3 | 9.0 | 4.8 | 71 |
| *cry1-MAT* | | | 180 | 0 | 8 | 2.1 | 0.7 | 93 |
| *cry1-MAT* | | | 83 | 0 | 4 | 2.3 | 1.1 | 27 |
| *cry1-MAT* | | | 25 | 0 | 1 | 1.9 | 1.9 | 27 |
| *cry1-MAT* | | | 97 | 0 | 9 | 4.3 | 1.4 | 67 |
| *cry1-MAT* | | | 1,276 | 2 | 106 | 4.3 | 0.5 | G. Sprague and J. Rine, pers. comm. |
| *cry1-MAT* | | | 28 | 0 | 1 | 1.8 | 1.7 | J. McCusker and J. Haber, pers. comm. |
| Total | | | 1,689 | 2 | 129 | 3.9 | 0.4 | |
| *cry1-tsm1* | | | 202 | 0 | 24 | 5.4 | 1.1 | G. Sprague and J. Rine, pers. comm. |
| *cry1-tsm1* | | | 27 | 0 | 2 | 3.5 | 2.4 | J. McCusker and J. Haber, pers. comm. |
| Total | | | 229 | 0 | 26 | 5.2 | 1.0 | |
| *MAT-tsm1* | | | 221 | 0 | 2 | 0.5 | 0.3 | G. Sprague and J. Rine, pers. comm. |
| *MAT-tsm1* | | | 51 | 0 | 4 | 3.7 | 1.8 | J. McCusker and J. Haber, pers. comm. |
| Total | | | 272 | 0 | 6 | 1.1 | 0.4 | |
| *MAT-thr4* | | | 29 | 0 | 24 | 24.1 | 3.9 | 54 |
| *MAT-thr4* | | | 268 | 4 | 162 | 21.8 | 1.9 | 70 |
| *MAT-thr4* | | | 23 | 0 | 41 | 35.1 | 3.9 | Y. Kassir and I. Herskowitz, pers. comm. |
| *MAT-thr4* | | | 58 | 1 | 37 | 22.6 | 4.2 | 106 |
| *MAT-thr4* | | | 214 | 1 | 114 | 18.3 | 1.6 | 99 |
| *MAT-thr4* | | | 387 | 5 | 165 | 17.7 | 1.7 | 99 |
| *MAT-thr4* | | | 56 | 0 | 40 | 20.8 | 2.5 | 50 |
| *MAT-thr4* | | | 1,092 | 23 | 730 | 23.9 | 1.0 | T. Takahashi, pers. comm. |
| *MAT-thr4* | | | 273 | 2 | 161 | 19.9 | 1.5 | J. McCusker and J. Haber, pers. comm. |
| *MAT-thr4* | | | 34 | 2 | 15 | 32.8 | 19.4 | 59 |
| Total | | | 2,434 | 38 | 1,489 | 21.9 | 0.6 | |
| *MAT-rad18* | | | 29 | 1 | 22 | 27.7 | 7.7 | 71 |
| *MAT-rad18* | | | 13 | 3 | 26 | 63.7 | 24.0 | 85 |
| *MAT-rad18* | | | 44 | 2 | 52 | 33.3 | 5.5 | J. McCusker and J. Haber, pers. comm. |
| Total | | | 86 | 6 | 100 | 37.2 | 5.2 | |
| *MAT-tsm5* | | | 18 | 2 | 20 | 45.3 | 18.6 | G. Fink, pers. comm. |
| *MAT-tsm5* | | | 225 | 6 | 238 | 29.5 | 2.0 | J. McCusker and J. Haber, pers. comm. |
| Total | | | 243 | 8 | 258 | 30.1 | 1.9 | |
| *MAT-tup1* | | | 35 | 0 | 37 | 27.6 | 3.5 | 106 |
| *MAT-tup1* | | | 33 | 1 | 45 | 32.5 | 4.8 | 106 |
| *MAT-tup1* (*umr7*) | | | 15 | 1 | 46 | 42.2 | 5.5 | 54 |
| *MAT-tup1* | | | 20 | 3 | 40 | 49.5 | 12.0 | J. McCusker and J. Haber, pers. comm. |
| Total | | | 103 | 5 | 168 | 36.3 | 3.0 | |

TABLE 3—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *MAT-SUP61* | | | 35 | 3 | 53 | 40.7 | 7.6 | 71 |
| *MAT-SUP61* | | | 18 | 0 | 27 | 32.8 | 4.6 | 7 |
| Total | | | 53 | 3 | 80 | 36.8 | 4.7 | |
| *MAT-SAD1* | | | 95 | 9 | 141 | 42.0 | 5.1 | Y. Kassir and I. Herskowitz, pers. comm. |
| *MAT-mak14* | | | 67 | 15 | 74 | 89.1 | 44.4 | 111 |
| *MAT-cdc39* | | | 61 | 6 | 132 | 43.4 | 4.6 | J. Shuster, pers. comm. |
| *MAT-MAL2* | | | 22 | 9 | 46 | 105.2 | 60.1 | Y. Kassir and I. Herskowitz, pers. comm. |
| *MAT-HMR* | | | 17 | 2 | 41 | 45.6 | 8.8 | Y. Kassir and I. Herskowitz, pers. comm. |
| *MAT-HMR* | | | 63 | 13 | 138 | 56.4 | 8.3 | 32 |
| Total | | | 80 | 15 | 179 | 53.7 | 6.5 | |
| *thr4-rad18* | | | 47 | 1 | 12 | 16.4 | 8.2 | J. McCusker and J. Haber, pers. comm. |
| *thr4-tup1* | | | 43 | 0 | 34 | 23.4 | 3.2 | 106 |
| *thr4-tup1* (*umr7*) | | | 27 | 0 | 28 | 27.3 | 4.0 | 54 |
| *thr4-tup1* | | | 25 | 0 | 35 | 31.8 | 3.9 | J. McCusker and J. Haber, pers. comm. |
| Total | | | 95 | 0 | 97 | 27.1 | 2.1 | |
| *thr4-SUP61* | | | 31 | 0 | 14 | 16.2 | 3.7 | 7 |
| *thr4-SAD1* | | | 15 | 0 | 16 | 27.8 | 5.3 | Y. Kassir and I. Herskowitz, pers. comm. |
| *thr4-mak14* | | | 38 | 0 | 8 | 8.9 | 2.9 | 111 |
| *thr4-cdc39* | | | 31 | 2 | 34 | 36.0 | 8.7 | J. Shuster, pers. comm. |
| *thr4-HMR* | | | 42 | 4 | 62 | 42.1 | 7.7 | A. Klar, pers. comm. |
| *thr4-MAL2* | | | 39 | 3 | 59 | 39.5 | 6.7 | A. Klar, pers. comm. |
| *thr4-MAL2* | | | 18 | 2 | 41 | 44.9 | 8.7 | Y. Kassir and I. Herskowitz, pers. comm. |
| *thr4-MAL2* | | | 29 | 4 | 50 | 48.4 | 10.9 | 59 |
| *thr4-MAL2* | | | 73 | 27 | 144 | 97.0 | 28.4 | J. McCusker and J. Haber, pers. comm. |
| Total | | | 159 | 36 | 294 | 62.6 | 7.6 | |
| *rad18-tup1* | | | 31 | 1 | 26 | 28.2 | 6.7 | J. McCusker and J. Haber, pers. comm. |
| *rad18-tup1* (*cyc9*) | | | 28 | 0 | 14 | 17.3 | 4.0 | 85 |
| Total | | | 59 | 1 | 40 | 23.2 | 4.0 | |
| *SAD1-HMR* | | | 17 | 1 | 25 | 36.9 | 8.7 | Y. Kassir and I. Herskowitz, pers. comm. |
| *SAD1-MAL2* | | | 13 | 4 | 20 | 99.0 | 91.1 | Y. Kassir and I. Herskowitz, pers. comm. |

TABLE 3—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *SUP61-MAL2* | | | 23 | 0 | 21 | 25.5 | 4.4 | 7 |
| *HMR-MAL2* | | | 105 | 0 | 2 | 1.0 | 0.7 | A. Klar, pers. comm. |
| *HMR-MAL2* | | | 52 | 0 | 2 | 1.9 | 1.4 | 49a |
| Total | | | 157 | 0 | 4 | 1.3 | 0.6 | |

[a] See footnote *a* of Table 1.

## TETRAD DATA ANALYSIS

Map distances usually are determined from tetrad analysis data, using the equation derived by Perkins (77a), i.e.,

$$x_p = \frac{100}{2} \cdot \left( \frac{T + 6NPD}{PD + NPD + T} \right)$$

This equation is valid only for short distances (≤35 cM) because it assumes that the probability of more than two exchanges in an interval is zero. Snow (96) has developed a set of equations for calculating map distances that considers all exchange classes. These equations are complex and must be solved by iteration using a computer. They yield, for each set of PD, NPD, and T values, values for the map distance $x'$ and chiasma interference coefficient $k$. The values of $x'$ for different sets of tetrad data are always equal to or larger than $x_p$. The difference between $x'$ and $x_p$ is small for distances up to about 35 cM but becomes progressively larger at greater distances. For example, the tetrad data (PD:NPD:T) for genes *cyh2* and *trp5*, which are located on the left arm of chromosome VII, are 692:14:1181. The $x'$ and $x_p$ values determined from these data are 42.0 and 40.4 cM, respectively. These distances differ by only 3.9%. For the gene pair *ura3-hom3*, located on chromosome V, the cumulative PD:NPD:T data are 538:101:1467. The $x'$ and $x_p$ values are 52.4 and 49.2 cM, respectively, and the error in using $x_p$ would be 6.5%. The tetrad data for *ade5,7-lys5* on chromosome VII are 100:26:240. These data yield $x'$ and $x_p$ values of 62.6 and 54.1 cM, respectively. In this case, the $x_p$ value differs from the $x'$ value by 13.6%. At still greater distances, the differences become much larger.

Because all exchange classes are considered, we believe that the equations for $x'$ yield more accurate representations of the true map distances and accordingly have presented only these values in Tables 1 through 18. However, we have determined values of $x_p$, as well, for all of these data, and a plot of $x'$ versus $x_p$ is presented in Fig. 2. This plot can be used to estimate $x'$ after first determining $x_p$ from the Perkins (77a) equation.

Gene-centromere distances normally are calculated as one-half of the second-division segregation frequency. This calculation assumes complete chiasma interference, which does not apply. We again used the Snow equations to calculate $x'$ from second-division segregation values. A plot of $x'$ versus second-division segregation for different interference values is presented in Fig. 3. The average interference for several intervals in yeast is 0.36 (96; R. K. Mortimer and D. Schild, unpublished data).

## COMMENTS ON THE CHROMOSOMES AND FRAGMENTS

The data in Tables 1 through 18, in most cases, permit unambiguous determinations of the relative orders of most of the genes on the different chromosomes; however, several ambiguities in sequence remain. These sequence ambiguities, as well as other mapping information pertaining to each of the chromosomes, are discussed below.

### Chromosome I

Chromosome I was identified originally by centromere-linked gene *ade1* (56a). Nine genes are now located on this chromosome, and its total length is approximately 90 cM. On the left arm, the relative arrangements of *tsl1, cyc3,* and *pyk1* (*cdc19*) are tentative. The order of centromere *let1-ade1-cdc15* is known because exchanges in the *let1-ade1* and *ade1-cdc15* intervals have been observed. Although several earlier publications had presented evidence indicating that a significant fraction of the ribosomal ribonucleic acid (RNA) genes are located on chromosome I, recent studies by Petes (78) have shown that this is unlikely and that instead all of these genes are on chromosome XII. The *pyk1* gene (pyruvate kinase) has been shown to be an allele of the cell division cycle mutation *cdc19* (48).

TABLE 4. *Tetrad analysis data for chromosome IV*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | x' (cM) | SE | |
| *SUC-HO* | | | 40 | 1 | 27 | 24.7 | 5.8 | 48; G. Kawasaki, pers. comm. |
| *HO-cdc9* | | | 19 | 0 | 24 | 30.3 | 4.6 | 48; G. Kawasaki, pers. comm. |
| *cdc9-ste7* | | | 53 | 0 | 5 | 4.4 | 1.9 | J. Shuster, pers. comm. |
| *cdc9-cdc2* | | | 20 | 1 | 24 | 34.2 | 8.5 | 33 |
| *cdc36-ste7* | | | 73 | 0 | 2 | 1.3 | 0.9 | J. Shuster, pers. comm. |
| *cdc36-cdc2* | | | 11 | 0 | 5 | 16.3 | 6.3 | J. Shuster, pers. comm. |
| *ste7-cdc2* | | | 17 | 0 | 10 | 19.4 | 5.2 | J. Shuster, pers. comm. |
| *pho2-rna11* | | | 35 | 3 | 58 | 41.1 | 7.0 | A. Toh-e, pers. comm. |
| *pho2-trp1* | | | 74 | 15 | 193 | 54.3 | 6.0 | A. Toh-e, pers. comm. |
| *pho2-mak21* | | | 34 | 9 | 105 | 59.0 | 9.3 | A. Toh-e, pers. comm. |
| *cdc2-mar1* | | | 22 | 1 | 21 | 31.7 | 9.0 | 49 |
| *cdc2-trp1* | | | 23 | 3 | 75 | 47.1 | 6.0 | 71 |
| *cdc2-trp1* | | | 19 | 6 | 32 | 92.3 | 57.2 | 111 |
| Total | | | 42 | 9 | 107 | 55.8 | 8.7 | |
| *mar1-trp1* | | | 25 | 0 | 30 | 29.5 | 4.1 | 49 |
| *rna11-trp1* | | | 60 | 0 | 30 | 17.4 | 2.7 | 71 |
| *rna11-trp1* | | | 84 | 0 | 45 | 18.2 | 2.3 | 111 |
| *rna11-trp1* | | | 64 | 0 | 33 | 17.7 | 2.6 | A. Toh-e, pers. comm. |
| Total | | | 208 | 0 | 108 | 17.8 | 1.5 | |
| *rna11-mak21* | | | 37 | 3 | 47 | 37.8 | 6.8 | A. Toh-e, pers. comm. |
| *cdc7-trp1* | | | 15 | 0 | 2 | 6.0 | 4.0 | 71 |
| *cdc7-trp1* | | | 108 | 0 | 8 | 3.5 | 1.2 | 77 |
| Total | | | 123 | 0 | 10 | 3.8 | 1.2 | |
| *cen4-trp1* | 2,112 | 20 | | | | 0.5 | 0.3 | 70 |
| *cen4-trp1* | 3,893 | 35 | | | | 0.4 | 0.1 | T. Takahashi, pers. comm. |
| Total | 6,005 | 55 | | | | 0.45 | 0.12 | |
| *lts4-cen4* | 68 | 3 | | | | 2.1 | 1.2 | 91 |
| *lts10-cen4* | 35 | 0 | | | | 0 | | 91 |
| *trp1-lts4* | | | 34 | 0 | 1 | 1.5 | 1.4 | 91 |
| *trp1-lts10* | | | 35 | 0 | 0 | 0 | | 91 |
| *trp1-gal3* | | | 123 | 0 | 1 | 0.4 | 0.4 | 18 |
| *trp1-rad57* | | | 12 | 0 | 2 | 7.3 | 4.9 | 24 |
| *trp1-rad57* | | | 29 | 0 | 1 | 1.7 | 1.7 | 77 |
| Total | | | 41 | 0 | 3 | 3.5 | 1.9 | |

TABLE 4—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | *x'* (cM) | SE | |
| *trp1-SUP27* | | | 91 | 0 | 30 | 12.8 | 2.1 | 77 |
| *trp1-rad55* | | | 24 | 2 | 61 | 42.6 | 5.7 | 71 |
| *cen4-ts225* | 33 | 43 | | | | 32.2 | 4.0 | F. Hilger, pers. comm. |
| *trp1-ts225* | | | 14 | 2 | 25 | 49.0 | 15.5 | F. Hilger, pers. comm. |
| *trp1-nu13* | | | 14 | 6 | 44 | 78.3 | 26.6 | 71 |
| *trp1-mak21* | | | 71 | 10 | 218 | 47.9 | 3.8 | 111 |
| *trp1-mak24* | | | 52 | 2 | 44 | 29.4 | 5.7 | A. Toh-e, pers. comm. |
| Total | | | 123 | 12 | 262 | 43.3 | 3.2 | |
| *rad57-SUP27* | | | 54 | 1 | 14 | 15.5 | 6.7 | 77 |
| *SUP27-rad55* | | | 35 | 2 | 19 | 31.8 | 14.1 | 77 |
| *mak21-aro1* | | | 66 | 9 | 121 | 48.0 | 6.7 | 111 |
| *nul3-aro1* | | | 52 | 0 | 31 | 19.6 | 2.9 | 71 |
| *aro1-hom2* | | | 329 | 0 | 90 | 11.0 | 1.1 | 70 |
| *aro1-hom2* | | | 57 | 0 | 5 | 4.1 | 1.8 | 71 |
| *aro1-hom2* | | | 28 | 0 | 2 | 3.4 | 2.3 | R. Contopoulou, pers. comm. |
| Total | | | 414 | 0 | 97 | 9.7 | 0.9 | |
| *aro1-sup35* | | | 65 | 1 | 37 | 21.1 | 3.9 | 36 |
| *aro1-arg82* | | | 43 | 0 | 16 | 14.0 | 3.1 | F. Hilger, pers. comm. |
| *aro1-pet14* | | | 87 | 2 | 91 | 28.8 | 3.1 | 111 |
| *aro1-pet14* | | | 10 | 0 | 15 | 32.9 | 6.2 | R. Contopoulou, pers. comm. |
| *aro1-pet14* | | | 19 | 0 | 42 | 38.6 | 4.1 | F. Hilger, pers. comm. |
| Total | | | 116 | 2 | 148 | 30.2 | 2.2 | |
| *aro1-rad50* | | | 10 | 1 | 16 | 42.9 | 15.1 | R. Contopoulou, pers. comm. |
| *hom2-sup35* | | | 46 | 0 | 4 | 4.1 | 2.0 | 70 |
| *hom2-pet14* | | | 19 | 0 | 40 | 37.9 | 4.1 | 71 |
| *sup35-pet14* | | | 20 | 0 | 20 | 26.8 | 4.7 | 71 |
| *arg82-pet14* | | | 47 | 0 | 42 | 25.1 | 3.1 | F. Hilger, pers. comm. |
| *arg82-SUP2* | | | 18 | 7 | 68 | 67.5 | 14.7 | F. Hilger, pers. comm. |
| *pet14-rad50* | | | 18 | 0 | 10 | 18.7 | 5.0 | R. Contopoulou, pers. comm. |
| *pet14-SUP2* | | | 33 | 0 | 27 | 23.9 | 3.7 | 71 |
| *pet14-SUP2* | | | 24 | 2 | 37 | 40.5 | 8.8 | F. Hilger, pers. comm. |
| Total | | | 57 | 2 | 64 | 31.3 | 4.4 | |
| *pet14-lys4* | | | 15 | 1 | 10 | 34.9 | 20.5 | R. Contopoulou, pers. comm. |

TABLE 4—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | *x'* (cM) | SE | |
| *rad50-fol1* | | | 121 | 0 | 7 | 2.8 | 1.0 | J. Game and J. Little, pers. comm. |
| *rad50-lys4* | | | 9 | 0 | 11 | 29.8 | 6.8 | R. Contopoulou, pers. comm. |
| *SUP2-trp4* | | | 17 | 0 | 46 | 41.5 | 4.0 | 71 |
| *asp1-trp4* | | | 136 | 1 | 68 | 18.1 | 2.2 | 46 |
| *asp1-trp4* | | | 35 | 0 | 11 | 12.3 | 3.3 | 45 |
| Total | | | 171 | 1 | 79 | 17.0 | 1.9 | |
| *asp1-ade8* | | | 10 | 5 | 26 | 108.5 | 78.7 | 45 |
| *trp4-ade8* | | | 31 | 1 | 29 | 29.2 | 6.3 | 71 |
| *trp4-ade8* | | | 14 | 1 | 28 | 40.3 | 8.4 | 45 |
| *trp4-ade8* | | | 40 | 3 | 69 | 39.9 | 5.8 | T. Takahashi, pers. comm. |
| Total | | | 85 | 5 | 126 | 36.9 | 3.9 | |
| *ade8-pur5* | | | 21 | 0 | 6 | 11.4 | 4.2 | 2 |
| *ade8-rna3* | | | 23 | 2 | 36 | 41.0 | 9.2 | 71 |

[a] See footnote *a* of Table 1.

## Chromosome II

Chromosome II was originally identified by centromere-linked gene *gal1* (56a). Twenty-nine genes have been mapped on this chromosome, which now has a total genetic length of approximately 270 cM. Lindegren et al. (57) reported a cycloheximide resistance gene near the centromere of chromosome II and, although complementation tests have not been run, it is probably allelic to *cyh1*. The order *gal7-gal10-gal1* was established by examination of rare recombinants between these tightly linked, functionally related genes (6). Because many genes on the right arm of this chromosome have not been mapped against each other, several areas of sequence ambiguity exist, particularly in the interval between *lys2* and *met8*. Of the genes in this interval, the proximal-to-distal order of *lys2-cdc28-tyr1-pet11-dur1-dur2-met8* is known (12, 71). However, the order of *lys2*, *mak4*, and *cyc8* with regard to each other and with regard to outside markers is not known. Likewise, the orders of *glc1-sup45-mak5-pgi1-cdc28-fdp1* and *tyr1-pet11-sup46* are still tentative. *sup45* and *sup46* both are omnipotent suppressors; i.e., they act on all three nonsense codons. Several studies have reported only two such suppressor loci; one has been mapped on chromosome II and one has been mapped on chromosome IV (36). *sup46* has not been tested for linkage to *sup45*, and it is possible they are alleles even though they have been tentatively placed in different locations on chromosome II. The *dur1,2* locus appears to code for one peptide which has two functions (12). *rna5* has recently been shown to be proximal rather than distal to *his7* (71; G. Kawasaki, personal communications). The relative order of *MGL2-SUC3-MAL3* has been determined (B. Rockmill, personal communication), but it has not been determined whether *MGL2* or *MAL3* is the most distal.

## Chromosome III

The "mating type" chromosome is about 150 cM in length and has 22 mapped genes distributed along its length. The left arm constitutes about one-third of the chromosome. Of special interest are genes *HML*, *HMR*, and *MAT*, which are all involved in determining the mating type of a cell. *HML* and *HMR* are normally the silent "cassettes" of the mating type alleles $\alpha$ and **a**, respectively, that can be inserted at *MAT* under the direction of the homothallism gene *HO*. *MAT* is the functional locus that expresses either **a** or $\alpha$ information (for a review, see reference 36a). Several uncertainties in sequences of genes exist. *HML* and *glk1* have both been mapped against *his4* and *leu2* and are

TABLE 5. *Tetrad analysis data for chromosome V*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | x' (cM) | SE | |
| *can1-prb1* | | | 176 | 0 | 4 | 1.1 | 0.6 | B. Jones, A. Mitchell, and G. Zubenko, pers. comm. |
| *can1-mak10* | | | 119 | 0 | 16 | 6.0 | 1.4 | 89 |
| *can1-mak10* | | | 52 | 1 | 9 | 14.1 | 9.6 | 109 |
| *can1-mak10* | | | 156 | 0 | 24 | 6.8 | 1.3 | B. Jones, A. Mitchell, and G. Zubenko, pers.comm. |
| Total | | | 327 | 1 | 49 | 7.3 | 1.2 | |
| *can1-min1* | | | 20 | 1 | 13 | 30.2 | 13.6 | 89 |
| *mak10-min1* | | | 114 | 1 | 11 | 7.5 | 4.2 | 89 |
| *can1-cyc7* | | | 74 | 1 | 58 | 24.2 | 3.1 | 89 |
| *can1-cyc7* | | | 171 | 5 | 113 | 25.4 | 3.1 | 88 |
| Total | | | 245 | 6 | 171 | 25.0 | 2.3 | |
| *can1-ura3* | | | 50 | 1 | 73 | 31.9 | 3.2 | S. Fogel and R. Mortimer, pers. comm. |
| *can1-ura3* | | | 31 | 5 | 60 | 51.2 | 10.7 | 71 |
| *can1-ura3* | | | 414 | 49 | 798 | 45.5 | 2.2 | 80 |
| *can1-ura3* | | | 6 | 0 | 23 | 46.3 | 6.0 | 109 |
| *can1-ura3* | | | 103 | 10 | 173 | 42.6 | 4.4 | 88 |
| Total | | | 604 | 65 | 1,127 | 44.2 | 1.8 | |
| *can1-cho1* | | | 19 | 8 | 76 | 69.1 | 14.5 | 3 |
| *prb1-mak10* | | | 160 | 0 | 20 | 5.6 | 1.2 | B. Jones, A. Mitchell, and G. Zubenko, pers. comm. |
| *mak10-ura3* | | | 10 | 0 | 19 | 36.4 | 5.8 | 109 |
| *SUS1-ura3* | | | 41 | 2 | 41 | 32.6 | 6.7 | 70 |
| *min1-cyc7* | | | 147 | 1 | 24 | 8.9 | 2.5 | 89 |
| *cyc7-ura3* | | | 198 | 1 | 113 | 19.1 | 1.7 | 89 |
| *cyc7-ura3* | | | 176 | 1 | 106 | 19.8 | 1.8 | 88 |
| Total | | | 374 | 2 | 219 | 19.4 | 1.2 | |
| *ura3-mnn1* | | | 78 | 0 | 10 | 5.7 | 1.8 | 1 |
| *ura3-cen5* | 512 | 58 | | | | 5.2 | 0.7 | 70 |
| *ura3-cen5* | 4,060 | 772 | | | | 8.2 | 0.3 | T. Takahashi, pers. comm. |
| *ura3-cen5* | 235 | 57 | | | | 10.6 | 1.4 | 89 |
| Total | 4,807 | 887 | | | | 8.0 | 0.3 | |
| *ura3-SUP71* | | | 32 | 0 | 10 | 12.3 | 3.5 | 71 |
| *ura3-arg9* | | | 52 | 0 | 9 | 7.5 | 2.4 | 70 |
| *ura3-arg9* | | | 139 | 0 | 32 | 9.6 | 1.6 | R. Snow, pers. comm. |
| Total | | | 191 | 0 | 41 | 9.0 | 1.3 | |
| *ura3-cho1* | | | 70 | 3 | 97 | 34.3 | 3.8 | 57 |
| *ura3-cho1* | | | 58 | 4 | 44 | 35.6 | 9.4 | 3 |
| *ura3-cho1* | | | 25 | 0 | 17 | 21.3 | 4.3 | R. Snow, pers. comm. |
| Total | | | 153 | 7 | 158 | 32.3 | 3.2 | |
| *ura3-hom3* | | | 73 | 2 | 131 | 34.8 | 2.6 | 70 |
| *ura3-hom3* | | | 203 | 43 | 703 | 53.2 | 2.7 | S. Fogel, pers. comm. |
| *ura3-hom3* | | | 147 | 41 | 354 | 65.3 | 6.9 | T. Takahashi, pers. comm. |

TABLE 5—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *ura3-hom3* | | | 69 | 4 | 148 | 39.3 | 3.2 | R. Snow, pers. comm. |
| *ura3-hom3* | | | 46 | 11 | 131 | 57.3 | 8.0 | 69 |
| Total | | | 538 | 101 | 1,467 | 52.4 | 2.0 | |
| *mnn1-cen5* | 41 | 0 | | | | 0 | | 1 |
| *cen5-SUP71* | 39 | 2 | | | | 2.5 | 1.7 | 71 |
| *cen5-arg9* | 72 | 5 | | | | 3.3 | 1.5 | 70 |
| *cen5-arg9* | 385 | 32 | | | | 3.9 | 0.6 | T. Takahashi, pers. comm. |
| Total | 457 | 37 | | | | 3.8 | 0.6 | |
| *arg9-hom3* | | | 14 | 1 | 21 | 38.7 | 10.7 | 70 |
| *arg9-hom3* | | | 57 | 16 | 165 | 61.7 | 8.4 | T. Takahashi, pers. comm. |
| *arg9-hom3* | | | 55 | 7 | 180 | 46.9 | 3.8 | R. Snow, pers. comm. |
| Total | | | 126 | 24 | 366 | 52.3 | 3.8 | |
| *cho1-hom3* | | | 48 | 1 | 57 | 29.9 | 3.7 | 3 |
| *cho1-his1* | | | 41 | 0 | 64 | 33.4 | 3.0 | 3 |
| *cho1-his1* | | | 17 | 0 | 25 | 32.6 | 4.7 | R. Snow, pers. comm. |
| *cho1-his1* | | | 23 | 0 | 21 | 25.5 | 4.4 | 57 |
| Total | | | 81 | 0 | 110 | 31.3 | 2.2 | |
| *cho1-arg6* | | | 20 | 0 | 26 | 30.7 | 4.5 | 57 |
| *hom3-his1* | | | 38 | 0 | 3 | 3.7 | 2.1 | 70 |
| *hom3-his1* | | | 3,566 | 0 | 181 | 2.4 | 0.2 | 21 |
| *hom3-his1* | | | 875 | 0 | 44 | 2.4 | 0.4 | S. Fogel, pers. comm. |
| *hom3-his1* | | | 38 | 0 | 3 | 3.7 | 2.1 | 75 |
| *hom3-his1* | | | 102 | 0 | 6 | 2.8 | 1.1 | 3 |
| *hom3-his1* | | | 313 | 0 | 18 | 2.7 | 0.6 | T. Takahashi, pers. comm. |
| *hom3-his1* | | | 28 | 0 | 1 | 1.8 | 1.7 | R. Snow, pers. comm. |
| *hom3-his1* | | | 205 | 0 | 19 | 4.3 | 0.9 | 69 |
| *hom3-his1* | | | 42 | 0 | 2 | 2.3 | 1.6 | J. Game and J. Little, pers. comm. |
| *hom3-his1* | | | 8,257 | 3 | 419 | 2.5 | 0.1 | 87 |
| Total | | | 13,464 | 3 | 696 | 2.5 | 0.1 | |
| *hom3-arg6* | | | 3,241 | 3 | 1,016 | 12.1 | 0.3 | 21 |
| *hom3-arg6* | | | 403 | 1 | 110 | 11.3 | 1.1 | T. Takahashi, pers. comm. |
| *hom3-arg6* | | | 197 | 1 | 46 | 10.7 | 1.8 | R. Snow, pers. comm. |
| Total | | | 3,841 | 5 | 1,172 | 12.0 | 0.3 | |
| *hom3-ilv1* | | | 82 | 0 | 56 | 21.4 | 2.4 | 39 |
| *hom3-ilv1* | | | 168 | 2 | 78 | 18.3 | 2.4 | R. Snow, pers. comm. |
| Total | | | 250 | 2 | 134 | 19.0 | 1.6 | |
| *hom3-ilv1* | | | 1,669 | 70 | 2,083 | 33.3 | 0.8 | 21 |
| *hom3-ilv1* | | | 316 | 19 | 435 | 36.6 | 2.2 | T. Takahashi, pers. comm. |
| *hom3-ilv1* | | | 108 | 3 | 79 | 26.1 | 3.6 | R. Snow, pers. comm. |
| Total | | | 2,093 | 92 | 2,597 | 33.5 | 0.8 | |
| *BOR1-his1* | | | 66 | 0 | 4 | 2.9 | 1.4 | 75 |
| *BOR1-arg6* | | | 54 | 0 | 12 | 9.3 | 2.5 | 75 |
| *BOR1-trp2* | | | 34 | 4 | 25 | 53.0 | 29.1 | 75 |

TABLE 5—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *his1-arg6* | | | 2,987 | 2 | 731 | 10.0 | 0.3 | 21 |
| *his1-arg6* | | | 63 | 0 | 9 | 6.3 | 2.0 | 70 |
| *his1-arg6* | | | 63 | 0 | 6 | 4.4 | 1.7 | 75 |
| *his1-arg6* | | | 829 | 5 | 108 | 7.5 | 1.0 | S. Fogel, pers. comm. |
| *his1-arg6* | | | 41 | 0 | 7 | 7.4 | 2.6 | 57 |
| *his1-arg6* | | | 183 | 0 | 38 | 8.8 | 1.3 | T. Takahashi, pers. comm. |
| *his1-arg6* | | | 138 | 0 | 28 | 8.6 | 1.5 | 69 |
| *his1-arg6* | | | 30 | 0 | 1 | 1.6 | 1.6 | R. Snow, pers. comm. |
| *his1-arg6* | | | 7,504 | 4 | 1,171 | 6.9 | 0.2 | 87 |
| Total | | | 11,838 | 11 | 2,099 | 7.8 | 0.2 | |
| *his1-SUP20* | | | 37 | 0 | 1 | 1.3 | 1.3 | 71 |
| *his1-SUP19* | | | 73 | 0 | 9 | 5.6 | 1.8 | B. Ono, J. Stewart, and F. Sherman, pers. comm. |
| *his1-ilv1* | | | 49 | 0 | 20 | 15.0 | 2.9 | 70 |
| *his1-ilv1* | | | 21 | 0 | 8 | 14.3 | 4.4 | S. Sora, pers. comm. |
| *his1-ilv1* | | | 26 | 0 | 14 | 18.3 | 4.2 | 57 |
| *his1-ilv1* | | | 38 | 0 | 15 | 14.6 | 3.3 | R. Snow, pers. comm. |
| Total | | | 134 | 0 | 57 | 15.5 | 1.8 | |
| *his1-trp2* | | | 41 | 2 | 39 | 32.2 | 6.9 | 75 |
| *his1-trp2* | | | 18 | 0 | 19 | 27.6 | 4.9 | 57 |
| *his1-trp2* | | | 1,635 | 50 | 1,759 | 30.2 | 0.8 | 21 |
| *his1-trp2* | | | 17 | 1 | 22 | 36.0 | 9.6 | R. Snow, pers. comm. |
| *his1-trp2* | | | 172 | 9 | 158 | 32.7 | 3.6 | T. Takahashi, pers. comm. |
| Total | | | 1,883 | 62 | 1,997 | 30.5 | 0.8 | |
| *his1-met5* | | | 15 | 0 | 14 | 25.8 | 5.4 | S. Sora, pers. comm. |
| *SUP19-arg6* | | | 76 | 0 | 6 | 3.7 | 1.5 | B. Ono, J. Stewart, and F. Sherman, pers. comm. |
| *arg6-ilv1* | | | 117 | 0 | 23 | 8.4 | 1.6 | 39 |
| *arg6-ilv1* | | | 188 | 0 | 35 | 7.9 | 1.2 | R. Snow, pers. comm. |
| Total | | | 305 | 0 | 58 | 8.0 | 1.0 | |
| *arg6-trp2* | | | 2,470 | 30 | 1,478 | 21.0 | 0.6 | 21 |
| *arg6-trp2* | | | 27 | 0 | 14 | 17.8 | 4.1 | 70 |
| *arg6-trp2* | | | 44 | 1 | 25 | 22.6 | 5.8 | 75 |
| *arg6-trp2* | | | 512 | 5 | 435 | 24.5 | 1.1 | S. Fogel, pers. comm. |
| *arg6-trp2* | | | 506 | 9 | 350 | 23.6 | 1.4 | T. Takahashi, pers. comm. |
| *arg6-trp2* | | | 132 | 0 | 60 | 16.2 | 1.8 | R. Snow, pers. comm. |
| *arg6-trp2* | | | 47 | 0 | 31 | 20.9 | 3.1 | 69 |
| *arg6-trp2* | | | 5,361 | 29 | 3,289 | 20.0 | 0.3 | 87 |
| Total | | | 9,099 | 74 | 5,682 | 20.7 | 0.3 | |
| *ilv1-trp2* | | | 56 | 0 | 13 | 9.6 | 2.5 | 70 |
| *ilv1-trp2* | | | 28 | 0 | 8 | 11.4 | 3.7 | 57 |
| *ilv1-trp2* | | | 213 | 1 | 32 | 7.8 | 1.8 | 39 |
| *ilv1-trp2* | | | 153 | 0 | 28 | 7.9 | 1.4 | R. Snow, pers. comm. |
| Total | | | 450 | 1 | 81 | 8.2 | 1.0 | |
| *ilv1-met5* | | | 23 | 0 | 6 | 10.6 | 4.0 | S. Sora, pers. comm. |
| *trp2-met5* | | | 35 | 0 | 1 | 1.4 | 1.4 | 57 |
| *trp2-rad51* | | | 338 | 0 | 21 | 2.9 | 0.6 | 69 |

TABLE 5—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *rad51-rad4* | | | 89 | 28 | 244 | 67.1 | 8.4 | 69 |
| *rad4-rad3* | | | 19 | 0 | 8 | 15.4 | 4.7 | 95 |
| *rad4-rad3* | | | 71 | 0 | 25 | 13.4 | 2.4 | 69 |
| *rad4-rad3* | | | 44 | 2 | 13 | 28.2 | 20.1 | J. Game and J. Little, pers. comm. |
| Total | | | 134 | 2 | 46 | 16.4 | 3.2 | |
| *rad3-r*$^1_s$ | | | 40 | 0 | 2 | 2.4 | 1.7 | F. Eckardt, J. Game, and J. Little, pers. comm. |

[a] See footnote *a* of Table 1.

positioned 27 and 24 cM, respectively, distal to *his4*. These values are not significantly different. These genes have not been included in a cross that also includes *his4*, and so their relative positions on the map are unknown. Genes *rad18*, *mak14*, *tup1* (*umr7*, *cyc9*, *flk1*), *SUP61*, and *SAD1* likewise have been positioned only by crosses to proximal (*MAT* or *thr4* or both) and distal (*HMR* or *MAL2* or both) genes. None of these five genes has been intercrossed. The *his4* locus contains three cistrons that code for three of the histidine biosynthetic enzymes. It has recently been shown that this gene codes for a single polypeptide that has all three enzymatic activities (G. Fink, personal communication). The *cly9* marker can no longer be scored reliably and has been removed from the map.

## Chromosome IV

The genetic length of chromosome IV, a metacentric chromosome, is in excess of the 430 cM, and 34 genes have been positioned along its length. Of particular interest is homothallism gene *HO*, which is on the left arm of this chromosome (48). Several sequence uncertainties, as indicated in Fig. 1 by parentheses, exist. On the left arm, the relative order of *rna11* and *mar1* relative to the centromere is uncertain because these genes have not been included in the same cross. However, the data suggest strongly that *mar1* is distal to *rna11* (29.5 ± 4.1 versus 17.8 ± 1.5). Similarly, the order of *rad55* and *mak21* relative to outside markers is uncertain because these genes have not been intercrossed. The distances of these two genes relative to *trp1* are 42.6 ± 5.7 and 43.3 ± 3.2, respectively; these values do not differ significantly, so there is no basis for assigning a preferred order relative to the centromere. Other uncertainties exist about the relative order of *rad50*, *fol1*, *SUP2*, and *lys4*. Genes *rad50* and *lys4* have been ordered relative to *pet14*. The marker *fol1* is close to *rad50*, and *SUP2* and *lys4* are about the same distance distal to *pet14*. Thus, the preferred proximal-to-distal order is: *pet14*-(*rad50-fol1*)-(*SUP2-lys4*). Finally, *pur5* has been mapped only against *ade8*; thus, the order of these two genes relative to the outside markers *trp4* and *rna3* is unknown.

A genetic length of 430 cM for a single chromosome is exceptional. The total map length of the four *Drosophila* sp. chromosomes is 285 cM, and the seven *Neurospora* sp. chromosomes have a total length of about 1,000 cM.

## Chromosome V

Chromosome V was originally defined by centromere-linked gene *ura3* (35, 56b). Twenty-five genes are distributed along its length. Gene *prt3* is placed distal to *can1* on the basis of random spore data (71). This linkage has not yet been confirmed by tetrad analysis. Although the order from the centromere of *ura3-cyc7-min1-mak10-prb1-can1* has been established, the location of *SUS1* in this group is uncertain. On the basis of its distance from *ura3*, *SUS1* should be close to *min1*. Also uncertain is the location of *BOR1* relative to *hom3*. This resistance gene is located 2.9 cM proximal to *his1* (75), which places it very close to *hom3*. *SUP19* and *SUP21* are weak ochre suppressors that were isolated independently (36; B. Ono, J. Stewart, and F. Sherman, personal communication). Both map close to and distal to *his1*, and it is likely that they are alleles. Genes *arg5* and *arg6* code for two of the arginine biosynthetic enzymes. They appear to be under operon-type regulation (68a). Both *met5* and *rad51* have been placed distal to *trp2*, at 1.4 and 2.9 cM, respectively. These values are not significantly different so that the relative order of these two genes on the chromosome is still unknown. Finally, the order of *rad3* and *r*$^1_s$ relative to *rad4* has not been determined.

Lindegren et al. (57) mapped four genes in the region proximal to *his1*. The location of *cho1* has been confirmed, but attempts to identify and

TABLE 6. *Tetrad analysis data for chromosome VI*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *SUF9-cdc4* | | | 57 | 1 | 18 | 16.5 | 5.7 | 16 |
| *SUF9-cen6* | 53 | 23 | | | | 16.0 | 3.0 | 16 |
| *cdc4-cen6* | 59 | 11 | | | | 8.1 | 2.3 | 71 |
| | 62 | 14 | | | | 9.5 | 2.3 | 16 |
| Total | 121 | 25 | | | | 8.8 | 1.7 | |
| *cdc4-SUP11* | | | 13 | 0 | 3 | 9.6 | 5.1 | 71 |
| *cdc4-his2* | | | 15 | 2 | 21 | 48.7 | 18.7 | 71 |
| *let6-cen6* | 45 | 6 | | | | 6.0 | 2.3 | 73 |
| *let6-his2* | | | 14 | 1 | 36 | 41.6 | 6.8 | 73 |
| *cen6-SUP11* | 308 | 20 | | | | 3.1 | 0.7 | 36 |
| *cen6-cly3* | 35 | 10 | | | | 11.5 | 3.4 | 71 |
| *cen6-his2* | 702 | 404 | | | | 19.6 | 0.9 | 70 |
| *cen6-his2* | 205 | 177 | | | | 25.5 | 1.6 | T. Takahashi, pers. comm. |
| *cen6-his2* | 756 | 491 | | | | 21.3 | 0.8 | S. Fogel, and R. Mortimer, pers. comm. |
| Total | 1,663 | 1,072 | | | | 21.1 | 0.6 | |
| *cen6-cdc14* | 70 | 71 | | | | 28.1 | 2.7 | 71 |
| *cen6-SUP6* | 68 | 91 | | | | 32.7 | 2.8 | 36 |
| *cen6-SUP6* | 578 | 664 | | | | 30.1 | 1.0 | S. Fogel and R. Mortimer, pers. comm. |
| Total | 646 | 755 | | | | 30.4 | 0.9 | |
| *SUP11-his2* | | | 65 | 1 | 41 | 22.2 | 3.8 | 36 |
| *SUP11-his2* | | | 46 | 4 | 37 | 40.5 | 12.9 | 12a; B. Cox, pers. comm. |
| Total | | | 111 | 5 | 78 | 29.4 | 5.0 | |
| *cly3-his2* | | | 17 | 0 | 11 | 20.7 | 5.2 | 71 |
| *his2-cdc14* | | | 43 | 0 | 7 | 7.1 | 2.5 | 71 |
| *his2-cdc14* | | | 9 | 0 | 2 | 9.4 | 6.1 | G. Kawasaki, pers. comm. |
| *his2-cdc14* | | | 1,859 | 2 | 147 | 3.4 | 0.4 | 17 |
| *his2-cdc14* | | | 55 | 0 | 8 | 6.4 | 2.2 | A. Toh-e, pers. comm. |
| Total | | | 1,966 | 2 | 164 | 4.1 | 0.4 | |
| *his2-SUP6* | | | 18 | 0 | 5 | 11.2 | 4.5 | 36 |
| *his2-SUP6* | | | 42 | 0 | 8 | 8.2 | 2.7 | 71 |
| *his2-SUP6* | | | 1,661 | 1 | 166 | 4.7 | 0.4 | 17 |
| *his2-SUP6* | | | 862 | 1 | 187 | 9.2 | 0.6 | S. Fogel and R. Mortimer, pers. comm. |
| Total | | | 2,583 | 2 | 366 | 6.4 | 0.3 | |
| *his2-met10* | | | 77 | 0 | 49 | 20.4 | 2.4 | 70 |
| *his2-met10* | | | 50 | 2 | 44 | 30.0 | 5.8 | 57 |
| *his2-met10* | | | 34 | 1 | 26 | 26.7 | 6.4 | 60 |
| *his2-met10* | | | 48 | 0 | 15 | 12.3 | 2.8 | A. Toh-e, pers. comm. |
| Total | | | 209 | 3 | 134 | 22.1 | 2.1 | |
| *his2-cdc26* | | | 8 | 0 | 5 | 20.3 | 7.5 | G. Kawasaki, pers. comm. |
| *his2-PHO82* | | | 102 | 0 | 38 | 14.0 | 2.0 | A. Toh-e, pers. comm. |

TABLE 6—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *his2-hxk1* | | | 19 | 3 | 49 | 50.5 | 12.5 | 60 |
| *cdc14-SUP6* | | | 2,039 | 0 | 34 | 0.82 | 0.14 | 17 |
| *cdc14-SUP6* | | | 46 | 0 | 4 | 4.0 | 2.0 | 71 |
| Total | | | 2,085 | 0 | 38 | 0.89 | 0.14 | |
| *cdc14-met10* | | | 1,848 | 0 | 192 | 4.8 | 0.3 | 17 |
| *cdc14-met10* | | | 9 | 0 | 1 | 5.1 | 4.9 | G. Kawasaki, pers. comm. |
| *cdc14-met10* | | | 56 | 0 | 6 | 4.9 | 1.9 | A. Toh-e, pers. comm. |
| Total | | | 1,913 | 0 | 199 | 4.8 | 0.3 | |
| *cdc14-cdc26* | | | 18 | 0 | 5 | 11.2 | 4.5 | G. Kawasaki, pers. comm. |
| *cdc14-PHO82* | | | 98 | 0 | 23 | 9.7 | 1.9 | A. Toh-e, pers. comm. |
| *SUP6-met10* | | | 16 | 0 | 0 | 0 | | 36 |
| *SUP6-met10* | | | 52 | 0 | 3 | 2.8 | 1.6 | 71 |
| *SUP6-met10* | | | 1.992 | 0 | 78 | 1.9 | 0.2 | 17 |
| *SUP6-met10* | | | 1,186 | 0 | 63 | 2.5 | 0.3 | S. Fogel, D. Hurst, and R. Mortimer, pers. comm. |
| Total | | | 3,246 | 0 | 144 | 2.1 | 0.2 | |
| *met10-cdc26* | | | 8 | 0 | 2 | 10.3 | 6.7 | G. Kawasaki, pers. comm. |
| *met10-PHO82* | | | 47 | 0 | 7 | 6.6 | 2.4 | A. Toh-e, pers. comm. |
| *met10-hxk1* | | | 41 | 2 | 26 | 29.7 | 9.5 | 60 |

[a] See footnote *a* of Table 1.

map the other three genes have been unsuccessful (S. Fogel, personal communication).

## Chromosome VI

The centromere-linked gene *his2* served initially to define chromosome VI (35). It is one of the shortest known chromosomes in *S. cerevisiae*, with a length of ca. 100 cM. Thirteen genes are positioned along its length, and no ambiguities in sequence of these genes exist. Of interest are the locations of two nonsense suppressors, one frame-shift suppressor, and three cell division cycle loci on this chromosome.

## Chromosome VII

Chromosome VII is one of the longest in *S. cerevisiae*. It was originally defined by centromere-linked genes *leu1*, *trp5*, and *ade6* (35). Roman (84a) had shown previously that *MAL1*, *SUC1*, and *ade3* were linked mitotically to *ade6*. To date, 37 genes have been mapped on this chromosome. Even though *cly8* and *SUC1* are linked mitotically, they do not show meiotic linkage (H. Roman, personal communication; Table 7). The tetrad data establish that the *cly8-SUC1* interval is at least 100 cM in length. No recombination events have been observed between *aro2* and *lts3* or between *cyh2* and *tsm437*. Therefore, the relative order of these two pairs of genes on the chromosome is unknown. Genes *BOR2*, *cyh3*, *til1*, *ant1*, *AMY1*, and *oli1* are expressed as resistance to various antibiotics. They have been isolated independently, and all map close to and distal to *leu1*. It has been proposed that they are all alleles of a single locus (86). Resistance gene *AXE1* (axenomycin resistance) does not appear to be part of this cluster. It is very close to *leu1* (no recombination events in 171 asci). However, it has been placed proximal to *leu1* by analysis of mitotic recombinants (S. Sora, personal communication). The only sequence ambiguity among the right-arm markers involves *MAL1* and *SUC1*. These two fermentation markers are very close, and gene conversion events frequently involve both sites (S. Fogel, personal communication). Industrial yeast strains used in brewing and baking are usually found to have one or the other, but not both, of these fermentation genes (70a).

## Chromosome VIII

Chromosome VIII contains 13 mapped genes and is at least 275 cM in length. Even though

TABLE 7. *Tetrad analysis data for chromosome VII*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | x' (cM) | SE | |
| *hxk2-ade5* | | | 41 | 0 | 21 | 17.7 | 3.3 | Z. Lobo, and P. Maitra, pers. comm. |
| *hxk2-lys5* | | | 11 | 4 | 55 | 60.5 | 11.8 | Z. Lobo and P. Maitra, pers. comm. |
| *ade5-kex1* | | | 38 | 0 | 35 | 25.6 | 3.4 | 110 |
| *ade5,7-lys5* | | | 28 | 9 | 59 | 77.9 | 25.9 | 70 |
| *ade5,7-lys5* | | | 34 | 9 | 80 | 63.7 | 13.8 | 74 |
| *ade5,7-lys5* | | | 17 | 3 | 44 | 51.5 | 11.2 | Z. Lobo and P. Maitra, pers. comm. |
| *ade5,7-lys5* | | | 21 | 5 | 57 | 57.8 | 12.6 | 110 |
| Total | | | 100 | 26 | 240 | 62.6 | 7.6 | |
| *ade5,7-aro2* | | | 39 | 17 | 110 | 85.2 | 21.0 | 70 |
| *ade5,7-aro2* | | | 19 | 7 | 56 | 72.3 | 20.2 | 110 |
| Total | | | 58 | 24 | 166 | 80.5 | 15.0 | |
| *ade5,7-lts3* | | | 11 | 2 | 24 | 53.2 | 17.4 | 91 |
| *ade5,7-met13* | | | 245 | 142 | 855 | 96.0 | 9.3 | 80 |
| *kex1-lys5* | | | 30 | 1 | 38 | 32.2 | 5.4 | 110 |
| *kex1-aro2* | | | 22 | 2 | 46 | 42.5 | 7.5 | 110 |
| *kex1-met13* | | | 22 | 2 | 45 | 42.5 | 7.6 | 110 |
| *ski1-lys5* | | | 59 | 1 | 12 | 13.7 | 6.9 | 103 |
| *ski1-aro2* | | | 53 | 1 | 22 | 19.0 | 5.5 | 103 |
| *ski1-met13* | | | 34 | 0 | 29 | 24.5 | 3.6 | 103 |
| *ski1-cyh2* | | | 46 | 6 | 115 | 46.9 | 5.6 | 103 |
| *lys5-aro2* | | | 139 | 1 | 22 | 8.9 | 2.7 | 70 |
| *lys5-aro2* | | | 107 | 1 | 15 | 9.1 | 3.8 | 74 |
| *lys5-aro2* | | | 76 | 0 | 9 | 5.4 | 1.7 | 110 |
| *lys5-aro2* | | | 256 | 2 | 55 | 10.9 | 1.9 | 90 |
| *lys5-aro2* | | | 66 | 0 | 8 | 5.5 | 1.9 | 103 |
| Total | | | 644 | 4 | 109 | 9.0 | 1.1 | |
| *lys5-lts3* | | | 32 | 0 | 7 | 9.2 | 3.2 | 91 |
| *lys5-met13* | | | 74 | 0 | 10 | 6.0 | 1.8 | 110 |
| *lys5-met13* | | | 167 | 3 | 123 | 24.3 | 2.4 | 90 |
| *lys5-met13* | | | 28 | 0 | 12 | 15.6 | 3.9 | 91 |
| Total | | | 269 | 3 | 145 | 19.7 | 1.8 | |
| *lys5-cyh2* | | | 44 | 1 | 40 | 27.3 | 4.6 | 110 |
| *lys5-cyh2* | | | 109 | 9 | 172 | 40.5 | 4.0 | 90 |
| *lys5-cyh2* | | | 13 | 2 | 31 | 49.4 | 12.5 | 70 |
| Total | | | 166 | 12 | 243 | 38.7 | 3.2 | |
| *lys5-ole1* | | | 15 | 2 | 34 | 47.2 | 10.9 | 90 |
| *lys5-trp5* | | | 59 | 34 | 192 | 102.0 | 23.1 | 90 |

TABLE 7—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | *x'* (cM) | SE | |
| *lys5-leu1* | | | 61 | 41 | 177 | 168.7 | 107.2 | 90 |
| *lys5-leu1* | | | 25 | 11 | 93 | 73.2 | 15.1 | T. Takahashi, pers. comm. |
| Total | | | 86 | 52 | 270 | 113.5 | 25.7 | |
| *aro2-lts3* | | | 39 | 0 | 0 | 0 | | 91 |
| *aro2-met13* | | | 85 | 0 | 2 | 1.2 | 0.8 | 110 |
| *aro2-met13* | | | 238 | 0 | 97 | 15.0 | 1.3 | 90 |
| *aro2-met13* | | | 34 | 0 | 5 | 6.5 | 2.7 | 91 |
| *aro2-met13* | | | 53 | 1 | 26 | 20.4 | 5.1 | 70 |
| *aro2-met13* | | | 83 | 1 | 39 | 18.5 | 3.4 | 74 |
| Total | | | 493 | 2 | 169 | 13.7 | 1.1 | |
| *aro2-cyh2* | | | 56 | 1 | 31 | 21.3 | 4.6 | 110 |
| *aro2-cyh2* | | | 136 | 6 | 153 | 32.7 | 3.2 | 90 |
| Total | | | 192 | 7 | 184 | 30.1 | 2.7 | |
| *aro2-ole1* | | | 27 | 6 | 60 | 58.5 | 13.5 | 90 |
| *aro2-trp5* | | | 75 | 33 | 224 | 82.6 | 13.5 | 90 |
| *aro2-leu1* | | | 67 | 43 | 228 | 111.9 | 26.3 | 90 |
| *lts3-met13* | | | 34 | 0 | 5 | 6.5 | 2.7 | 91 |
| *lts3-cyh2* | | | 17 | 0 | 22 | 30.6 | 4.9 | 91 |
| *met13-cyh2* | | | 50 | 1 | 29 | 22.2 | 5.0 | 70 |
| *met13-cyh2* | | | 78 | 2 | 43 | 23.0 | 4.7 | 74 |
| *met13-cyh2* | | | 957 | 2 | 303 | 12.5 | 0.7 | 80 |
| *met13-cyh2* | | | 56 | 1 | 30 | 21.0 | 4.7 | 110 |
| *met13-cyh2* | | | 32 | 1 | 19 | 24.9 | 8.0 | R. Wickner, pers. comm. |
| *met13-cyh2* | | | 192 | 1 | 94 | 17.5 | 1.7 | 90 |
| Total | | | 1,365 | 8 | 518 | 15.0 | 0.7 | |
| *met13-mak24* | | | 21 | 2 | 27 | 41.9 | 12.5 | R. Wickner, pers. comm. |
| *met13-ole1* | | | 24 | 7 | 62 | 65.4 | 16.1 | 90 |
| *met13-trp5* | | | 82 | 20 | 226 | 58.3 | 6.4 | 90 |
| *met13-trp5* | | | 332 | 86 | 846 | 61.3 | 3.8 | 80 |
| Total | | | 414 | 106 | 1,072 | 60.6 | 3.3 | |
| *met13-leu1* | | | 236 | 128 | 902 | 84.1 | 6.6 | 80 |
| *met13-leu1* | | | 61 | 36 | 234 | 90.5 | 15.1 | 90 |
| Total | | | 297 | 164 | 1,136 | 85.4 | 6.0 | |
| *tsm437-cyh2* | | | 25 | 0 | 0 | 0 | | 71 |
| *cyh2-ole1* | | | 30 | 2 | 42 | 37.6 | 7.4 | 90 |
| *cyh2-trp5* | | | 44 | 5 | 111 | 45.3 | 5.1 | 70 |
| *cyh2-trp5* | | | 34 | 3 | 86 | 43.0 | 5.0 | 74 |
| *cyh2-trp5* | | | 491 | 49 | 753 | 42.8 | 2.2 | 80 |
| *cyh2-trp5* | | | 13 | 1 | 23 | 40.2 | 10.1 | J. McCusker and J. Haber, pers. comm. |
| *cyh2-trp5* | | | 9 | 0 | 25 | 41.9 | 3.9 | S. Sora, pers. comm. |
| *cyh2-trp5* | | | 101 | 6 | 183 | 38.3 | 3.1 | 90 |
| Total | | | 692 | 64 | 1,181 | 42.5 | 1.6 | |

TABLE 7—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | x' (cM) | SE | |
| *cyh2-mak24* | | | 51 | 0 | 16 | 12.3 | 2.8 | 108 |
| *cyh2-leu1* | | | 309 | 90 | 895 | 62.9 | 3.8 | 80 |
| *cyh2-leu1* | | | 9 | 2 | 25 | 55.8 | 17.4 | J. McCusker and J. Haber, pers. comm. |
| *cyh2-leu1* | | | 4 | 1 | 29 | 52.4 | 9.7 | S. Sora, pers. comm. |
| *cyh2-leu1* | | | 81 | 13 | 202 | 50.0 | 4.9 | 90 |
| Total | | | 403 | 106 | 1,151 | 59.9 | 3.0 | |
| *ole1-rad6* | | | 17 | 0 | 8 | 16.7 | 5.1 | 24 |
| *ole1-trp5* | | | 33 | 0 | 14 | 15.4 | 3.6 | 84 |
| *ole1-trp5* | | | 46 | 0 | 47 | 25.3 | 2.6 | 90 |
| Total | | | 79 | 0 | 61 | 21.8 | 2.1 | |
| *ole1-leu1* | | | 24 | 0 | 23 | 26.2 | 4.3 | 84 |
| *ole1-leu1* | | | 46 | 6 | 67 | 47.9 | 10.0 | 90 |
| Total | | | 70 | 6 | 90 | 40.3 | 6.2 | |
| *ole1-ade6* | | | 30 | 14 | 73 | 106.3 | 45.9 | 90 |
| *mak24-trp5* | | | 17 | 3 | 34 | 53.2 | 15.2 | R. Wickner, pers. comm. |
| *rad6-trp5* | | | 29 | 0 | 9 | 12.2 | 3.7 | 24 |
| *rad6-trp5* | | | 4 | 0 | 19 | 49.0 | 6.8 | J. Game, pers. comm. |
| Total | | | 33 | 0 | 28 | 24.4 | 3.7 | |
| *lts1-trp5* | | | 45 | 0 | 0 | 0 | | 91 |
| *lts1-leu1* | | | 27 | 0 | 18 | 20.1 | 3.7 | 91 |
| *trp5-BOR2* | | | 93 | 1 | 55 | 20.6 | 2.9 | 75 |
| *trp5-oli1* | | | 23 | 0 | 9 | 14.6 | 4.3 | 86 |
| *trp5-AMY1* | | | 20 | 0 | 2 | 4.6 | 3.2 | 62 |
| *trp5-axe1* | | | 19 | 0 | 15 | 23.4 | 4.9 | S. Sora, pers. comm. |
| *trp5-cyh3* | | | 42 | 0 | 22 | 17.9 | 3.3 | 70 |
| *trp5-leu1* | | | 27 | 0 | 19 | 21.8 | 4.1 | 91 |
| *trp5-leu1* | | | 171 | 6 | 100 | 25.8 | 3.8 | T. Takahashi, pers. comm. |
| *trp5-leu1* | | | 256 | 4 | 100 | 17.6 | 2.3 | 90 |
| *trp5-leu1* | | | 19 | 0 | 15 | 23.4 | 4.9 | S. Sora, pers. comm. |
| *trp5-leu1* | | | 115 | 1 | 78 | 21.7 | 2.3 | 75 |
| *trp5-leu1* | | | 829 | 2 | 465 | 18.4 | 0.7 | 80 |
| *trp5-leu1* | | | 77 | 0 | 46 | 19.6 | 2.4 | 74 |
| *trp5-leu1* | | | 33 | 0 | 14 | 15.4 | 3.6 | 84 |
| *trp5-leu1* | | | 81 | 0 | 51 | 20.3 | 2.4 | J. McCusker and J. Haber, pers. comm. |
| *trp5-leu1* | | | 365 | 0 | 132 | 13.7 | 1.1 | 70 |
| *trp5-leu1* | | | 226 | 0 | 61 | 10.9 | 1.3 | 35 |
| *trp5-leu1* | | | 17 | 0 | 5 | 11.7 | 4.7 | 81; C. Reed and S. Liebman, pers. comm. |
| Total | | | 2,216 | 13 | 1,086 | 17.6 | 0.5 | |

TABLE 7—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | x' (cM) | SE | |
| *trp5-cen7* | 132 | 61 | | | | 16.7 | 1.9 | 35 |
| *trp5-cen7* | 239 | 153 | | | | 21.0 | 1.5 | T. Takahashi, pers. comm. |
| *trp5-cen7* | 389 | 188 | | | | 17.3 | 1.1 | 70 |
| Total | 760 | 402 | | | | 18.5 | 0.8 | |
| *trp5-SUP54* | | | 23 | 0 | 2 | 4.1 | 2.8 | 81; C. Reed and S. Liebman, pers. comm. |
| *SUP54-leu1* | | | 16 | 0 | 7 | 15.8 | 5.2 | 81; C. Reed and S. Liebman, pers. comm. |
| *trp5-cyh3* | | | 42 | 0 | 22 | 18.5 | 3.2 | 70 |
| *trp5-ade6* | | | 32 | 12 | 62 | 101.2 | 48.5 | 35 |
| *trp5-ade6* | | | 274 | 106 | 921 | 70.4 | 4.5 | 80 |
| *trp5-ade6* | | | 31 | 4 | 57 | 47.0 | 9.2 | 90 |
| *trp5-ade6* | | | 25 | 7 | 69 | 62.5 | 13.5 | J. McCusker and J. Haber, pers. comm. |
| Total | | | 362 | 129 | 1,109 | 69.5 | 4.1 | |
| *trp5-cly8* | | | 232 | 141 | 925 | 90.3 | 7.5 | 80 |
| *AMY1-leu1* | | | 95 | 0 | 11 | 5.3 | 1.5 | 62 |
| *ant1-leu1* | | | 223 | 0 | 16 | 3.4 | 0.8 | 9 |
| *BOR2-leu1* | | | 149 | 0 | 10 | 3.2 | 1.0 | 75 |
| *oli1-leu1* | | | 51 | 0 | 1 | 1.0 | 1.0 | 86 |
| *oli1-ade6* | | | 18 | 0 | 25 | 31.7 | 4.7 | 86 |
| *axe1-leu1* | | | 171 | 0 | 0 | 0 | | S. Sora, pers. comm. |
| *cyh3-leu1* | | | 53 | 0 | 12 | 9.4 | 2.5 | 70 |
| *cyh3-cen7* | 52 | 13 | | | | 10.3 | 2.7 | 70 |
| *leu1-cen7* | 850 | 39 | | | | 2.2 | 0.3 | 35 |
| *leu1-cen7* | 1,726 | 147 | | | | 4.0 | 0.3 | T. Takahashi, pers. comm. |
| *leu1-cen7* | 1,518 | 78 | | | | 2.5 | 0.3 | 70 |
| Total | 4,094 | 264 | | | | 3.1 | 0.2 | |
| *leu1-til1* | | | 31 | 0 | 8 | 10.5 | 3.4 | P. Magee, pers. comm. |
| *leu1-til1* | | | 34 | 0 | 3 | 4.1 | 2.3 | J. Stiles and F. Sherman, pers. comm. |
| Total | | | 65 | 0 | 11 | 7.4 | 2.1 | |
| *leu1-rme1* | | | 44 | 0 | 16 | 13.8 | 3.1 | G. Sprague and I. Herskowitz, pers. comm. |
| *leu1-ade6* | | | 125 | 6 | 175 | 35.1 | 3.0 | 35 |
| *leu1-ade6* | | | 208 | 9 | 290 | 34.4 | 2.2 | 70 |
| *leu1-ade6* | | | 171 | 10 | 197 | 35.2 | 3.3 | T. Takahashi, pers. comm. |
| *leu1-ade6* | | | 366 | 42 | 894 | 45.4 | 1.8 | 80 |
| *leu1-ade6* | | | 340 | 14 | 589 | 36.0 | 1.4 | S. Fogel, pers. comm. |
| *leu1-ade6* | | | 30 | 2 | 58 | 39.6 | 5.7 | J. McCusker and J. Haber, pers. comm. |

TABLE 7—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *leu1-ade6* | | | 43 | 6 | 108 | 47.8 | 6.0 | 90 |
| *leu1-ade6* | | | 61 | 2 | 91 | 33.7 | 3.4 | 52 |
| Total | | | 1,344 | 91 | 2,402 | 39.2 | 0.9 | |
| *leu1-cly8* | | | 10 | 2 | 25 | 54.3 | 17.0 | 71 |
| *leu1-cly8* | | | 251 | 83 | 965 | 61.9 | 3.2 | 80 |
| Total | | | 261 | 85 | 990 | 61.7 | 3.2 | |
| *cen7-ade6* | 175 | 234 | | | | 32.7 | 1.7 | 35 |
| *cen7-ade6* | 470 | 458 | | | | 27.4 | 1.1 | T. Takahashi, pers. comm. |
| *cen7-ade6* | 355 | 371 | | | | 28.6 | 1.2 | 70 |
| Total | 1,000 | 1,063 | | | | 28.8 | 0.8 | |
| *rme1-ade6* | | | 39 | 0 | 19 | 17.1 | 3.4 | G. Sprague and I. Herskowitz, pers. comm. |
| *ade6-cly8* | | | 27 | 0 | 17 | 20.3 | 4.1 | 71 |
| *ade6-cly8* | | | 878 | 9 | 418 | 18.2 | 1.0 | 80 |
| Total | | | 905 | 9 | 435 | 18.2 | 0.9 | |
| *cly8-SUC1* | | | 118 | 126 | 506 | NL[b] | | H. Roman, pers. comm. |
| *MAL1-SUC1* | | | 108 | 0 | 0 | 0 | | 70 |
| *MAL1-fol2* | | | 15 | 0 | 2 | 6.0 | 4.0 | J. Game and J. Little, pers. comm. |
| *MAL1-fol2* | | | 66 | 0 | 29 | 15.8 | 2.6 | B. Rockmill, pers. comm. |
| Total | | | 81 | 0 | 31 | 14.3 | 2.3 | |
| *MAL1-mes1* | | | 21 | 0 | 18 | 24.6 | 4.6 | D. Schild, pers. comm. |
| *MAL1-rad2* | | | 36 | 1 | 70 | 35.6 | 3.5 | D. Schild, pers. comm. |
| *mes1-rad2* | | | 14 | 0 | 3 | 9.1 | 4.8 | 71 |
| *mes1-rad2* | | | 29 | 0 | 10 | 13.2 | 3.7 | D. Schild, pers. comm. |
| Total | | | 43 | 0 | 13 | 11.9 | 3.0 | |
| *mes1-ade3* | | | 3 | 0 | 11 | 45.7 | 8.6 | D. Schild, pers. comm. |
| *rad2-ade3* | | | 4 | 0 | 10 | 40.4 | 8.5 | D. Schild, pers. comm. |
| *MAL1-ade3* | | | 42 | 7 | 89 | 51.4 | 8.5 | 70 |
| *MAL1-fro1* | | | 6 | 5 | 21 | NL | | 102 |
| *MAL1-fro2* | | | 4 | 6 | 15 | NL | | 102 |
| *SUC1-ser2* | | | 85 | 23 | 239 | 61.0 | 6.9 | 44 |
| *SUC1-ADE15* | | | 76 | 28 | 197 | 77.4 | 13.0 | 44 |
| *fol2-ade3* | | | 21 | 1 | 46 | 38.5 | 5.2 | J. Game and J. Little, pers. comm. |
| *ser2-ADE15* | | | 270 | 0 | 23 | 4.6 | 0.9 | 44 |
| *ade3-fro1* | | | 50 | 0 | 21 | 15.3 | 2.9 | 102 |

TABLE 7—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | x' (cM) | SE | |
| *ade3-fro2* | | | 20 | 6 | 34 | 85.4 | 45.9 | 102 |
| *fro1-fro2* | | | 13 | 0 | 7 | 18.3 | 5.9 | 101 |
| *fro1-fro2* | | | 47 | 0 | 35 | 22.6 | 3.1 | 101 |
| *fro1-fro2* | | | 10 | 0 | 8 | 23.6 | 6.7 | 102 |
| Total | | | 70 | 0 | 50 | 22.0 | 2.5 | |

[a] See footnote *a* of Table 1.
[b] NL, Not linked.

there are two tight clusters of genes, *arg4-spo13* and *pet3-SUF8-mak18*, no ambiguities exist in the sequence of genes on this chromosome. Gene *mak20* was placed on chromosome VIII by trisomic analysis (108). It does not show mitotic linkage to markers on the right arm and could not be tested for mitotic linkage to left-arm markers. Therefore, its location on this chromosome is considered to be tentative. Gene *arg4*, which is on the right arm of this chromosome, has been the subject of many gene conversion studies (21a).

## Chromosome IX

Thirteen genes have now been located on chromosome IX, which was originally identified by centromere-linked genes *his6* and *lys1* (35). The only ambiguity in the sequence of genes on this chromosome is the position of *bar1* (*sst1*). It has not been determined yet on which side of *cdc29* it is located. The serine-inserting suppressor *SUP24* is located on chromosome IX and appears to be distal to *SUP22*, but its location has not been determined precisely (Ono et al., personal communication). On the right arm is a cluster of three tightly linked genes (*dal1*, *dal4*, and *dal2*) involved in allantoin utilization; the sequence of these genes and *lys1* has been determined unambiguously (11). The supertriploid method was used to localize *mak13* to chromosome IX, and mitotic recombination with *lys1* placed it on the right arm of this chromosome (108).

## Chromosome X

Chromosome X was first identified by centromere-linked gene *met3* (57), and 19 genes are now localized on it. Although unlinked to *ura2*, *mak17* was placed on the distal left arm of chromosome X by supertriploid and mitotic mapping techniques (108). Recent data (F. Hilger, personal communication) show linkage between *arg3* and *SUP7* (PD = 24, NPD = 0, T = 37) but no significant linkage between *ura2* and *SUP7* (PD = 7, NPD = 2, T = 44), indicating the order *ura2-arg3-SUP7*. Four suppressor genes are located near the centromere, but these may represent only two loci because the suppressors were isolated in separate laboratories (36, 55, 77). *SUP29* and *SUP30* are both leucine-inserting ochre suppressors and are probably allelic (77). *SUP51* and *SUP52* are both leucine-inserting amber suppressors and are also probably allelic (55). *SUP51* and *SUP30* are probably not allelic since in 1 of 42 asci, *SUP30* segregated 3:1 while *SUP51* segregated 2:2 (71). The regions flanking *cyc1* (cytochrome *c*) have been examined extensively. Besides containing gene *cyc1*, this region has been shown to contain a *Ty1* sequence in some strains. *Ty1* is a sequence found in many places in the yeast genome and has been shown to undergo transposition (8a). The gene order of (*cyc1*, *osm1*) *rad7*, *SUP4*, and *cdc8* has been determined unambiguously by tetrad analysis (51) and deletion mapping (92), and the pattern of restriction fragments from deletions has been used to order *cyc1* and *osm1* (J. I. Stiles, T. S. Cardillo, and F. Sherman, personal communication).

## Chromosome XI

Chromosome XI was originally defined by centromere-linked gene *met14* (40), and 13 additional genes have since been positioned on it. Genes *met1* and *ura1* were originally assigned to opposite arms of an unknown chromosome by trisomic and mitotic crossover analyses (70). Later, it was shown that these genes are on chromosome XI (71). Most of the other genes on this chromosome were originally mapped relative to either *met1* or *ura1*. The long chromosomal segment containing *mak9*, *fas1*, *mnn4*, *trp3*, *ura1*, *dbl1*, and *cly7* is assigned to chromosome XI only by trisomic analysis. None of these genes shows linkage to other chromosome XI markers. Accordingly, the orientation of this block of genes on the chromosome is unknown. Gene *cly7* is linked to *ura1* but fails to show

TABLE 8. *Tetrad analysis data for chromosome VIII*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | x' (cM) | SE | |
| *mak7-arg4* | | | 52 | 9 | 131 | 51.3 | 6.5 | 109 |
| *mak7-arg4* | | | 28 | 6 | 48 | 62.0 | 18.9 | 107 |
| Total | | | 80 | 15 | 179 | 53.7 | 6.5 | |
| *spo11-cen8* | 39 | 25 | | | | 21.1 | 3.6 | S. Klapholz and R. Easton-Esposito, pers. comm. |
| *spo11-arg4* | | | 30 | 2 | 30 | 35.9 | 9.8 | S. Klapholz and R. Easton-Esposito, pers. comm. |
| *cen8-pet1* | 293 | 34 | | | | 5.3 | 0.9 | 35 |
| *cen8-pet1* | 559 | 49 | | | | 4.1 | 0.6 | 70 |
| Total | 852 | 83 | | | | 4.5 | 0.5 | |
| *cen8-arg4* | 449 | 85 | | | | 8.2 | 0.8 | 35 |
| *cen8-arg4* | 935 | 189 | | | | 8.6 | 0.6 | 70 |
| *cen8-arg4* | 874 | 376 | | | | 15.9 | 0.7 | F. Tavares and R. Mortimer, pers. comm. |
| *cen8-arg4* | 930 | 336 | | | | 13.9 | 0.7 | S. Fogel and R. Mortimer, pers. comm. |
| *cen8-arg4* | 1,527 | 428 | | | | 11.4 | 0.5 | T. Takahashi, pers. comm. |
| Total | 4,715 | 1,414 | | | | 12.0 | 0.3 | |
| *cen8-thr1* | 189 | 144 | | | | 23.6 | 1.7 | 35 |
| *cen8-thr1* | 288 | 234 | | | | 24.6 | 1.4 | 70 |
| *cen8-thr1* | 367 | 244 | | | | 21.6 | 1.2 | T. Takahashi, pers. comm. |
| Total | 844 | 622 | | | | 23.1 | 0.8 | |
| *pet1-arg4* | | | 163 | 0 | 18 | 5.0 | 1.1 | 35 |
| *pet1-arg4* | | | 371 | 0 | 30 | 3.8 | 0.7 | 70 |
| Total | | | 534 | 0 | 48 | 4.2 | 0.6 | |
| *spo13-arg4* | | | 52 | 0 | 1 | 0.9 | 0.1 | S. Klapholz and R. Easton-Esposito, pers. comm. |
| *arg4-thr1* | | | 453 | 0 | 138 | 12.0 | 0.9 | 70 |
| *arg4-thr1* | | | 443 | 2 | 178 | 15.3 | 1.1 | T. Takahashi, pers. comm. |
| *arg4-thr1* | | | 152 | 0 | 43 | 11.3 | 1.6 | 109 |
| *arg4-thr1* | | | 295 | 0 | 123 | 15.2 | 1.2 | S. Fogel and R. Mortimer, pers. comm. |
| *arg4-thr1* | | | 801 | 2 | 296 | 14.0 | 0.8 | F. Tavares and R. Mortimer, pers. comm. |
| *arg4-thr1* | | | 841 | 1 | 280 | 12.7 | 0.7 | S. Fogel and R. Mortimer, pers. comm. |
| Total | | | 2,985 | 5 | 1,058 | 13.4 | 0.4 | |
| *arg4-cdc12* | | | 21 | 6 | 78 | 58.6 | 10.0 | 109 |
| *thr1-CUP1* | | | 259 | 2 | 225 | 24.4 | 1.4 | 70 |
| *thr1-CUP1* | | | 560 | 6 | 624 | 27.8 | 0.9 | F. Tavares and R. Mortimer, pers. comm. |
| *thr1-CUP1* | | | 602 | 8 | 582 | 26.5 | 1.0 | S. Fogel and R. Mortimer, pers. comm. |
| *thr1-CUP1* | | | 393 | 15 | 496 | 32.8 | 1.6 | S. Fogel and R. Mortimer, pers. comm. |
| Total | | | 1,814 | 31 | 1,927 | 28.1 | 0.6 | |
| *thr1-cdc12* | | | 27 | 2 | 82 | 42.7 | 4.3 | 109 |

TABLE 8—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *thr1-mak19* | | | 13 | 10 | 43 | NL[b] | | R. Wickner, pers. comm. |
| *cdc12-SUF8* | | | 229 | 0 | 79 | 13.2 | 1.3 | 16 |
| *cdc12-pet3* | | | 227 | 0 | 81 | 13.6 | 1.3 | 16 |
| *cdc12-pet3* | | | 18 | 1 | 27 | 36.6 | 8.1 | 109 |
| Total | | | 245 | 1 | 108 | 16.1 | 1.5 | |
| *SUF8-pet3* | | | 305 | 0 | 3 | 0.5 | 0.3 | 16 |
| *mak18-pet3* | | | 56 | 0 | 2 | 1.7 | 1.2 | 108 |
| *cdc12-mak19* | | | 33 | 7 | 64 | 59.1 | 14.1 | R. Wickner, pers. comm. |
| *pet3-mak19* | | | 45 | 6 | 58 | 49.3 | 12.0 | R. Wickner, pers. comm. |

[a] See footnote *a* of Table 1.
[b] NL, Not linked.

linkage to *fas1* (111). Therefore, *cly7* and *fas1* were placed on opposite ends of this segment. Genes *mak11* and *cdc16* are very close, and their order relative to the centromere is unknown. No other sequence ambiguities exist among the mapped genes on this chromosome.

## Chromosome XII

Eleven miscellaneous genes plus the 100 to 140 ribosomal RNA genes have been positioned along chromosome XII. The left arm is marked by *mak12*. Gene *mak22* is tentatively located distal to *mak12*. It was placed on chromosome XII by trisomic analysis and shown not to be on the right arm of this chromosome by mitotic crossover analysis (108). The centromere marker of this chromosome is *asp5*, which is located 18.2 ± 1.1 cM from the centromere on the right arm. Distal to this gene are *rad5*, *ROC1*, and *suh1*, at distances of 4.1 ± 1.5, 4.4 ± 1.9, and 7.9 ± 5.2 cM, respectively. These map distance values are not significantly different, so the relative order of these genes is unknown. Genes *gal2* and *pep16* are further out on the right arm; they have not recombined so their relative order is unknown. Distal to *gal2* is *RDN1*, the structural genes for ribosomal RNA synthesis. These genes were located in this position by trisomic, mitotic crossing over, and tetrad analyses (78). Interestingly, even though there are 100 to 140 contiguous genes, the frequency of recombination within this cluster was only about 0.05 per meiosis. Since 3.5 to 5 exchanges per cell would be expected based on the amount of DNA that codes for ribosomal RNA, these results indicate that meiotic exchanges between homologs are greatly depressed in this region. Genes *car2*, *ura4*, and *SUP26* are positioned distal to *RDN1* because *ura4* shows mitotic but not meiotic linkage to *RDN1* and *car2* and *SUP26* show linkage to *ura4*. The relative orientation of this cluster on the chromosome is unknown.

## Chromosome XIII

Marker *lys7* originally defined chromosome XIII (70). Subsequently, *rad52* was positioned across the centromere from *lys7* (83), and nine additional genes have since been positioned along this chromosome. On the left arm, *SUF7* and *cdc5* are located distal to *rad52*. There is uncertainty about the location of *cdc5*, however. Two studies (16, 71) place the gene 1.5 and 15.1 cM from the centromere, respectively. It is very likely that the original *cdc5* mutant (33) contains two linked mutations and that a different one of these mutations was analyzed in each of the two studies (R. Contopoulou, personal communication). Gene *eth2* shows significant linkage to *lys7* and is closely linked to *met6* (65). However, it is anomalous that no evidence of linkage between *lys7* and *met6* exists. Because of this, it is possible that *eth2* and *met6* are located elsewhere in the genome. *SUP8* was placed on the right arm by mitotic crossover analysis, and *rna1* was shown to be linked to *SUP8* (71, 108). The killer-maintenance gene *mak27* is close to *rna1*, but the order of these two genes relative to *SUP8* is unknown. Likewise, the orientation of the

TABLE 9. *Tetrad analysis data for chromosome IX*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *SUC2-his5* | | | 11 | 1 | 19 | 41.9 | 12.5 | 70 |
| *SUC2-his5* | | | 84 | 30 | 251 | 70.3 | 9.0 | 76 |
| *SUC2-his5* | | | 89 | 20 | 180 | 60.4 | 8.7 | 57 |
| Total | | | 184 | 51 | 450 | 64.6 | 5.9 | |
| *SUC2-lys11* | | | 73 | 14 | 216 | 52.3 | 5.0 | 57 |
| *SUP22-his5* | | | 27 | 0 | 4 | 6.6 | 3.1 | B. Ono, J. Stewart, and F. Sherman, pers. comm. |
| *SUP22-SUP17* | | | 14 | 2 | 31 | 48.3 | 12.2 | B. Ono, J. Stewart, and F. Sherman, pers. comm. |
| *his5-lys11* | | | 12 | 1 | 6 | 44.2 | 52.5 | 76 |
| *his5-lys11* | | | 215 | 4 | 107 | 20.5 | 2.5 | 57 |
| *his5-lys11* | | | 24 | 0 | 14 | 19.3 | 4.3 | 70 |
| Total | | | 251 | 5 | 127 | 20.9 | 2.4 | |
| *his5-SUP17* | | | 192 | 28 | 349 | 49.4 | 4.2 | 76 |
| *his5-his6* | | | 14 | 7 | 40 | 97.7 | 47.5 | 71 |
| *lys11-SUP17* | | | 269 | 1 | 94 | 13.8 | 1.4 | 76 |
| *SUP17-his6* | | | 41 | 2 | 61 | 35.6 | 5.0 | 76 |
| *SUP17-lys1* | | | 259 | 174 | 880 | 120.3 | 16.1 | 76 |
| *cdc29-his6* | | | 29 | 0 | 7 | 10.0 | 3.5 | 33 |
| *cdc29-cen9* | 42 | 14 | | | | 13.1 | 3.2 | 33 |
| *sst1, bar1-his6* | | | 31 | 0 | 5 | 7.1 | 3.0 | R. Chan, pers. comm. |
| *sst1, bar1-his6* | | | 38 | 0 | 8 | 8.9 | 2.9 | G. Sprague and I. Herskowitz, pers. comm. |
| Total | | | 69 | 0 | 13 | 8.1 | 2.1 | |
| *his6-lys1* | | | 75 | 8 | 130 | 44.0 | 5.4 | 35 |
| *his6-lys1* | | | 119 | 20 | 284 | 50.9 | 4.4 | T. Takahashi, pers. comm. |
| *his6-lys1* | | | 27 | 11 | 74 | 81.6 | 23.4 | 76 |
| *his6-lys1* | | | 138 | 17 | 256 | 46.2 | 4.2 | 70 |
| Total | | | 359 | 56 | 744 | 50.2 | 2.8 | |
| *sst1, bar1-cen9* | 31 | 12 | | | | 14.7 | 3.8 | R. Chan, pers. comm. |
| *his6-cen9* | 207 | 100 | | | | 17.3 | 1.5 | 35 |
| *his6-cen9* | 379 | 226 | | | | 20.1 | 1.2 | T. Takahashi, pers. comm. |
| *his6-cen9* | 60 | 50 | | | | 25.0 | 3.0 | 76 |
| Total | 646 | 376 | | | | 19.7 | 0.9 | |
| *cen9-lys1* | 71 | 85 | | | | 30.8 | 2.7 | 35 |
| *cen9-lys1* | 269 | 457 | | | | 36.9 | 1.4 | T. Takahashi, pers. comm. |
| *cen9-lys1* | 39 | 79 | | | | 40.1 | 3.6 | 76 |
| Total | 379 | 621 | | | | 36.2 | 1.2 | |
| *his6-dal2* | | | 43 | 14 | 97 | 75.6 | 18.4 | 52 |

TABLE 9—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *dal1-dal2* | | | 94 | 0 | 9 | 4.4 | 1.4 | 52 |
| *dal1-dal2* | | | 1,154 | 0 | 89 | 3.6 | 0.4 | 11 |
| Total | | | 1,248 | 0 | 98 | 3.7 | 0.4 | |
| *dal1-dal4* | | | 347 | 0 | 18 | 2.5 | 0.6 | 11 |
| *dal2-dal4* | | | 351 | 0 | 14 | 1.9 | 0.5 | 11 |
| *dal1-lys1* | | | 80 | 0 | 10 | 5.6 | 1.7 | 52 |
| *dal1-lys1* | | | 23 | 0 | 1 | 2.1 | 2.1 | 52 |
| *dal1-lys1* | | | 1,059 | 0 | 184 | 7.5 | 0.5 | 11 |
| Total | | | 1,162 | 0 | 195 | 7.3 | 0.5 | |
| *dal4-lys1* | | | 320 | 0 | 45 | 6.2 | 0.8 | 11 |
| *dal2-lys1* | | | 92 | 0 | 7 | 3.6 | 1.3 | 52 |
| *dal2-lys1* | | | 28 | 0 | 2 | 3.4 | 2.3 | 52 |
| *dal2-lys1* | | | 1,129 | 0 | 114 | 4.6 | 0.4 | 11 |
| Total | | | 1,249 | 0 | 123 | 4.5 | 0.4 | |

[a] See footnote *a* of Table 1.

*SUP8-rna1* segment on the right arm is unknown.

## Chromosome XIV

Gene *pet8* serves as the centromere marker of chromosome XIV. Three other genes, *SUF10*, *spo1*, and *rna2*, are tightly linked to *pet8* and to the centromere. Cummins et al. (16) assigned *SUF10* to the left arm of chromosome XIV, across the centromere from *pet8*. Their data are more consistent with placing *SUF10* on the right arm distal to *pet8* but proximal to *rna2*. Sporulation gene *spo1* has not recombined with *pet8*, so the order of these two genes on the chromosome is unknown. The group of genes *mak26*, *ski4*, *kex2*, *petx*, and *ski3* all show meiotic linkage. The have been assigned to chromosome XIV by aneuploid analyses and to the left arm of this chromosome by a mitotic crossover analysis (103, 108, 110).

## Chromosome XV

Centromere-linked genes *pet17* and *SUP3* originally defined chromosome XV (36). A long segment of linked genes (fragment 1) was later shown to be part of the right arm of chromosome XV (71). Gene *ade2*, which is part of this segment, shows significant linkage to *pet17*. Gene *his3* (*his8*), which is distal to *ade2*, was one of the first yeast genes to be cloned in *Escherichia coli* (98a). Three other genes, *met7*, *tra3*, and *cpa1*, are distal to *his3*. Gene *prt1* shows clear mitotic linkage to *ade2* (71) but so far has not shown linkage to any right-arm marker. Tentatively, it is located distal to *cpa1*. The left arm is marked by *SUP3*, and distal to this suppressor locus are *arg1*, *spe2*, and *arg8* (37). Genes *arg1* and *spe2* had originally been assigned to a new chromosome, XVIII (10). Twenty-six genes are located on chromosome XV. The map distance from *arg8* to *cpa1* is about 300 cM. If *prt1* is located distal to *cpa1*, the total length of this chromosome could be 350 to 400 cM.

## Chromosome XVI

Marker *aro7* was used to define chromosome XVI (36). Thirteen genes are located on the two arms, and the total length from *pho85* on the left arm to *rad56* on the right arm is approximately 100 cM. Galactose regulatory gene *gal4* has been mapped distal to *rad1* on the left arm by mitotic analysis; these two genes do not show meiotic linkage, however (PD:NPD:T = 21:17:87; J. McCusker and J. E. Haber, personal communication). Genes *aro7* and *osm2* have not recombined, and so their relative arrangement on the chromosome is unknown (92). No other sequence ambiguities exist.

TABLE 10. *Tetrad analysis data for chromosome X*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *ura2-arg3* | | | 32 | 0 | 21 | 20.8 | 3.8 | F. Hilger, pers. comm. |
| *ura2-cdc6* | | | 8 | 0 | 14 | 35.2 | 6.6 | F. Hilger, pers. comm. |
| *ura2-cdc6* | | | 17 | 0 | 17 | 26.8 | 5.0 | 48 |
| Total | | | 25 | 0 | 31 | 30.0 | 4.0 | |
| *arg3-cdc6* | | | 5 | 1 | 15 | 53.0 | 19.3 | F. Hilger, pers. comm. |
| *SUP7-cen10* | 116 | 122 | | | | 28.7 | 2.1 | 36 |
| *SUP7-ilv3* | | | 32 | 0 | 22 | 21.5 | 3.8 | 36 |
| *SUP7-SUP4* | | | 47 | 11 | 121 | 58.0 | 8.9 | 25 |
| *let3-cen10* | 24 | 3 | | | | 5.7 | 3.1 | 73 |
| *let5-cen10* | 49 | 22 | | | | 16.4 | 3.1 | 73 |
| *let3-ilv3* | | | 16 | 0 | 11 | 21.5 | 5.3 | 73 |
| *let5-ilv3* | | | 38 | 3 | 30 | 38.3 | 12.9 | 73 |
| *SUP30-ilv3* | | | 14 | 0 | 3 | 9.1 | 4.8 | 36 |
| *SUP30-ilv3* | | | 58 | 0 | 15 | 10.5 | 2.5 | 71 |
| Total | | | 72 | 0 | 18 | 10.2 | 2.2 | |
| *SUP51-ilv3* | | | 17 | 0 | 2 | 5.4 | 3.6 | 36 |
| *SUP51-ilv3* | | | 59 | 0 | 18 | 12.0 | 2.6 | 71 |
| Total | | | 76 | 0 | 20 | 10.7 | 2.2 | |
| *SUP30-SUP51* | | | 42 | 0 | 0 | 0 | | 71 |
| *SUP52-met3* | | | 57 | 0 | 2 | 1.7 | 1.2 | 55 |
| *SUP29-met3* | | | 102 | 0 | 4 | 1.9 | 0.9 | 77 |
| *SUP29-SUP52* | | | 46 | 0 | 0 | 0 | | 77 |
| *cen10-met3* | 174 | 13 | | | | 3.5 | 1.0 | 70 |
| *cen10-met3* | 186 | 43 | | | | 9.7 | 1.4 | 51 |
| *cen10-met3* | 1,588 | 78 | | | | 2.4 | 0.3 | T. Takahashi, pers. comm. |
| Total | 1,948 | 134 | | | | 3.3 | 0.2 | |
| *cen10-SUP51* | 36 | 0 | | | | 0 | | 36 |
| *cen10-SUP52* | 58 | 1 | | | | 0.8 | 0.8 | 55 |
| *met3-ilv3* | | | 69 | 0 | 5 | 3.4 | 1.5 | 70 |
| *met3-ilv3* | | | 153 | 0 | 32 | 8.8 | 1.4 | 51 |
| Total | | | 222 | 0 | 37 | 7.3 | 1.1 | |
| *cen10-ilv3* | 459 | 199 | | | | 16.0 | 1.0 | 51 |
| *cen10-ilv3* | 93 | 13 | | | | 6.3 | 1.7 | 70 |
| Total | 552 | 212 | | | | 14.6 | 0.9 | |

TABLE 10—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *ilv3-cyc1* | | | 485 | 11 | 342 | 24.7 | 1.6 | 51 |
| *ilv3-SUP4* | | | 27 | 0 | 11 | 15.0 | 4.0 | 36 |
| *ilv3-cdc8* | | | 21 | 0 | 20 | 26.1 | 4.6 | 71 |
| *cyc1-rad7* | | | 246 | 0 | 6 | 1.2 | 0.5 | 51 |
| *rad7-SUP4* | | | 247 | 0 | 1 | 0.2 | 0.2 | 51 |
| *SUP4-cdc8* | | | 219 | 0 | 0 | 0 | | 51 |
| *SUP4-cdc8* | | | 17 | 0 | 0 | 0 | | 71 |
| Total | | | 236 | 0 | 0 | 0 | | |
| *SUP4-cyc1* | | | 689 | 0 | 23 | 1.6 | 0.3 | 51 |
| *cdc8-cdc11* | | | 17 | 0 | 10 | 19.4 | 5.2 | 71 |
| *SUP4-cdc11* | | | 37 | 0 | 22 | 19.5 | 3.5 | 51 |

[a] See footnote *a* of Table 1.

## Chromosome XVII

Chromosome XVII is the only chromosome that has not been defined by a centromere-linked gene. The two fragments containing *met4-lys10* and *pet2-met2-pha2* were eliminated from chromosomes I to XVI by trisomic analysis (71). These analyses also showed that these two groups of linked genes were on the same chromosome. In addition to these five genes, *lap3*, *pet2*, and *kar1* have been located on chromosome XVII.

## Fragments

A total of eleven fragments of linked genes have been described (36, 70, 71). These fragments represented groups of two or more linked genes that were not yet associated with any of the established chromosomes. Presently, only three fragments, F6, F8, and F11, remain unassociated.

Fragment 6 contains the genes *thi1*, *SUP50*, *gal5*, and *pdx2* (71). To our knowledge, there has been no attempt to assign this fragment to any of the chromosomes.

Fragment 8 contains *gal80*, *SUP5*, and *arg81*. Attempts to locate *SUP5* by mitotic analyses using markers representing all but seven of the chromosome arms were unsuccessful (71). Likewise, *gal80* failed to show mitotic linkage with markers representing all of the chromosome arms (McCusker and Haber, personal communication). It is possible that this fragment is located far out on one of the chromosome arms and, if so, would be expected to cosector with a marker near a centromere only rarely. Conversely, fragment 8 might be part of an 18th chromosome.

Fragment 11 contains two mutator genes, *mut1* and *mut2* (26). No effort has been made to assign this fragment to any of the chromosomes.

## IS THERE AN EIGHTEENTH CHROMOSOME?

Because of the small size of the nucleus and chromosomes of *S. cerevisiae*, it has not been possible, by cytological methods, to obtain a reliable estimate of the chromosome number. Genetic analyses establish only a minimum number. For example, it is possible that additional chromosomes exist for which centromere-linked genes have yet to be identified. Two such centromere-linked genes that might identify an additional chromosome(s) are *KRB1* and *AMY2*.

Wickner and Leibowitz (110a) have identified a gene, *KRB1*, that is tightly linked to a centromere (<2 cM). This marker has been eliminated from chromosomes I to XVI by conventional tetrad analysis. Because it is dominant, trisomic analysis could not be used to eliminate it from chromosome XVII. Thus, it may be the centromere marker of chromosome XVII or represent a new chromosome. Similarly, Lucchini et al.

TABLE 11. *Tetrad analysis data for chromosome XI*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *cly7-ura1* | | | 23 | 4 | 40 | 54.1 | 15.4 | 69; R. Mortimer and D. Hawthorne, pers. comm. |
| *mak9-fas1* | | | 37 | 0 | 5 | 6.1 | 2.6 | 111 |
| *mak9-trp3* | | | 57 | 6 | 101 | 43.8 | 6.0 | 111 |
| *mak9-ura1* | | | 59 | 11 | 135 | 53.4 | 7.3 | 111 |
| *fas1-trp3* | | | 27 | 1 | 51 | 36.3 | 4.6 | 111 |
| *fas1-trp3* | | | 56 | 3 | 110 | 38.3 | 3.7 | 14 |
| *fas1-trp3* | | | 127 | 5 | 203 | 35.1 | 2.4 | 8 |
| Total | | | 210 | 9 | 364 | 36.2 | 1.9 | |
| *fas1-ura1* | | | 47 | 3 | 72 | 37.8 | 5.3 | 111 |
| *fas1-ura1* | | | 36 | 3 | 120 | 43.8 | 3.7 | 14 |
| *fas1-ura1* | | | 114 | 9 | 297 | 42.3 | 2.5 | 8 |
| Total | | | 197 | 15 | 489 | 41.9 | 1.9 | |
| *mnn4-trp3* | | | 13 | 0 | 4 | 12.1 | 5.5 | 4 |
| *mnn4-ura1* | | | 43 | 1 | 38 | 27.1 | 4.8 | 4 |
| *trp3-ura1* | | | 258 | 1 | 42 | 8.0 | 1.5 | 111 |
| *trp3-ura1* | | | 42 | 0 | 5 | 5.4 | 2.3 | 70 |
| *trp3-ura1* | | | 108 | 0 | 21 | 8.3 | 1.7 | T. Takahashi, pers. comm. |
| *trp3-ura1* | | | 138 | 0 | 18 | 5.8 | 1.3 | 14 |
| *trp3-ura1* | | | 341 | 0 | 44 | 5.8 | 0.8 | 8 |
| Total | | | 887 | 1 | 130 | 6.7 | 0.6 | |
| *mnn4-dbl1* | | | 15 | 3 | 7 | 50.0 | | 4 |
| *trp3-dbl1* | | | 12 | 1 | 9 | 39.7 | 26.2 | 4 |
| *ura1-dbl1* | | | 25 | 0 | 10 | 14.8 | 4.1 | 4 |
| *ura1-dbl1* | | | 11 | 1 | 10 | 41.2 | 24.0 | 22 |
| Total | | | 36 | 1 | 20 | 23.6 | 7.3 | |
| *mak11-cdc16* | | | 112 | 1 | 3 | 3.8 | | A. Toh-e, pers. comm. |
| *mak11-cdc16* | | | 52 | 0 | 0 | 0 | | 111 |
| Total | | | 164 | 1 | 3 | 2.7 | | |
| *mak11-met14* | | | 45 | 1 | 24 | 22.0 | 5.8 | 111 |
| *cdc16-cen14* | 41 | 14 | | | | 13.3 | 3.2 | 33 |
| *cdc16-met14* | | | 25 | 0 | 13 | 17.9 | 4.2 | 33 |
| *cen11-met14* | 577 | 37 | | | | 3.0 | 0.5 | T. Takahashi, pers. comm. |
| *cen11-met14* | 82 | 2 | | | | 1.2 | 0.8 | 40 |
| *cen11-met14* | 133 | 4 | | | | 1.5 | 0.7 | 70 |
| Total | 792 | 43 | | | | 2.6 | 0.4 | |
| *met-14-met1* | | | 38 | 5 | 66 | 47.5 | 9.0 | 71 |

TABLE 11—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | x' (cM) | SE | |
| *met1-SUP25* | | | 55 | 0 | 8 | 6.5 | 2.2 | 36 |
| *met1-SUP25* | | | 97 | 0 | 17 | 7.6 | 1.7 | 71 |
| Total | | | 152 | 0 | 25 | 7.2 | 1.4 | |
| *met1-mak15* | | | 55 | 1 | 22 | 18.5 | 5.3 | 111 |
| *met1-MAL4* | | | 40 | 3 | 37 | 37.4 | 10.1 | 70 |
| *met1-MAL4* | | | 71 | 3 | 59 | 30.0 | 5.3 | 71 |
| Total | | | 111 | 6 | 96 | 32.6 | 4.9 | |
| *SUP25-MAL4* | | | 40 | 0 | 15 | 14.1 | 3.2 | 71 |
| *SUP25-MAL4* | | | 9 | 0 | 14 | 33.4 | 6.4 | 36 |
| Total | | | 49 | 0 | 29 | 19.5 | 3.0 | |
| *mak15-MAL4* | | | 12 | 0 | 7 | 19.3 | 6.1 | 111 |

[a] See footnote *a* of Table 1.

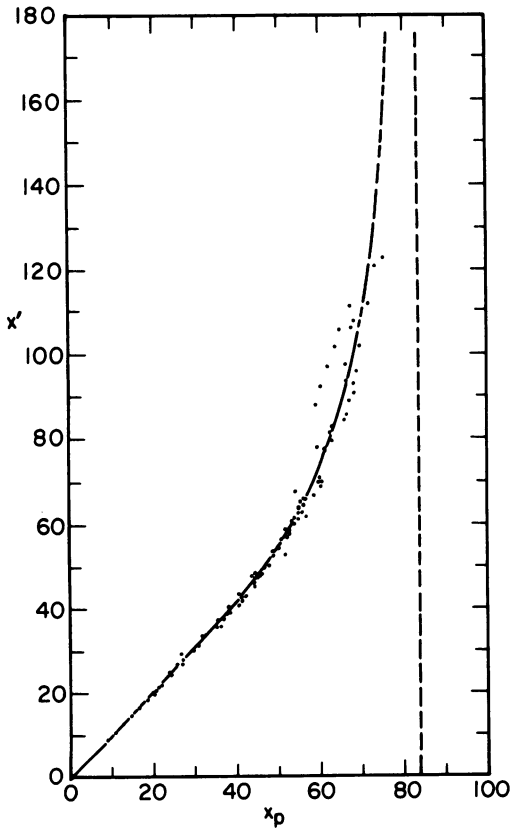


FIG. 2. *Map distances x', calculated by the method of Snow (96), plotted against the map distances $x_p$, calculated for the same sets of data using the formula derived by Perkins (77a). The line is drawn as a best-fit line. The scatter of points about the line is because of variation in the degree of chiasma interference for different intervals; the relationship between x' and $x_p$ is dependent on the interference parameter (k).*

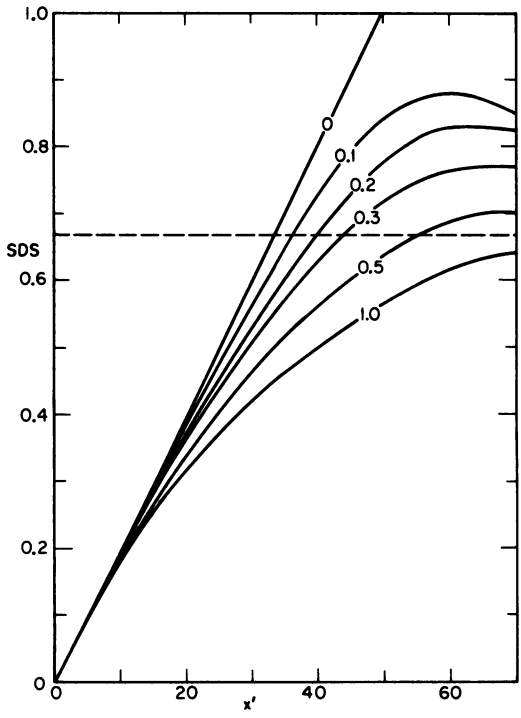


FIG. 3. *Second-division segregation frequencies plotted against map distance (x') for different values of the interference parameter (k). The curves were calculated using the equations derived by Snow (96). SDS, Second-division segregation.*

(62) have described a gene, *AMY2*, that confers resistance to the drug antimycin A and that is tightly linked to a centromere. The ascus-type ratios against *trp1* are 48:54:9 (8.1% second-division segregation). These data indicate that

TABLE 12. *Tetrad analysis data for chromosome XII*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *mak12-cen12* | 46 | 56 | | | | 31.1 | 3.4 | 111 |
| *mak12-asp5* | | | 45 | 9 | 88 | 57.0 | 11.1 | 111 |
| *cen12-asp5* | 127 | 56 | | | | 16.2 | 1.9 | 111 |
| *cen12-asp5* | 129 | 48 | | | | 14.2 | 1.9 | 70 |
| *cen12-asp5* | 77 | 56 | | | | 22.9 | 2.6 | T. Takahashi, pers. comm. |
| *cen12-asp5* | 32 | 21 | | | | 21.4 | 4.0 | 78 |
| *cen12-asp5* | 16 | 16 | | | | 27.8 | 5.7 | 41 |
| Total | 381 | 197 | | | | 18.2 | 1.1 | |
| *cen12-suh1* | 12 | 3 | | | | 10.3 | 5.5 | 69 |
| *cen12-ROC1* | 72 | 76 | | | | 28.7 | 2.7 | 70 |
| *asp5-rev2* (*rad5*) | | | 80 | 0 | 7 | 4.1 | 1.5 | 53 |
| *asp5-suh2* | | | 11 | 0 | 2 | 7.9 | 5.2 | 71 |
| *asp5-ROC1* | | | 53 | 0 | 5 | 4.4 | 1.9 | 70 |
| *asp5-gal2* | | | 32 | 0 | 31 | 26.3 | 3.7 | 70 |
| *asp5-gal2* | | | 13 | 0 | 12 | 25.6 | 5.8 | 18 |
| *asp5-gal2* | | | 19 | 2 | 36 | 43.9 | 9.7 | 78 |
| Total | | | 64 | 2 | 79 | 31.7 | 3.7 | |
| *asp5-RDN1* | | | 16 | 4 | 35 | 63.0 | 20.9 | 78 |
| *gal2-RDN1* | | | 16 | 2 | 37 | 46.4 | 9.9 | 78 |
| *pep16-gal2* | | | 16 | 0 | 0 | 0 | | B. Jones, A. Mitchell, and G. Zubenko, pers. comm. |
| *RDN1-ura4* | | | 11 | 6 | 39 | 89.2 | 36.6 | 78 |
| *car2-ura4* | | | 18 | 2 | 13 | 50.4 | 36.6 | F. Hilger, pers. comm. |
| *SUP26-ura4* | | | 133 | 0 | 1 | 0.4 | 0.4 | 77 |

[a] See footnote *a* of Table 1.

TABLE 13. *Tetrad analysis data for chromosome XIII*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *SUF7-cdc5* | | | 93 | 1 | 76 | 24.2 | 2.6 | 16 |
| *SUF7-cen13* | 93 | 85 | | | | 26.4 | 2.4 | 16 |
| *SUF7-lys7* | | | 45 | 11 | 117 | 59.1 | 9.4 | 16 |
| *rad52-lys7* | | | 18 | 2 | 40 | 44.8 | 8.9 | 71 |
| *rad52-lys7* | | | 8 | 0 | 6 | 22.7 | 7.5 | R. Contopoulou and R. Mortimer, pers. comm. |
| Total | | | 26 | 2 | 46 | 40.2 | 7.1 | |
| *rad52-cen13* | 78 | 39 | | | | 17.7 | 2.5 | 83 |
| *rad52-cen13* | 12 | 1 | | | | 3.9 | 3.8 | R. Contopoulou and R. Mortimer, pers. comm. |
| Total | 90 | 40 | | | | 16.3 | 2.3 | |
| *cdc5-cen13* | 8 | 5 | | | | 20.7 | 8.0 | R. Contopoulou and R. Mortimer, pers. comm. |
| *cdc5-cen13* | 52 | 21 | | | | 15.1 | 3.0 | 71 |
| *cdc5-cen13* | 168 | 5 | | | | 1.5 | 0.7 | 16 |
| Total | 228 | 31 | | | | 6.1 | 1.0 | |
| *cdc5-lys7* | | | 20 | 3 | 32 | 50.8 | 15.6 | 71 |
| *cdc5-lys7* | | | 56 | 0 | 64 | 28.8 | 2.7 | 16 |
| *cdc5-lys7* | | | 13 | 4 | 22 | 88.6 | 62.4 | 32 |
| Total | | | 89 | 7 | 118 | 39.2 | 5.0 | |
| *cen13-arg80* | 13 | 18 | | | | 33.3 | 6.3 | F. Hilger, pers. comm. |
| *cen13-arg80* | 14 | 17 | | | | 31.0 | 6.1 | F. Hilger, pers. comm. |
| Total | 27 | 35 | | | | 32.2 | 4.4 | |
| *cen13-lys7* | 15 | 16 | | | | 28.9 | 5.9 | F. Hilger, pers. comm. |
| *cen13-lys7* | 17 | 14 | | | | 24.8 | 5.6 | F. Hilger, pers. comm. |
| *cen13-lys7* | 384 | 340 | | | | 25.9 | 1.2 | 70 |
| *cen13-lys7* | 183 | 243 | | | | 32.6 | 1.7 | T. Takahashi, pers. comm. |
| *cen13-lys7* | 97 | 79 | | | | 24.6 | 2.3 | 16 |
| Total | 696 | 692 | | | | 27.7 | 0.9 | |
| *cen13-let1* | 28 | 44 | | | | 35.5 | 4.3 | 73 |
| *arg80-lys7* | | | 27 | 0 | 4 | 6.6 | 3.1 | F. Hilger, pers. comm. |
| *cdc5-rad52* | | | 8 | 0 | 6 | 22.7 | 7.5 | R. Contopoulou and R. Mortimer, pers. comm. |
| *lys7-eth2* | | | 14 | 3 | 27 | 59.6 | 22.1 | 65 |
| *lys7-met6* | | | 4 | 9 | 15 | NL | | 65 |
| *lys7-let1* | | | 16 | 3 | 53 | 51.5 | 9.2 | 73 |
| *eth2-met6* | | | 30 | 0 | 5 | 7.3 | 3.1 | 65 |
| *SUP8-rna1* | | | 28 | 1 | 43 | 34.3 | 5.1 | 108 |
| *mak27-rna1* | | | 165 | 0 | 7 | 2.0 | 0.8 | 111 |

[a] See footnote *a* of Table 1.
[b] NL, Not linked.

TABLE 14. *Tetrad analysis data for chromosome XIV*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *mak26-petx* | | | 29 | 0 | 23 | 23.4 | 3.9 | 108 |
| *kex2-petx* | | | 44 | 0 | 7 | 7.0 | 2.5 | 110 |
| *ski4-kex2* | | | 97 | 0 | 2 | 1.0 | 0.7 | 103 |
| *kex2-ski3* | | | 34 | 8 | 48 | 74.7 | 30.9 | 103 |
| *cen14-pet8* | 316 | 15 | | | | 2.3 | 0.6 | 16 |
| *cen14-pet8* | 47 | 2 | | | | 2.1 | 1.4 | T. Takahashi, pers. comm. |
| *cen14-pet8* | 242 | 0 | | | | 0 | | 70 |
| Total | 605 | 17 | | | | 1.4 | 0.3 | |
| *cen14-SUF10* | 313 | 18 | | | | 2.7 | 0.6 | 16 |
| *cen14-rna2* | 105 | 11 | | | | 4.8 | 1.4 | 71 |
| *cen14-rna2* | 272 | 59 | | | | 9.2 | 1.1 | 16 |
| Total | 377 | 70 | | | | 8.0 | 0.9 | |
| *pet8-spo1* | | | 19 | 0 | 0 | 0 | | S. Klapholz, pers. comm. |
| *pet8-SUF10* | | | 327 | 0 | 4 | 0.6 | 0.6 | 16 |
| *SUF10-rna2* | | | 313 | 0 | 18 | 2.7 | 0.6 | 16 |
| *pet8-rna2* | | | 73 | 0 | 9 | 5.6 | 1.8 | 71 |
| *pet8-rna2* | | | 284 | 0 | 47 | 7.2 | 1.0 | 16 |
| *pet8-rna2* | | | 35 | 0 | 2 | 2.7 | 1.9 | 110 |
| Total | | | 392 | 0 | 58 | 6.5 | 0.8 | |
| *pet8-lys9* | | | 23 | 3 | 40 | 47.3 | 11.4 | 71 |
| *pet8-lys9* | | | 24 | 0 | 22 | 25.5 | 4.3 | 110 |
| *pet8-lys9* | | | 24 | 2 | 25 | 39.4 | 12.7 | 70 |
| Total | | | 71 | 5 | 87 | 37.5 | 5.6 | |
| *rna2-lys9* | | | 27 | 3 | 36 | 44.7 | 12.2 | 71 |
| *rna2-lys9* | | | 23 | 1 | 15 | 28.6 | 11.2 | 110 |
| Total | | | 50 | 4 | 51 | 38.7 | 8.7 | |

[a] See footnote *a* of Table 1.

TABLE 15. *Tetrad analysis data for chromosome XV*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *arg8-arg1* | | | 72 | 17 | 220 | 56.3 | 5.8 | 37 |
| *arg1-spe2* | | | 63 | 0 | 4 | 3.0 | 1.5 | 10 |
| *arg1-SUP3* | | | 74 | 6 | 139 | 41.0 | 4.2 | 37 |
| *SUP3-pet17* | | | 15 | 0 | 7 | 16.6 | 5.4 | 36 |
| *SUP3-pet17* | | | 31 | 0 | 27 | 24.8 | 3.8 | 37 |
| Total | | | 46 | 0 | 34 | 22.5 | 3.1 | |
| *SUP3-cen15* | 181 | 70 | | | | 14.7 | 1.6 | 36 |
| *SUP3-cen15* | 57 | 31 | | | | 18.8 | 3.0 | 37 |
| Total | 238 | 101 | | | | 15.7 | 1.4 | |
| *SUP3-tcm1* | | | 53 | 0 | 34 | 20.5 | 2.9 | 28 |
| *spd1-cen15* | 25 | 9 | | | | 13.9 | 4.2 | I. Dawes, pers. comm. |
| *spd1-pet17* | | | 11 | 1 | 8 | 42.3 | 32.2 | I. Dawes, pers. comm. |
| *cen15-cyc2* | 172 | 48 | | | | 11.3 | 1.5 | 85 |
| *cen15-mak1* | 75 | 0 | | | | 0 | | 109 |
| *cen15-tup4* | 77 | 10 | | | | 5.9 | 1.8 | J. McCusker and J. Haber, pers. comm. |
| *cen15-tup4* | 59 | 13 | | | | 9.3 | 2.4 | 109 |
| Total | 136 | 23 | | | | 7.4 | 1.5 | |
| *cen15-tup7* | 216 | 3 | | | | 0.7 | 0.4 | L. Bisson, pers. comm. |
| *cen15-pet17* | 63 | 29 | | | | 16.7 | 2.7 | 36 |
| *cen15-pet17* | 79 | 53 | | | | 21.7 | 2.6 | T. Takahashi, pers. comm. |
| Total | 142 | 82 | | | | 19.6 | 1.9 | |
| *cen15-cdc21* | 28 | 34 | | | | 31.0 | 4.3 | 7a |
| *cen15-cdc21* | 17 | 34 | | | | 39.8 | 5.5 | 110 |
| Total | 45 | 68 | | | | 34.8 | 3.4 | |
| *mak1-tup4* | | | 16 | 0 | 2 | 5.6 | 3.8 | 109 |
| *mak1-tup7* | | | 35 | 0 | 2 | 2.7 | 1.9 | L. Bisson, pers. comm. |
| *mak1-pet17* | | | 95 | 4 | 59 | 27.9 | 5.6 | 109 |
| *mak1-ade2* | | | 20 | 4 | 50 | 54.3 | 12.0 | 109 |
| *tup4-tup7* | | | 44 | 0 | 13 | 11.7 | 2.9 | L. Bisson, pers. comm. |
| *tup4-pet17* | | | 43 | 0 | 22 | 17.6 | 3.2 | 109 |
| *tup4-ade2* | | | 7 | 0 | 31 | 48.1 | 5.3 | 109 |
| *tup4-ade2* | | | 2 | 3 | 15 | NL[b] | | L. Bisson, pers. comm. |
| *tup4-ade2* | | | 11 | 11 | 65 | NL | | J. McCusker and J. Haber, pers. comm. |
| Total | | | 20 | 14 | 111 | NL | | |

TABLE 15—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *tup7-pho80* | | | 42 | 0 | 0 | 0 | | L. Bisson, pers. comm. |
| *cyc2-pet17* | | | 30 | 1 | 13 | 23.3 | 10.7 | 85 |
| *pet17-mak8* | | | 61 | 0 | 0 | 0 | | 109 |
| *pet17-suf11* | | | 76 | 0 | 16 | 8.9 | 2.1 | M. Culbertson, pers. comm. |
| *pet17-cdc21* | | | 113 | 0 | 46 | 15.0 | 1.9 | 109 |
| *mak8-cdc21* | | | 23 | 1 | 9 | 26.5 | 17.7 | 109 |
| *pet17-ade2* | | | 64 | 10 | 158 | 49.6 | 5.5 | 71 |
| *pet17-ade2* | | | 23 | 1 | 67 | 40.2 | 3.9 | M. Culbertson, pers. comm. |
| *pet17-ade2* | | | 33 | 4 | 58 | 46.0 | 8.9 | 109 |
| *pet17-ade2* | | | 17 | 1 | 25 | 36.9 | 8.7 | 85 |
| Total | | | 137 | 16 | 308 | 45.3 | 3.3 | |
| *tmp1-cdc21* | | | 30 | 0 | 0 | 0 | | 23 |
| *cdc21-ade2* | | | 35 | 2 | 24 | 32.3 | 11.1 | F. Hilger, pers. comm. |
| *cdc21-ade2* | | | 46 | 2 | 62 | 34.1 | 4.8 | 109 |
| *cdc21-ade2* | | | 16 | 2 | 20 | 47.7 | 19.5 | 23 |
| *cdc21-ade2* | | | 26 | 2 | 43 | 39.9 | 7.6 | 23 |
| *cdc21-ade2* | | | 18 | 1 | 19 | 34.2 | 10.5 | M. Brendel, pers. comm. |
| Total | | | 141 | 9 | 168 | 36.3 | 3.8 | |
| *tcm1-pet17* | | | 130 | 0 | 3 | 1.1 | 0.6 | 28 |
| *tcm1-ade2* | | | 15 | 3 | 91 | 50.8 | 5.2 | 28 |
| *suf11-ade2* | | | 31 | 2 | 59 | 39.2 | 5.6 | M. Culbertson, pers. comm. |
| *cyh4-ade2* | | | 107 | 5 | 124 | 33.4 | 3.6 | 70 |
| *cdc21-8740* | | | 31 | 1 | 19 | 25.5 | 8.1 | F. Hilger, pers. comm. |
| *8740-ade2* | | | 38 | 0 | 13 | 13.1 | 3.3 | F. Hilger, pers. comm. |
| *ade2-SUF5* | | | 106 | 0 | 34 | 12.5 | 1.9 | 15 |
| *ade2-ser1* | | | 30 | 0 | 28 | 25.8 | 3.8 | 43 |
| *ade2-ser1* | | | 100 | 1 | 109 | 27.4 | 2.2 | 70 |
| *ade2-ser1* | | | 22 | 2 | 25 | 41.0 | 13.3 | 61 |
| Total | | | 152 | 3 | 162 | 28.5 | 2.2 | |
| *ade2-ade9* | | | 23 | 0 | 16 | 21.6 | 4.4 | 70 |
| *ade2-ade9* | | | 37 | 6 | 99 | 49.9 | 6.8 | 15 |
| Total | | | 60 | 6 | 115 | 43.3 | 5.2 | |
| *ade2-his8* | | | 90 | 4 | 198 | 38.2 | 2.4 | 70 |
| *ade2-his8* | | | 65 | 18 | 260 | 57.1 | 5.0 | T. Takahashi, pers. comm. |
| *ade2-his8* | | | 18 | 3 | 29 | 53.7 | 18.4 | 61 |
| *ade2-his8* | | | 21 | 7 | 107 | 58.4 | 7.7 | 15 |
| Total | | | 194 | 32 | 594 | 49.9 | 2.6 | |

TABLE 15—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *ser1-his8* | | | 249 | 0 | 68 | 11.0 | 1.2 | 70 |
| *ser1-his8* | | | 32 | 0 | 17 | 18.1 | 3.7 | 61 |
| *ser1-his8* | | | 119 | 0 | 39 | 12.7 | 1.8 | 43 |
| Total | | | 400 | 0 | 124 | 12.2 | 1.0 | |
| *SUF5-ade9* | | | 50 | 1 | 89 | 34.0 | 2.9 | 15 |
| *SUF5-his8* | | | 35 | 2 | 100 | 41.1 | 3.6 | 15 |
| *ade9-his8* | | | 16 | 0 | 5 | 12.3 | 4.9 | 70 |
| *ade9-his8* | | | 100 | 0 | 36 | 13.7 | 2.0 | 15 |
| Total | | | 116 | 0 | 41 | 13.5 | 1.9 | |
| *his8-met7* | | | 288 | 1 | 244 | 23.5 | 1.2 | 61 |
| *his8-tra3* | | | 24 | 0 | 35 | 32.4 | 4.0 | 61 |
| *his8-cpa1* | | | 4 | 0 | 13 | 44.1 | 7.8 | F. Hilger, pers. comm. |
| *met7-cpa1* | | | 8 | 0 | 9 | 28.6 | 7.3 | F. Hilger, pers. comm. |
| *met7-tra3* | | | 51 | 0 | 8 | 6.9 | 2.3 | 61 |

[a] See footnote *a* of Table 1.
[b] NL, Not linked.

TABLE 16. *Tetrad analysis data for chromosome XVI*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *pho85-rad1* | | | 112 | 0 | 48 | 15.5 | 2.0 | A. Toh-e, pers. comm. |
| *rad1-sot1* | | | 109 | 0 | 1 | 0.5 | 0.5 | 82 |
| *rad1-swi1* | | | 81 | 0 | 10 | 5.6 | 1.7 | J. Haber and L. Rowe, pers. comm. |
| *rad1-chl1* | | | 38 | 0 | 12 | 12.4 | 3.2 | 58 |
| *rad1-cen16* | 60 | 36 | | | | 20.1 | 2.9 | J. Haber and L. Rowe, pers. comm. |
| *rad1-cen16* | 77 | 43 | | | | 19.2 | 2.5 | T. Takahashi, pers. comm. |
| Total | 137 | 79 | | | | 19.6 | 1.9 | |
| *sot1-cen16* | 101 | 12 | | | | 5.4 | 1.5 | 82 |
| *swi1-cen16* | 58 | 29 | | | | 17.7 | 2.9 | J. Haber and L. Rowe, pers. comm. |
| *chl1-cen16* | 136 | 19 | | | | 6.3 | 1.4 | 58 |
| *rad1-aro7* | | | 16 | 4 | 47 | 58.1 | 13.7 | 58 |
| *rad1-aro7* | | | 15 | 0 | 16 | 27.8 | 5.3 | J. Game, pers. comm. |
| *rad1-aro7* | | | 16 | 3 | 19 | 65.8 | 40.5 | 83 |
| *rad1-aro7* | | | 37 | 8 | 83 | 57.5 | 11.0 | 88 |
| Total | | | 84 | 15 | 165 | 53.6 | 7.1 | |
| *chl1-aro7* | | | 100 | 1 | 111 | 27.6 | 2.2 | 58 |
| *cen16-mak6* | 41 | 6 | | | | 6.5 | 2.5 | 109 |
| *cen16-mak6* | 66 | 12 | | | | 7.9 | 2.2 | 76 |
| Total | 107 | 18 | | | | 7.4 | 1.8 | |
| *cen16-SUP15* | 16 | 18 | | | | 29.8 | 5.7 | 36 |
| *cen16-mak3* | 41 | 60 | | | | 34.3 | 3.5 | 109 |
| *cen16-mak3* | 32 | 29 | | | | 26.3 | 4.1 | 76 |
| Total | 73 | 89 | | | | 31.1 | 2.7 | |
| *cen16-aro7* | 98 | 194 | | | | 39.7 | 2.3 | 109 |
| *cen16-aro7* | 228 | 244 | | | | 28.9 | 1.5 | 36 |
| *cen16-aro7* | 71 | 161 | | | | 42.2 | 2.7 | F. Hilger, pers. comm. |
| Total | 397 | 599 | | | | 34.8 | 1.2 | |

TABLE 16—*Continued*

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | $x'$ (cM) | SE | |
| *cen16-rad56* | 17 | 25 | | | | 34.3 | 5.5 | 24 |
| *mak6-aro7* | | | 37 | 0 | 34 | 25.6 | 3.5 | 109 |
| *mak6-aro7* | | | 33 | 3 | 42 | 41.1 | 9.7 | 76 |
| Total | | | 70 | 3 | 76 | 32.2 | 4.5 | |
| *mak3-aro7* | | | 69 | 0 | 6 | 4.0 | 1.6 | 109 |
| *mak3-aro7* | | | 35 | 0 | 4 | 5.2 | 2.5 | F. Hilger, pers. comm. |
| *mak3-aro7* | | | 61 | 1 | 11 | 11.8 | 6.7 | 76 |
| Total | | | 165 | 1 | 21 | 7.4 | 2.3 | |
| *mak3-ts4572* | | | 26 | 1 | 26 | 30.8 | 7.3 | F. Hilger, pers. comm. |
| *aro7-osm2* | | | 8 | 0 | 0 | 0 | | 92 |
| *mak3-SUP16* | | | 13 | 0 | 7 | 18.3 | 5.9 | 76 |
| *aro7-SUP15* | | | 34 | 0 | 5 | 6.5 | 2.8 | 56 |
| *aro7-SUP15* | | | 28 | 0 | 6 | 8.9 | 3.6 | 36 |
| Total | | | 62 | 0 | 11 | 7.7 | 2.2 | |
| *aro7-SUP16* | | | 122 | 0 | 35 | 11.4 | 1.7 | 76 |
| *aro7-ts4572* | | | 35 | 0 | 36 | 27.2 | 3.5 | F. Hilger, pers. comm. |
| *aro7-rad56* | | | 15 | 2 | 24 | 48.0 | 15.9 | 24 |

[a] See footnote *a* of Table 1.

TABLE 17. *Tetrad analysis data for chromosome XVII*[a]

| Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|
| | FD | SD | PD | NPD | T | x' (cM) | SE | |
| *lap3-pet2* | | | 90 | 0 | 54 | 19.7 | 2.2 | R. Trumbly, pers. comm. |
| *lap3-met2* | | | 63 | 1 | 92 | 31.5 | 2.7 | R. Trumbly, pers. comm. |
| *lap3-pha2* | | | 26 | 15 | 99 | 89.1 | 22.5 | R. Trumbly, pers. comm. |
| *pet2-prt2* | | | 33 | 0 | 0 | 0 | | 71 |
| *pet2-met2* | | | 102 | 0 | 33 | 12.6 | 2.0 | 70 |
| *pet2-met2* | | | 96 | 0 | 55 | 19.1 | 2.2 | 71 |
| *pet2-met2* | | | 147 | 1 | 54 | 14.9 | 2.2 | R. Trumbly, pers. comm. |
| Total | | | 345 | 1 | 142 | 15.2 | 1.2 | |
| *prt2-met2* | | | 10 | 0 | 7 | 21.8 | 6.7 | S. Dutcher, pers. comm. |
| *prt2-kar1* | | | 7 | 1 | 11 | 49.7 | 25.6 | S. Dutcher, pers. comm. |
| *pet2-pha2* | | | 48 | 8 | 95 | 51.9 | 8.6 | 71 |
| *met2-kar1* | | | 12 | 0 | 11 | 25.5 | 6.1 | S. Dutcher, pers. comm. |
| *met2-pha2* | | | 60 | 1 | 87 | 31.5 | 2.8 | 70 |
| *met2-pha2* | | | 57 | 4 | 85 | 38.5 | 5.2 | 71 |
| *met2-pha2* | | | 71 | 6 | 136 | 41.5 | 4.3 | R. Trumbly, pers. comm. |
| Total | | | 188 | 11 | 308 | 37.6 | 2.4 | |
| *kar1-pha2* | | | 13 | 0 | 10 | 23.0 | 5.9 | S. Dutcher, pers. comm. |

[a] See footnote *a* of Table 1.

TABLE 18. *Tetrad analysis data for fragments*[a]

| Fragment | Interval | Segregation (no.) | | Ascus type (no.) | | | Map distance | | Reference |
|---|---|---|---|---|---|---|---|---|---|
| | | FD | SD | PD | NPD | T | x' (cM) | SE | |
| 6 | *thi1-SUP50* | | | 41 | 0 | 3 | 3.5 | 1.9 | 36 |
| | *SUP50-pdx2* | | | 44 | 0 | 9 | 8.7 | 2.7 | 36 |
| | *thi1-pdx2* | | | 60 | 0 | 18 | 11.9 | 2.5 | 70 |
| | *gal5-SUP50* | | | 17 | 0 | 1 | 2.8 | 2.8 | 71 |
| | *gal5-thi1* | | | 53 | 0 | 8 | 6.7 | 2.2 | 18 |
| 8 | *arg81-SUP5* | | | 24 | 0 | 27 | 28.5 | 4.2 | F. Hilger, pers. comm. |
| | *gal80-SUP5* | | | 101 | 0 | 7 | 3.3 | 1.2 | A. Klar, pers. comm. |
| | *gal80-SUP5* | | | 20 | 0 | 0 | 0 | | 20 |
| | Total | | | 121 | 0 | 7 | 2.8 | 1.0 | |
| 11 | *mut1-mut2* | | | 13 | 2 | 19 | 52.3 | 22.5 | 26 |

[a] See footnote *a* of Table 1.

TABLE 19. *Glossary of gene symbols*

| Gene symbol | Phenotype |
|---|---|
| *ade* | Adenine requiring |
| *AMY* | Antimycin resistance |
| *ant* | Antibiotic resistance |
| *arg* | Arginine requiring |
| *aro* | Aromatic amino acid requiring |
| *asp* | Aspartic acid requiring |
| *AXE* | Axenomycin resistance |
| *bar* | a cells lack barrier effect on α factor |
| *BOR* | Borrelidin resistance |
| *can* | Canavanine resistance |
| *car* | Arginine catabolism defective |
| *cdc* | Cell division cycle block at 36°C |
| *cen* | Centromere |
| *chl* | Chromosome loss |
| *cho* | Choline requiring |
| *cly* | Cell lysis at 36°C |
| *cpa* | Arginine requiring in presence of excess uracil |
| *cry* | Cryptopleurine resistance |
| *CUP* | Copper resistance |
| *cyc* | Cytochrome *c* deficiency |
| *cyh* | Cycloheximide resistance |
| *cys* | Cysteine requiring |
| *dal* | Allantoin degradation deficient |
| *dbl* | Alcian blue dye binding deficient |
| *dur* | Urea degradation deficient |
| *eth* | Ethionine resistance |
| *fas* | Fatty acid synthetase deficient |
| *fdp* | Unable to grow on glucose, fructose, sucrose, or mannose |
| *flk* | Resistance to catabolite repression |
| *FLO* | Flocculation |
| *fol* | Folinic acid requiring |
| *fro* | Frothing |
| *gal* | Galactose nonutilizer |
| *glc* | Glycogen storage |
| *glk* | Glucokinase deficient (unable to use glucose) |
| *his* | Histidine requiring |
| *HML* | Mating type cassette |
| *HMR* | Mating type cassette |
| *HO* | Homothallic switching |
| *hom* | Homoserine requiring |
| *hxk* | Hexokinase deficient |
| *ils* | Isoleucyl-tRNA synthetase deficient; no growth at 36°C |
| *ilv* | Isoleucine-plus-valine requiring |
| *kar* | Nuclear fusion defective |
| *kex* | Unable to express killer phenotype |
| *lap* | Leucine aminopeptidase deficient |
| *let* | Lethal |
| *leu* | Leucine requiring |
| *lts* | Low-temperature sensitive |
| *lys* | Lysine requiring |
| *mak* | Maintenance of killer deficient |
| *MAL* | Maltose fermentation positive |
| *mar* | Partial expression of mating type cassettes |
| *MAT* | Mating type locus |
| *mes* | Methionyl-tRNA synthetase defective; no growth at 36°C |
| *met* | Methionine requiring |
| *MGL* | α-Methyl glucoside fermenter |
| *min* | Inhibited by methionine |
| *mnn* | Mannan synthesis defective |
| *mut* | Elevated spontaneous mutation rate |
| *nul* | Nonmater |
| *ole* | Oleic acid requiring |
| *oli* | Oligomycin resistance |
| *osm* | Sensitive to low osmotic pressure |
| *pdx* | Pyridoxine requiring |
| *pep* | Proteinase deficient |
| *pet* | Petite; unable to grow on nonfermentable carbon sources |
| *pgi* | Phosphoglucose isomerase deficient |
| *pgk* | 3-Phosphoglycerate kinase deficient |
| *pha* | Phenylalanine requiring |
| *pho* | Phosphatase deficient |
| *prb* | Proteinase deficient |
| *prt* | Protein synthesis defective at 36°C |
| *pur* | Purine excretion |
| *pyk* | Pyruvate kinase deficient |
| $r_s^1$ | Radiation sensitive |
| *rad* | Radiation (UV or ionizing) sensitive |
| *RDN* | Ribosomal DNA structural genes |
| *rev* | Nonrevertible |
| *ROC* | Roccal resistance |
| *rme* | Meiosis independent of mating type heterozygosity |
| *rna* | Unable to grow at 36°C; block in RNA synthesis |
| *SAD* | Sporulation regulation |
| *ser* | Serine requiring |
| *ski* | Super-killer |
| *sot* | Suppression of dTMP uptake |
| *spd* | Sporulation not repressed on rich media |
| *spe* | Spermidine resistance |
| *spo* | Sporulation deficient |
| *sst* | Supersensitive to α factor |
| *ste* | Sterile |
| *SUC* | Sucrose fermenter |
| *SUF/suf* | Suppression of frameshift mutation |
| *suh* | Suppression of *his2-1* |
| *SUP/sup* | Suppression of nonsense mutation |
| *SUS* | Suppression of *ser1* |
| *swi* | Homothallic switching deficient |
| *tcm* | Trichodermin resistance |
| *thi* | Thiamine requiring |
| *thr* | Threonine requiring |
| *til* | Thiaisoleucine resistance |
| *tmp* | Thymidine monophosphate requiring |
| *tra* | Triazylalanine resistant |
| *trp* | Tryptophan requiring |
| *ts* | Lethal, temperature sensitive |
| *tsl* | Lethal, temperature sensitive |
| *tsm* | Lethal, temperature sensitive |
| *tup* | dTMP uptake positive |
| *tyr* | Tyrosine requiring |
| *umr* | Non-UV revertible |
| *ura* | Uracil requiring |

[a] Abbreviations: RNA, ribonucleic acid; tRNA, transfer RNA; UV, ultraviolet; DNA, deoxyribonucleic acid; dTMP, deoxythymidine 5′-monophosphate.

TABLE 20. *List of mapped genes*[a]

| Gene | Map position | Reference |
|---|---|---|
| *ade1* | 1R | 70, 85 |
| *ade2* | 15R | 70 |
| *ade3* | 7R | 44, 70, 102 |
| *ade5* | 7L | 70, 74, 110 |
| *ade6* | 7R | 35, 80, 84a, 90 |
| *ade8* | 4R | 2, 45, 71 |
| *ade9* | 15R | 15, 70 |
| *ADE15* | 7R | 44 |
| *AMY1* | 7L | 62 |
| *ant1* | 7L | 9 |
| *arg1* | 15L | 10, 37 |
| *arg3* | 10L | F. Hilger, pers. comm. |
| *arg4* | 8R | 35, 70, 108, 109 |
| *arg5,6* | 5R | 21, 57, 69, 70, 75 |
| *arg8* | 15L | 37 |
| *arg9* | 5R | 70 |
| *arg80* | 13R | F. Hilger, pers. comm. |
| *arg81* | F8 | F. Hilger, pers. comm. |
| *arg82* | 4R | F. Hilger, pers. comm. |
| *aro1* | 4R | 70, 71, 111 |
| *aro2* | 7L | 70, 74, 90, 110 |
| *aro7* | 16R | 36, 56, 77, 109 |
| *asp1* | 4R | 45, 46 |
| *asp5* | 12R | 18, 41, 70, 78 |
| *AXE1* | 7L | S. Sora, pers. comm. |
| *bar1* | 9L | G. Sprague and I. Herskowitz, pers. comm. |
| *BOR1* | 5R | 75 |
| *BOR2* | 7L | 75 |
| *can1* | 5L | 71, 89, 109 |
| *car2* | 12R | F. Hilger, pers. comm. |
| *cdc2* | 4L | 33, 49, 71, 111 |
| *cdc4* | 6L | 16, 71 |
| *cdc5* | 13L | 16, 71 |
| *cdc6* | 10L | 48; F. Hilger, pers. comm. |
| *cdc7* | 4L | 71, 77 |
| *cdc8* | 10R | 51, 71 |
| *cdc9* | 4L | 33, 71 |
| *cdc10* | 3L | 13, 71 |
| *cdc11* | 10R | 51, 71 |
| *cdc12* | 8R | 16, 109 |
| *cdc14* | 6R | 16, 71 |
| *cdc15* | 1R | 71 |
| *cdc16* | 11L | 33, 111 |
| *cdc19* | 1L | 48 |
| *cdc21* | 15R | 23, 109 |
| *cdc26* | 6R | 48 |
| *cdc28* | 2R | 12, 33, 109 |
| *cdc29* | 9L | 33 |
| *cdc36* | 4L | J. Shuster, pers. comm. |
| *cdc39* | 3R | J. Shuster, pers. comm. |
| *chl1* | 16L | 58 |
| *cho1* | 5R | 3, 57 |
| *cly3* | 6R | 71 |
| *cly7* | 11L | 71 |
| *cly8* | 7R | 71, 80 |
| *cpa1* | 15R | F. Hilger, pers. comm. |
| *cry1* | 3R | 27, 67, 93 |
| *CUP1* | 8R | 35, 70 |
| *cyc1* | 10R | 51, 71 |
| *cyc2* | 15R | 85 |
| *cyc3* | 1L | 85 |
| *cyc7* | 5L | 88, 89 |
| *cyc8* | 2R | 85 |
| *cyc9* | 3R | 85 |
| *cyh1* | 2L | 70 |
| *cyh2* | 7L | 70, 74, 80, 90 |
| *cyh3* | 7L | 70 |
| *cyh4* | 15R | 70 |
| *cyh10* | 2R | 91 |
| *cys1* | 1L | 30, 85, 11 |
| *dal1* | 9R | 11, 52 |
| *dal2* | 9R | 11, 52 |
| *dal4* | 9R | 11, 52 |
| *dbl1* | 11L | 4, 22 |
| *dur1,2* | 2R | 12 |
| *eth2* | 13R | 65, 66 |
| *fas1* | 11L | 8, 14 |
| *fdp1* | 2R | 105 |
| *flk1* | 3R | H. Stark, pers. comm. |
| *FLO1* | 1R | 38, 85, 98 |
| *FLO4* | | See *FLO1* |
| *fol1* | 4R | J. Game and J. Little, pers. comm. |
| *fol2* | 7R | J. Game J. Little, and B. Rockmill, pers. comm. |
| *fro1* | 7R | 101, 102 |
| *fro2* | 7R | 101, 102 |
| *gal1* | 2R | 6, 18, 57, 70 |
| *gal2* | 12R | 18, 70, 78 |
| *gal3* | 4R | 18, 42 |
| *gal4* | 16L | J. Haber, pers. comm. |
| *gal5* | F6 | 19 |
| *gal7* | 2R | 6, 18, 57, 70 |
| *gal10* | 2R | 6, 18, 57, 70 |
| *gal80* | F8 | 19, 20 |
| *glc1* | 2R | J. Pringle, pers. comm. |
| *glk1* | 3L | P. Maitra and Z. Lobo, pers. comm. |
| *his1* | 5R | 21, 57, 70, 75 |
| *his2* | 6R | 17, 36, 70, 71 |
| *his3* | 15R | 15, 70 |
| *his4* | 3L | 13, 35, 102, 106 |
| *his5* | 9L | 57, 70, 76 |
| *his6* | 9L | 35, 71, 76 |
| *his7* | 2R | 70, 80 |
| *his8* | | See *his3* |
| *HML* | 3L | 32 |
| *HMR* | 3R | 32 |
| *HO* | 4L | 48; G. Kawasaki, pers. comm. |
| *hom2* | 4R | 70, 71 |
| *hom3* | 5R | 21, 70, 75 |
| *hxk1* | 6R | 60 |
| *hxk2* | 7L | P. Maitra, pers. comm. |
| *ils1* | 2L | 68 |
| *ilv1* | 5R | 39, 57, 70 |
| *ilv3* | 10R | 36, 51, 70, 71 |
| *kar1* | 17R | S. Dutcher, pers. comm. |
| *kex1* | 7L | 110 |
| *kex2* | 14L | 103, 110 |
| *lap3* | 17R | R. Trumbly, pers. comm. |
| *let1* | 1R | 71 |

TABLE 20—*Continued*

| Gene | Map position | Reference |
|---|---|---|
| *let1M* | 13R | 73 |
| *let3* | 10L | 73 |
| *let5* | 10L | 73 |
| *let6* | 6L | 73 |
| *leu1* | 7L | 35, 60, 70, 90 |
| *leu2* | 3L | 13, 35, 57, 70 |
| *lts1* | 7L | 91 |
| *lts3* | 7L | 91 |
| *lts4* | 4R | 91 |
| *lts10* | 4R | 91 |
| *lys1* | 9R | 11, 35, 52, 57, 76 |
| *lys2* | 2R | 12, 35, 70, 80, 109 |
| *lys4* | 4R | R. Contopoulou, pers. comm. |
| *lys5* | 7L | 70, 74, 90, 110 |
| *lys7* | 13R | 16, 32, 70, 71 |
| *lys9* | 14R | 70, 71, 110 |
| *lys10* | 17L | 71 |
| *lys11* | 9L | 57, 70, 76 |
| *mak1* | 15C | 109 |
| *mak3* | 16R | 77, 109 |
| *mak4* | 2R | 109 |
| *mak5* | 2R | 109 |
| *mak6* | 16R | 77, 109 |
| *mak7* | 8L | 108, 109 |
| *mak8* | 15R | 109 |
| *mak9* | 11L | 111 |
| *mak10* | 5L | 89, 109 |
| *mak11* | 11L | 111 |
| *mak12* | 12L | 111 |
| *mak13* | 9R | 108 |
| *mak14* | 3R | 111 |
| *mak15* | 11R | 111 |
| *mak16* | 1L | 111 |
| *mak17* | 10L | 108 |
| *mak18* | 8R | 108 |
| *mak19* | 8R | 108 |
| *mak20* | 8L | 108 |
| *mak21* | 4R | 111 |
| *mak22* | 12L | 108 |
| *mak24* | 7L | 108 |
| *mak26* | 14L | 108 |
| *mak27* | 13R | 111 |
| *MAL1* | 7R | 44, 70, 102 |
| *MAL2* | 3R | 7, 35, 60 |
| *MAL3* | 2R | 48, 64 |
| *MAL4* | 11R | 36, 70, 71, 111 |
| *mar1* | 4L | 49 |
| *MAT* | 3R | 27, 35, 67, 70, 93 |
| *mes1* | 7R | D. Schild, pers. comm. |
| *met1* | 11R | 35, 70, 71 |
| *met2* | 17R | 71 |
| *met3* | 10R | 51, 70, 77 |
| *met4* | 17L | 71 |
| *met5* | 5R | 57 |
| *met6* | 13R | 65, 66 |
| *met7* | 15R | 61 |
| *met8* | 2R | 12, 36, 70 |
| *met10* | 6R | 17, 48, 57, 60, 70 |
| *met13* | 7L | 70, 74, 90, 92, 110 |
| *met14* | 11R | 33, 40, 70, 111 |
| *MGL2* | 2R | 48, 64 |
| *min1* | 5L | 89 |
| *mnn1* | 5C | 1 |
| *mnn2* | 2R | 4 |
| *mnn4* | 11L | 4 |
| *mut1* | F11 | 26 |
| *mut2* | F11 | 26 |
| *nul3* | 4R | 71 |
| *ole1* | 7L | 84, 90 |
| *oli1* | 7L | 86 |
| *osm1* | 10R | 92 |
| *osm2* | 16R | 92 |
| *pdx2* | F6 | 35 |
| *pep16* | 12R | B. Jones, pers. comm. |
| *pet1* | 8R | 35, 70 |
| *pet2* | 17R | 70, 71 |
| *pet3* | 8R | 16, 71, 108, 109 |
| *pet8* | 14R | 16, 70, 71, 110 |
| *pet9* | 2L | 18, 68, 70 |
| *pet11* | 2R | 12, 36, 70 |
| *pet14* | 4R | 71, 111 |
| *pet17* | 15R | 36, 71, 85, 109 |
| *pet18* | 3R | 71, 109 |
| *petx* | 14L | 110 |
| *pgi1* | 2R | 64 |
| *pgk1* | 3R | 50 |
| *pha2* | 17R | 70, 71 |
| *pho2* | 4L | A. Toh-e, pers. comm. |
| *pho3,5* | 2R | 31, 94, 100, 104 |
| *pho4* | 6R | A. Toh-e, pers. comm. |
| *pho80* | 15R | L. Bisson, pers. comm. |
| *PHO82* | 6R | A. Toh-e, pers. comm. |
| *pho85* | 16L | A. Toh-e, pers. comm. |
| *prb1* | 5L | B. Jones, A. Mitchell, and G. Zubenko, pers. comm. |
| *prt1* | 15R | 71 |
| *prt2* | 17R | 71 |
| *prt3* | 5L | 71 |
| *pur5* | 4R | 2 |
| *pyk1* | 1L | 63, 85, 97 |
| $r_s^1$ | 5R | F. Eckardt, J. Game, and J. Little, pers. comm. |
| *rad1* | 16L | 58, 82, 83, 88 |
| *rad2* | 7R | D. Schild, pers. comm. |
| *rad3* | 5R | 69, 95 |
| *rad4* | 5R | 69, 95 |
| *rad5* | 12R | 53 |
| *rad6* | 7L | 24 |
| *rad7* | 10R | 51 |
| *rad18* | 3R | 71, 85 |
| *rad50* | 4R | R. Contopoulou, pers. comm. |
| *rad51* | 5R | 69 |
| *rad52* | 13L | 85 |
| *rad55* | 4R | 71 |
| *rad56* | 16R | 24 |
| *rad57* | 4R | 24, 77 |
| *RDN1* | 12R | 78 |
| *rev2* | | See *rad5* |
| *rme1* | 7R | G. Sprague and I. Herskowitz, pers. comm. |
| *ROC1* | 12R | 70 |
| *rna1* | 13R | 71, 108, 111 |

TABLE 20—*Continued*

| Gene | Map position | Reference |
|---|---|---|
| *rna2* | 14R | 16, 71, 110 |
| *rna3* | 4R | 71 |
| *rna5* | 2R | 48, 71 |
| *rna11* | 4L | 71, 111; A. Toh-e, pers. comm. |
| *SAD1* | 3R | Y. Kassir and I. Herskowitz, pers. comm. |
| *ser1* | 15R | 43, 61, 70 |
| *ser2* | 7R | 44 |
| *ski1* | 7L | 103 |
| *ski3* | 14L | 103 |
| *ski4* | 14L | 103 |
| *sot1* | 16L | 82 |
| *spd1* | 15L | I. Dawes, pers. comm. |
| *spe2* | 15L | 10, 37 |
| *spo1* | 14R | S. Klapholz and R. Easton-Esposito, pers. comm. |
| *spo11* | 8L | S. Klapholz and R. Easton-Esposito, pers. comm. |
| *spo13* | 8R | S. Klapholz and R.Easton-Esposito, pers. comm. |
| *sst1* | 9L | R. Chan, pers. comm. |
| *ste7* | 4L | J. Shuster, pers. comm. |
| *SUC* | 4L | 48 |
| *SUC1* | 7R | 44, 70, 84a, 102 |
| *SUC2* | 9L | 57, 70, 76 |
| *SUC3* | 2R | 48, 64 |
| *SUF2* | 3R | 13 |
| *SUF5* | 15R | 15 |
| *SUF7* | 13L | 16 |
| *SUF8* | 8R | 16 |
| *SUF9* | 6L | 16 |
| *SUF10* | 14L | 16 |
| *suf11* | 15R | M. Culbertson, pers. comm. |
| *suh2* | 12R | 71 |
| *SUP2* | 4R | 71 |
| *SUP3* | 15L | 36, 37 |
| *SUP4* | 10R | 25, 51, 71 |
| *SUP5* | F8 | 20 |
| *SUP6* | 6R | 17, 36, 71 |
| *SUP7* | 10L | 25, 36 |
| *SUP8* | 13R | 71, 108 |
| *SUP11* | 6R | 17, 36, 71 |
| *SUP15,16* | 16R | 36, 56, 77 |
| *SUP17* | 9L | 76 |
| *SUP19,20* | 5R | 71, 77 |
| *SUP22* | 9L | 76 |
| *SUP25* | 11R | 36, 71 |
| *SUP26* | 12R | 77 |
| *SUP27* | 4R | 77 |
| *SUP29* | 10C | 77 |
| *SUP30* | 10C | 71 |
| *sup35* | 4R | 70 |
| *sup45* | 2R | 36, 94 |
| *sup46* | 2R | B. Ono, J. W. Stewart, and F. Sherman, pers. comm. |
| *SUP50* | F6 | 70, 71 |
| *SUP51* | 10C | 71 |
| *SUP52* | 10L | 55 |
| *SUP53* | 3L | 81; C. Reed and S. Liebman, pers. comm. |
| *SUP54* | 7L | 81; C. Reed and S. Liebman, pers. comm. |
| *SUP61* | 3R | 7, 71 |
| *SUP71* | 5R | 71 |
| *SUS1* | 5L | 70 |
| *swi1* | 16L | 29; J. Haber and L. Rowe, pers. comm. |
| *tcm1* | 15R | 28 |
| *thi1* | F6 | 20, 70, 71 |
| *thr1* | 8R | 35, 71 |
| *thr4* | 3R | 50, 51, 54, 70, 99, 106 |
| *til1* | 7L | J. I. Stiles and F. Sherman, pers. comm. |
| *tmp1* | 15R | 7a, 23, 109 |
| *tra3* | 15R | 61 |
| *trp1* | 4R | 18, 24, 34, 70, 71, 77, 111 |
| *trp2* | 5R | 21, 57, 70, 75 |
| *trp3* | 11L | 4, 8, 14, 70, 111 |
| *trp4* | 4R | 45, 46, 71 |
| *trp5* | 7L | 35, 70, 74, 75, 80, 84, 90, 92 |
| *ts4572* | 16R | F. Hilger, pers. comm. |
| *tsl1 (tse)* | 1L | 47; J. McCusker and J. Haber, pers. comm. |
| *tsm1* | 3R | G. Sprague and I. Herskowitz, pers. comm. |
| *tsm5* | 3R | G. Fink, pers. comm.; J. McCusker and J. Haber, pers. comm. |
| *tsm134* | 2R | 31, 64, 71 |
| *tsm225* | 4L | F. Hilger, pers. comm. |
| *tsm437* | 7L | 71 |
| *tup1* | 3R | 54, 106 |
| *tup4* | 15L | 109 |
| *tup7* | 15R | L. Bisson, pers. comm. |
| *tyr1* | 2R | 12, 31, 70, 80, 85 |
| *umr7* | 3R | 54 |
| *ura1* | 11L | 4, 8, 14, 70, 111 |
| *ura2* | 10L | 48, 71 |
| *ura3* | 5L | 1, 3, 70, 71, 89 |
| *ura4* | 12R | 71, 78 |
| *8740* | 15R | F. Hilger, pers. comm. |

[a] The following sets of gene symbols are known to be synonyms: *pyk1–cdc19*, *FLO1–FLO4*, *tup1–cyc9–umr7–flk1*, *bar1–sst1*, *rad5–rev2*, *cdc21–tmp1* and *his3–his8*. pers. comm., Personal communication.

*AMY2* is about 4 cM from its centromere. Crosses to the centromere markers of chromosomes I to XVI failed to reveal significant linkage to any of these genes. Lucchini et al. (62) also used mitotic crossover analyses to eliminate this gene from both arms of chromosome XVII. Thus, *AMY2* could be near the centromere of an 18th chromosome. However, the tetrad data against *met3*, the centromere marker of chromosome X, are anomalous. The number of tetratype asci (7 of 11) for this gene pair is much higher than would be predicted from the second-division segregation frequencies of these two genes. Only 1.4 tetratype asci are expected in a sample of 11 asci. Thus, it is possible that another *met* gene was scored in this cross and that *AMY2* may be near the centromere of X. Fragment 8 (discussed above) has been eliminated from many of the chromosome arms and may be part of an 18th chromosome.

## ACKNOWLEDGMENTS

We are very pleased to acknowledge the invaluable assistance of Richard Snow for his efforts in development of the various computer programs used in the analyses of the data presented in this article. Fred Abrams and Elena Vasquez typed the tables and text and made valuable editorial suggestions. Finally, and most importantly, we thank the many investigators who provided unpublished data and made corrections on earlier drafts of the tables and map.

This work was supported by Public Health Service grant T32 CA09272, awarded by the National Cancer Institute to D.S., and by the Office of Health and Environmental Research of the U.S. Department of Energy under contract W-7405-ENG-48.

## LITERATURE CITED

1. **Antalis, C., S. Fogel, and C. E. Ballou.** 1973. Genetic control of yeast mannan structure: mapping the first gene concerned with mannan biosynthesis. J. Biol. Chem. **248**:4655–4659.
2. **Armitt, S., and R. A. Woods.** 1970. Purine-excreting mutants of *Saccharomyces cerevisiae*. I. Isolation and genetic analysis. Genet. Res. **15**:7–17.
3. **Atkinson, K. D., B. Jensen, A. I. Kolat, E. M. Storm, S. A. Henry, and S. Fogel.** 1980. Yeast mutants auxotrophic for ethanolamine or choline. J. Bacteriol. **141**:558–564.
4. **Ballou, D. L.** 1975. Genetic control of yeast mannan structure: mapping genes *mnn2* and *mnn4* in *Saccharomyces cerevisiae*. J. Bacteriol. **123**:616–619.
5. **Barratt, R. W., D. Newmeyer, D. D. Perkins, and L. Garnjobst.** 1954. Map construction in *Neurospora crassa*. Adv. Genet. **6**:1–93.
6. **Bassel, J., and R. Mortimer.** 1971. Genetic order of the galactose structural genes in *Saccharomyces cerevisiae*. J. Bacteriol. **108**:179–183.
7. **Brandriss, M. C., J. W. Stewart, F. Sherman, and D. Botstein.** 1976. Substitution of serine caused by a recessive lethal suppressor in yeast. J. Mol. Biol. **102**:467–476.

7a. **Brendel, M., and W. W. Fath.** 1974. Isolation and characterization of mutants of *Saccharomyces cerevisiae* auxotrophic and conditionally auxotrophic for 5'-dTMP. Z. Naturforsch. **29**: 733–738.

8. **Burkl, G., H. Castorph, and E. Schweizer.** 1972. Mapping of a complex gene locus coding for part of the *Saccharomyces cerevisiae* fatty acid synthetase multienzyme complex. Mol. Gen. Genet. **119**:315–322.

8a. **Cameron, J. R., E. Y. Loh, and R. W. Davis.** 1979. Evidence for transposition of dispersed repetitive DNA families in yeast. Cell **16**:739–751.

9. **Cohen, J. D., and N. R. Eaton.** 1979. Genetic analysis of multiple drug cross resistance in *Saccharomyces cerevisiae*: a nuclear-mitochondrial gene interaction. Genetics **91**:19–33.
10. **Cohn, M. S., C. W. Tabor, and H. Tabor.** 1978. Isolation and characterization of *Saccharomyces cerevisiae* mutants deficient in *S*-adenosylmethionine decarboxylase, spermidine, and spermine. J. Bacteriol. **135**:208–213.
11. **Cooper, T. G., M. Gorski, and V. Turoscy.** 1979. A cluster of three genes responsible for allantoin degradation in *Saccharomyces cerevisiae*. Genetics **92**:383–396.
12. **Cooper, T. G., C. Lam, and V. Turoscy.** 1980. Structural analysis of the *dur* loci in *Saccharomyces cerevisiae*: two domains of a single multifunctional gene. Genetics **94**:555–580.

12a. **Cox, B. S.** 1971. A recessive lethal super-suppressor mutation in yeast and other $\psi$ phenomena. Heredity **26**:211–232.

13. **Culbertson, M. R., L. Charnas, M. T. Johnson, and G. R. Fink.** 1977. Frameshifts and frameshift suppressors in *Saccharomyces cerevisiae*. Genetics **86**:745–764.
14. **Culbertson, M. R., and S. Henry.** 1973. Genetic analysis of hybrid strains trisomic for the chromosome containing a fatty acid synthetase gene complex (*fas1*) in yeast. Genetics **75**:441–458.
15. **Culbertson, M. R., K. N. Underbrink, and G. R. Fink.** 1980. Frameshift suppressors in *Saccharomyces cerevisiae*. II. Genetic properties of group II suppressors. Genetics, in press.
16. **Cummins, C. M., R. F. Gaber, M. R. Culbertson, R. Mann, and G. R. Fink.** 1980. Frameshift suppression in *Saccharomyces cerevisiae*. II. Isolation and genetic properties of group III suppressors. Genetics, in press.
17. **di Caprio, L., and P. J. Hastings.** 1976. Gene conversion and intragenic recombination at the *SUP6* locus and the surrounding region in *Saccharomyces cerevisiae*. Genetics **84**:697–721.
18. **Douglas, H. C., and D. C. Hawthorne.** 1964. Enzymatic expression and genetic linkage of genes controlling galactose utilization in Saccharomyces. Genetics **49**:837–844.
19. **Douglas, H. C., and D. C. Hawthorne.** 1966.

Regulation of genes controlling synthesis of the galactose pathway enzymes in yeast. Genetics **54**:911–916.

20. **Douglas, H. C., and D. C. Hawthorne.** 1972. Uninducible mutants in the *gali* locus of *Saccharomyces cerevisiae*. J. Bacteriol. **109**:1139–1143.
21. **Fogel, S., and D. D. Hurst.** 1967. Meiotic gene conversion in yeast tetrads and the theory of recombination. Genetics **57**:455–481.

21a. **Fogel, S., R. Mortimer, K. Lusnak, and F. Tavares.** 1979. Meiotic gene conversion: a signal of the basic recombination event in yeast. Cold Spring Harbor Symp. Quant. Biol. **43**: 1325–1341.

22. **Friis, J., and P. Ottolenghi.** 1970. The genetically determined binding of alcian blue by a minor fraction of yeast cell walls. C. R. Trav. Lab. Carlsberg **37**:327–341.
23. **Game, J. C.** 1976. Yeast cell-cycle mutant *cdc21* is a temperature-sensitive thymidylate auxotroph. Mol. Gen. Genet. **146**:313–315.
24. **Game, J. C., and R. K. Mortimer.** 1974. A genetic study of X-ray sensitive mutants in yeast. Mutat. Res. **24**:281–292.
25. **Gilmore, R.** 1966. Super-suppressors in *Saccharomyces cerevisiae*. Ph.D. thesis, University of California, Berkeley.
26. **Gottlieb, D. J. C., and R. C. von Borstel.** 1976. Mutators in *Saccharomyces cerevisiae, mut1-1, mut1-2,* and *mut2-1*. Genetics **83**:655–666.
27. **Grant, P. G., L. Sanchez, and A. Jimenez.** 1974. Crytopleurine resistance: genetic locus for a 40S ribosomal component in *Saccharomyces cerevisiae*. J. Bacteriol. **120**:1308–1314.
28. **Grant, P. G., D. Schindler, and J. E. Davies.** 1976. Mapping of trichodermine resistance in *Saccharomyces cerevisiae*: a genetic locus for a component of the 60S ribosomal subunit. Genetics **83**:667–673.
29. **Haber, J. E., and B. Garvik.** 1977. A new gene affecting the efficiency of mating type interconversions in homothallic strains of *Saccharomyces cerevisiae*. Genetics **87**:33–50.
30. **Halos, S.** 1976. Cysteine mutants in *Saccharomyces cerevisiae*. Ph.D. thesis, University of California, Berkeley.
31. **Hansche, P. E., V. Beres, and P. Lange.** 1978. Gene duplication in *Saccharomyces cerevisiae*. Genetics **88**:673–687.
32. **Harashima, S., and Y. Oshima.** 1976. Mapping of the homothallic genes, *HMα* and *HMa* in Saccharomyces yeasts. Genetics **84**:437–451.
33. **Hartwell, L. H., R. K. Mortimer, J. Culotti, and M. Culotti.** 1973. Genetic control of the cell division cycle in yeast. V. Genetic analysis of *cdc* mutants. Genetics **74**:267–286.
34. **Hawthorne, D. C.** 1955. The use of linear asci for chromosome mapping in Saccharomyces. Genetics **40**:511–518.
35. **Hawthorne, D. C., and R. K. Mortimer.** 1960. Chromosome mapping in Saccharomyces: centromere-linked genes. Genetics **45**:1085–1110.
36. **Hawthorne, D. C., and R. K. Mortimer.** 1968. Genetic mapping of nonsense suppressors in yeast. Genetics **60**:735–742.

36a. **Herskowitz, I., L. Blair, D. Forbes, J. Hicks, Y. Kassir, P. Kushner, J. Rine, G. Sprague, Jr., and J. Strathern.** 1980. Control of cell type in the yeast *Saccharomyces cerevisiae* and a hypothesis for development in higher eukaryotes. *In* W. Loomis and T. Leighton, (ed.), The molecular genetics of development, in press. Academic Press, Inc., New York.

37. **Hilger, F., and R. K. Mortimer.** 1980. Genetic mapping of *arg1* and *arg8* in *Saccharomyces cerevisiae* by trisomic analysis combined with interallelic complementation. J. Bacteriol. **141**: 270–274.
38. **Holmberg, S., and M. C. Kielland-Brandt.** 1978. A ts mutant in yeast flocculation. Carlsberg Res. Commun. **43**:37–47.
39. **Hurst, D. D., and S. Fogel.** 1964. Mitotic recombination and heteroallelic repair in *Saccharomyces cerevisiae*. Genetics **50**:435–458.
40. **Hwang, Y. L., G. Lindegren, and C. C. Lindegren.** 1963. Mapping the eleventh centromere of Saccharomyces. Can. J. Genet. Cytol. **5**:290–298.
41. **Hwang, Y. L., G. Lindegren, and C. C. Lindegren.** 1964. The twelfth chromosome of Saccharomyces. Can. J. Genet. Cytol. **6**:373–380.
42. **James, A. P., and B. Lee-Whiting.** 1955. Radiation-induced genetic segregations in vegetative cells of diploid yeast. Genetics **40**:826–831.
43. **Johnston, J. R.** 1962. Studies in meiotic and mitotic recombination in *Saccharomyces cerevisiae*. Ph.D. thesis, University of California, Berkeley.
44. **Jones, E. W., and K. Lam.** 1973. Mutations affecting levels of tetrahydrofolate interconversion enzymes in *Saccharomyces cerevisiae*. II. Map positions on chromosome VII of *ade3-41* and *ADE15*. Mol. Gen. Genet. **123**:209–218.
45. **Jones, G. E.** 1970. L-Asparaginase degradation in *Saccharomyces cerevisiae*: genetic control and biochemical properties of yeast l-asparaginase. Ph.D. thesis, University of California, Berkeley.
46. **Jones, G. E., and R. K. Mortimer.** 1970. L-Asparaginase-deficient mutants of yeast. Science **167**:181–182.
47. **Kaback, D. B., and H. O. Halvorson.** 1978. Ribosomal DNA magnification in *Saccharomyces cerevisiae*. J. Bacteriol. **134**:237–245.
48. **Kawasaki, G.** 1979. Karyotypic instability and carbon source effects in cell cycle mutants of *Saccharomyces cerevisiae*. Ph.D. thesis, University of Washington, Seattle.
49. **Klar, A. J. S., S. Fogel, and K. MacLeod.** 1979. *MAR1*—a regulator of the *HMa* and *HMα* loci in *Saccharomyces cerevisiae*. Genetics **93**:37–50.

49a. **Kushner, P.** 1979. Control of cell type by mobile genes. Ph.D. thesis, University of Oregon, Eugene.

50. **Lam, K.-B., and J. Marmur.** 1977. Isolation and characterization of *Saccharomyces cerevisiae* glycolytic pathway mutants. J. Bacte-

riol. **130**:746–749.

51. **Lawrence, C. W., F. Sherman, M. Jackson, and R. A. Gilmore.** 1975. Mapping and gene conversion studies with the structural gene for iso-1-cytochrome c in yeast. Genetics **81**:615–629.
52. **Lawther, R. P., E. Riemer, B. Chojnacki, and T. G. Cooper.** 1974. Clustering of the genes for allantoin degradation in *Saccharomyces cerevisiae*. J. Bacteriol. **119**:461–468.
53. **Lemontt, J. F.** 1971. Mutants of yeast defective in ultraviolet light-induced mutation. Genetics **68**:21–33.
54. **Lemontt, J. F., D. R. Fugit, and V. L. MacKay.** 1980. Pleiotropic mutations at the *TUP1* locus that affect the expression of mating-type-dependent functions in *Saccharomyces cerevisiae*. Genetics **94**:899–920.
55. **Liebman, S. W., J. W. Stewart, J. H. Parker, and F. Sherman.** 1977. Leucine insertion caused by a yeast amber suppressor. J. Mol. Biol. **109**:13–22.
56. **Liebman, S. W., J. W. Stewart, and F. Sherman.** 1975. Serine substitutions caused by an ochre suppressor in yeast. J. Mol. Biol. **94**:595–610.

56a. **Lindegren, C. C.** 1949. The yeast cell, its genetics and cytology. Educational Publishers, Inc., St. Louis.

56b. **Lindegren, C. C., G. Lindegren, E. E. Shult, and S. Desborough.** 1959. Chromosome maps of *Saccharomyces*. Nature (London) **183**:800–802.

57. **Lindegren, C. C., G. Lindegren, E. Shult, and Y. L. Hwang.** 1962. Centromeres, sites of affinity and gene loci on the chromosomes of Saccharomyces. Nature (London) **194**:260–265.
58. **Liras, P., J. McCusker, S. Mascioli, and J. E. Haber.** 1978. Characterization of a mutation in yeast causing nonrandom chromosome loss during mitosis. Genetics **88**:651–671.
59. **Lobo, Z.** 1976. Sugar phosphorylating enzymes in yeast: genetic and biochemical studies. Ph.D. thesis, University of Bombay, Bombay, India.
60. **Lobo, Z., and P. K. Maitra.** 1977. Genetics of yeast hexokinase. Genetics **86**:727–744.
61. **Lowenstein, R.** 1973. Genetic studies in *Saccharomyces cerevisiae*. Ph.D. thesis, Cornell University, Ithaca, N.Y.
62. **Lucchini, G., M. L. Carbone, M. Cocucci, and M. L. Sensi.** 1979. Nuclear inheritance of resistance to antimycin A in *Saccharomyces cerevisiae*. Mol. Gen. Genet. **177**:139–144.
63. **Maitra, P. K., and Z. Lobo.** 1977. Pyruvate kinase mutants of *Saccharomyces cerevisiae*: biochemical and genetic characterization. Mol. Gen. Genet. **152**:193–200.
64. **Maitra, P. K., and Z. Lobo.** 1977. Genetic studies with a phosphoglucose isomerase mutant of *Saccharomyces cerevisiae*. Mol. Gen. Genet. **156**:55–60.
65. **Masselot, M., and H. de Robichon-Szulmajster.** 1974. Methionine biosynthesis in *Saccharomyces cerevisiae*: mutations at the regulatory locus *ETH2*. I. Genetic data. Mol. Gen. Genet. **129**:339–348.
66. **Masselot, M., and H. de Robichon-Szulmajster.** 1975. Methionine biosynthesis in *Saccharomyces cerevisiae*. I. Genetical analysis of auxotrophic mutants. Mol. Gen. Genet. **139**: 121–132.
67. **Meade, J. H., M. I. Riley, and T. R. Manney.** 1977. Expression of cryptopleurine resistance in *Saccharomyces cerevisiae*. J. Bacteriol. **129**: 1428–1434.
68. **McLaughlin, C. S., and L. H. Hartwell.** 1969. A mutant of yeast with a defective methionyl-tRNA synthetase. Genetics **61**:557–566.

68a. **Minet, M., J. C. Jauniaux, P. Thuriaux, M. Grenson, and J. M. Wiame.** 1979. Organization and expression of a two-gene cluster in the arginine biosynthesis of *Saccharomyces cerevisiae*. Mol. Gen. Genet. **168**:299–308.

69. **Morrison, D. P.** 1978. Repair parameters in mutator mutants of *Saccharomyces cerevisiae*. Ph.D. thesis, University of Alberta, Edmonton, Alberta, Canada.
70. **Mortimer, R. K., and D. C. Hawthorne.** 1966. Genetic mapping in Saccharomyces. Genetics **53**:165–173.

70a. **Mortimer, R. K., and D. C. Hawthorne.** 1969. Yeast genetics, p. 385. *In* A. H. Rose and J. S. Harrison (ed.), The yeast I. Academic Press, Inc., New York.

71. **Mortimer, R. K., and D. C. Hawthorne.** 1973. Genetic mapping in Saccharomyces. IV. Mapping of temperature-sensitive genes and use of disomic strains in localizing genes. Genetics **74**: 33–54.
72. **Mortimer, R. K., and D. C. Hawthorne.** 1975. Genetic mapping in yeast. Methods Cell Biol. **11**:221–233.
73. **Munz, P.** 1972. Clone size distribution among haploid yeast segregants carrying a UV-induced recessive lethal mutation. Arch. Genet. **45**:173–180.
74. **Nakai, S., and R. K. Mortimer.** 1969. Studies of the genetic mechanism of radiation-induced mitotic segregation in yeast. Mol. Gen. Genet. **103**:329–338.
75. **Nass, G., and K. Poralla.** 1976. Genetics of borreliden resistant mutants of *Saccharomyces cerevisiae* and properties of their threonyl-tRNA-synthetase. Mol. Gen. Genet. **147**:39–43.
76. **Ono, B., J. W. Stewart, and F. Sherman.** 1979. Yeast UAA suppressors effective in $\psi^+$ strains: serine-inserting suppressors. J. Mol. Biol. **128**: 81–100.
77. **Ono, B., J. W. Stewart, and F. Sherman.** 1979. Yeast UAA suppressors effective in $\psi^+$ strains: leucine-inserting suppressors. J. Mol. Biol. **132**:507–520.

77a. **Perkins, D. D.** 1949. Biochemical mutants in the smut fungus *Ustilago maydis*. Genetics **34**: 607–626.

78. **Petes, T. D.** 1979. Meiotic mapping of yeast ribosomal DNA on chromosome XII. J. Bacteriol. **138**:185–192.

79. **Plischke, M. E., R. C. von Borstel, R. K. Mortimer, and W. E. Cohn.** 1976. Genetic markers and associated products in *Saccharomyces cerevisiae*, p. 767–832. *In* G. D. Fasman (ed)., Handbook of biochemistry and molecular biology: Nucleic acids section, vol. 2, 3rd ed. CRC Press, Cleveland.

80. **Plotkin, D. J.** 1978. Commitment to meiotic recombination: a temporal analysis. Ph.D. thesis, University of Chicago, Chicago, Ill.

81. **Reed, C. R., and S. W. Liebman.** 1979. New amber suppressors in *Saccharomyces cerevisiae*. Genetics **91**:s102.

82. **Remer, S., A. Sherman, E. Kraig, and J. E. Haber.** 1980. A suppressor of deoxythymidine monophosphate uptake mutants in *Saccharomyces cerevisiae*. J. Bacteriol. **138**:638–652.

83. **Resnick, M. A.** 1969. Genetic control of radiation sensitivity in *Saccharomyces cerevisiae*. Genetics **62**:519–531.

84. **Resnick, M. A., and R. K. Mortimer.** 1966. Unsaturated fatty acid mutants of *Saccharomyces cerevisiae*. J. Bacteriol. **92**:597–600.

84a. **Roman, H.** 1956. A system selective for mutations affecting the synthesis of adenine in yeast. C. R. Trav. Lab. Carlsberg Ser. Physiol. **26**: 299–314.

85. **Rothstein, R. J., and F. Sherman.** 1980. Genes affecting the expression of cytochrome-c in yeast: genetic mapping and genetic interactions. Genetics **94**:871–889.

86. **Saunders, G. W., G. H. Rank, B. Kustermann-Kuhn, and C. P. Hollenberg.** 1979. Inheritance of multiple drug resistance in *Saccharomyces cerevisiae*: linkage to *leu1* and analyses of 2 μm DNA in partial revertants. Mol. Gen. Genet. **175**:45–52.

87. **Savage, E.** 1979. A comparative analysis of recombination at the *his1* locus among five related diploid strains of *Saccharomyces cerevisiae*. Ph.D. thesis, University of Alberta, Edmonton, Alberta, Canada.

88. **Sherman, F., and C. Helms.** 1978. A chromosomal translocation causing overproduction of iso-2-cytochrome c in yeast. Genetics **88**:689–707.

89. **Sherman, F., J. W. Stewart, C. Helms, and J. A. Downie.** 1978. Chromosome mapping of the *CYC7* gene determining yeast iso-2-cytochrome c: structural and regulatory regions. Proc. Natl. Acad. Sci. U.S.A. **75**:1437–1441.

90. **Shult, E. E., G. Lindegren, and C. C. Lindegren.** 1967. Hybrid specific linkage relations in Saccharomyces. Can. J. Genet. Cytol. **9**:723–759.

91. **Singh, A., and T. R. Manney.** 1974. Genetic analysis of mutations affecting growth of *Saccharomyces cerevisiae* at low temperature. Genetics **77**:651–659.

92. **Singh, A., and F. Sherman.** 1978. Deletions of the iso-1-cytochrome c and adjacent genes of yeast: discovery of the *OSM1* gene controlling osmotic sensitivity. Genetics **89**:653–665.

93. **Skogerson, L., C. McLaughlin, and E. Wakatama.** 1973. Modification of ribosomes in cryptopleurine-resistant mutants of yeast. J. Bacteriol. **116**:818–822.

94. **Smirnov, M., N. Krasnopevtseva, S. Inge-Vechtomov, and A. Yanoolaitis.** 1974. Isolation of mutants for acid phosphatase in the yeast *Saccharomyces cerevisiae*. Issled. Genet. **5**:59–62.

95. **Snow, R.** 1967. Mutants of yeast sensitive to ultraviolet light. J. Bacteriol. **94**:571–575.

96. **Snow, R.** 1979. Maximum likelihood estimation of linkage and interference from tetrad data. Genetics **92**:231–245, **93**:285.

97. **Sprague, G. F.** 1977. Isolation and characterization of a *Saccharomyces cerevisiae* mutant deficient in pyruvate kinase activity. J. Bacteriol. **130**:232–241.

98. **Stewart, G. G., and I. Russell.** 1977. The identification, characterization, and mapping of a gene for flocculation in *Saccharomyces* sp. Can. J. Microbiol. **23**:441–447.

98a. **Struhl, K., J. R. Cameron, and R. W. Davis.** 1976. Functional genetic expression of eukaryotic DNA in *Escherichia coli*. Proc. Natl. Acad. Sci. U.S.A. **73**:1471–1475.

99. **Takano, I., and Y. Oshima.** 1970. Mutational nature of an allele specific conversion of the mating type by the homothallic gene *HO* in Saccharomyces. Genetics **65**:421–427.

100. **Ter-Avanesyan, M. D., S. Inge-Vechtomov, and M. Petrashan.** 1974. Genetical and biochemical studies of acid phosphatases in yeast *Saccharomyces cerevisiae*. Genetika **10**:101–109. (In Russian.)

101. **Thornton, R. J.** 1978. Investigations on the genetics of foaming in wine yeasts. Eur. J. Appl. Microbiol. Biotechnol. **5**:103–107.

102. **Thornton, R. J.** 1978. The mapping of two dominant genes for foaming in wine yeasts. FEMS Microbiol. Lett. **4**:207–209.

103. **Toh-e, A., P. Guerry, and R. Wickner.** 1978. Chromosomal superkiller mutants of *Saccharomyces cerevisiae*. J. Bacteriol. **136**:1002–1007.

104. **Toh-e, A., Y. Ueda, S. Kakimoto, and Y. Oshima.** 1973. Isolation and characterization of acid phosphatase mutants in *Saccharomyces cerevisiae*. J. Bacteriol. **113**:727–738.

105. **van de Poll, K., and D. Schamhart.** 1977. Characterization of a regulatory mutant of fructose 1,6-bisphosphatase in *Saccharomyces carlsbergensis*. Mol. Gen. Genet. **154**:61–66.

106. **Wickner, R. B.** 1974. Mutants of *Saccharomyces cerevisiae* that incorporate deoxythymidine-5-monophosphate into deoxyribonucleic acid in vivo. J. Bacteriol. **117**:252–260.

107. **Wickner, R. B.** 1978. Twenty-six chromosomal genes needed to maintain the killer double-stranded RNA plasmid in *Saccharomyces cerevisiae*. Genetics **88**:419–425.

108. **Wickner, R. B.** 1979. Mapping chromosomal genes of *Saccharomyces cerevisiae* using an improved genetic mapping method. Genetics **92**:803–821.

109. **Wickner, R. B., and M. J. Leibowitz.** 1976.

Chromosomal genes essential for replication of a double-stranded RNA plasmid of *Saccharomyces cerevisiae*: the killer character of yeast. J. Mol. Biol. **105**:427–434.

110. **Wickner, R. B., and M. J. Leibowitz.** 1976. Two chromosomal genes required for killing expression in killer strains of *Saccharomyces cerevisiae*. Genetics **82**:429–442.

110a. **Wickner, R. B., and M. J. Leibowitz.** 1977. Dominant chromosomal mutation bypassing chromosomal genes needed for killer RNA plasmid replication in yeast. Genetics **87**:453–469.

111. **Wickner, R. B., and M. J. Leibowitz.** 1979. *mak* mutants of yeast: mapping and characterization. J. Bacteriol. **140**:154–160.