Novel RNA-binding Properties of Pop3p Support a Role for Eukaryotic RNase P Protein Subunits in Substrate Recognition*  

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Ribonuclease P (RNase P) catalyzes the 5′-end maturation of transfer RNA molecules. Recent evidence suggests that the eukaryotic protein subunits may provide substrate-binding functions (True, H. L., and Celander, D. W. (1998) J. Biol. Chem. 273, 7193–7196). We now report that Pop3p, an essential protein subunit of the holoenzyme inSaccharomyces cerevisiae, displays novel RNA-binding properties. A recombinant form of Pop3p (H6Pop3p) displays a 3-fold greater affinity for binding pre-tRNA substrates relative to tRNA products. The recognition sequence for the H6Pop3p-substrate interaction in vitro was mapped to a 39-nucleotide long sequence that extends from position –21 to +18 surrounding the natural processing site in pre-tRNA substrates. H6Pop3p binds a variety of RNA molecules with high affinity ($K_d = 16–25$ nM) and displays a preference for single-stranded RNAs. Removal or modification of basic C-terminal residues attenuates the RNA-binding properties displayed by the protein specifically for a pre-tRNA substrate. These studies support the model that eukaryotic RNase P proteins bind simultaneously to the RNA subunit and RNA substrate.

Ribonuclease P (RNase P)$^1$ is the endoribonuclease responsible for the generation of mature 5′-termini of transfer RNA (tRNA) molecules (1, 2). Although the holoenzyme is universally composed of both RNA and protein, the subunit composition differs dramatically among the holoenzymes derived from bacteria and eukaryotes (3). A single protein component and RNA molecule constitute the bacterial RNase P holoenzyme, whereas as many as nine proteins play a role in the nuclear RNase P function ofSaccharomyces cerevisiae (3, 4). The RNase P RNAs derived from bacterial and some archaeal sources catalyze precursor tRNA (pre-tRNA) cleavage in vitro under appropriate ionic conditions in the absence of protein (5, 6). Although the eukaryotic RNase P RNAs contain many of the secondary structural elements present in the prokaryotic RNA subunits, a demonstrable catalytic activity in RNA-alone reactions has not been established for any eukaryotic RNAs.

We have previously reported that proteins constitute significant components of the active site architecture for the eukaryotic RNase P holoenzyme (7). These findings were based upon the observation that for RNase P enzymes from both Tetrathyaina thermophila and human HeLa cell sources, proteins rather than RNA were able to form efficient cross-linked products with photo-reactive substrates. Conversely, the protein complement of theEscherichia coli RNase P was not required for the RNA subunit to form a corresponding cross-linked product with substrate. One potential role for protein components in the eukaryotic system may be to position the pre-tRNA substrate in the active site for efficient and accurate processing.

Our previous work with RNase P preparations derived from T. thermophila and HeLa sources illustrated that a single protein component of the holoenzyme resides in proximity to the substrate (7). For example, a 36-kDa protein component of the T. thermophila holoenzyme (p36) forms a specific protein-RNA adduct with pre-tRNA substrates. The proximity of an RNase P protein subunit to the substrate does not prove that the protein component contacts the substrate within the active site. Furthermore, our previous cross-linking studies were not of sufficient resolution to reveal details about the pre-tRNA substrate surface that lie proximal to the protein to which the RNA was ultimately cross-linked.

To address these questions, we have extended our biochemical analyses to study substrate-protein interactions for the RNase P holoenzyme derived from S. cerevisiae. RNA binding experiments reveal that one protein component of the yeast nuclear RNase P, Pop3p, possesses high affinity RNA-binding properties with preferences for single-stranded RNA. Consistent with this observation, Pop3p interacts with a 39-nucleotide-long region that surrounds the RNase P cleavage site within a pre-tRNA substrate. Mutational studies reveal that the highly charged C-terminal region of Pop3p is involved in RNA-binding interactions and may provide a direct role in substrate recognition. The results described here provide further evidence for the model that proteins facilitate substrate binding in the active site for eukaryotic RNase P function.

EXPERIMENTAL PROCEDURES

Materials—All buffer solutions were prepared with sterile water that was initially deionized using a Millipore MilliQ water purification system. T7 RNA polymerase and restriction enzymesBstNI, HindIII, andBamHI were purchased from New England Biolabs; [α-32P]ATP (3000 Ci/mmol), [γ-32P]ATP (6000 Ci/mmol), and [5′-32P]Cytidine 3′,5′-bisphosphate (3000 Ci/mmol) were obtained from PerkinElmer Life Sciences; calf intestinal alkaline phosphatase was obtained from United States Biochemicals; T4 RNA ligase was purchased from Promega; all oligonucleotides were obtained from Operon, Inc.

POP3 Gene Amplification and Cloning—Genomic DNA from S. cerevisiae was isolated using the procedure described by Hoffman and Winston (8). Oligonucleotides complementary to the 5′-terminus (5′-WT oligo) of POP3 plus an additional restriction site 5′-CCGGATCCATGTCGGGTCGTTAAAATCTC-3′, BamHI site underlined) and 3′-terminus (3′-WT oligo) plus an additional restriction site 5′-CCCCAGCTCTACTTTTGCCCTCTCTAGAC-3′, HindIII site underlined) were used as gene-specific primers for DNA amplification using genomic

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1 The abbreviations used are: RNase P, ribonuclease P; poly(A), poly-cytidylic acid; WT, wild type; pre-tRNA, precursor tRNA.

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DNA as a template. Following amplification, the DNA was subsequently digested with restriction enzymes, and the DNA corresponding to POP3 was cloned into the expression vector pQE30 (Qiagen). Several POP3 mutants were created for the identification of a RNA-binding domain of the protein. The following oligonucleotides were used to create the mutants used in the protein expression:

1. WT oligo: (5’-CCGCGATCCCGCGGAGAACTGCTGTT-3’) and 3’ WT oligo: (5’-GGGTTTCGGGGATCCCTGGTGGTGA-3’).
2. C-8: 5’ WT oligo and (5’-CCGCGATCCCGCGGAGAACTGCTGTT-3’).
3. CAATTGGCAC-3’/H11032 TGTAGTTTTCAACAG-3’.
4. WT oligo: (5’-CGGCGATCCCGCGGAGAACTGCTGTT-3’) and (5’-CCGCGATCCCGCGGAGAACTGCTGTT-3’).
5. N-64: (5’-CGCAAGCTTCTATGGCAC-3’/H11032 N-64: (5’-CGCAAGCTTCTATGGCAC-3’/H11032).
6. CAATTGGCAC-3’/H11032 TGTAGTTTTCAACAG-3’.

Pop3p Recombinant Protein Expression and Purification—The QiAexpress (Qiagen) pQE expression system utilizes an isopropylthiogalactopyranoside-inducible T5 promoter and two lac operator sequences to ensure efficient repression. An N-terminal 6xHis tag was incorporated into the coding sequence during cloning to facilitate rapid affinity purification of the recombinant protein using Ni(II)-nitrilotriacetic acid chromatography. An N-terminal sequencing of the natural coding sequence does not interfere with Pop3p function, because a Protein A-Pop3p fusion protein is biologically active in vivo (9). This recombinant form of Pop3p (designated as H6Pop3p) was used for all of the experiments described herein. E. coli strain MG13009(pREP4) was transformed with plasmids p2020P3P and pQE30-Pop3p using ampicillin and kanamycin antibiotic selection. Protein expression was induced with isopropylthiogalactopyranoside to a final concentration of 1 mM for an additional 3 h at 37°C. The recombinant protein was purified from crude lysates by Ni(II)-nitrilotriacetic acid chromatography (Qiagen) according to the manufacturer’s instructions. Fractionations were diluted 1:10 and analyzed by SDS-polyacrylamide gel electrophoresis. Peak fractions were pooled and dialyzed versus R150 buffer (50 mM citrate, 150 mM NaCl, 5 mM β-mercaptoethanol, 20% glycerol, pH 6.5) for a total of five 1-liter exchanges at 4°C. Typical yields from this procedure range from 8 to 12 mg of soluble protein per liter of induced culture. H6Pop3p is stable at 4°C in R150 buffer for several months. Protein could also be stored at -80°C for >6 months without losing activity, as assessed by filter binding with S. cerevisiae RNase P RNA (described below). Protein concentration was determined spectrophotometrically as described by Mach et al. (10).

Preparation of Nucleic Acids—Mature RNase P RNA from S. cerevisiae was transcribed in vitro from a BstNI-linearized pGEM7 DNA template using T7 RNA polymerase. The tRNA used in the tRNA expression reaction was gel-purified and refolded using previously described procedures (7).

End-labeled RNAs were prepared for use in the filter retention experiments. For the 5’-end labeling of pre-tRNA, 500 pmol of pre-tRNA was dephosphorylated in a 100-μl reaction with 5 units of calf-intestinal alkaline phosphatase at 45°C for 30 min. The RNA was extracted twice each with phenol, phenol-chloroform, chloroform, and ether. The RNA was then precipitated with 100% ethanol was added to facilitate precipitation of the RNA overnight at -20°C. For the 5’-end labeling reaction, 50 pmol of dephosphorylated pre-tRNA was reacted with 3.3 pmol of [γ-32P]ATP in the presence of 10 units of T4 polynucleotide kinase and kinase buffer (70 mM Tris-HCl (pH 8.0)/0.001 M Na2EDTA) containing 2% SDS for 2 h. This reaction was applied to a BA85 Protran nitrocellulose filter with 500 nM, based upon their calculated mole transcript concentrations. The competitor nucleic acids of unknown length were used in the range of 0.1–500 nts, based on their calculated mole concentration. These transcripts were gel-purified for use in filter binding assays.

Filter Binding Assays—A modified filter binding assay was used for the determination of dissociation constants assuming a bimolecular equilibrium for each experiment. H6Pop3p was initially preincubated with 1 μg of a deproteinized, total yeast RNA hydrolysesate preparation at 37°C for 10 min to limit nonspecific protein-RNA interactions. Typically, a fixed concentration of pre-labeled RNA (100 pm) was incubated with various H6Pop3p concentrations (0.1–500 nM) in a 100-μl reaction volume and placed on ice for 0.5–1 h. An 80-μl aliquot of the reaction was applied to a BA85 Protran nitrocellulose filter with an underlying NA45-DEAE membrane (Schleicher and Schuell) under vacuum using a double-filter dot-blot apparatus (Schleicher and Schuell) described by Wong and Lohman (12). The nitrocellulose filters were soaked in R150 buffer for at least 30 min prior to filtration. The DEAE membranes were soaked immediately before use. Following filtration, each filter was dried and quantitated on a PhosphorImager (Molecular Dynamics) or a Cyclone Storage phosphor system (Packard). For the competition experiments, a fixed concentration of H6Pop3p (100 nM) was incubated with a mixture of nucleic acids consisting of a fixed concentration of internally labeled S. cerevisiae RNase P RNA (100 pm) and a varying concentration of unlabelled competitor nucleic acids. The competitor nucleic acids of defined length were used in the range of 0.1–500 nts, based on their calculated mole concentration. These transcripts were gel-purified for use in filter binding assays.

RESULTS

H6Pop3p Binds RNA with High Affinity—To explore the nucleic acid binding characteristics of this protein, protein-RNA mixtures were subjected to a modified filter binding assay in which a modified dot-blot apparatus was fitted with a nitrocellulose filter and an underlying DEAE filter (12). The data were fitted to a retention efficiency and a Kd value assuming a bimolecular equilibrium. As seen in Fig. 1A, H6Pop3p binds to the S. cerevisiae RNase P RNA with high affinity. A dissociation constant (Kd) value of 16.3 ± 1.5 mM has been calculated that represents an average of five independent experiments. A Hill analysis of the data yields a Hill coefficient of 1.2, suggesting that this interaction is non-cooperative (Fig. 1B).

H6Pop3p was also tested for its ability to bind substrate pre-tRNA and mature tRNA. H6Pop3p prefers to bind substrate relative to product by roughly 3-fold (Fig. 1C).

The stability of H6Pop3p to interact with RNA under a variety of buffer conditions was also tested. Specifically, the dependence of H6Pop3p on MgCl2 was explored using various concentrations of MgCl2 or MgCl2(CH3OH)2 in the binding reactions. As seen in Fig. 2A, magnesium(II) has no effect on the interaction within the range of 0–100 mM. In addition, the ionic strength dependence of the H6Pop3p-RNase P RNA interaction was tested in binding reactions containing varying concentrations of either...
CH$_3$CO$_2$NH$_4$ or NH$_4$Cl. The results shown in Fig. 2 indicate that the RNA-protein interaction is hindered by high ionic strength conditions above 0.5 M, suggesting a role for ionic contacts in the formation of the RNA-protein complex.

**Single-strand Specificity of the H6Pop3p-RNA Interaction**—A competition assay was used to investigate the interaction of H6Pop3p with a wide variety of nucleic acid molecules. The nucleic acids chosen included both single- and double-stranded RNA molecules as well as DNA molecules. The H6Pop3p concentration (100 nM) was held constant above the K$_d$ level for H6Pop3p- S. cerevisiae RNase P RNA interaction (16.3 nM), and the labeled S. cerevisiae RNase P RNA remained constant at 100 pM. Unlabeled competitor nucleic acids were included in the reaction mixtures at varying concentrations. Some RNA molecules were also shown to possess a high affinity to H6Pop3p as revealed by direct titration of each RNA as an internally labeled molecule with H6Pop3p. None of the DNA molecules served as efficient competitor nucleic acids to H6Pop3p-RNase P RNA binding. As summarized in Table I, H6Pop3p preferentially binds single-stranded RNAs or complex RNAs with some single-stranded character.

**H6Pop3p Binds to Pre-tRNA Sequences Surrounding the Scissile Bond**—Although H6Pop3p did not show specificity for a given RNA molecule, the data suggested that the protein prefers to bind single-stranded RNAs and prefers to bind pre-tRNA relative to tRNA. To determine more precisely the RNA-binding site on pre-tRNA, we used a filter retention procedure with end-labeled substrates. End-labeled pre-tRNAs that contain $^{32}$P at either the 5’ or 3’ terminus were randomly fragmented by hydrolysis and used as substrates in binding reactions containing H6Pop3p. The RNA products that were retained by the nitrocellulose filter by virtue of binding H6Pop3p were extracted and analyzed on a sequencing gel to determine the minimal length of RNA that interacted with H6Pop3p. The results of a representative experiment are shown in Fig. 3. When the pre-tRNA is 5’-end-labeled, the smallest RNA that H6Pop3p is able to retain extends from the 5’ terminus to nucleotide positions +14 to +18 (Fig. 3A). When the pre-tRNA is labeled at the 3’ terminus, the smallest RNAs that H6Pop3p is able to retain extend from the 3’-end to nucleotide position −21 (Fig. 3B). These experiments permit the inference that Pop3p displays a preference for binding a ~39-nucleotide-long region near the 5’-end of pre-tRNA (Fig. 4). This region surrounds the cleavage site for pre-tRNA processing.
TABLE I
Specificity of H6Pop3p-nucleic acid interaction

| Nucleic acid        | Direct titration a | Competition c |
|---------------------|--------------------|---------------|
|                     | nM                 | pM            |
| S. cerevisiae       |                    |               |
| RNase P RNA         | 16.3 ± 1.5         | 6.6 ± 0.7     |
| pre-tRNA            | 42.5 ± 7.5         | ND1           |
| tRNA                | 125.0 ± 15.0       | ND            |
| T. thermophila      |                    |               |
| L-21/Scl RNA        | 19.5 ± 0.5         | 8.2 ± 0.2     |
| Poly(A)             | NA                 | 8.8 ± 1.3     |
| Poly(U)             | NA                 | 4.0 ± 0.1     |
| poly(I)/poly(C)     | NA                 | 25 ± 5.0      |
| Single-strand DNA   | ND                 | 135 ± 40      |
| Plasmid DNA         | ND                 | 210 ± 40      |

a The nucleic acids were defined and prepared according to procedures stated under "Experimental Procedures." Dissociation constants calculated from at least three independent filter binding experiments with internally labeled RNA molecules.

b Mole nucleotide concentration of unlabeled competitor nucleic acid at fraction bound = 50%.

c ND, not determined.

The plasmid used was pTSSP6, an SP6 RNA polymerase expression vector.

The sequence of the single-strand DNA oligo is: 5'-CGATAAGC-CAGCTGCATTAATG-3'.

The plasmid used was pTSSP6, an SP6 RNA polymerase expression vector.

FIG. 3. H6Pop3p filter retention of alkaline-hydrolyzed pre-tRNA

Deletions were engineered that removed the first 20 or 64 amino acids, respectively. A gene that encoded a C-terminal deletion was also engineered that removed the last eight amino acids of the protein. Fig. 5 shows a diagram of the Pop3p mutant constructs. Filter binding assays with these proteins demonstrated that the removal of the highly charged C-terminal residues dramatically reduces the affinity of the protein to RNA (Table II).

Site-specific mutations were created to reveal the identity of residues important for RNA binding activity (Fig. 5). The attenuation of Pop3p's high affinity binding properties suggests that the 3 lysine residues may play a role in pre-tRNA binding activity (Table II). These residues have a more pronounced affect on binding substrate than on binding the RNase P RNA subunit (Table II), suggesting that these residues may provide substrate recognition and interaction functions.

DISCUSSION

The lack of a demonstrable catalytic activity for eukaryotic RNase P RNAs suggests a more critical role for protein subunits in eukaryotes than the protein subunit provides in the bacterial holoenzyme. The lack of catalytic activity in eukaryotic RNase P RNA-alone reactions and the apparent abundance of protein subunits in the eukaryotic holoenzyme that lie in the vicinity of the pre-tRNA substrate led to our original proposal that the eukaryotic RNase P holoenzyme possesses a protein-rich active site (7). Cross-linking analyses with a photoreactive substrate pre-tRNA and an RNase P holoenzyme preparation from S. cerevisiae confirmed that several protein species lie in proximity to the substrate.2 As is evident for holoenzymes from HeLa cells and the ciliated protozoa T. thermophila, proteins of the S. cerevisiae holoenzyme may provide a critical role in active site architecture formation. The data presented in this study provide further support that protein(s) may provide substrate recognition for eukaryotic RNase P holoenzymes.

Three observations implicated Pop3p as a component of the active site topology of the S. cerevisiae RNase P holoenzyme.

2 E. M. Brusca, H. L. True, and D. W. Celander, unpublished observations.
RNA-binding Properties of Pop3p

First, the recombinant form of Pop3p shows a marked preference for single-stranded RNA versus double-stranded RNA. This intriguing observation is consistent with recent findings that have shown that single-stranded RNA homopolymers inhibit the nuclear RNase P reaction, whereas double-stranded non-substrate RNA molecules had little inhibitory effect (18). In this regard, Pop3p or other protein components that are associated with the active site may discriminate among potential substrate RNA molecules and provide to the active site only those RNA molecules with requisite features, i.e., a 5'-leader sequence. Second, Pop3p prefers to bind pre-tRNA relative to tRNA. The ability of the protein to distinguish substrates and proteins may also be required to interact with the RNA-binding motif of RNase P or RNase MRP (21). This interaction is presumably reliant on conserved structural features among the two RNA components, because little primary sequence is conserved between them. Protein binding sites on RNA molecules are often characterized by a set of secondary and tertiary features that allow the RNA to fold into a unique three-dimensional array of nucleotide phosphates allowing ionic contact sites to contribute to specificity in RNA-protein interactions (22). The H6Pop3p-P RNA interaction is inhibited by elevated salt concentrations, supporting a role for ionic contacts in the binding interaction. Specificity may be resolved in the context of the holoenzyme where protein-protein interactions are likely to provide further scaffolding in these complex ribonucleoproteins.

Following the biochemical purification and identification of holoenzyme components from the S. cerevisiae RNase P, it was noted that eight of the nine essential protein components shared a short region of highly charged residues (4). Although this stretch of amino acid sequence does not comprise a known RNA-binding motif, it was speculated that these regions may be involved in RNA-binding interactions for the ribozyme. Pop3p has several stretches of basic residues within the natural open reading frame. In general, protein components of RNase P holoenzymes from diverse phylogenetic origins do not share a high degree of amino acid sequence conservation. However, it is noteworthy that modification of a short stretch of basic residues common in most of the S. cerevisiae RNase P proteins significantly alters the RNA-binding properties of Pop3p. Interestingly, the C-terminal domain of Pop3p appears to play a role in substrate recognition and RNA-binding in general.

This study represents the first detailed biochemical analysis for a protein-RNA interaction for a eukaryotic RNase P. The roles proteins play in eukaryotic RNase P holoenzyme function have yet to be elucidated. Proteins may provide RNA-chaperone and stabilization activities, assist in subcellular localization, or play more direct roles in the catalytic cycle. Pop3p constitutes the first identified protein essential for RNase P activity in S. cerevisiae that is able to recognize a pre-tRNA substrate in a biochemically relevant manner. Thus, a protein-rich active site in which proteins facilitate substrate recognition and positioning for efficient processing is consistent with the role of protein subunits in other eukaryotic organisms (7).

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RNA-binding Properties of Pop3p

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