GENEALOGY OF PRINCIPAL STRAINS OF THE YEAST GENETIC STOCK CENTER

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ABSTRACT

We have constructed a genealogy of strain S288C, from which many of the mutant and segregant strains currently used in studies on the genetics and molecular biology of *Saccharomyces cerevisiae* have been derived. We have determined that its six progenitor strains were EM93, EM126, NRRL YB-210 and the three baking strains Yeast Foam, FLD and LK. We have estimated that approximately 88% of the gene pool of S288C is contributed by strain EM93. The principal ancestral genotypes were those of segregant strains EM93-1C and EM93-3B, initially distributed by C. C. LINDEGREN to several laboratories. We have analyzed an isolate of a lyophilized culture of strain EM93 and determined its genotype as *MATa/MATα SUC2/SUC2 GAL2/gal2 MAL/MAL mel/mel CUP1/cup1 FLO1/flo1*. Strain EM93 is therefore the probable origin of genes *SUC2*, *gal2*, *CUP1* and *flo1* of S288C. We give details of the current availability of several of the progenitor strains and propose that this genealogy should be of assistance in elucidating the origins of several types of genetic and molecular heterogeneities in Saccharomyces.

THE recent explosion of interest in the genetics and molecular biology of the yeast *Saccharomyces cerevisiae* has resulted in a rapid expansion of our knowledge of this organism. Several lines of evidence have recently shown various heterogeneities among strains in, for example, the distribution of restriction sites (OLSON, LOUGHNEY and HALL 1979), in position and numbers of transposable elements (EIBEL *et al.* 1980) and in chromosome polymorphisms (CARLE and OLSON 1985). To assess the relative contributions to these heterogeneities from recent events, as opposed to differences introduced in the development of the initial breeding stocks, we have developed a pedigree of some of the most common laboratory strains.

During the 1930s and 1940s O. WINGE of the Carlsberg Laboratories in Denmark pioneered research on the genetics of yeast. Although his scientific career extended back to 1907, he started work on yeast in 1933, using strains that had been stored in 10% sucrose many years earlier (as early as 1886) by the microbiologist EMIL HANSEN (WINGE and HJORT 1935). Along with O. LAUSTEN and C. ROBERTS, WINGE elegantly elucidated the life cycle of several

yeasts and began the genetic analyses of sucrose and maltose fermentation (WINGE and ROBERTS 1952). WINGE and ROBERTS (1949) characterized the first gene for homothallism (symbolized *D* for diploidization and now designated *HO*). CARL LINDEGREN began research on the genetics of Saccharomyces in the 1940s following his study of the genetics and life cycle of *Neurospora crassa*, upon which BEADLE and TATUM later based their pioneering studies in microbial genetics. LINDEGREN used yeast strains from a limited number of sources in the United States and, in contrast to the breeding strains used by WINGE, developed strains that were heterothallic, thus greatly facilitating genetic research in yeast. We have attempted to review these earlier studies in our effort to develop a pedigree of many of the current breeding stocks of *S. cerevisiae*, concentrating primarily on the studies of LINDEGREN and later workers. Part of the studies described here has appeared in earlier abstracts (JOHNSTON and MORTIMER 1984; MORTIMER and JOHNSTON 1984).

ANALYSIS AND RESULTS

CARL LINDEGREN (1949) published a book entitled *The Yeast Cell: Its Genetics and Cytology*, in which he presented much of his early work on yeast. Included in this book is a pedigree of the breeding stocks that he and GERTRUDE LINDEGREN used in many of their early studies. Part of this pedigree, showing in particular the ancestry of strains 1426 and 1428 (LINDEGREN numbers) and including some information given elsewhere in the book, is redrawn as Figure 1. The equivalence of strains that were designated by LINDEGREN as 4 and 93-1C (recommended designation EM93-1C) is assumed, but seems likely from the information recorded. Strain FLD is listed by LINDEGREN as a commercial baking yeast. Strains EM93 and EM126 were isolated by EMIL MRAK of the University of California, Davis, in 1938 and 1939, respectively, from rotting figs near Merced, California (H. PHAFF and M. MIRANDA, personal communication). Whether these strains were originally part of the figs' flora or were spoilage organisms originating as commercial baking and/or brewing yeasts is unknown. Strain NRRL-210 was isolated from rotting bananas from Costa Rica in 1942 (C. KURTZMAN, personal communication) and was originally classified as *S. microellipsoideus*. It has since been identified as *S. cereviseae* (D. YARROW, personal communication) or *S. uvarum* (*S. bayanus*) (C. KURTZMAN, personal communication).

The LINDEGRENS also made a major contribution to yeast genetics by distributing haploid breeding strains to several other early yeast geneticists; namely, POMPER and BURKHOLDER (1949); REAUME and TATUM (1949); ROMAN, HAWTHORNE and DOUGLAS (1951); and ZIRKLE and TOBIAS (1949). Our investigations have revealed that in every case those haploids were derived from strain EM93 and, in particular, were most probably the meiotic segregant strains EM93-1C (α) and EM93-3B (**a**). POMPER and BURKHOLDER (1949) simply identified these latter strains as "α" and "**a**" (strains 63 and 62; S. POMPER, personal communication). ROMAN, HAWTHORNE and DOUGLAS (1951) designated EM93-1C as "clone 1" (H. ROMAN, personal communication) and as strain 287 (HAWTHORNE 1956) and ZIRKLE and TOBIAS (1949) used both

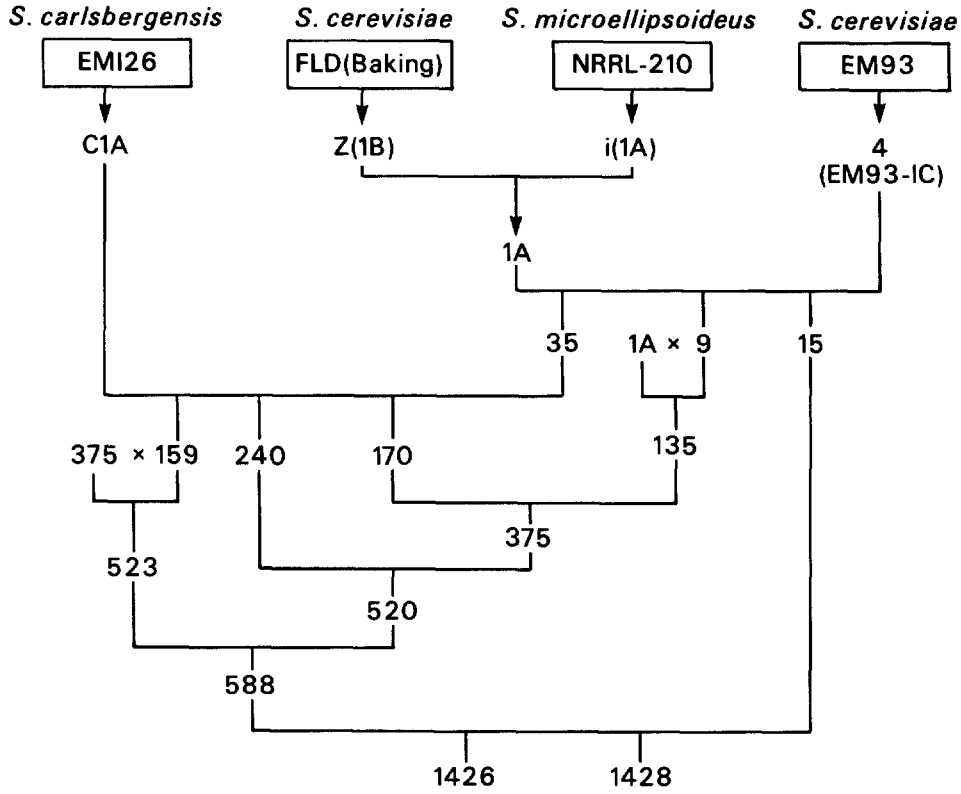

FIGURE 1.—Pedigree of the LINDEGREN strains 1426 and 1428. The diagram is essentially a reconstruction from LINDEGREN (1949). We have concluded that the LINDEGREN strains designated 4 and EM93-1C (distributed to other laboratories) are equivalent. Strain NRRL-210, originally classified as *S. microellipsoideus*, is now classified under either *S. cereviseae* (D. YARROW, personal communication) or *S. uvarum* (C. KURTZMAN, personal communication). It has been proposed that *S. carlsbergensis* be included in *S. uvarum* and that *S. uvarum* be included in *S. cerevisiae* (YARROW 1984). However, it has also been recently proposed that *S. cerevisiae*, *S. bayanus* (including *S. uvarum*) and possibly also *S. carlsbergensis* constitute different species (MARTINI and KURTZMAN 1986).

strains EM93 (SC6) and EM93-1C (SC7). (An error in denoting strain EM93-3B as 93-3P was perpetuated over a number of years.) One of us (R.K.M.) began research in yeast genetics in the TOBIAS laboratory, Berkeley, using strain EM93-1C (SC7) together with some strains obtained from S. E. REAUME (in the TATUM laboratory, Stanford). These additional strains were Y02022 and Y02587, and from information originally obtained from REAUME and TATUM, and more recently from POMPER, we have determined that these strains also derive entirely from strain EM93.

The strain S288C was isolated through genetic crosses by one of us (R.K.M.) as a parental strain to be used for isolation of biochemical mutants. Conditions established for this strain were that it be nonclumpy (nonflocculent)—*i.e.*, dispersed as single cells in liquid culture—and that it have a minimal number of nutritional requirements. In fact, S288C requires only biotin, a nitrogen

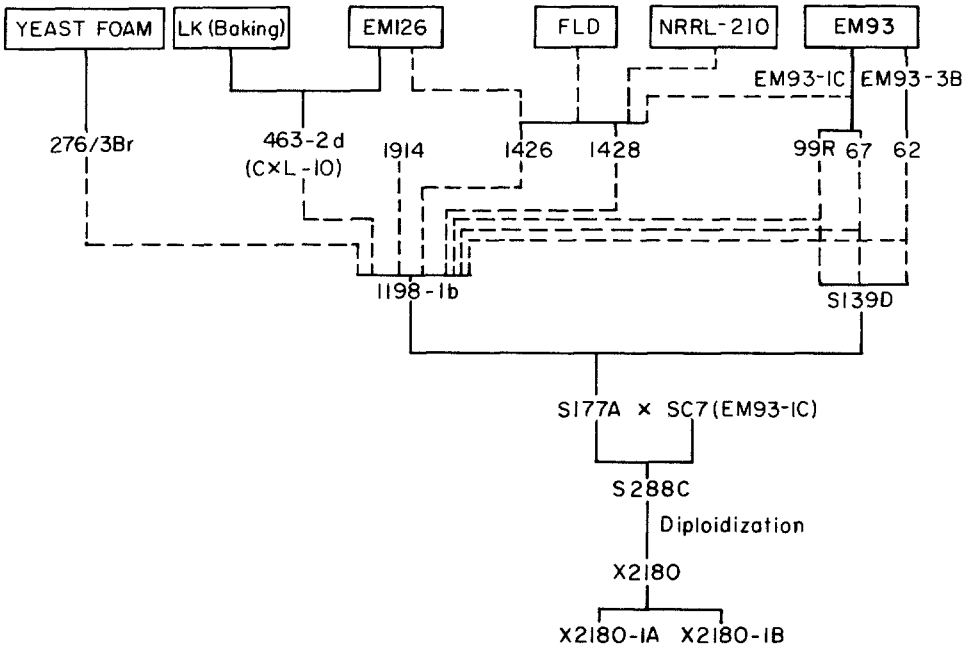

FIGURE 2.—Progenitor strains of S288C, X2180-1A and X2180-1B. In addition to the four strains, EM126, FLD, NRRL-210 and EM93 (Figure 1), from which the LINDEGREN strains 1426 and 1428 were derived, are strains Yeast Foam and LK, both baking yeasts. Solid lines show direct crosses; broken lines indicate that there were intervening crosses. The origins of laboratory strains can be allocated as follows: MRAK: EM93 and EM126; WICKERHAM: NRRL-210; LINDEGREN: EM93-1C, EM93-3B, 1426, 1428, C × L-10; POMPER: 62 and 67; REAUME: 99R; EPHRUSSI: 276/3Br; ROMAN and DOUGLAS: 463-2d; RAUT: 1914; HAWTHORNE: 1198-1b; MORTIMER: S139D, S177A, S288C.

source, glucose and an asssortment of salts and trace elements. The ancestry, with the omission of many intervening crosses, of strain S288C is shown in Figure 2. The immediate parents were strains EM93-1C (SC7) and S177A. One parent, S139D, of the latter strain was derived (by R.K.M.) entirely from the LINDEGREN strains EM93-1C and EM93-3B via strains 99R (REAUME and TATUM), 67 and 62 (POMPER). Strain 67 (POMPER and BURKHOLDER 1949) was obtained from REAUME, but as far as we can determine was strain 93-1C. The other parent of S177A, *1198-1b*, resulted from a large number of crosses made by D. C. HAWTHORNE in order to study genetic segregation for the fermentation of sucrose, maltose, α-methylglucoside and galactose (HAWTHORNE 1956). These crosses involved (D. HAWTHORNE, personal communication) the progenitor strains of POMPER, REAUME and TATUM, LINDEGREN's 1426 and 1428 (Figure 1), strain 463-2d (ROMAN and DOUGLAS) derived from the LINDEGREN diploid strain C × L-10 (LINDEGREN 1949) strain 276/3Br (EPHRUSSI, HOTTINGUER and TAVLITZKI 1949) and the strain 1914. This final strain was received from C. RAUT, and although we have been unable to trace its specific pedigree, it appears likely (RAUT 1953) that it was derived from the same ancestral strains as were LINDEGREN strains 1426 and 1428 (Figure 1). The

other seven progenitor strains of 1198-1b were descendants of the same four original strains shown in Figure 1 and, in addition, the baking yeasts LK (LINDEGREN 1949), where L apparently symbolizes Lallemand (C. KURTZMAN, personal communication) and "Yeast Foam" (EPHRUSSI, HOTTINGUER and TAVLITZKI 1949). This latter yeast is heterothallic and originated as a bakers' yeast from Northwestern Yeast Company, Chicago (WINGE and ROBERTS 1984). Figure 2 also shows the derivation of strain X2180, by self-diploidisation of S288C, and the isogenic *MAT***a** and *MATα* haploid strains, X2180-1A and X2180-1B, derived from this diploid.

Strain S288C or an *ade2-1* mutant of it, DV147, were used to isolate the original alleles of most of the nutritional mutants currently used in yeast genetics research (HAWTHORNE and MORTIMER 1960; MORTIMER and HAWTHORNE 1966). For example, all, or nearly all, of the mutants in the arginine, histidine, tryptophan, uracil, threonine-methionine, leucine, lysine and serine pathways were isolated from these strains. Analysis of the pedigrees illustrated in Figures 1 and 2 shows that strain EM93 contributes approximately 90% of the genome of S288C. Strains EM126, NRRL-210, FLD, LK and Yeast Foam contribute the balance.

Mutants of S288C (*MATα*) were brought together in various combinations to provide many of the strains for the Yeast Genetic Stock Center, which has been in operation formally since 1970 and informally since 1960. Backcrosses were made using *MAT***a** strains Y02587, 1198-1b and 4209A. The first of these strains is derived entirely from strain EM93. We have estimated that the contribution of strain EM93 to strain 1198-1b is approximately 30%. Strain 4209A was obtained from H. ROMAN and was derived from the same progenitor strains as shown in Figure 2, but with an increased contribution of Yeast Foam through the mutant 276/3Br (*ade2*).

In the course of our investigations we were fortunate to find samples of the diploid strain EM93 (SC6) that had been lyophilized in the TOBIAS laboratory, Berkeley, in 1951. Several isolates of these samples were cultured and classified. They all sporulated well, but varied in their level of ascospore viability. In particular, a few apparently segregated for a recessive lethal mutation, perhaps resulting from the lyophilization process. Isolate 10 yielded the highest recovery of viable tetrads, and we selected this strain for tetrad analysis. LINDEGREN (1949) reported heterozygosity of strain EM93 for mating type, galactose fermentation and the characteristic "dispersed" *vs.* "flaky" growth. Tetrad analysis of our isolate of strain EM93 confirms these segregations. We have shown by linkage and complementation tests that the genes segregating are *MAT*, *gal2* and *FLO1*; in addition, strain EM93 is heterozygous for *CUP1*/*cup1* (R. CONTOPOULOU, unpublished results; DE ZOYSA 1985).

DISCUSSION

In elucidating the genealogy of strain S288C, and its derivative strains X2180-1A and X2180-1B, we have determined that strain EM93, through its segregant strains EM93-1C and EM93-3B, is the principal progenitor strain. We have calculated the contribution of these segregants of strain EM93 to the

gene pool of strain S288C as approximately 88%. We have also concluded that, in turn, strain S288C (or strains closely related to it) is a major source of the gene pool of most laboratory strains. Our tetrad analysis of an isolate of strain EM93, lyophilized in Berkeley in 1951, showing it to be heterozygous for *gal2* and *CUP1* and homozygous for *SUC2* is evidence that strain EM93 is the origin of these genes which are present in strain S288C.

The genotype of strain 1198-1b was *mal mel gal2 suc*, but it is likely that the source of *gal2* in this strain was also strain EM93. The gene *gal1* originated in the LINDEGREN strain 1426 (HAWTHORNE 1956). We have determined that the source of the *mal* gene in strains 1198-1b and S288C is progenitor strain NRRL-210 (C. KURTZMAN, personal communication).

Fortunately, several progenitor strains and strains derived from them are still available in different stock collections. Strain EM93 is in culture at the University of California, Davis (M. MIRANDA and H. PHAFF, personal communication) and at the Food Research Institute, Norwich, England [National Collection of Yeast Cultures (NCYC), strain NCYC 292]. The latter strain was deposited by S. JACKSON, who received the strain from C. LINDEGREN in 1951 (NCYC Catalog, June 1981). Strain EM126 is also in culture at the University of California, Davis. The isolate of strain EM93, on which we have performed tetrad analysis, is available from the Yeast Genetic Stock Center, Berkeley, and the University of Strathclyde, Glasgow. Although the strains EM93-1C and EM93-3B are apparently no longer available, mutant strains 99R (REAUME and TATUM 1949) and 200, which we believe are derivatives of the former strains, respectively, are also available from the Yeast Genetic Stock Center (R. K. MORTIMER and C. R. CONTOPOULOU, YGSC Catalog, January 1984). Of the remaining four progenitor strains of S288C, two are available. Strain NRRL YB-210, also designated as NRRL Y-1350, is in culture at the Northern Regional Research Center, Peoria, Illinois, and (as strain CBS 6333) at the Centraalbureau voor Schimmelcultures, Delft, The Netherlands (C. KURTZMAN, D. YARROW, personal communications). The strain "Yeast Foam" (or "American Yeast Foam") is listed as culture NCYC 232 (NCYC Catalog, June, 1981) and as culture CBS 1428 (D. YARROW, personal communication).

In addition to strain S288C, several other strains have played a key role in the development of yeast genetics. These include FL100 (LACROUTE 1968, Σ 1278b (GRENSON *et al.* 1966) and A364A (HARTWELL 1967). The relationships of these strains to strain EM93 and S288C remain to be fully determined, although our preliminary analyses indicate that FL100 and A364A are closely related to S288C. Strain Σ 1278b is a segregant of a cross between a segregant of Yeast Foam and strain 1422-11D (HAWTHORNE), which we believe was derived from the same progenitor strains as shown in Figure 2. Another bakers' yeast, referred to as Boulangerie II, was the source of the nuclear petite mutant, *pet1* (CHEN, EPHRUSSI and HOTTINGUER 1950).

A major frustration in our analysis was the practice of several investigators to change the designations of strains sent to them. For example, strain EM93-1C has been assigned several synonyms by different investigators, including LINDEGREN (Table 1). Table 1 presents a record of synonyms and culture

TABLE 1

Recommended and other strain designations of several progenitor strains of YGSC

Recommended strain designation	Saccharomyces species	Original isolate by (from)	Synonymous strain designation	Reference	Culture collection number(s)
EM93	*S. cerevisiae*	E. MRAK	MRAK 93	LINDEGREN (1949)	NCYC 292
			93; SC6	ZIRKLE and TOBIAS (1949)	
EM93-1C	*S. cerevisiae*	C. LINDEGREN	93-1C; Wild type	REAUME and TATUM (1949)	
			4 (assumed)	LINDEGREN (1949)	
			α	POMPER and BURKHOLDER (1949)	
			63	S. POMPER (personal communication)	
			Clone 1	ROMAN, HAWTHORNE and DOUGLAS (1951)	
			287	HAWTHORNE (1956)	
			93-1C; SC7	ZIRKLE and TOBIAS (1949)	
EM93-3B	*S. cerevisiae*	C. LINDEGREN	**a**	POMPER and BURKHOLDER (1949)	
			62	POMPER (1952)	
			93-3B; SC8	ZIRKLE and TOBIAS (1949)	
EM126	*S. carlsbergensis*[a]	E. MRAK	MRAK 126	LINDEGREN (1949)	
NRRL Y-1350[b]	*S. microellipsoideus*[a]	L. WICKERHAM	NRRL YB-210	C. KURTZMAN (personal communication)	CBS 6333 (formerly CBS 428)
			NRRL-210		
			NRRL-B210	LINDEGREN (1949)	
Yeast foam	*S. cerevisiae*	Northwestern Yeast Company, Chicago	American Yeast Foam	WINGE and ROBERTS (1948)	NCYC 232 CBS 1428 (formerly CBS 237)

[a]For comments on current taxonomy, see the caption to Figure 1.
[b]Recommended current collection number (C. KURTZMAN, personal communication).

collection numbers, along with recommended designations for several of the progenitor strains of S288C. We would recommend most strongly that investigators, if they choose to use new strain designations, also present the previous or original strain designations as synonyms in publications or communications.

We hope that the genealogy described in this paper will be of value in the analyses of various strain heterogeneities. For example, structural heterology of a region of chromosome *III* has been shown between the species *S. cerevisiae* and *S. carlsbergensis* by the techniques of classical and molecular genetics (NILSSON-TILLGREN *et al.* 1981; HOLMBERG, 1982). DNA sequence polymorphisms of the *RDN1* gene (PETES 1979), on chromosome *XII*, and the *HIS4* gene (chromosome *III*) among various yeast strains, including those of the species *S. cereviseae*, *S. uvarum* and *S. carlsbergensis* have also been described (PEDERSEN 1983). In addition, polymorphisms in chromosome size (CARLE and OLSON 1985), restriction sites (OLSON, LOUGHNEY and HALL 1979) and *TY1* number and chromosome location (EIBEL *et al.* 1980) have been found.

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