Identification of Two Novel TAF Subunits of the Yeast Saccharomyces cerevisiae TFIID Complex*

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The general transcription initiation factor TFII D1 plays a central role in the initiation of DNA-dependent RNA polymerase II (RNAP II) transcription. TFII D is the only general transcription initiation factor (GTF) with a specific TATA box binding activity, and binding of TFII D to the TATA box is the first rate-limiting step in formation of a complex competent to initiate transcription. TFIID (1) is composed of TBP, the TATA box binding protein, and 14 distinct TBP-associated factors (TAFs), which range in size from 17 to 150 kDa. Twelve of the TAF subunits have been previously identified, but two, TAF48p and TAF65p, are novel. TAF48p exhibits significant sequence similarity to the conserved C-terminal region of Drosophila TAF110p, human TAF130p, and human TAF105p and is encoded by a previously identified gene MPT1. TAF65p shows no significant sequence homology to any previously identified TAF. The genes encoding TAF48p and TAF65p are single copy and essential for normal yeast cell growth. Furthermore, neither TAF48p nor TAF65p are associated with the histone acetylase Spt-Ada-Gcn5 complex or other non-TFIID TBF/TAF complexes. The significance of these results in terms of TFIID structure, function, and organization is discussed.

Using a combination of ion exchange and immunofinity chromatography, we have purified the general transcription initiation factor TFII D to near homogeneity from Saccharomyces cerevisiae. Yeast TFII D is composed of TBP, the TATA box binding protein, and 14 distinct TBP-associated factors (TAFs), which range in size from 17 to 150 kDa. Twelve of the TAF subunits have been previously identified, but two, TAF48p and TAF65p, are novel. TAF48p exhibits significant sequence similarity to the conserved C-terminal region of Drosophila TAF110p, human TAF130p, and human TAF105p and is encoded by a previously identified gene MPT1. TAF65p shows no significant sequence homology to any previously identified TAF. The genes encoding TAF48p and TAF65p are single copy and essential for normal yeast cell growth. Furthermore, neither TAF48p nor TAF65p are associated with the histone acetylase Spt-Ada-Gcn5 complex or other non-TFIID TBF/TAF complexes. The significance of these results in terms of TFIID structure, function, and organization is discussed.

The general transcription initiation factor TFII D1 plays a central role in the initiation of DNA-dependent RNA polymerase II (RNAP II) transcription. TFII D is the only general transcription initiation factor (GTF) with a specific TATA box binding activity, and binding of TFII D to the TATA box is the first rate-limiting step in formation of a complex competent to initiate transcription in vivo. TATA box element is found in the promoter of many mRNA encoding genes and is required for specific transcription initiation both in vitro and in vivo.

Biochemical studies published to date from yeast, human, and Drosophila systems have revealed TFII D to be a multbsubunit complex comprised of TBP, the TATA box binding protein, and 10–12 TBP-associated factors (TAFs) (2–4). TBP is responsible for the TATA box binding activity of TFII D and is conserved throughout eukaryotes. Like TBP, TAFs are highly conserved throughout eukaryotes, but their exact role in TFII D function has been an area of considerable debate (see Ref. 5 for review). Studies in yeast have clearly demonstrated a critical role for TAFs in mediating RNAP II transcription in vivo (6–10). Whether this role can be directly ascribed to TFII D function has been difficult to interpret as a subset of TFII D TAF subunits, specifically TAF90p, TAF61p, TAF60p, TAF25p, and TAF17p, have been identified as integral subunits of the yeast histone acetylase Spt-Ada-Gcn5 (SAGA) complex (11). However, a recent study has shown that loss of TAF40p function (TAF40p is believed to be specific to TFII D) severely impairs ongoing high level RNAP II-mediated transcription in vivo (12). This result strongly argues that TFII D is required for the transcription of many RNAP II-dependent genes in vivo.

Studies in the yeast system have proven invaluable in understanding the role of TAFs, and thus TFII D function, in mediating RNAP II transcription in vivo. It is somewhat surprising then that yeast TFII D is rather poorly defined biochemically. Independently, we and others have used a combination of biochemical purification and protein sequence comparison to identify 12 yeast TFII D TAF subunits (13–17). Although these studies clearly suggest the existence of a yeast TFII D complex composed of TBP plus 12 TAFs, this fact has not been directly shown biochemically. Indeed, it is not clear at present whether this is the minimal or core TFII D assembly. Of the 12 known yeast TFIID subunits, only one, TAF47p, does not have a known metazoan homologue (see Table I). Conversely, metazoan TAFs dTAF110p and hTAF130p, which have been shown to mediate transcription by the glutamine-rich transactivator Sp1 (18, 19), do not have a known yeast homologue. Thus it has been suggested that yeast may be evolutionarily distinct from metazoans and lacking the co-activator(s) necessary to mediate transcription by glutamine-rich activators, as it was initially reported that Sp1 could not stimulate transcription in yeast (20). However, this conclusion seems contradictory because native yeast activators such as Hap2p and Mcm1p both contain glutamine-rich domains, which by themselves are capable of transactivation (21). Furthermore, Sp1 can stimulate transcription in yeast when the reporter gene of interest is carried on a high copy plasmid, but not when integrated into the genome (21). Additionally, a recent report has identified a potentially novel histone-like pair in hTAF20p and hTAF130p (22). hTAF20p has a yeast homologue in yeast TAF61p. Because other histone-like pairs are highly conserved between yeast and humans, it would be surprising if yeast did not have an equivalent interacting pair to hTAF20p and hTAF130p. Together, these results suggest the possibility of an unidentified yeast equivalent to metazoan dTAF110p and hTAF130p.

As a first step toward a concise biochemical analysis of yeast TFII D, we have purified TFII D from Saccharomyces cerevisiae to near homogeneity. We find that yeast TFII D is reproducibly composed of TBP plus 12 distinct TAFs. Two of the 14 TAFs,
TAF48p and TAF65p, are novel. Immunoprecipitation experiments indicate that TAF48p and TAF65p are TFIID-specific TAFs and that these TAFp are not components of the yeast SAGA complex. The genes encoding TAF48p and TAF65p are both single copy and essential for vegetative growth. TAF65p does not resemble any previously identified metazoan TAF, but TAF48p is similar to the conserved C-terminal region of dTAF110p, hTAF130p, and hTAF105p. The significance of these results is discussed below.

MATERIALS AND METHODS

Strains and Plasmids—Escherichia coli strain XL-1 Blue (23) was used for routine plasmid propagation. Plasmid pDP15-HATBP was derived from pTBP (24) by insertion of an oligo encoding one copy of the influenza hemagglutinin (HA) epitope (25) into the SacI site at the N terminus of the TBP open reading frame (ORF). pRS313-HATF130 was derived from pRS313-HA, TAF130 (24) by deleting the second and third HA repeats using site-directed mutagenesis. E. coli expression plasmids for TAF48p and TAF65p were created by polymerase chain reaction amplification of the appropriate ORF and ligation into pRSET-A (Invitrogen). An E. coli expression plasmid for Dr1p was made in a similar fashion except the ORF was ligated into pET15b (Novagen).

Standard laboratory protocols and techniques for DNA manipulations were used (26), and all plasmids were verified by DNA sequencing. Standard laboratory protocols and techniques for DNA manipulations were followed for yeast manipulations (32).

RESULTS

Purification of TFIID from S. cerevisiae—A, outline of TFIID purification scheme. See “Materials and Methods” for details. B, pooled peak fractions of either Mono S-purified HATBP or HATAF130p (indicated at top) were resolved using NuPAGE (Novex) gel with MOPS running buffer and visualized by Coomassie staining. Labels on the right, TFIID subunits; labels on the left, molecular weight standards. Asterisk, novel TAF subunits described in this study. Note that TAF30p and HATBP comigrate in the gel system utilized.

FIG. 1. Purification of TFIID from S. cerevisiae. A, outline of TFIID purification scheme. See “Materials and Methods” for details. B, pooled peak fractions of either Mono S-purified HATBP or HATAF130p (indicated at top) were resolved using NuPAGE (Novex) gel with MOPS running buffer and visualized by Coomassie staining. Labels on the right, TFIID subunits; labels on the left, molecular weight standards. Asterisk, novel TAF subunits described in this study. Note that TAF30p and HATBP comigrate in the gel system utilized.

searches were performed with BLAST 2.0 software (NCBI), and ClustalW alignments were performed with MacVector 6.5 software (Oxford Molecular).

Antibodies and Immunoprecipitations—Recombinant protein production and generation of affinity-purified polyclonal antibodies for Dr1p, TAF48p, and TAF65p were performed as described (10). Polyclonal antibodies against other TFIID subunits and Gen5p have been described (10). Horseradish peroxidase-conjugated anti-HA (mAb 3F10, Roche) was utilized for immunoblotting HA-tagged proteins. For immunoprecipitations, 50 ηmole units aliquots of exponentially growing yeast cells were harvested, washed with distilled H₂O, transferred to a 1.5-mL microcentrifuge tube, frozen on dry ice, and stored at −80 °C. All subsequent steps were performed at 4 °C. Cells were resuspended in 0.6 mL of lysis buffer (20 mM HEPES-KOH (pH 7.6), 10% glycerol, 300 mM KOAc, 0.1% Nonidet P-40, 1 mM diethiothreitol, 1 mM EDTA, plus protease inhibitors), −0.7 mL of glass beads were added, and samples were lysed by a 30-s burst with a Mini-Beadbeater-8 (BioSpec). Cell debris was pelleted by centrifugation (10 min at 15,000 × g). Typically 0.2–0.3 mL of whole cell extract (~7 mg/mL) was recovered. The extract was pre-cleared by addition of a one-half volume of protein A-Sepharose, which had been washed and slurried to 1:1 in lysis buffer. The resin-extract slurry was incubated for 5 min, the beads were pelleted by a brief spin in a microcentrifuge, and an aliquot of the cleared extract was taken as input. To 50 μL of the cleared extract was added: 5–10 μg of anti-HA (mAb 12CA5, Roche) cross-linked to 2.5 mL of protein A-Sepharose (Sigma) and added to the slurry was incubated 12 to 14 h on a tilted board. The resin was collected in a 10-mL column and washed extensively with BA300 plus 0.1% Nonidet P-40, then with BA290 plus 0.001% Nonidet P-40. Elution was performed by adding 1 volume of BA200 containing 0.001% Nonidet P-40 with 2 mg/mL 3 × HA peptide (14). The slurry was incubated 30 to 40 min at 24 °C, the elute was collected by a brief spin at 1000 rpm, and a second elution was performed as above. Elutes were pooled, and bovine serum albumin was added to a final concentration of 50 μg/mL. The TFIID fraction was applied to a HR 5/5 Mono S column (Amersham Pharmacia Biotech) equilibrated in BA200 plus 0.001% Nonidet P-40. Neither the 3 × HA peptide nor major protein contaminants bound to the column. Bound proteins were resolved with a 15-mL linear gradient from BA1000 plus 0.001% Nonidet P-40. TFIID eluted in a single peak at ~375 mM KOAc. Peak fractions (3–4 mL) were pooled, dialyzed against BA200 with 30% glycerol, aliquoted, and stored at −80 °C.

Protein Identification—The identification of previously known TFIID subunits was confirmed in the Mono S fraction by immunoblotting. The identification of unknown protein contaminations was performed as follows. Mono S-purified HATBP TFIID was resolved using SDS-polyacrylamide gel electrophoresis (PAGE) on a 10% NuPAGE (Novex) gel and stained with Coomassie Brilliant Blue. Each of the unknown bands was excised and subjected to in-gel tryptic digestion and MALDI-TOF mass spectrometry (Borealis Biosciences Inc.). The identified peptides covered 40–50% of the total protein sequence for each identified protein. Protein sequence searches were performed with BLAST 2.0 software (NCBI), and ClustalW alignments were performed with MacVector 6.5 software (Oxford Molecular).
untagged strains were identical (data not shown). SDS-PAGE and Coomassie staining of pooled peak fractions from the final Mono S column indicated that these TFIID preparations contained 17 polypeptides, which were consistently copurified (Fig. 1B). Immunoblotting confirmed the identity of TBP and all 12 previously identified TAF subunits believed to comprise yeast TFIID (Fig. 1B and data not shown). Four additional unknown polypeptides with apparent molecular masses of \( \approx 65 \) kDa and a triplet of proteins of \( \approx 48 \) kDa also were consistently copurified in the TFIID fraction (see TAF48p* and TAF65p*, in Fig. 1B and below). Importantly, the composition of TFIID was essentially identical whether purified from the \( HATBP \) or \( HATAF130 \) strain. These results, together with the fact that immunoblotting indicated that the major fraction (70–100%) of those TFIID TAF subunits previously believed to be specific to TFIID (TAF130p, TAF67p, TAF47p, TAF40p, and TAF19p) were recovered in the 1M Bio-Rex 70 fraction (data not shown), suggest that the major form of TFIID in \( S. cerevisiae \) is composed of TBP plus 14 distinct TAFs.

Identification of Novel TAFs—As described above, four unknown polypeptides were consistently copurified in the TFIID fractions. Each of the unknown polypeptide bands were excised from a Coomassie-stained gel and subjected to in-gel trypsin digestion and MALDI-TOF mass spectrometry for identification. Peptide sequence from the unknown 65-kDa protein identified a previously predicted ORF, YML114c, which encodes a protein with a deduced molecular mass of 58 kDa with no known function. We refer to the protein encoded by YML114c as TAF65p. BLAST search analysis revealed no significant homology to any protein of known function. However, TAF65p does contain a potential coiled-coiled domain similar to that of myosin (data not show). Gene disruption in a diploid strain followed by tetrad analysis indicated that TAF65 is essential for yeast cell viability (data not shown).

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Peptide sequence from the three \( \approx 48 \) kDa polypeptides indicated that they represented differentially phosphorylated forms of the same protein (data not shown) encoded by the previously identified ORF MPT1. MPT1 is an essential yeast gene (data not shown) previously predicted to encode a protein with a deduced molecular mass of 42 kDa required for protein synthesis.2 We refer to the protein encoded by MPT1 as TAF65p. Interestingly, BLAST search analysis revealed that the C-terminal region of TAF48p bears significant similarity to the conserved C termini of metazoan dTAF110p, hTAF130p, and hTAF105p (Fig. 2). This result was quite unexpected, because previous BLAST search analysis of the complete \( S. cerevisiae \) genome with dTAF110p and hTAF130p sequence had

\[2\] Estey, L. A., and Douglas, M. G. (1994) Saccharomyces Genome Database, direct submission.
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not revealed an obvious sequence homologue. In retrospect, however, this result may not be surprising, because the region of similarity between TAF48p and its metazoan counterparts is quite small.

To confirm the identity of TAF48p and TAF65p in TFIID, recombinant protein and affinity-purified polyclonal antibodies directed against either TAF48p or TAF65p were generated. Immunoblotting of the HATBP and HATA130p TFIID fractions shown in Fig. 1B indicated that the antibodies specifically recognized the appropriate polypeptides identified by mass spectroscopy (data not shown).

To further test whether TAF65p and TAF48p where indeed TFIID TAF subunits, immunoprecipitations were performed with either anti-Flag or anti-HA antibodies utilizing whole cell extracts prepared from yeast strains with either wt (untagged) or HA$_3$-tagged alleles of MPT1 (TAF48) or TAF65. It is important to note that the genomic copy of each allele harbors the HA$_3$ tag, thus the epitope-tagged allele is the sole source of either TAF48p or TAF65p in the cell. A HA$_3$TAF25 strain was utilized as a control. Immunoblotting with anti-HA indicated that each HA$_3$-tagged protein was specifically precipitated with anti-HA antibody but not with the control anti-Flag antibody (data not shown). Immunoblotting of precipitates indicated that TFIID subunits TBP, TAF130p, TAF90p, TAF67p, TAF61p, TAF60p, TAF47p, TAF40p, TAF25p, and TAF19p, and TAF17p were specifically co-immunoprecipitated with anti-HA antibody from each HA$_3$-tagged strain in the input, Dr1p was not detected in the precipitate from any strain (Fig. 3). To further test the specificity of TAF48p and TAF65p, immunoprecipitations were performed from HA$_3$TAF25, HA$_3$ MOT1, and HA$_3$ BRF1 strains as described above. Mot1p is in a TBF-TAF complex distinct from TFIID (37), and BRF1p is a TAF subunit of the RNAP III-specific GTF TFIIB (33, 38). As expected, TBP was specifically co-immunoprecipitated from each HA$_3$-tagged strain with anti-HA antibody (Fig. 4A). However, TAF48p and TAF65p were specifically co-immunoprecipitated with only HA$_3$TAF25p (Fig. 4A). These results indicate that TAF48p and TAF65p are specific to the TFIID TBF-TAF complex.

Because a subset of TAFs (TAF90p, TAF61p, TAF60p, TAF25p, and TAF17p) have been identified as subunits of the yeast histone acetylase SAGA complex (11), we tested whether or not TAF48p and TAF65p were SAGA components. Immunoprecipitations from wt, HA$_3$TAF48, HA$_3$TAF65, and HA$_3$TAF25 strains were probed for Gcn5p, the histone acetylase component of SAGA (39). Whereas Gcn5p specifically co-immunoprecipitated with HA$_3$TAF25p, an integral subunit of both TFIID and SAGA, Gcn5p was not associated with either HA$_3$TAF48p or HA$_3$TAF65p (Fig. 3). Additionally, both TAF90p and TAF60p, but not TAF48p or TAF65p, were specifically co-immunoprecipitated by anti-HA antibody from a strain that harbors an HA$_3$ADA3 allele as the sole source of Ada3p in the cell (Fig. 4B). Ada3p is an integral subunit of the SAGA complex (39). Together these results strongly argue that TAF48p and TAF65p are not components of the yeast histone acetylase SAGA complex.

**DISCUSSION**

Here we describe the use of a combination of ion exchange and immunofinity chromatography to purify the GTF TFIID from *S. cerevisiae*. Yeast TFIID is composed of TBP plus 14 distinct TAF subunits. A comparison of yeast TFIID with known metazoan TFIID subunits indicates that two yeast TAF subunits, TAF47p and TAF65p, currently do not have known
Comparison of yeast and metazoan TFIID subunits

| Yeast     | Human  | Drosophila |
|-----------|--------|------------|
| TBP       | TBP    | TBP        |
| TAF150    | TAF150 | TAF150     |
| TAF130(145)| TAF250 | TAF250     |
| TAF90     | TAF100 | TAF60      |
| TAF67     | TAF55  | TAF55      |
| TAF65<sup>a</sup> | TAF20 | TAF30      |
| TAF68(70) | TAF68(70) | TAF62     |
| TAF130(105) | TAF130(105) | TAF110   |
| TAF47     | TAF47  | TAF47      |
| TAF40     | TAF30  | TAF40      |
| TAF30     | AF-9ENL<sup>b</sup> | TAF30 |
| TAF25     | TAF25  | TAF25      |
| TAF19     | TAF19  | TAF19      |
| TAF17     | TAF31(32) | TAF42     |

<sup>a</sup> This study.

<sup>b</sup> Based on sequence homology.

<sup>c</sup> See Ref. 41.

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<sup>a</sup> I. Davidson, personal communication.
<sup>b</sup> S. Buratowski, personal communication.
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