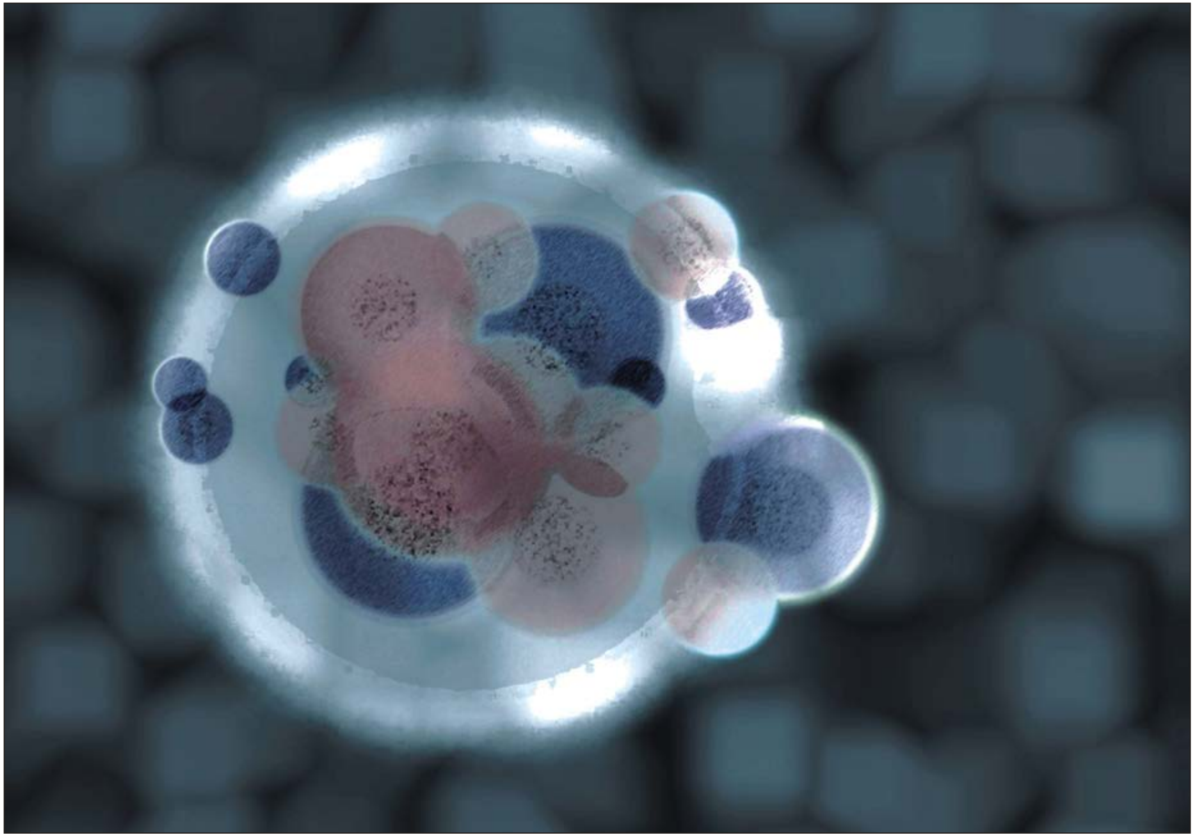

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Molecular Cloning and Characterization of a cDNA Encoding L10 Ribosomal Protein from *Mucor racemosus* PTCC 5305

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Abstract: The present research aims to study the molecular characterization of a new 60S ribosomal protein L10 (RPL10) from *Mucor racemosus* PTCC5305 and its coding sequence. A full-length complementary DNA (cDNA) encoding 60S ribosomal protein L10 was isolated from *Mucor racemosus* cDNA library. The cDNA of 766 base pairs contains a 652 base pairs open reading frame and 5'- and 3'- flanking regions including a polyadenylation sequence. The deduced protein of 216 amino acid residues had an isoelectric point (pI) of 10.16 and a calculated molecular mass of about 24.5 kDa. Sequence analysis of RPL10 revealed 78% identity and 89% similarity with fungus *Pyrenophora tritici*. Also it showed 73% identity and 84% similarity with *Homo sapiens*. Phylogenetic tree analysis based on the conserved domain of Ribosomal_L16_L10e super family exhibited that *Mucor racemosus* RPL10 is closely related to that of *Candida glabrata*.

Key words: RPL10, *Mucor racemosus*, phylogenetic analysis, QM protein

INTRODUCTION

Ribosomes are the macromolecular machines responsible for protein biosynthesis in living organisms. The ribosome has some specific interactions with different ribonucleic acids and some of the nonribosomal protein cofactors which guarantee the correct initiation, elongation and termination of polypeptide biosynthesis (Maguire and Zimmermann, 2001). The eukaryotic ribosomes are ribonucleoprotein particles composed of a small (40S) and a large (60S) subunit with well defined tasks. The small ribosomal subunit contains the decoding site where the correct base pairing between aminoacyl-tRNAs and codons of the mRNA takes place and ensures the fidelity of translation. The large ribosomal subunit contains the peptidyltransferase center which catalyses peptide bind formation and is responsible for channeling the nascent proteins through their exit tunnel. Together these subunits are composed of 4 RNA species and approximately 80 structurally distinct proteins. The exact number of the each subunit components relates to the ribosomal source (Zarivach *et al*., 2004). For instance, the mammalian 60S and 40S subunits are composed of 47 and 32 Ribosomal Proteins (RPs), respectively (Wool *et al*., 1995). Because of the fundamental function and the evolutionary structure of the ribosome, the composition and primary structure of the ribosomal components have been considered as an important tool in modern phylogenetic studies (Olsen and Woese, 1993; Lecompte *et al*., 2002). RPs play a pivotal role in protein biosynthesis. Their cellular level variations during growth steps have been studied in bacteria and fungi (Cujec and Tyler, 1996; Milne *et al*., 1975). The rRNA cores of the subunits are surrounded by RPs. Many of the large subunit RPs have a globular, surface exposed domain with long finger-like projections that extend into the rRNA core to stabilize its structure (Maguire and Zimmermann, 2001). This RNA chaperon activity of large ribosomal subunit proteins during ribosomal assembly and translation has been fully investigated and shown that nearly a third of them have high levels of RNA chaperon activity (Semrad *et al*., 2004).

L10 is an essential protein component of the large ribosomal subunits of archeal and eukaryotic cytosol and is homologue of bacterial L16. Although L16 and L10 show structural differences at the N-terminus, they belong to the ribosomal_L16_L10e super-family (Harms *et al*., 2002). Eukaryotic L10 participates in a variety of cellular activities including joining the 40S and 60s subunits (Eisinger *et al*., 1997; Zemp and Kutay, 2007). L10 incorporation into the large ribosomal subunit is one of the key steps in the ribosomal assembly process. The process mainly takes place in the nucleus and then exported to the cytoplasm through the nucleopores (Johnson *et al*., 2002). It is revealed that L10 involved in a late step of the 60S subunit assembly and is added to

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the 60S ribosomal subunit in the cytoplasm and not in the nucleus (Nguyen *et al*., 1998) although; all of the protein components of the small ribosomal subunit are incorporated in the nucleus (Fromont-Racine *et al*., 2003).

Extra ribosomal functions of eukaryotic L10 have also been studied. Human RPL10, known as QM protein, has been revealed to have role in tumor suppression as it was first identified as a high level cDNA transcript in a non-tumourigenic Wilm's tumour microcell hybrid in comparison with the tumourigenic parentral cell line (Dowdy *et al*., 1991). The role of RPL10 homologues in regulation of transcription factor has also been reported by Monteclaro and Vogt (1993), Inada *et al*. (1997) and Oh *et al*. (2002).

Several studies have been carried out on the function and characterization of the RPs, including L10 and their encoding genes (Chávez-Rios *et al*., 2003; Hofer *et al*., 2007; Lillico *et al*., 2002). Moreover, RPs are highly represented in cDNA libraries (Karsi *et al*., 2002; Patterson *et al*., 2003; Manchado *et al*., 2007), which caused to the increase of their related sequences from different organisms in databases. In addition, L10 and L30 are the only members of eukaryotic ribosomal components whose crystal structures are studied in detail (Mao and Williamson, 1999; Nishimura *et al*., 2008). Based on all these reasons, RPL10 can be proposed as a useful molecular marker for phylogenetic analysis.

Mucor racemosus is a saprophytic zygomecete with a dimorphic character. In the presence of oxygen, it shows filamentous growth but under an anaerobic condition and availability of a fermentable hexose, it grows as single-celled budding yeast (Cihlar, 1985). Its relatively small genome facilitates molecular genetic investigation on this organism (Casale *et al*., 1990). *Mucor racemosus* PTCC 5305 was isolated in a soil screening project aiming to study biologically important proteins in our laboratory. Here, we describe the isolation and characterization of the cDNA encoding for RPL10 from *M. racemosus* PTCC 5305 cDNA library. Evolutionary comparison with other species is also discussed. To our knowledge this is the first report on a ribosomal protein of the large subunit of the *Mucor* genus. Regarding to the importance of the ribosomal proteins in the phylogenetic studies, cloning and molecular characterization of *Mucor* RPL10 could be useful for discussion about the evolutionary routes of *Mucor* genus in eukaryotic kingdom.

MATERIALS AND METHODS

Culture of *M. racemosus* PTCC 5305: The microorganism was cultured in a basic medium consisting of maltose (0.6% w/v), uric acid (0.7% w/v), Vogel trace elements solution (2% v/v), $CuSO_4$ (0.5 μM). The pH of the medium was adjusted to 6±0.05. The culture was incubated at 30°C with a shaking rate of 150 rpm for 24 h.

Extraction of total RNA: A 100 mg of cultured mycelium was collected by filtration, which was grounded in liquid nitrogen using a mortar and pestle. The cells were lysed under highly denaturing conditions, in a solution containing guanidine isothiocyanate (5.4 M, pH 6.5). The cell lysate was centrifuged at 10000 g and the supernatant subjected for total RNA extraction by RNeasy Plant Minikit (Qiagen) as instructed by the manufacturer. The quality and quantity of extracted RNA was monitored by spectrophotometric method and denatured agarose gel (1%) electrophoresis.

cDNA library construction and identification of RPL10 cDNA: Double stranded cDNA was constructed by using cDNA synthesis system (Roche) using 15 μg total RNA as the starting material according to the producer's manual. The blunted ds-cDNA was then ligated into the *SmaI* cut pUC19 using T4 DNA Ligase (Fermentase) according to kit instruction manual. The ligated plasmid was transformed to competent *E. coli* DH5α according to Sambrook *et al*. (2001). The resulted colonies were subjected to PCR, using the pUC19 specific designed primers (B1R: 5'-CACATTTCCCCGAAAAGTGC-3' and B1F: 5'-ACGGTTCCTGGCCTTTTGC-3'). The selected clones contained the inserted fragment of interest with the size ranging from 800-1200 bp. These clones were then sent for sequencing using M13 sequencing primers. The resulted sequences were analyzed for homologies. The one which showed the most homology to RPL10 was selected for further analysis.

Molecular Analysis of Nucleotide and Amino Acid Sequences: For sequence analysis of cDNA fragment in order to determine presence of potential open reading frame, BLASTX program was used. Search for related sequences and amino acid sequences comparison was carried out using BLASTP and CLUSTAL W software, respectively. A phylogenetic tree was generated with CLUSTALW based on alignment of conserved Ribosomal_L10_L16e region of each protein sequence and drawn by DRAWGRAM program.

RESULTS AND DISCUSSION

Isolation and sequence analysis of the cDNA clone encoding *M. racemosus* RPL10: Sequence analysis of about 80 inserted fragments sized by 800-1200 bp of

selected positive clones, resulted in identification of two cDNA clones containing ORF for RPL10. It showed a good representation of RPL10 in a *M. racemosus* cDNA library.

The *M. racemosus* RPL10 cDNA consists of 766 base pairs, including 5'- and 3'- noncoding sequences (GenBank accession no. EU195426). The 3'- flanking region contains about 10 bp of poly(A) and a typical polyadenylation signal for eukaryotic organisms, AATAAA, 38 nucleotides upstream of the poly(A) tail. A kozak sequence of CCCATGG was also found in the 5' end and considered as translation initiation site (Fig. 1).

Characteristics of recombinant RPL10: The *M. racemosus* RPL10 cDNA sequence predicts a polypeptide of 216 amino acid residues with a calculated molecular mass of 24553.73 Da. The protein contains a high level of charged amino acids and has an estimated isoelectric point of 10.16. These data are in accordance with earlier reports from human and other organisms (Dowdy *et al.*, 1991; Lillico *et al.*, 2002). Using conserved domain search at NCBI (Marchler-Bauer *et al.*, 2005), a highly conserved domain between residues 43-166 was detected which confirmed that the recombinant protein belongs to the Ribosomal_L16_L10e super family. The protein interfaces with different rRNA and some protein components of large ribosomal subunits have also been determined and shown in the Fig. 2. It has been reported that protein kinase C is capable of phosphorylating QM *in vitro* (Inada *et al.*, 1997). A putative protein kinase phosphorylation site (SxR) was identified between residues 137-139.

The secondary structure analysis of RPL10 was carried out by SOPMA (Geourjon and Deleage, 1995) and the result showed that the protein contained 35.35 helix, 20 extended strand, 8.84 beta turn and 35.81% random coil (Fig. 3). The location of two distinct helices (between residues 54-79 and 145-156) and their near beta sheets are in accordance with the results taken from crystal structure of human ribosomal protein L10 (Nishimura *et al.*, 2008).

Sequence similarities and phylogenetic analysis: Alignment of the predicted amino acid sequence of RPL10 from *M. racemosus* with the corresponding sequences of some higher and lower eukaryotic organisms

```
  1 ccatgattacgccaagcttgcatgcctgcaggtcgactctagaggat
 48 cccatgggtcgccgtccccctcgttgttatcgttactgtaagaac
       M  G  R  R  P  P  R  C  Y  R  Y  C  K  N
 93 aagccttatcccaagtctagatactgtcgtggtgtccctgatgcc
    K  P  Y  P  K  S  R  Y  C  R  G  V  P  D  A
138 aagctcagaatctacgatttaggtcgtaagaaggcatctgtcgac
    K  L  R  I  Y  D  L  G  R  K  K  A  S  V  D
183 gacttccctctctttgttcacttggtttccaacgagtacgaacaa
    D  F  P  L  F  V  H  L  V  S  N  E  Y  E  Q
228 ttgtctgccgaagctctcgaagctggtcgtatttgtgccaacaag
    L  S  A  E  A  L  E  A  G  R  I  C  A  N  K
273 tacatgtccaagacttctggtaaggattccttccacatgcgtatc
    Y  M  S  K  T  S  G  K  D  S  F  H  M  R  I
318 cgtgtccacccttaccatgtcacccgtatcaacaaaatgttgtct
    R  V  H  P  Y  H  V  T  R  I  N  K  M  L  S
363 tgtgctggtgccgatagattgcaaactggtatgcgtggtgctttc
    C  A  G  A  D  R  L  Q  T  G  M  R  G  A  F
408 ggtaagcctaacggtcttgtcgctcgtgtcaacattggtcaaatc
    G  K  P  N  G  L  V  A  R  V  N  I  G  Q  I
453 attttctctgttcgtaccaaggactccaacaaggctgtcgttatt
    I  F  S  V  R  T  K  D  S  N  K  A  V  V  I
498 gaagccttgagacgttgtaagtacaagttccctggtcaacaaaag
    E  A  L  R  R  C  K  Y  K  F  P  G  Q  Q  K
543 atcattatctccaagaagtggggtttcactcctcttgctcgtgct
    I  I  I  S  K  K  W  G  F  T  P  L  A  R  A
588 gaatacgttgaagctcgtgctgctggtaagctcagacctgatggt
    E  Y  V  E  A  R  A  A  G  K  L  R  P  D  G
633 tgttacgtcaagtttgttccccaaagaggtcctctcgccaactac
    C  Y  V  K  F  V  P  Q  R  G  P  L  A  N  Y
678 ttcaaggaagctggcaaggtttaaatttctttttcaataaaatta
    F  K  E  A  G  K  V  *
723 tgaaaggcaattttcttctcttttaaaaaacccaaaaaaaaaa
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Fig. 1: Nucleotide sequence and deduced amino acid sequence of *M. racemosus* RPL10 cDNA. The putative initial methionine code is in bold type and the stop codon is indicated by *. A putative protein kinase C phosphorylation site is bold underlined

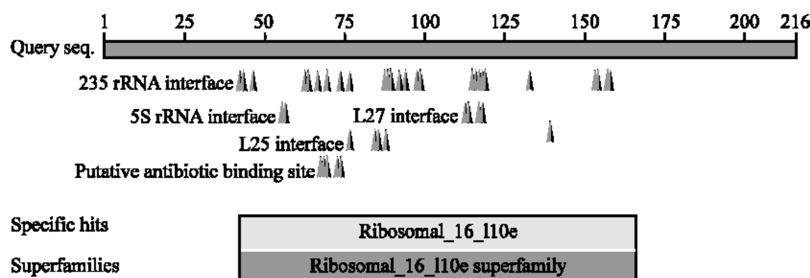

Fig. 2: Graphical summary of *M. racemosus* RPL10 conserved domains. The amino acid residues which are conserved in large ribosomal subunit rRNA and proteins interfaces are indicated by ▲

50 100 150 200

Fig. 3: Secondary structure prediction of *M. racemosus* RPL10. The alpha helix, beta sheet, turn and coil were indicated with the longest, second longest, medium and the shortest vertical lines, respectively

```
M._racemosus        MGRRPPRCYRYCKNKPYPKSRYCRGVPDAKLRIYD[illegible]
P._tritici          MARRPARCYRYCKNKPYPKSRFNRGVPDAKIRIFD[illegible]
N._crassa           MARRPARCYRYCKNKPYPKSRFNRGVPDPKIRIFD[illegible]
S._pombe            MARRPARCYRYCKNKPYPKSRYNRAVPDSKIRIFD[illegible]
P._guilliermondii   MARRPARCYRYCKNKPYPKSRYNRAVPDAKIRIYD[illegible]
R._norvegicus       MGRRPARCYRYCKNKPYPKSRFCRGVPDAKIRIFD[illegible]
H._sapiens          MGRRPARCYRYCKNKPYPKSRFCRGVPDAKIRIFD[illegible]
                    *.***.***************: *.***.*:**:*[illegible]

M._racemosus        [illegible]
P._tritici          [illegible]
N._crassa           [illegible]
S._pombe            [illegible]
P._guilliermondii   [illegible]
R._norvegicus       [illegible]
H._sapiens          [illegible]

M._racemosus        [illegible]KKWGFTPLARAE
P._tritici          [illegible]KNWGFTPLKRDE
N._crassa           [illegible]KNWGFTPLRREE
S._pombe            [illegible]KKWGFSQYARDE
P._guilliermondii   [illegible]KKWGFTPLNRDE
R._norvegicus       [illegible]KKWGFTKFNADE
H._sapiens          [illegible]KKWGFTKFNADE
                    [illegible]*:***:     *

M._racemosus        YVEARAAGKLRPDGCYVKFVPQRGPLANYFKEAGKV-----
P._tritici          YVEQRQAGKVKIDGAYVQFLRNKGNLANNIKRFPTAFENAA
N._crassa           YLEKKAAGKLLIDGAYVQFLGNRGSLERNMKRFPDAFATEA
S._pombe            YIEKRSRGEIIPDGCYAKFLNKRGSLQEKLDLFPEASFNLA
P._guilliermondii   YIAKKTNGEVKDDGAYVKFLTKKGPLEENLRQFPNYHYEA-
R._norvegicus       FEDMVAEKRLIPDGCGVKYIPNRGPLDKWRALHS-------
H._sapiens          FEDMVAEKRLIPDGCGVKYIPSRGPLDKWRALHS-------
                   :       .:  **. .::: .:* *  .
```

Fig. 4: Amino acid sequence alignment of *M. racemosus* RPL10 with those of other organisms. The accession numbers for RPL10 homologues of *Pyrenophora tritici, Neurospora crassa, Pichia guilliermondii, Schizosaccharomyces pombe*, *Rattus norvegicus* and *Homo sapiens* are XP_001932198, XP_960786, XP_001487794, NP_595850, NP_112362, NP_006004, respectively. *, : and . are indicative for single, fully conserved residue, conservation of strong groups and conservation of weak groups, respectively. The "Ribosomal L16-L10e" region in all sequences is marked

revealed that it most similar to the *Pyrenophora tritici* RPL10 (89% similarity and 78% identity). Also, it revealed a considerable identity and similarity, 73 and 84%, respectively, with Human QM protein (Fig. 4). For investigation on the evolutionary relationships, a phylogenetic tree was drawn based on Ribosomal_L16_L10e conserved domain (Fig. 5). The constructed tree showed that all of the studied organisms have a common ancestor in the evolution although the *Mucor* has the shortest distance to *Candida glabrata* in this respect.

Neurospora crassa
Aspergillus clavatus
Schizosaccharomyces pombe
Pyernophora tritci
Mucor recemosus
Candida glabrata

Fig. 5: Phylogenetic tree of *M. racemosus* RPL10 and some of other fungal related homologues

In conclusion, we could successfully clone and analyze the cDNA encoding *Mucor racemosus* RPL10 and it was used for evolutionary studies.

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