Review on Important Yeast Genes Used for Yeast Genetics Study

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Abstract: Yeasts are unicellular fungi taxonomical classifications under the phylum Ascomycetes, class Hemiascomycetes. S. cerevisiae has been the model system for much of molecular genetic research because the basic cellular mechanics of replication, recombination, cell division and metabolism are generally conserved between yeast and larger eukaryotes, including mammals. S. cerevisiae contains a haploid set of 16 well-characterized chromosomes, ranging in size from 200 to 2,200 kb. The total sequence of chromosomal DNA, constituting 12,052 kb. A total of 6,183 open-readingframes (ORF) of over 100 amino acids long were reported, and approximately 5,800 of them were predicated to correspond to actual protein-coding genes. Several genes and promoters are commonly employed for genetic manipulations and studies with yeast. Some of these genes have special properties, whereas others were originally choosen arbitarily and are conveniently available in strains and plasmids. Several of the genes most commonly used for a variety of purposes. Some of important genes used for genetics studies are URA3 and LYS2 yeast genes, ADE1 and ADE2 yeast genes, GAL1 Promoter, RAD54 and RAD51 genes, lacZ and Other Reporters. There are three genetic techniques to isolate and characterize unknown mutations in S. cerevisiae. These techniques are molecular cloning, genetic complementation, and tetrad dissection.
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Introduction:

Yeasts are unicellular fungi; precise classification uses the characteristics of the cell, ascospore and colony. Budding yeasts are true fungi of the phylum Ascomycetes, class Hemiascomycetes. The true yeasts are separated into one main order Saccharomycetales. The awesome power of yeast genetics is partially due to the ability to quickly map a phenotype-producing gene to a region of the S. cerevisiae genome. S. cerevisiae has been the model system for much of molecular genetic research because the basic cellular mechanics of replication, recombination, cell division and metabolism are generally conserved between yeast and larger eukaryotes, including mammals. S. cerevisiae can stably exist in both haploid and diploid states. Foreign DNA in the form of plasmids or linear nucleotides can easily be transformed in S. cerevisiae. S. cerevisiae has a strong homologous recombination pathway and a high rate of gene conversion. There are hundreds of genetic markers available in S. cerevisiae since the genome sequence of S. cerevisiae are known (Sherman F., 2002).

A wild-type yeast cell that has the ability to synthesize its own nutritional requirement is called a prototroph. Its mutant counterpart that loses the ability to synthesize an essential nutrient due to a DNA mutation somewhere in the biosynthetic pathway is called an auxotroph. An auxotrophic marker is then defined as a wild-type allele of a gene that encodes a key enzyme for the production of an essential monomer used in biosynthesis, Some examples of the commonly used auxotrophic markers in S. cerevisiae are URA3, LYS2, LEU2, TRI1, HIS3, MET15 and ADE2 (1). All these marker genes encode essential enzymes for de novo nucleic acid and amino acid synthesis. Two immediate applications for yeast auxotrophic markers are the stable maintenance of expression vectors and the introduction of knockout mutations (Barnett JA., 2007).

S. cerevisiae contains a haploid set of 16 well-characterized chromosomes, ranging in size from 200 to 2,200 kb. The total sequence of chromosomal DNA, constituting 12,052 kb. A total of 6,183 open-readingframes (ORF) of over 100 amino acids long were reported, and approximately 5,800 of them were predicated to correspond to actual protein-coding genes. the yeast genome is highly compact, with genes representing 72% of the total sequence (<2% in the human genome!). The average size of yeast genes is 1.45 kb, or 483 codons, with a range from 40 to 4,910 codons. A total of 3.8% of the ORF contain introns. Approximately 30% of the genes already have been characterized experimentally. Of the remaining 70% with unknown function Genetic analyses and transformation can be performed with a number of

taxonomically distinct varieties of yeast, extensive studies have been limited primarily to the many freely interbreeding species of the budding yeast Saccharomyces and to the fission yeast Schizo saccharomyces. The haploid strain S288C (MATa SUC2 mal mel gal2 CUP1 flo1 flo8-1 hap1) is often used as a normal standard because the sequence of its genome has been determined (Goffeau *et al*., 1996).

Yeast genes are given 3 letter names with one or two digits after them, such as CDC33. Classically, yeast gene names were given for the phenotype of the mutant. Thus ste genes such as ste2, ste3, etc., confer a sterile phenotype and his3 mutants require histidine. Genes can also be named after the proteins or RNAs they encode, an example being CMD1, which encodes calmodulin. The genetic nomenclature for chromosomal genes of the yeast S. cerevisiae is now more-or-less universally accepted, whenever possible, each gene, allele, or locus is designated by three italicized letters, e.g., *ARG*, which is usually a describer, followed by a number, e.g., *ARG*2. Wild-type genes are designated with a superscript "plus" (*sup*6+ or *ARG*2+). Alleles are designated by a number separated from the locus number by a hyphen, e.g., arg2-9. The symbol Δ can denote complete or partial deletions, e.g., arg2-Δ1. Insertion of genes follow the bacterial nomenclature by using the symbol "::". For example, arg2::LEU2 denotes the insertion of the LEU2 gene at the ARG2 locus, in which LEU2 is dominant (and functional), and arg2 is recessive (and defective) (Schneiter R., 2004) and (Chen X. J., and Butow R. A., 2005).

Phenotypes are sometimes denoted by cognate symbols in roman type and by the superscripts + and -. For example, the independence and requirement for arginine can be denoted by Arg+ and Arg-, respectively. Proteins encoded by ARG2, for example, can be denoted Arg2p, or simply Arg2 protein. However, gene symbols are generally used as adjectives for other nouns, for example, ARG2 mRNA, ARG2 strains, etc. The general form YCRXXw is now used to designate genes uncovered by systematically sequencing the yeast genome, where Y designates yeast; C (or A, B, etc.) designates the chromosome III (or I, II, etc.); R (or L) designates the right (or left) arm of the chromosome; XX designates the relative position of the start of the open-reading frame from the centromere; and w (or c) designates the Watson (or Crick) strand. (Schneiter R., 2004) and (Chen X. J., Butow R. A., 2005).

Yeast Genes Important For Genetic Studies

Several genes and promoters are commonly employed for genetic manipulations and studies with yeast. Some of these genes have special properties, whereas others were originally choosen arbitarily and are conveniently available in strains and plasmids. Several of the genes most commonly used for a variety of purposes (Schneiter R., 2004).

URA3 and LYS2

The URA3 and LYS2 yeast genes have a marked advantage because both positive and negative selections are possible. Positive selection is carried out by auxotrophic complementation of the ura3 and lys2 mutations, whereas negative selection is based on specific inhibitors, 5-fluoro-orotic acid (FOA) and αaminoadipic acid (αAA), respectively, that prevent growth of the prototrophic strains but allows growth of the ura3 and lys2 mutants, respectively. URA3 encodes orotidine-5'phosphate decarboxylase, an enzyme which is required for the biosynthesis of uracil. Ura3- (or ura5-) cells can be selected on media containing FOA. The URA3+ cells are killed because FOA appears to be converted to the toxic compound 5-fluorouracil by the action of decarboxylase, whereas ura3- cells are resistant. The negative selection on FOA media is highly discriminating, and usually less than 10-2 FOA-resistant colonies are Ura+. The FOA selection procedure can be used to produce ura3 markers in haploid strains by mutation, and, more importantly, for expelling URA3-containing plasmids, including YCp and YEp replicating plasmids, and integated YIp plasmids. (Schneiter R., 2004).

Because of the negative selection and its small size, URA3 is the most widely used yeast marker in yeast vectors. The specific allele, ura352, which is the most commonly used host marker, contains a Ty1 insertion, is not revertible, and does not allow integation of YIp-URA3 plasmids at the URA3 chromosomal locus in most, but not all strains. LYS2 encodes α-aminoadipate reductase, an enzyme which is required for the biosynthesis of lysine. Lys2- and lys5- mutants, but not normal strains grow on a medium lacking the normal nitrogen source, but containing lysine and αAA. Apparently, lys2 and lys5 mutations cause the accumulation of a toxic intermediate of lysine biosynthesis that is formed by high levels of αAA, but these mutants still can use αAA as a nitrogen source. Numerous lys2 mutants and low frequencies of lys5 mutants can be conveniently obtained by simply plating high densities of normal cells on αAA medium. Similar with the FOA selection procedure, LYS2-containing plasmids can be conveniently expelled from lys2 hosts. Because of the large size of the LYS2 gene and the presence of numerous restriction sites, the FOA selection procedure with URA3 plasmids are more commonly used (Schneiter R., 2004).

ADE1 and ADE2

The ADE1 and ADE2 yeast genes encode phosphoribosylamino-imidazole-succinocarbozamide synthetase and phosphoribosylamino-imidazole-carboxylase, respectively, two enzymes in the

biosynthetic pathway of adenine. Ade1 and ade2 mutants, but no other ade- mutants, produce a red pigment that is apparently derived from the polymerization of the intermediate phosphoribosylamino-imidazole (denoted AIR). Furthermore, the formation of AIR is prevented by blocks preceding the ADE1 and ADE2 steps. For example ade2 strains are red, whereas ade3 and the double mutant ade2 ade3 are both white, similar to the color of normal strains. Red colonies and red-white sectored colonies are easily detected by visual inspection (Schneiter R., 2004).

The ade1 and ade2 red pigmentation, and the prevention of the coloration by ade3 or other ade- mutation has been incorporated as a detection scheme in a number of diverse genetic screens. Also, the ade2-1 UAA mutation, and the suppression of formation of the red pigment by the SUP4-o suppressor has been used in a variety of genetic screens. Most of the screens are based on the preferential loss, or the required retention of a plasmid containing a component involved in the formation of the red pigment. Examples of ade- red genetic screens include the detection of conditional mutations, isolation of synthetic lethal mutations, detection of Yeast Artificial Chromosomes (YAC) transformants, and the isolation of mutations that effect plasmid stability (Schneiter R., 2004).

GAL1 Promoter

Cloned genes can be expressed with constitutive or regulatable promoters. The most commonly-used regulated promoter for yeast studies is PGAL1. There are two regulatory proteins, Gal4p and Gal80p, which effect the transcription of the following structural genes: GAL1, a kinase; GAL2, a permease; GAL7, a transferase; GAL10, an epimerase; and MEL1, a galactosidase. Gal3p appears to be required for the production of the intracellular inducer from galactose. In presence of the inducer, Gal4p binds to sites in the UAS (upstream activation sequence), and activates transcription. In the absence of the inducer, such as when cells are grown in media containing non fermentable carbon sources, Gal80p binds to the carboxyl terminal region of Gal4p, masking the activation domain. Expression is repressed in cells exposed to glucose-containing media for several reasons in addition to the absence of the inducer, including the action of repressors at sites between the UAS and the TATA box and the inhibition of galactose uptake. Therefore, the addition of glucose to cells growing in galactose medium causes an immediate repression of transcription. The UAS of galactose structural genes contains one or more 17 base-pair palindromic sequences to which Gal4p binds, with the different levels of transcription determined by the number and combinations of the palindromes (Schneiter R., 2004).

The UAS of the divergently transcribed GAL1 and GAL10 is contained within a 365-bp fragment, denoted PGAL1 that is sufficient for maximal galactose induction and thorough glucose repression. PGAL1 can rapidly induce the expression of downstream fused-genes over 1000-fold after the addition of galactose to cells growing in media with a non fermentable carbon source. Furthermore, PGAL1 can be turned off by the addition of glucose to the galactose containing medium. PGAL1 has been used in a wide range of studies with yeast, including the overproduction of yeast proteins as well as heterologous proteins. Most importantly, the strong glucose repression of PGAL1 has been used to investigate the terminal phenotype of essential genes, in much the same way that temperature shifts are used to control the activity of temperature-sensitive mutations. Also, the PGAL1 system has been used to investigate suppression and growth inhibition by over expressed normal or mutant genes. PGAL1 is also an important component of one of the two hybrid systems (Schneiter R., 2004).

RAD54 and RAD51 genes

The RAD54 and RAD51 genes are involved in genetic recombination and double-strand break repair in the yeast Saccharomyces cerevisiae. The Rad51 protein is thought to be a yeast analogue of the Eschericia coli recA gene product and catalyzes strand exchange between homologous single- and double-stranded DNAs in vitro. RAD54 exhibits homologies to several known ATPases and is a member of the SWI2/MOT1 family. The Rad54 protein interacts with the Rad51 protein in vivo and in vitro and that the NH2-terminal 115 residues of the Rad54 protein are necessary for this interaction. The Rad54 protein is part of a multi protein yeast recombination complex. There is growing evidence that mitotic recombination in yeast is catalyzed by a multi protein complex containing several RAD gene products, including Rad51, Rad52, Rad55, Rad57, and probably many other factors as well (Jiang H. *et al*., 1996).

The function of the Rad54 protein in recombination is unknown and the protein has yet to be purified and characterized biochemically. It is homologous to a number of ATPases and appears to be a member of a family that includes Swi2/Snf2 and MOT1 ATPases involved in transcriptional regulation. The Swi-Snf complex is thought to remodel chromatin structure and may influence transcription factor binding. MOT1 protein has been shown to be a TATA-binding protein-associated factor that disrupts TATA-binding protein-DNA complexes in an ATP-dependent fashion. This raises the exciting possibility that Rad54 may be involved in allowing the

recombination machinery to access the DNA in a histone-occluded substrate. However, Rad54 protein is not required when the DNA is carried on a plasmid and is therefore part of a more accessible chromatin structure. Alternatively, it has been suggested that Rad54 protein might be a DNA helicase. (Jiang H. *et al*., 1996)

lacZ and Other Reporters

Activities of promoters and protein-protein and protein-DNA interactions involving promoter regions can be readily converted into selectable and quantifiable traits by fusing the promoter regions to reporter genes. Reporter genes can be used to determine the levels of transcription, or the levels of translation of the transcript, under various physiological conditions. The most common use of reporter genes has been to identify elements required for transcription by systematically examining series of mutations in promoter regions. Similarly, reporter genes have been used to identify trans acting factors that modulate expression by transcription or translation (Schneiter R., 2004).

The Escherichia coli lacZ gene, which encodes β-galactosidase, is the most commonly used reporter with yeast and other systems, because its activity can assayed semi quantitatively on plates and fully quantitatively by enzyme assay of liquid cultures. Rare events can be detected by the differential staining of colonies using X-gal (5-bromo-4-chloro-3-indolyl-b-D-galactoside). For positive selection, the reporter gene could include, for example, the translated region of the HIS3 gene, lacking a UAS (upstream-activating sequence). His+ colonies arise when active promoters are formed, such as in the cloning of heterologous components required for the activation of a defined DNA segment. Combining the HIS3 selection with a lacZ screen is a commomly used strategy; this approach of using two different reporters in parallel with the same promoter region is an efficient means for identifying trans-acting factors (Schneiter R., 2004).

Yeast vectors

A wide range of vectors are available to meet various requirements for insertion, deletion alteration and expression of genes in yeast. Most plasmids used for yeast studies are shuttle vectors, which contain sequences permitting them to be selected and propagated in E. coli, thus allowing for convenient amplification and subsequent alteration in vitro. The most common yeast vectors originated from pBR322 and contain an origin of replication (ori), promoting high copy-number maintenance in E. coli, and the selectable antibiotic markers, the b-lactamase gene, bla (or AmpR), and sometime to tetracycline-resistance gene, tet or (TetR), conferring resistance to, respectively, ampicillin and tetracycline. In addition, all yeast vectors contain markers that allow selection of transformants containing the desired plasmid. The most commonly used yeast markers include URA3, HIS3, LEU2, TRP1 and LYS2, which complement specific auxotrophic mutations in yeast, such as ura3-52, his3-Δ1, leu2-Δ1, trp1-Δ1 and lys2201. These complementable yeast mutations have been chosen because of their low reversion rate. Also, the URA3, HIS3, LEU2 and TRP1 yeast markers can complement specific E. coli auxotrophic mutations. The URA3 and LYS2 yeast genes have an additional advantage because both positive and negative selections are possible (Schneiter R., 2004).

YIp Vectors

The YIp integrative vectors do not replicate autonomously, but integrate into the genome at low frequencies by homologous recombination. Integration of circular plasmid DNA by homologous recombination leads to a copy of the vector sequence flanked by two direct copies of the yeast sequence. The site of integration can be targeted by cutting the yeast segment in the YIp plasmid with a restriction endonuclease and transforming the yeast strain with the linearized plasmid. The linear ends are recombinogenic and direct integration to the site in the genome that is homologous to these ends. In addition, linearization increases the efficiency of integrative transformation from 10- to 50-fold. The YIp vectors typically integrate as a single copy. However multiple integration does occur at low frequencies, a property that can be used to construct stable strains over expressing specific genes (Schneiter R., 2004).

YIp plasmids with two yeast segments, such as YFG1 and URA3 marker, have the potential to integrate at either of the genomic loci, whereas vectors containing repetitive DNA sequences, such as Ty elements or rDNA, can integrate at any of the multiple sites within genome. Strains constructed with YIp plasmids should be examined by PCR analysis, or other methods, to confirm the site of integration. The wild-type chromosomal YFG1+ allele can be replaced by the mutant yfg1-1 allele from a YIp integrating plasmid. The plasmid is first integrated in the chromosome corresponding to the site on the plasmid that was cleaved by a restriction endonuclease. Strains that have excised the URA3 marker in vivo by homologous recombination are selected on FOA medium. Either the original YFG1+ allele, or the yfg1-1 allele remains in the chromosome, depending on the site of the cross-over (Schneiter R., 2004).

YEp Vectors

The YEp yeast episomal plasmid vectors replicate autonomously because of the presence of a segment of the yeast 2 μm plasmid that serves as an origin of replication (2 μm ori). The 2 μm ori is responsible for the high copy-number and high

frequency of transformation of YEp vectors. YEp vectors contain either a full copy of the 2 μm plasmid, or, as with most of these kinds of vectors, a region which encompasses the ori and the REP3 gene. The REP3 gene is required in cis to the ori for mediating the action of the trans-acting REP1 and REP2 genes which encode products that promote partitioning of the plasmid between cells at division. Therefore, the YEp plasmids containing the region encompassing only ori and REP3 must be propagated in cir+ hosts containing the native 2 μm plasmid. Most YEp plasmids are relatively unstable, being lost in approximately 10-2 or more cells after each generation. Even under conditions of selective growth, only 60% to 95% of the cells retain the YEp plasmid (Schneiter R., 2004).

The copy number of most YEp plasmids ranges from 10-40 per cell of cir+ hosts. However, the plasmids are not equally distributed among the cells, and there is a high variance in the copy number per cell in populations. Several systems have been developed for producing very high copy-numbers of YEp plasmids per cell, including the use of the partially defective mutation leu2-d, whose expression is several orders of magnitude less than the wild-type LEU2+ allele. The copy number per cell of such YEp leu2-d vectors range from 200-300, and the high copy-number persists for many generations after growth in leucine-containing media without selective pressure. The YEp leu2-d vectors are useful in large-scale cultures with complete media where plasmid selection is not possible. The most common use for YEp plasmid vectors is to overproduce gene products in yeast (Schneiter R., 2004).

YCp Vectors

The YCp yeast centromere plasmid vectors are autonomously replicating vectors containing centromere sequences, CEN, and autonomously replicating sequences, ARS. The YCp vectors are typically present at very low copy numbers, from 1 to 3 per cell, and possibly more, and are lost in approximately 10-2 cells per generation without selective pressure. In many instances, the YCp vectors segregate to two of the four ascospore from an ascus, indicating that they mimic the behavior of chromosomes during meiosis, as well as during mitosis. The ARS sequences are believed to correspond to the natural replication origins of yeast chromosomes, and all of them contain a specific consensus sequence (Schneiter R., 2004).

The CEN function is dependent on three conserved domains, designated I, II, and III; all three of these elements are required for mitotic stabilization of YCp vectors. YRp vectors, containing ARS but lacking functional CEN elements, transform yeast at high frequencies, but are lost at too high a frequency, over 10% per generation, making them undesirable for general vectors. The stability and low copy-number of YCp vectors make them the ideal choice for cloning vectors, for construction of yeast genomic DNA libraries, and for investigating the function of genes altered in vivo. ARS1, which is in close proximity to TRP1, is the most commonly used ARS element for YCp vectors, although others have been used. CEN3, CEN4 and CEN11 are commonly used centromeres that can be conveniently manipulated. For example, the vector YCp50 contains CEN4 and ARS1 (Schneiter R., 2004).

Transformation In Yeast

The first functionally cloned yeast DNA fragments encoded biosynthetic enzymes for amino acids and pyrimidine bases and were inserted into pBR322. Linearization of the plasmids yielded more transformants, the majority of which had stably integrated at the homologous locus in the genome. plasmid YRp7. YRp7 contains the TRP1 gene as an EcoRI fragment inserted into pBR322. YRp7 was found to transform yeast with a high frequency and reduced mitotic stability. The sub fragment that conferred high frequency transformation was separable from TRP1 and was named ARS1 for autonomously replicating sequence. ARS1 turned out to be the first cloned eukaryotic replication origin. YRp plasmids can be made into more stable, high copy YEp plasmids with addition of sequences from the endogenous yeast 2 micron circle. YRp plasmids become highly stable, single copy YCp plasmids with the addition of a cloned yeast centromere. YACs have become favorite tools in mammalian positional cloning projects because they allow large pieces of DNA to be maintained in yeast. YACs are linear cloning vehicles with telomeres at each end and yeast selectable markers, such as URA3 and LEU2, to the right and left of a central insertion site. There are three main methods are currently used to transform yeast: those using spheroplasts, cells treated with lithium salts and the use of electroporation (Schneiter R., 2004).

Genetic Analyses

There are three genetic techniques to isolate and characterize unknown mutations in S. cerevisiae. These techniques are molecular cloning, genetic complementation, and tetrad dissection (Brown, A. J. P., and M. F. Tuite 1998).

Molecular cloning

In molecular cloning, a library of single-copy vectors containing inserts of random genomic fragments is transformed into the unknown mutant strains. The transformants are examined for the non-mutant (Yfg+) trait. Once the transformant with the desired phenotypes is identified, the vector is isolated. The identity of the random sequence on the vector can be further narrowed down by restriction digestion, or

identified by sequencing. Molecular cloning is particularly useful if there are no available mutant strains (Brown, A. J. P., and M. F. Tuite 1998).

Genetic complementation

Genetic complementation can be used to reveal the identity of an unknown mutation if this mutant exhibits the same phenotype as other mutant strains with known identity. Specifically, an unknown mutation in a haploid strain is crossed with a wild-type haploid strain of opposite mating type, as well as a set of haploid strains that exhibit the same phenotype. The diploid crosses are isolate and the unknown mutant phenotype is scored. The mutation is recessive if the heterozygous control diploids do not exhibit mutant phenotype. The diploid cross that exhibits the same mutant phenotype would indicate that the unknown mutation is the same as the known mutant that was initially crossed. For example genetic complementation is carried out by crossing the Yfg- MATa mutant to each of the tester strains MATα yfg1, MATα yfg2, etc., as well as the normal control strain MATα. These yfg1, yfg2, etc., are previously defined mutations causing the same phenotype. The diploid crosses are isolated and the Yfg trait is scored. The Yfg+ phenotype in the heterozygous control cross establishes that the Yfg- mutation is recessive. The Yfg- phenotype in MATa yfg1 cross, and the Yfg+ phenotype in the MATa yfg2, MATa yfg3, etc., crosses reveals that the original Yfg- mutant contains a yfg1 mutation (Brown, A. J. P., and M. F. Tuite 1998).

Tetrad dissection

Tetrad dissection can be used to identify the genetic linkage of a mutation and to determine if the unknown mutation is an alternation at a single genetic locus. In tetrad analysis, the haploid unknown mutant is crossed with a wild-type haploid strain or a strain with known genetic markers. The diploid cross is isolated and induced for sporulation. The resulting four spores from the same meiotic event are separated and scored for the desired phenotype. A 2:2 segregation pattern would indicate that the phenotype is the result of a single gene. Analyzing segregation pattern could reveal genetic linkages to other markers or centromere (Brown, A. J. P., and M. F. Tuite 1998).

1. Conclusion And Recommendation

Yeasts are eukaryotic organism at which some of its cellular structures are similar to that of mammalians cells at molecular level. Studying yeast genetics are important but most organisms of yeast genetics are not well studied except S. cerevisiae. S. cerevisiae is the first organism sequenced completely and its gene and genome are studied except some genes functions are not well known. Yeast genes important for genetics studies are small in number and restricted only in S. cerevisiae.

Therefore based on the above review and conclusion the following recommendations are forwarded:-

- ✓ Further and detail studies of yeast genes important in genetics studies are needed.
- ✓ Studies focused on other yeasts than S. cervicea to get new type of genes important for genetics studies.

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