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Eukaryotic Multi-subunit DNA dependent RNA Polymerases: An Insight into Their Active Sites and Catalytic Mechanism

Peramachi Palanivelu[1*]

[1]Department of Molecular Microbiology, School of Biotechnology, Madurai Kamaraj University, Madurai - 625021, India.

Author's contribution

The sole author designed, analysed, interpreted and prepared the manuscript.

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ABSTRACT

Aim: To analyze the most complex multi-subunit (MSU) DNA dependent RNA polymerases (RNAPs) of eukaryotic organisms and find out conserved motifs, metal binding sites and catalytic regions and propose a plausible mechanism of action for these complex eukaryotic MSU RNAPs, using yeast (*Saccharomyces cerevisiae*) RNAP II, as a model enzyme.
Study Design: Bioinformatics, Biochemical, Site-directed mutagenesis and X-ray crystallographic data were analyzed.
Place and Duration of Study: School of Biotechnology, Madurai Kamaraj University, Madurai, India, between 2007- 2013.
Methodology: Bioinformatics, Biochemical, Site-directed mutagenesis (SDM) and X-ray crystallographic data of the enzyme were analyzed. The advanced version of Clustal Omega was used for protein sequence analysis of the MSU DNA dependent RNAPs from various eukaryotic sources. Along with the conserved motifs identified by the bioinformatics analysis, the data already available by biochemical and SDM experiments and X-ray crystallographic analysis of these enzymes were used to confirm the possible amino acids involved in the active sites and catalysis.
Results: Multiple sequence alignment (MSA) of RNAPs from different eukaryotic organisms showed a large number of highly conserved motifs among them. Possible catalytic regions in the catalytic

**Corresponding author: E-mail: ppmkupp@gmail.com;*

subunits of the yeast Rpb2 (= β in eubacteria) and Rpb1 (= β' in eubacteria) consist of an absolutely conserved amino acid R, in contrast to a K that was reported for DNA polymerases and single subunit (SSU) RNAPs. However, the invariant 'gatekeeper/DNA template binding' YG pair that was reported in all SSU RNAPs, prokaryotic MSU RNAPs and DNA polymerases is also highly conserved in eukaryotic Rpb2 initiation subunits, but unusually a KG pair is found in higher eukaryotes including the human RNAPs. Like the eubacterial initiation subunits of MSU RNAPs, the eukaryotic initiation subunits, viz. Rpb2, exhibit very similar active site and catalytic regions but slightly different distance conservations between the template binding YG/KG pair and the catalytic R. In the eukaryotic initiation subunits, the proposed catalytic R is placed at the -9th position from the YG/KG pair and an invariant R is placed at -5 which are implicated to play a role in nucleoside triphosphate (NTP) selection as reported for SSU RNAPs (viral family) and DNA polymerases.

Similarly, the eukaryotic elongation subunits (Rpb1) are also found to be very much homologous to the elongation subunits (β') of prokaryotes. Interestingly, the catalytic regions are highly conserved, and the metal binding sites are absolutely conserved as in prokaryotic MSU RNAPs. In eukaryotes, the template binding YG pair is replaced with an FG pair. Another interesting observation is, similar to the prokaryotic β' subunits, in the eukaryotic Rpb1 elongation subunits also, the proposed catalytic R is placed double the distance, i.e., -18 amino acids downstream from the FG pair unlike in the SSU RNAPs and DNA polymerases where the distance is only -8 amino acids downstream from the YG pair. Thus, the completely conserved FG pair, catalytic R with an invariant R, at -6th position are proposed to play a crucial role in template binding, NTP selection and polymerization reactions in the elongation subunits of eukaryotic MSU RNAPs. Moreover, the Zn binding motif with the three completely conserved Cs is also highly conserved in the eukaryotic elongation subunits. Another important difference is that the catalytic region is placed very close to the N-terminal region in eukaryotes.

Conclusions: Unlike reported for the DNA polymerases and SSU RNA polymerases, the of eukaryotic MSU RNAPs use an R as the catalytic amino acid and exhibit a different distance conservation in the initiation and elongation subunits. An invariant Zn^{2+} binding motif found in the Rpb1 elongation subunits is proposed to participate in proof-reading function. Differences in the active sites of bacterial and human RNA polymerases may pave the way for the design of new and effective drugs for many bacterial infections, including the multidrug resistant strains which are a global crisis at present.

Keywords: Multi-subunit DNA dependent RNA polymerases; eukaryotic RNA polymerases; RNA polymerase II; Saccharomyces cerevisiae; conserved motifs; polymerase active site; polymerization mechanism; transcription slippage diseases; drug design.

1. INTRODUCTION

RNAPs (EC 2.7.7.6) are key enzymes which play a vital role in the flow of genetic information from DNA to proteins and the proteins are final players in all cellular processes. Therefore, they are found in all living organisms and play a crucial role in copying DNA sequences into RNA molecules which are subsequently translated into proteins. Thus, transcription forms the first step and a key control point in gene regulation and expression. Errors in the transcription process can potentially lead to aberrant gene products and ultimately lead to various diseases including cancer. One major class of transcription error, known as transcriptional slippages, are implicated in the development of a wide variety of diseases, such as colon cancer, non-familial Alzheimer's, Down's syndrome, etc. [1]. Recently the *in vitro* transcribed mRNAs have come into focus as a potential new class of drugs known as 'mRNA therapeutics' to deliver genetic information through mRNAs to correct the malfunction(s) [2] and also potential vaccines against cancer treatment [3]. In fact, many anti-cancer drugs act by inhibiting the transcription step itself. Therefore, understanding the mechanism and regulation of RNAPs have been a key goal of molecular biologists since its discovery. Interestingly, the sequences, overall 3D framework and functions of these DNA dependent RNAPs are universally conserved in viruses, bacteria, plants and animals with small but significant differences in their active sites and catalytic amino acids. For the discussion about the discovery and dynamics of the polymerization reactions [refer to Palanivelu 4]. Instead of a single type of RNAPs in prokaryotes, Robert Roeder and William Rutter discovered in1969 the existence of three different RNAPs in eukaryotic

cells that were responsible for transcription of all types of RNAs in the eukaryotic cells [5].

Though RNAPs are found in all organisms, their number and composition vary across taxa, possibly due to evolutionary consequences, changes in the genome structure and the complexity of the transcription process. However, the MSU RNAPs display a conserved core structure across all major domains of life, viz. viruses, bacteria, archaea and eucarya. For example, viruses contain mainly two different RNAPs, viz. DNA dependent RNAPs and RNA dependent RNAPs. Both eubacteria and archaebacteria contain a single type of MSU RNAPs, while eukaryotes contain at least five distinct types of MSU RNAPs (I-V). While the eubacterial enzymes are composed of 5 different subunits, the eukaryotic enzymes are made up of up to 12-16 different subunits. Despite such differences, there are striking similarities among the transcriptional mechanisms by various types of RNAPs across the three major domains of life [6 and references therein].

Transcription and transcriptional regulation are very important in eukaryotes as it underlies all aspects of cellular metabolism including oncogenesis (cancer) and morphogenesis (development). The major type of RNA polymerase, i.e., the RNA polymerase II, which involves in the transcription of genes, is a large (550 kDa) complex made up of 12 subunits. Unlike in prokaryotes, gene expression, and therefore, RNAP II activity is controlled by several proteins known as general transcription factors. In other words, as there are no Sigma like factors in eukaryotic cells for promoter recognition and to initiate transcription, the eukaryotic RNAPs interact with a variety of protein factors known as general transcription factors. Large volumes of genomic and protein sequence data are available for most of the prokaryotic and eukaryotic MSU RNAPs. Understanding the biological principles buried in these sequencing data is a significant challenge for scientists. Therefore, the purpose of the study is to analyze the available protein sequences of the MSU RNAPs from eukaryotes to find out the highly conserved motifs among them and to understand the structure- function relationships and mechanism of action of these key enzymes, along with the X-ray crystallographic and experimental data available on these enzymes from various sources. A comparative analysis of the bacterial and human RNAPs for their transcription mechanism will pave way to design new and effective drugs for many bacterial infections, including the antibiotic resistance, especially the multi-drug resistance, which has become a global crisis [7,8]. MSA has been proven to be very useful for assigning a function to a given sequence, by comparing the existing experimental data with the protein sequence data and thus, bridging the gap between the protein sequence and experimental data.

RNAPs catalyze the chemical reaction that synthesizes an RNA strand from a DNA template with all the 4 NTPs and a metal ion, usually a Mg^{2+} ion. RNA synthesis in eukaryotes involves four steps, viz. formation of pre-initiation complex, initiation, elongation and termination. The nucleotides are added one at a time to the growing 3' end. The newly formed RNA copies serve as blueprints for the synthesis of proteins during the next step of translation. The basic transcription unit is the distance between the sites of transcription start site (TSS) and transcription termination site (TTS), and may have one or more genes between them (e.g., mono or poly-cistronic mRNAs; poly-cistronic mRNAs are uncommon in eukaryotes).

2. TYPES OF MSU DNA DEPENDENT RNAPs OF PROKARYOTES AND EUKARYOTES

There are at least 4 different types of MSU RNAPs in living cells, viz.

1) MSU DNA dependent RNAPs of eubacteria
2) MSU DNA dependent RNAPs of archaebacteria
3) MSU DNA dependent RNAPs of chloroplasts (Plastid encoded)
4) MSU DNA dependent RNAPs of eukaryotes

2.1 Types of MSU DNA Dependent RNAPs in Eukaryotes

As mentioned elsewhere, bacteria and archaea have only a single RNAP to transcribe all of its genes whereas eukaryotic cells employ different RNAPs to transcribe different types of genes, viz. rRNAs, tRNAs and mRNAs (Table 1).

There are at least 7 major types of RNAPs in eukaryotes. The nuclear genome utilizes three

Table 1. Types and functions of prokaryotic and eukaryotic RNAPs

RNA polymerase type	Type of RNA(s) synthesized
1. RNA Polymerase I (Nuclear)	rRNA genes (5.8S, 18S, 28S rRNAS from 45S pre-rRNA)
2. RNA Polymerase II (Nuclear)	mRNAs, snRNAs, microRNAs
3. RNA Polymerase III (Nuclear)	tRNAs & 5S rRNA, scRNAs, U6 SnRNA
4. RNA Polymerase IV (Plant specific)	siRNAs in plants
5. RNA Polymerase V (Plant specific)	Plant specific RNAs involved in siRNA directed heterochromatin formation in plants.
6. MSU RNAP type (Genomic)	Eubacteria and Chloroplasts (rRNAs, tRNAs mRNAs)

major types of RNAPs which are localized in the nucleus. For example, the RNAP I is localized in the nucleolus and primarily involves in the synthesis of the rRNAs and the other two RNAPs, viz. RNAPs II and III are localized in the nucleoplasm and mainly involved in the synthesis of mRNAs and tRNAs, respectively (Table 1). Plants are unique among eukaryotes in having five nuclear MSU RNAPs. Two plant-specific RNAPs, polymerases IV and V are 12-subunit enzymes that are evolved as specialized forms of Pol II. (Pols IV and V are nonessential for viability but play important roles in RNA-mediated gene silencing pathways that tame transposons and defend against invading viruses [9]).

2.2 Basic Structure and Composition of the Eukaryotic RNAPs

All the 5 eukaryotic enzymes (RNAPs I-V) are MSU enzymes. The 12-subunit RNAP II is the enzyme largely responsible for transcription of protein-encoding genes and thus, forms the central component of the eukaryotic transcription machinery. Similarities between the eukaryotic and prokaryotic MSU enzymes, suggest a common lineage in the evolutionary tree. For example, counterparts for all the five core eubacterial RNAP subunits ($\alpha_2\beta\beta'\omega$) are found in the eukaryotic RNAPs I, II and III [10] (Table 2). The five orthologs include the two largest catalytic subunits Rpb1 and Rpb2, which correspond to the bacterial β' and β subunits, respectively [11]. Furthermore, Rpb3 and Rpb11 correspond to the two copies of the bacterial α subunit, and the Rpb6 subunit corresponds to the bacterial ω subunit [12]. In addition to, the two large subunits of RNAP II share some sequence homology and antigenic determinants with the corresponding subunits of RNAPs I and III [13] (Refer to also Mix and Match analysis Figs. 5 and 6). Rpb3 is involved in RNAP II assembly. The subunits Rpb4 and Rpb7 form a heterodimer and associate reversibly with the '10-subunit core polymerase' and involves in the initiation process which is otherwise defective in initiation. Rpb5, an evolutionarily highly conserved, universal eukaryotic RNAP subunit, shared by all three enzymes, facilitates communication between the RNAP core with a variety of basal and gene-specific transcription factors [14]. Rpb7 is essential for the functioning of the RNAP-II as deletion is also found to be lethal. A cleft is formed by jaws; the upper jaw is formed by regions of Rpb1, Rpb2 and Rpb9 whereas the lower jaw is formed by Rpb1 and Rpb5. The jaws are thought to grab the incoming DNA template [15] (Fig. 1).

Consistent with the increased complexity of the eukaryotic genome, all three major RNAPs of the eukaryotic transcriptional machinery have several additional subunits that do not have bacterial counterparts. Table 2 shows the subunit compositions of the three major types of nuclear MSU RNAPs. Apart from the five orthologs, as discussed above, the nuclear RNAPs share four common subunits, while the remaining subunits are RNAP dependent. Thus, the three major classes of eukaryotic RNAPs: I, II and III, in addition to comprising of two large catalytic subunits are also made up of 10-14 smaller subunits (Table 2).

2.3 Characteristics of the C-terminal Domain (CTD) in the Largest Subunit Rpb1

Though exact functions of all the eukaryotic RNAPs are more or less completely understood, yet much data are not available on the individual subunits except for the larger subunits. An interesting feature of the RNAP II, a 12-subunit complex, is its unique CTD in the largest subunit Rpb1. The Rpb1 elongation subunit consists of a tandem repeat of a conserved heptapeptide repeat sequences (-**YS**$^{\mathbf{2}}$P**TS**$^{\mathbf{5}}$P**S**$^{\mathbf{7}}$-). These

Table 2. Composition of the three major eukaryotic nuclear RNAPs

Features	Pol I	Pol II	Poll III
Subunits unique to each RNAP ($\alpha_2\beta\beta'\omega$- like)	5	5*	5
Common subunits to all 3 RNAPs	4	4	4
Additional unique subunits to each RNAPs	5	3	7
Total No. of subunits	**14**	**12**	**16**
Products	pre-rRNAS (45S RNA → 28S, 5.8S, 18S)	pre-mRNAs 5 snRNAs^ Sno RNAs, microRNAs	pre-tRNAs 5S & 7S RNAs[$], U6-snRNA
Sensitivity to α-Amanitin	Nil	High (1 µg/ml)	Moderate (10 µg /ml)
Sensitivity to Actinomycin-D#	0.05 µg/ml	0.5 µg/ml	5.0 µg/ml

*NB:*The largest subunit, Rpb1, has unique Carboxy Terminal Domain (CTD); # [16].*
Subunit nomenclatures RNAPs I, II & III: RP A1-A14; RP B1-B12; RP C1-C16
^U1-U5 of ~200 bases; involves in the formation of spliceosomes
[$]7S RNA from the signal recognition particle (SRP), which is involved in the transport of proteins into the endoplasmic reticulum

heptapeptide repeats are completely conserved in sequence and function from yeast to human with varying lengths from 25 to 52. (The CTD domain does not exist in RNAPs I and III suggesting its special importance to mRNA processing). The Ser residues are phosphorylated and dephosphorylated during the active transcription process. Therefore, the RNAP-II exists in two forms, i.e., unphos-phorylated and phosphorylated forms (II and II^P), respectively [17]. In fact, the transition between the two forms facilitates different functions during transcription. (The phosphorylation of CTD is catalyzed by TFII-H, one of the six general transcription factors associated with RNAP II. TFII-H plays a dual role: one is to unwind the DNA at the transcription start site and the other is to phosphorylate the heptapeptide repeats. (TFII-H is a large protein complex that contains among others the Cdk7/Cyclin-H kinase complex for phosphorylation of CTD and an ATP dependent DNA helicase to unwind the DNA and open up the transcription bubble at TSS). It also involves in transcription-coupled DNA mismatch repair. (Mutations in the human XPD kinase cause *Xeroderma pigmentosum* and *Trichothiodystrophy* [18].

The elongation of initiation is accomplished by the phosphorylation of Ser^5 of the heptapeptide, (-**Y**$\mathbf{S^2}$P**T**$\mathbf{S^5}$P**S-**) by the TFII-H. The Ser^5 phosphorylation recruits enzymes to cap the 5' end of the newly synthesized mRNA and the 3' processing factors to poly(A) sites. Once the second Ser is phosphorylated, i.e., Ser^2, elongation is activated. West and Corden have shown the substitution of Ala or Glu for Ser in positions 2 or 5 is lethal. In addition, changing Tyr in position 1 to Phe is also lethal [19]. In order to terminate elongation, dephosphorylation is accomplished by phosphatases. Once the domain is completely dephosphorylated, the RNAP II is "recycled" and catalyzes the same process with another initiation site. Thus, the CTD acts as a platform for various transcription factors as it binds or dissociates them, depending upon their requirements during the transcription process. Thus, the phosphorylation and dephosphorylation of the CTD is an important regulatory mechanism exhibited only by RNAP II [20]. Ser7 phosphorylation is required for the transcription of SnRNAs and a mutation of Ser7 to Ala causes a specific defect in snRNA expression [21].

The number of heptapeptide repeats in the CTD increases with genomic complexity; for example, 17 in Plasmodium, 26 in yeast, 32 in *Caenorhabditis elegans*, 45 in Drosophila, and 52 in mammals). The CTD deletion experiments have shown the CTD's central role in coupling transcription to all three of the main mRNA processing events [22]. For example, deletion of most of the CTD can result in inefficient capping, splicing, and polyadenylation *in vivo*. SDM experiments of the yeast RNAP II has found that at least 10 repeats are needed for the viability of the process [23,24].

2.4 Salient Features of the Yeast (*S. cerevisiae*) MSU RNAPs

To-date one of the most well-studied eukaryotic RNAPs is from the baker's yeast, *S. cerevisiae.* In fact, our present understanding of the eukaryotic transcription system is mainly based on the yeast system. (For solving the structure and molecular basis of transcription by the yeast RNAP II, Roger Kornberg was awarded Nobel Prize in chemistry in 2006). Like other eukaryotic cells, the yeast cells also contain 3 different polymerases as discussed above. All the three yeast polymerases have five core subunits that exhibit good homology to the β, β', α and ω subunits of *E. coli* RNAP. RNAPs I and III contain the same two non-identical α-like subunits, whereas polymerase II has two copies of a different α-like subunit. All three yeast polymerases share four other common subunits as mentioned elsewhere. In addition, each RNAP contains three to seven unique smaller subunits as shown in Table 3.

The yeast RNAP II, which involves in the production of mRNAs, is extensively characterized and a great deal of information is available. The yeast RNAP II is composed of 12 subunits and the largest subunit (Rpb1) contains the essential CTD, containing 26 heptapeptide repeats (YSPTSPS). Thus, the Rpb1, Rpb2, Rpb3 and Rpb11 subunits are related to the subunits of the eubacterial RNA polymerase core enzyme, whereas the 5 subunits, viz. Rpb5, Rpb6, Rpb8, Rpb10 and Rpb12 are shared among yeast RNA polymerases I, II and III [25] (Table 3).

The yeast RNAP II core enzyme is composed of 12 subunits (Fig. 1). The 7 subunits, viz. Rpb1-4, Rpb7, Rpb9 and Rpb11 are unique to RNAP II while the 5 subunits, viz. Rpb5, Rpb6, Rpb8, Rpb10 and Rpb12 are shared between the three RNAPs (Table 3). The Δ*rpb4* phenotypes can be suppressed by overexpression of Rpb7, and the high level of Rpb7 allows its interaction with RNAP II in the absence of Rpb4, suggesting that Rpb7 is the critical component of the Rpb4–Rpb7 complex and the role of Rpb4 is to stabilize the complex [26]. MSA analysis of the Rpb7 from various eukaryotic sources have shown 3 template binding pairs, possibly decide the right orientation of the template DNA by three-point attachment in addition to two long stretches of conserved motifs (data not shown). Rpb2, a protein of 138,750 Daltons, exists as a single copy in the haploid yeast genome and disruption of the gene is lethal to the yeast cell [11].

During the production of the primary transcript by RNAP-II, the phosphorylation state (P) of the CTD changes to allow the transcribing polymerase to associate with the capping, splicing, polyadenylation and mRNA export machinery [22]. X-ray crystallographic results also provide evidence for RNA exit in the vicinity of the carboxyl-terminal repeat domain, coupling synthesis to RNA processing by enzymes bound to this domain [28]. These associations are essential for normal processing of pre-mRNAs to generate mature mRNAs and to export them to the cytoplasm and also for normal termination of transcription by RNAP II. The subunit Rpb1 (*RPO21*) is the largest and catalytic component of RNAP II and similar to the eubacterial β'. Bacterial RNA polymerase subunit ω and eukaryotic RNA polymerase subunit Rpb6 (shared by RNAPs I, II, and III) are thesequence, structural, and functional homologs and promote RNA polymerase assembly [12].

Table 3. Composition of the MSU RNAP II *from S. cerevisiae*

Subunit	Size (~kDa)	Subunit	Size (~kDa)
Rpb1 (β')	192/E	Rpb7**	19/E
Rpb2 (β)	139/E	***Rpb8****	17E/S
Rpb3 (~α)	35/E	Rpb9	14/NE
Rpb4	25/NE	***Rpb10****	8.8/E/S
Rpb5*	25/E/S	Rpb11	14/E
***Rpb6* (ω)**	18/E/S	***Rpb12****	7.7/E/S

Adapted from [25]; E, Essential; NE, Nonessential; S, Shared.

**The 5 Rpb subunits, viz. 5, 6, 8, 10 and 12 are common for all 3 RNAPs, viz. RNAP I, II & III*

*The Rpb6 promotes RNAP assembly and contains 9 C2H2 zinc fingers [27]; ** Rpb7 is unique to RNAP II. (Rpbs7 and 4 form a dimer and initiate transcription, not required for elongation); Rpb3 is not absolutely equivalent to α subunit of E. coli.; Subunits Rpb1, Rpb2, Rpb3 and Rpb7 are absolutely required for activity; Rpb1 is known to bind strongly to Rpb5; Rpb12 interacts with Rpb3*

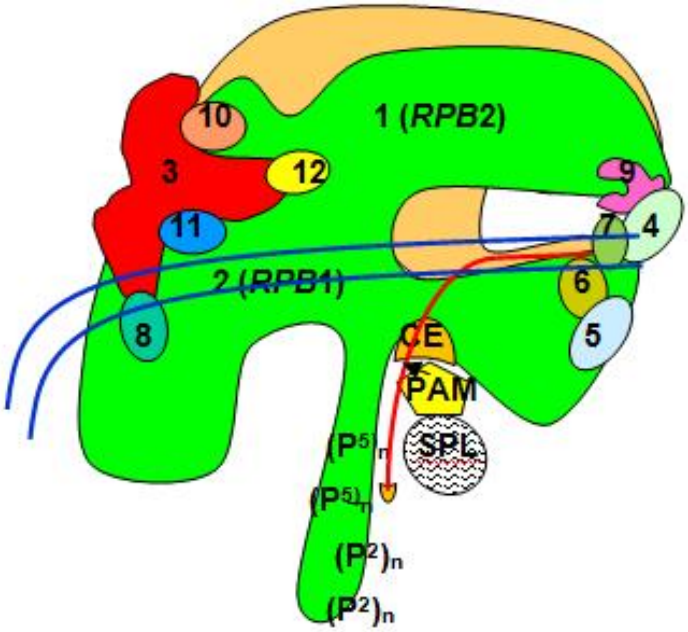


Fig. 1. A schematic diagram of the 12-subunit yeast MSU RNAP-II with the CTD and processing components

CE Capping Enzyme; PAM, Poly-Adenylation Machinery; SPL, Spliceosome; $(P^{5})_n$, phosphorylation at Ser5 positions (during initiation); $(P^{2})_n$ phosphorylations at Ser2 positions (during elongation)

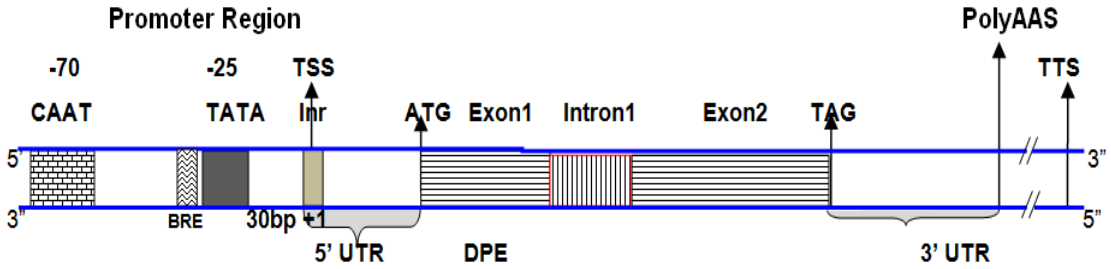


Fig. 2. Schematic diagram of a typical transcription unit in eukaryotes

NB: Blue lines, DNA strands; TATA, TATA box (Hogness box) (some promoters are TATAless), CAAT, CAAT box; The starting nucleotide (nt) is always an A in eukaryotes; UTR, UnTranslated Region); PolyAAS, Poly-A Addition Site (AATAAA); TSS, Transcription Start Site; Inr, Initiation region –pyTCACA-; DPE, Downstream Promoter Element (is seen ~ +30 bp in many genes, AGACA); TTS, Transcription Termination Site

In this communication, the yeast RNAP II is used as the model system and the structural studies of yeast RNAP II are directly relevant to RNAP II enzymes in higher organisms, as the yeast RNAP II subunits are very well conserved in sequence and function as discussed elsewhere. These analyses not only bridge the data obtained by protein sequence analysis and the experimental results obtained on the yeast RNAP II but also will pave for more SDM experiments and genetic analysis to dissect the transcription mechanism in eukaryotes in much detail. The following brief discussion on the basic structure of the transcription unit, transcription cycle and the participation of the RNAP II subunits will be useful to further understand the analysis and conclusions.

3. BASIC STRUCTURE OF THE TRANSCRIPTION UNITS IN EUKARYOTES

The transcription units in eukaryotes are slightly different from the one described in prokaryotes

[4] as most of the eukaryotic genes are interrupted with intervening sequences called introns. A typical transcription unit in eukaryotes is shown in Fig. 2.

[Some transcription units have an InR start site, TATA-like site, Down Stream Promoter Elements (DPE), Upstream activator elements/ Enhancer elements, Repressor and even Insulator and Silencer sequences. The poly-A cleavage site is about 30-35 or even 100 nucleotides downstream of the STOP codon (TAG). This sequence at the mRNAs' 3' end is called poly-A signal. The sequence present in the terminal region of the gene is TTATTT (poly-A signal) is usually followed by poly-U of 20 to 35 nts downstream from the poly-A signal.

5' UTR is the portion of an mRNA from the 5' end to the first codon; the 3' UTR is the portion of an mRNA from the last codon to the poly-A site. The UTRs play crucial roles in mRNA stability, transport, translation efficiency, etc].

4. TRANSCRIPTION PROCESSES IN EUKARYOTES

The basic transcription unit in eukaryotes is the distance between the sites of transcription start site (TSS) and transcription termination site (TTS), and the coding region is usually interrupted by one to many introns (Fig. 2)

The RNA synthesis in eukaryotes is carried out in the nucleus and involves four distinctive steps, viz. formation of pre-initiation complex (PIC), initiation, elongation and termination. It is interesting to note that the eukaryotic RNAPs do not possess any initiator subunits similar to the σ factors, as reported in prokaryotes., However, unlike in prokaryotes where the initiation starts with the specific binding of the single σ subunit, in eukaryotes, at least about half a dozen protein factors involve in the initiation of transcription and are collectively known as General Transcription factors (GTFs). These GTFs assemble at the promoter region to form the PIC. Once the PIC is formed and the RNAP is positioned at TSS, the initiation subunit Rpb2 initiates RNA synthesis by making short RNA primers of ~10 nts, from which the elongation subunit Rpb1 extends and terminates at TTS. In eukaryotes, there is no well-defined transcriptional terminator region as in prokaryotes and therefore, the transcription progresses well beyond 1000 or more nts downstream from the stop codon. Unlike RNAP I and III, RNAP II lacks any specific termination signals.

In my earlier communication, SSU RNAPs and MSU RNAPs (prokaryotic and prokaryotic type, i.e., plastid-encoded) RNAPs were analyzed in detail [29, 4, 30]. In this communication, the most complex MSU RNAPs of eukaryotic origin are analyzed for their conserved motifs, active sites, metal binding regions and based on these findings, a plausible mechanism of action is proposed for these MSU eukaryotic enzymes using the yeast MSU RNAP II as the model enzyme.

5. MATERIALS AND METHODS

A large number of MSU RNAPs from eubacteria and eukaryotes have been isolated, purified, characterized, cloned and sequenced [17,31,6]. Complete nucleic acid and protein sequence data are available for these enzymes from different eukaryotic sources. Thus, these data have become valuable tools in analyzing and understanding the structure-function relationships of these most complex enzymes which play a vital role gene expression. This communication presents a consensus model for initiation and elongation processes and also a plausible mechanism of action for these enzymes.

The *S. cerevisiae* DNA-dependent MSU RNAP II is used as the model system for delineating the polymerization mechanism. Biochemically and genetically as this is the most well-studied enzyme, a large amount of data on biochemical, SDM and X-ray analyses of its subunits make this enzyme a convenient model for investigating the physicochemical aspects of transcription in eukaryotes. For MSA of various eukaryotic RNAP II, the sequences were retrieved from SWISS-PROT and PUBMED sites and analyzed using Clustal Omega, an accurate, fast and widely accepted algorithm, available on their website.

6. RESULTS AND DISCUSSION

6.1 MSA of Eukaryotic MSU RNA Polymerases from Different Sources

The eukaryotic RNAP II is composed of various subunits as described elsewhere (Table 2). Only

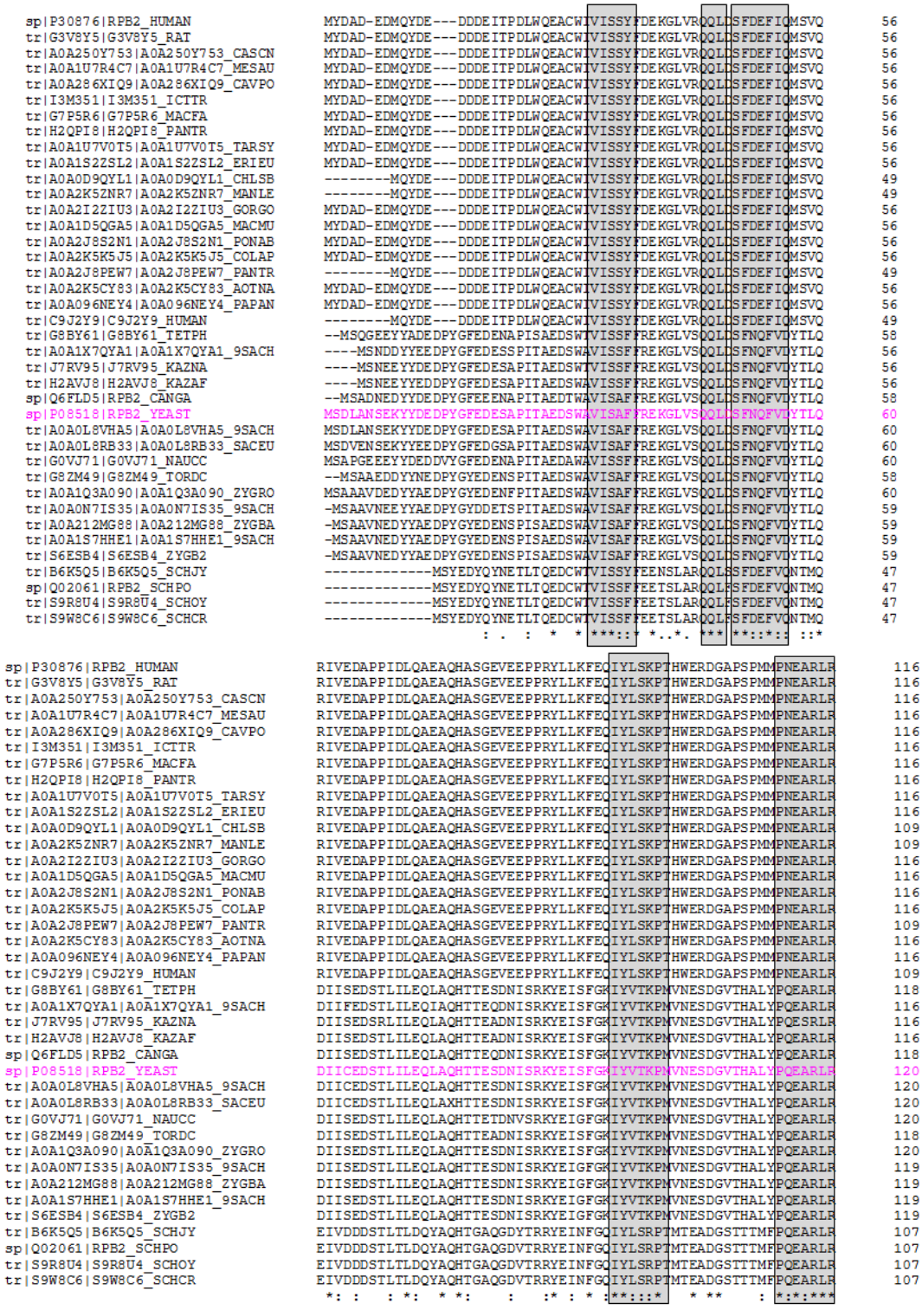
the two catalytic subunits, viz. Rpb2 and Rpb1 which involve in the initiation and elongation processes are analyzed to find out the conserved and active site regions among them. Figs. 3 and 4 show the MSA of the two catalytic subunits of MSU RNAP II from various eukaryotic sources. To reduce the length of the article, only the relevant and highly conserved regions are shown in the Figures. The possible catalytic, template and substrate binding motifs are highlighted in yellow and the metal binding regions are highlighted in green/orange. The subunit sequences of standard organisms are highlighted in yellow/magenta and used for numbering.

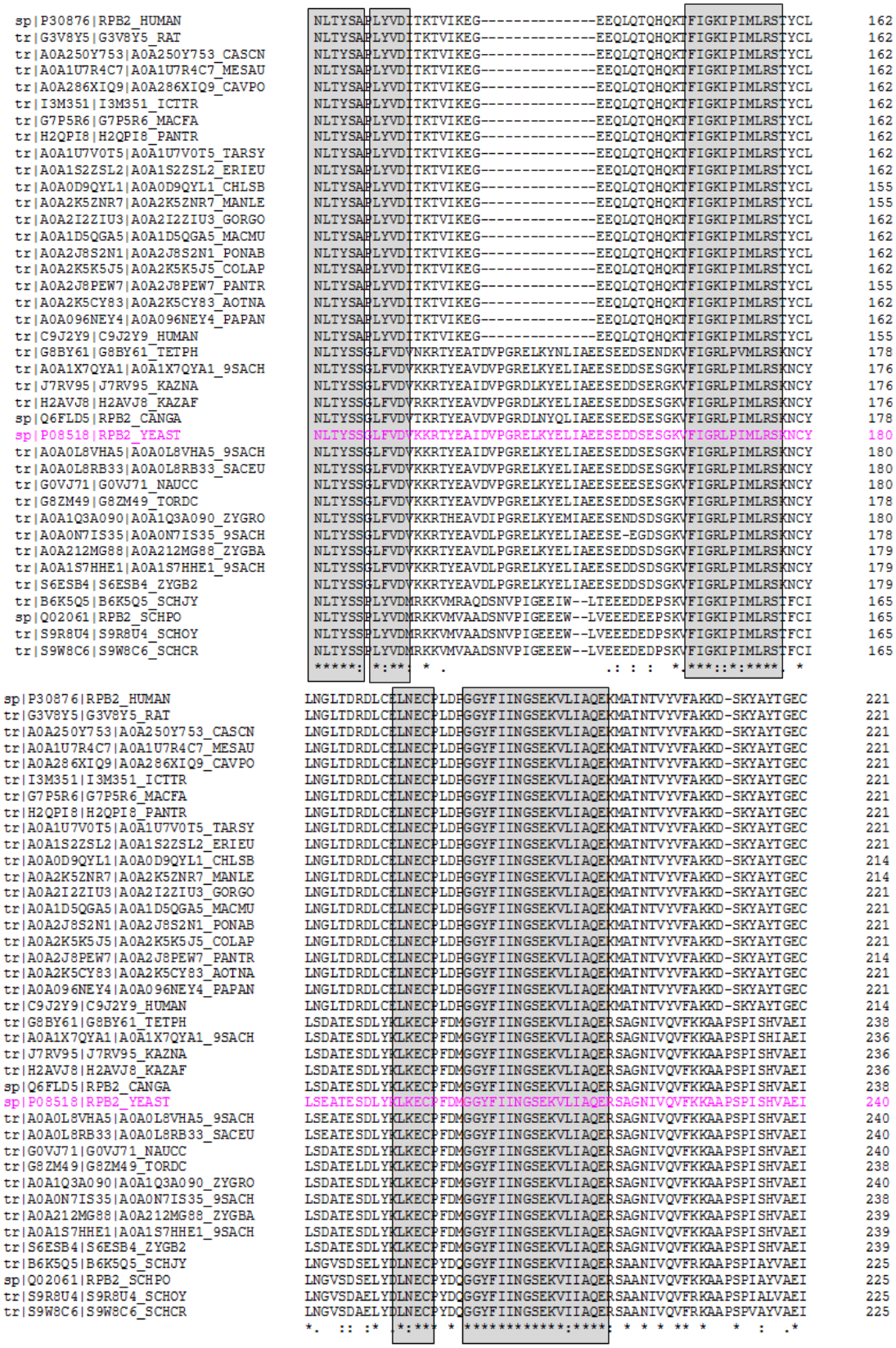
6.1.1 MSA of Rpb2 subunits of eukaryotic MSU RNAPs (RNAP II)

Fig. 3 shows the MSA analysis and conserved motifs of the Rpb2 initiation subunits in eukaryotic MSU RNAPs II. There are large numbers of conserved motifs are observed and some are found to be long stretches (highlighted). The yeast *(S. cerevisiae)* Rpb2 subunit (1224 amino acids) is used as the standard for numbering and highlighted in magenta. The catalytic region is found ~400 amino acids from the N-terminal. The invariant template binding YG is replaced by a KG pair in higher eukaryotes including human. The invariant catalytic R is placed at -9 from the template binding pair. This distance conservation is in close agreement with Pal and Luse findings that the transcription slippage abruptly stopped once the Rpb2 makes about 9 nts [32]. Interestingly, the transition from abortive to productive elongation cycle occurred once the RNAP register +10 nts [33]. The absolutely conserved R, which is implicated in NTP selection in SSU and MSU RNAPs and DNA polymerases, is placed at –5/6 positions. In fact, in all the eubacterial β subunits the catalytic R is placed at -7th position from the YG pair and completely conserved R is placed at -8th position downstream from the catalytic R. However, catalytic R is placed at -8th position from the YG pair the completely conserved R was at -4th position in SSU RNAPs and DNA polymerases [29,34]. This strongly suggests that the DNA polymerases, SSU and MSU RNAPs use the same set of amino acids for template, substrate binding and catalysis establishing a structure-function relationship among the DNA and RNA polymerases. The immediate upstream amino acid from catalytic K in DNA polymerases is usually a G or A [34], but in SSU viral RNA polymerases it is a Q [29] and in MSU eubacterial β subunits, it is a D in all [4] and in eukaryotic Rpb2 it is S/T, suggesting a possible role in the substrate binding and catalysis. Another catalytic like region is located in ~400 amino acids from the N-terminal but with a YG/FG pair and a catalytic R at -9 and long highly conserved stretches on both the sides. The Zn binding motif with 3 completely conserved Cs is found in the C-terminal region (highlighted in orange) which is followed by a long stretch of conservation till the C-terminal end. There are many highly conserved YG/FG/IG/LG pairs and a WG pair in the Rpb2 subunits. At least three of them may provide by three-point attachment for stereospecific binding on to the template DNA. However, the DNA polymerases show only one YG pair. Interestingly, the RNA dependent RNAPs do not have the YG pair [35]. A long stretch of the C-terminal region is highly conserved in all Rpb2 subunits. Interestingly the higher eukaryotic Rpb2 subunits show a completely conserved motif till the end of the C-terminal whereas the lower eukaryotic Rpb2 subunits also show a completely conserved stretch but not covering all the amino acids till the C- terminal with a consensus sequence “PYAxKLLFQELMx M”. A long stretch of highly conserved end suggests a possible role in the initiation process.

Fig. 4 shows the MSA analysis and conserved motifs in the Rpb1 elongation subunits in eukaryotic MSU RNAPs II. The yeast subunit with 1733 amino acids is used as standard and highlighted in magenta. Like the Rpb2 subunits, there are large numbers of conserved motifs and some are found to be long stretches (highlighted). However, the Rpb1 subunits are more conserved than the Rpb2 subunits. The ‘template binding’ pair is invariably an FG rather than a YG pair as reported in other MSU RNAPs. However, the catalytic R is completely conserved, including distance conservation in all the eukaryotic Rpb1 subunits and the upstream neighbour is mostly S/T but in lower eukaryotes like yeasts, it is N. Unlike in prokaryotic elongation subunit, the catalytic region is placed very close to the N-terminal (~ 100 amino acids). It is interesting to note that the distance between the catalytic R and the FG pair is 18 amino acids, i.e., placed exactly double the distance as compared to the Rpb2 initiation subunits. This distance closely agrees with the transcription bubble which extends ~ 20 bp from the TATA box [32]. The template binding and catalytic

CLUSTAL O (1.2.4) MSA of the Rpb2, initiation subunits of eukaryotic MSU RNAP II 3

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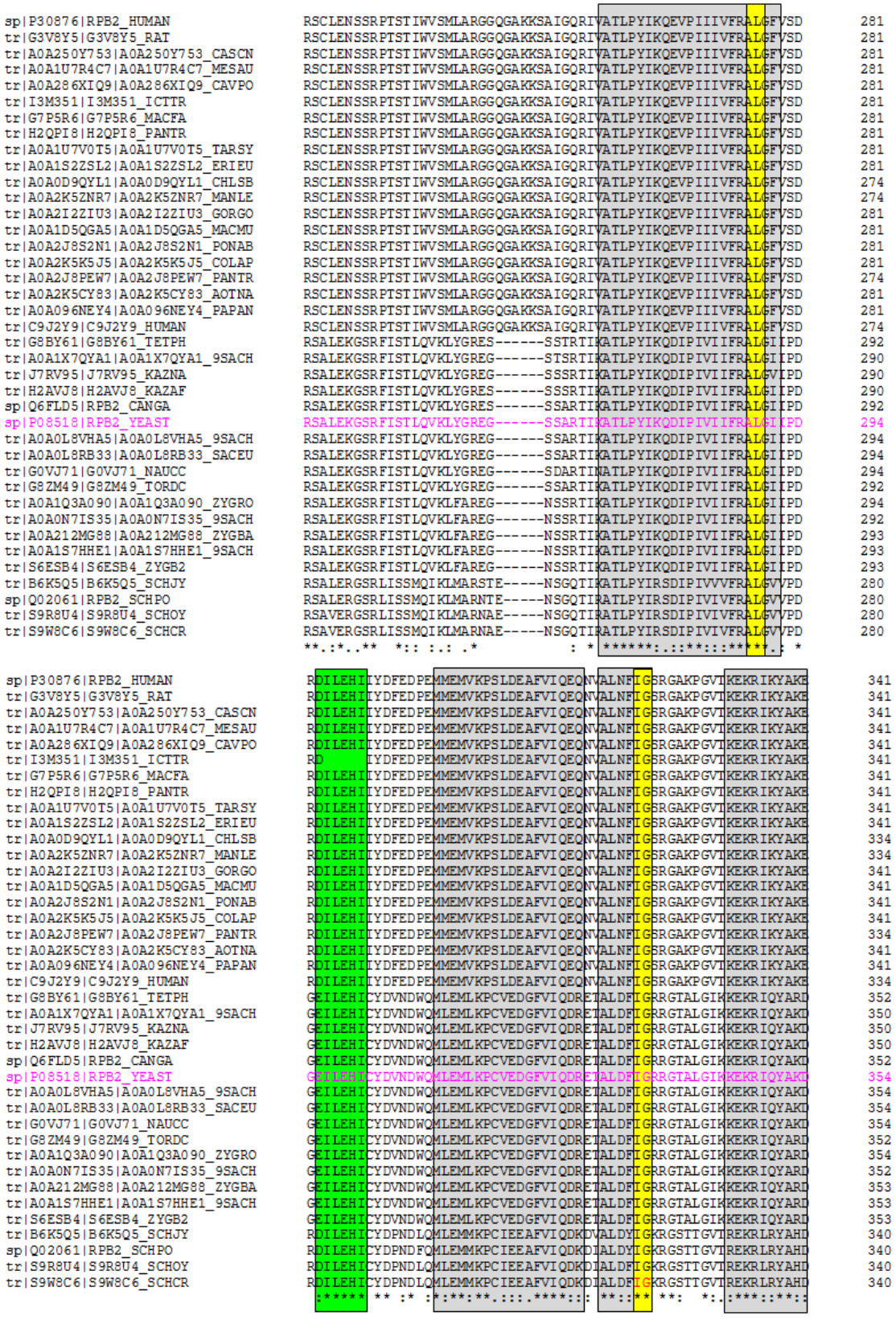
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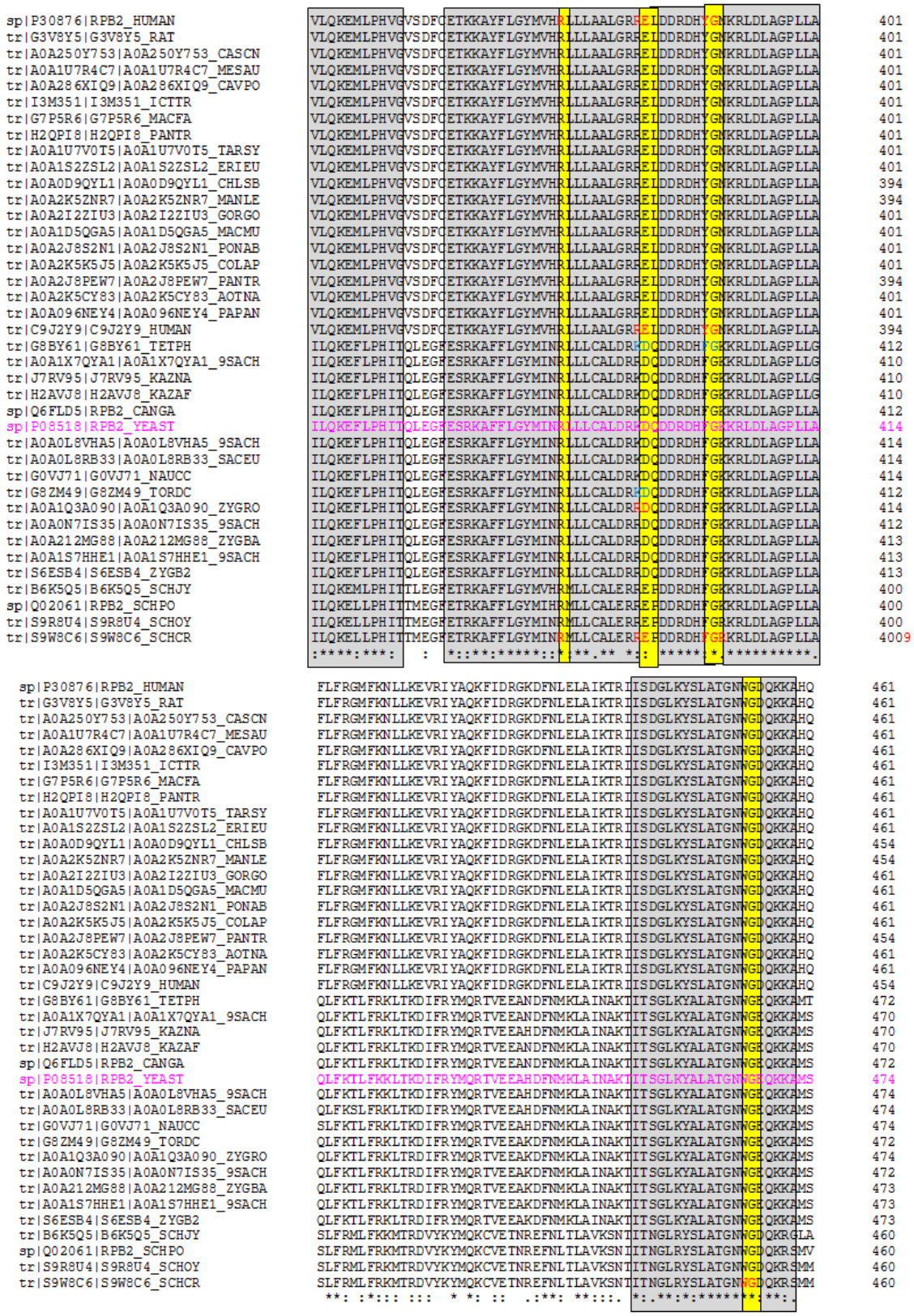
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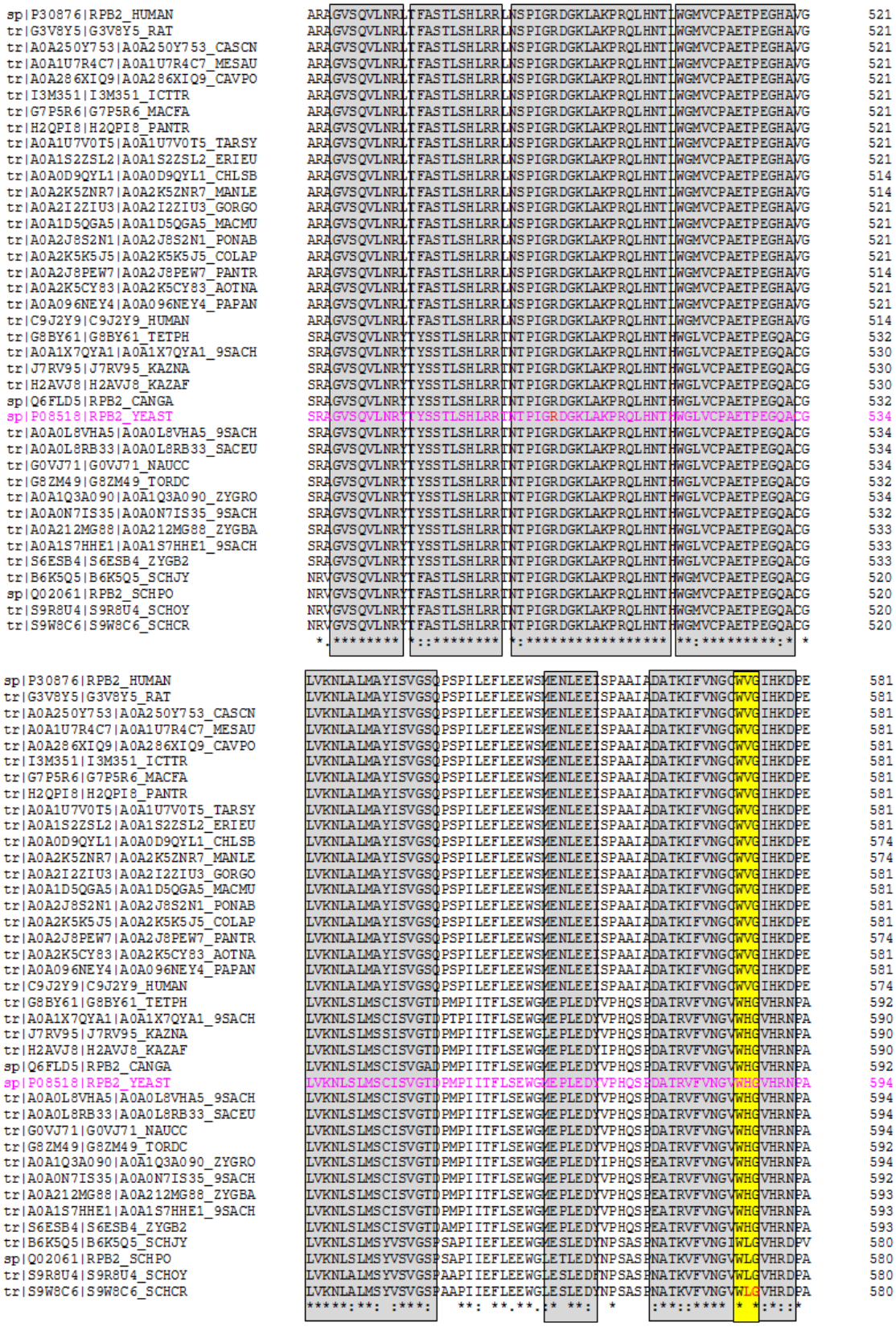
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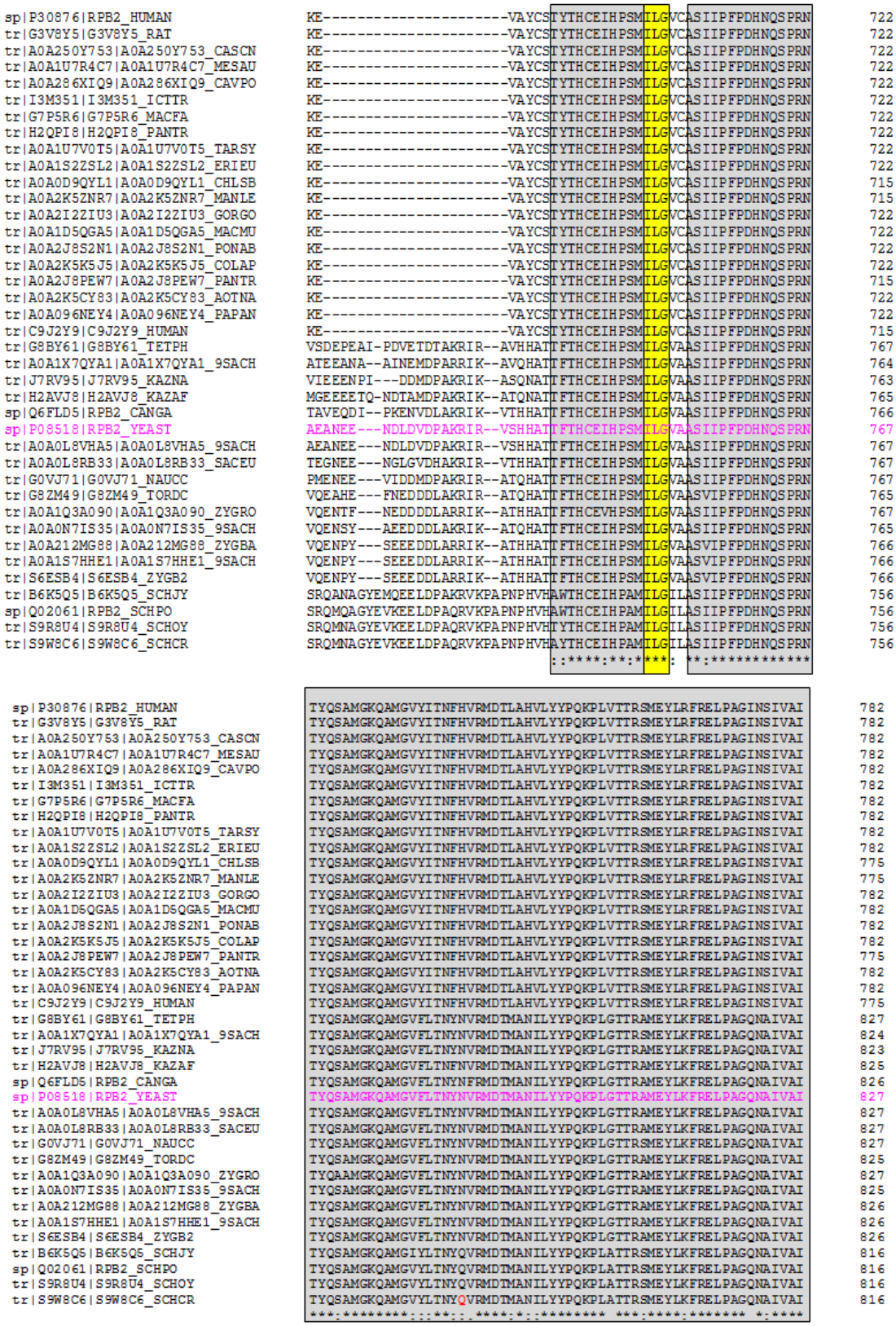
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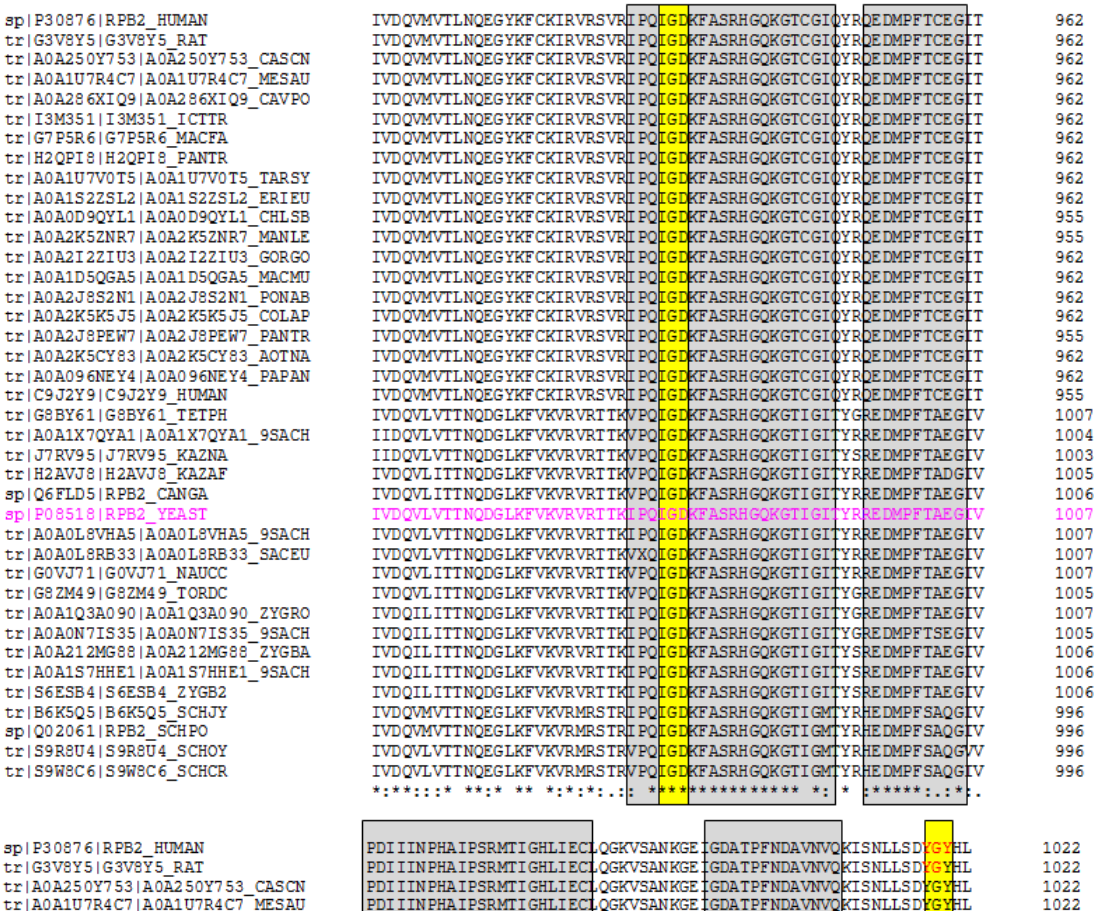
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tr|G0VJ71|G0VJ71_NAUCC IVDQVLITTNQDGLKFVKVRVRTTKVPQIGDKFASRHGQKGTIGITYRREDMPFTAEGIV 1007
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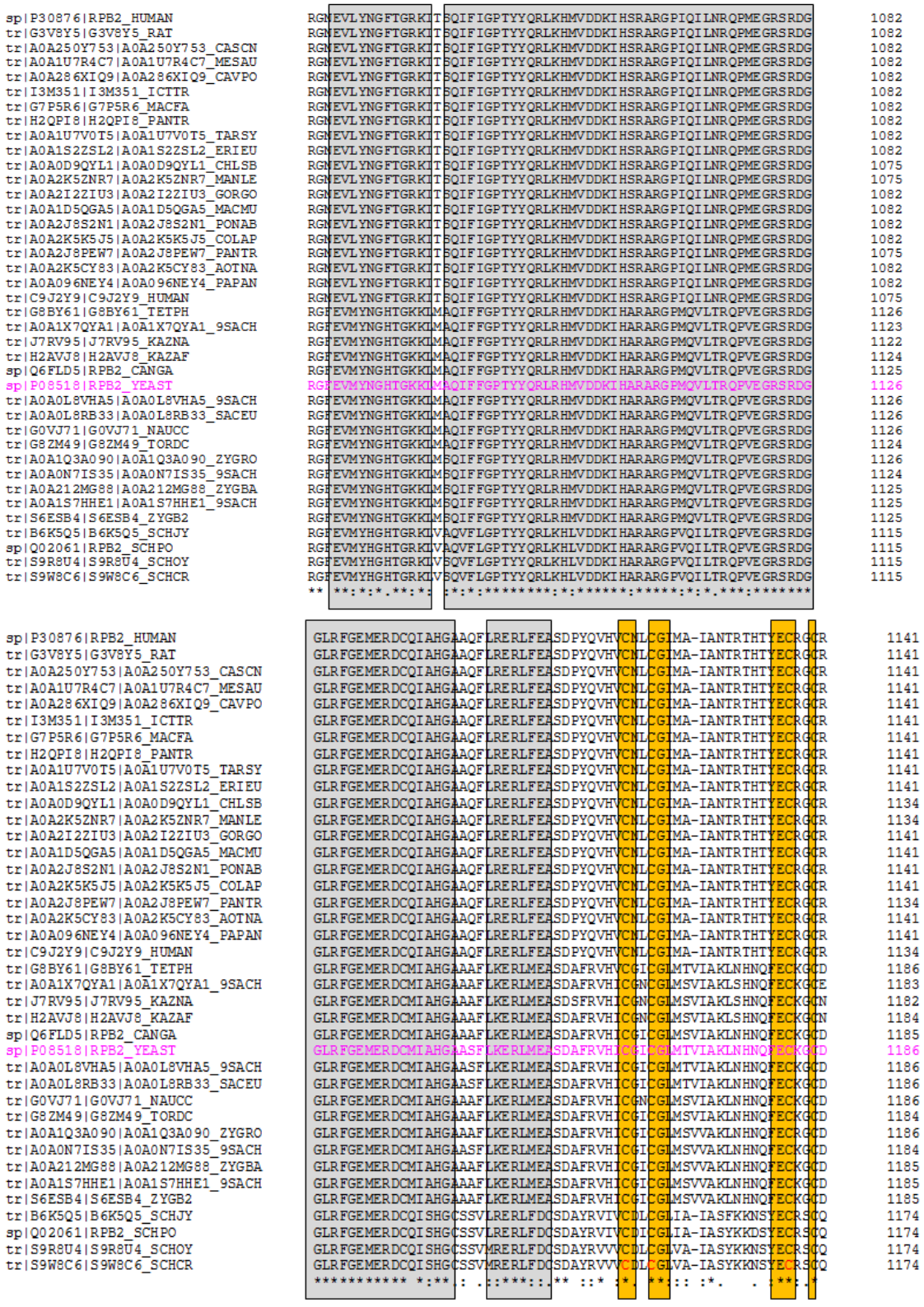
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tr|H2AVJ8|H2AVJ8_KAZAF
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sp|P08518|RPB2_YEAST
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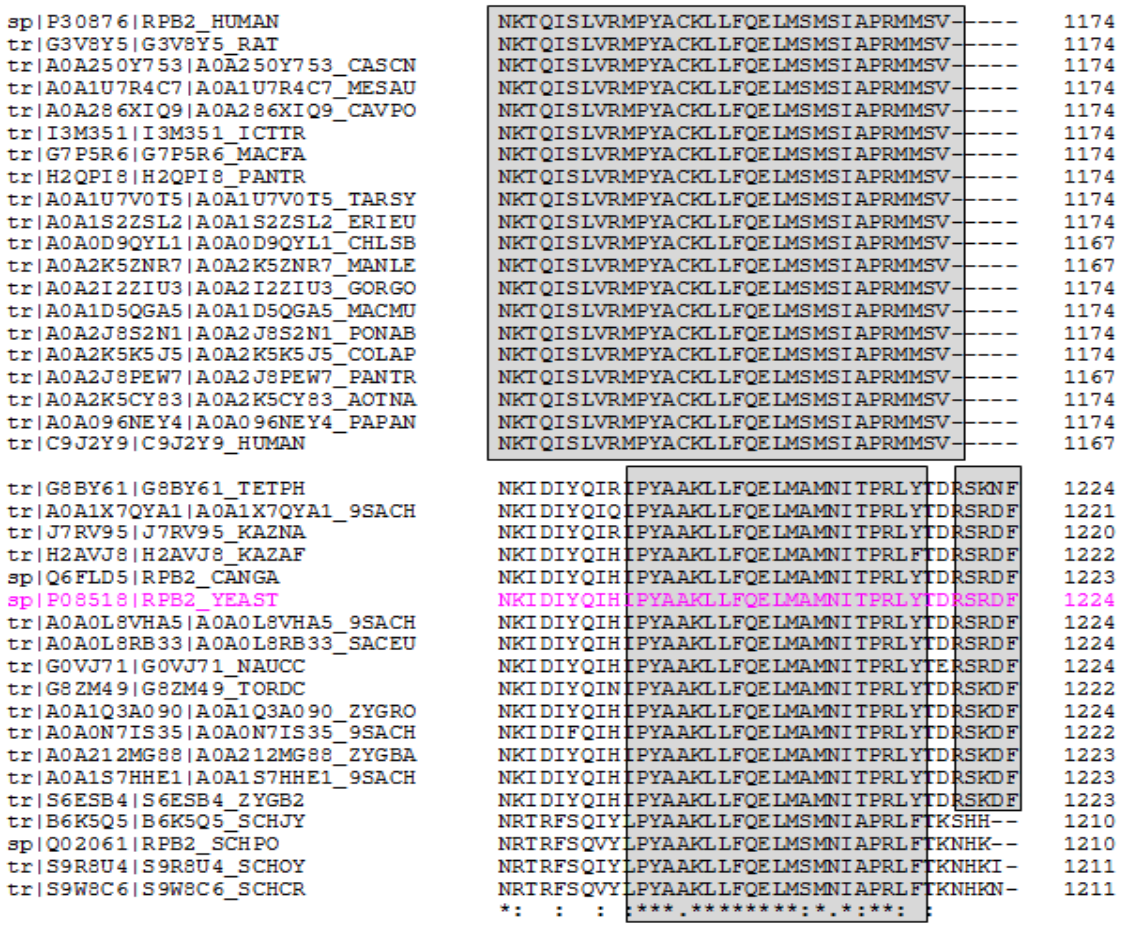

Fig. 3 MSA of the Rpb2, initiation subunits of eukaryotic RNAPs II

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G7P5R6_MACFA, *Macaca fascicularis*
I3M351_ICTTR, *Ictidomys tridecemlineatus*
H2QPI8_PANTR, *Pan troglodytes*
A0A1U7V0T5_TARSY, *Tarsiussyrichta*
A0A1S2ZSL2_ERIEU, *Erinaceus europaeus*
A0A0D9QYL1_CHLSB, *Chlorocebussabaeus*
A0A2K5K5J5_COLAP, *Colobus angolensis palliates*
A0A2I2ZIU3_GORGO, *Gorilla gorillagorilla*
A0A1D5QGA5_MACMU, *Macaca mulatta*
A0A2J8PEW7_PANTR, *Pan troglodytes*
A0A2K5CY83_AOTNA, *Aotus nancymaae*
A0A2J8S2N1_PONAB, *Pongo abelii*
A0A2K5ZNR7_MANLE, *Mandrillus leucophaeus*
A0A096NEY4|_PAPAN, *Papio Anubis*
C9J2Y9_HUMAN, *Homo sapiens*
G8BY61_TETPH, *Tetrapisisporaphaffii*
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H2AVJ8_KAZAF, *Kazachstania africana*
Q6FLD5_CANGA, *Candida glabrata*
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A0A1S7HHE1_9SACH, *Zygosaccharomyces parabailii*
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B6K5Q5_SCHJY, *Schizosaccharomyces japonicas*
Q02061_SCHPO, *Schizosaccharomyces pombe*
S9R8U4_SCHOY, Schizosaccharomyces *octosporus*
S9W8C6_SCHCR, *Schizosaccharomyces cryophilus*

conservations strongly suggest that the DNA, SSU and MSU RNA polymerases use the same set of amino acids for template, substrate binding and catalysis establishing a structure-function relationship among the DNA and RNAPs. Interestingly the catalytic region harbouring the Zn binding motif is found very close to the N-terminal region. This is in sharp contrast to the equivalent region in the β' subunit in all eubacteria (Table 1). The Zn binding motif was originally identified by X-ray crystallographic analysis in the equivalent β' subunit of the thermophilic bacterium, *Thermus aquaticus* [36]. The Zn binding 3 invariant Cs were located in the catalytic region and suggested in possible proof-reading activity during elongation. A completely conserved R found upstream from the catalytic R is located at -6th position which is implicated in NTP selection. It is interesting to note a completely conserved R found upstream from the catalytic R is missing in eubacteria (Table 1) [29, 34]. The immediate downstream amino acid from catalytic K in DNA polymerases is usually a G or A [29], but in viral RNA polymerases it is a K or R, in MSU β' subunits, it is a D and in all β' subunits it is an S and it is an S/T in eukaryotes suggesting a possible role in NTP selection. In SSU RNAPs, an invariant hydroxyl amino acid located very close to the YG pair is shown to involve in NTP selection by SDM experiments [37]. In addition to the template binding FG pair, there are 1 YG pair, 4 LG pairs and 3 I/VLG pairs in this subunit. A C- terminal conservation - **SPDDSDEEN**- (where the penultimate E is replaced with functionally equivalent D in some species) is seen in all higher forms of life and such sequence was conspicuously absent in the lower eukaryotes like yeasts and also not found in the initiation subunits, Rpb2. The –**D**XD- is a metal binding motif commonly found in glycosyl transferases and interestingly similar motif –**D**XDXT- in metal-dependent phosphatases (**D**xDXE in C-terminals of Rpb1 elongation subunits) where it plays a role for Ser phosphate removal from the CTD at the end of the cycle [38]. Interestingly, this motif invariably ends in N preceded by D/E in all the cases in Rpb1 (Fig 4). As expected the CTD is filled with the "heptapeptide repeats" (YSPTSPS) in all species and its role is discussed elsewhere (Not shown in the Figure) and results provide evidence for RNA exit in the vicinity of the carboxyl-terminal repeat domain, coupling synthesis to RNA processing by enzymes bound to this domain [28].

CLUSTAL O (1.2.4) MSA of the Rpb1, elongation subunits of MSU RNAPs- II 4

```
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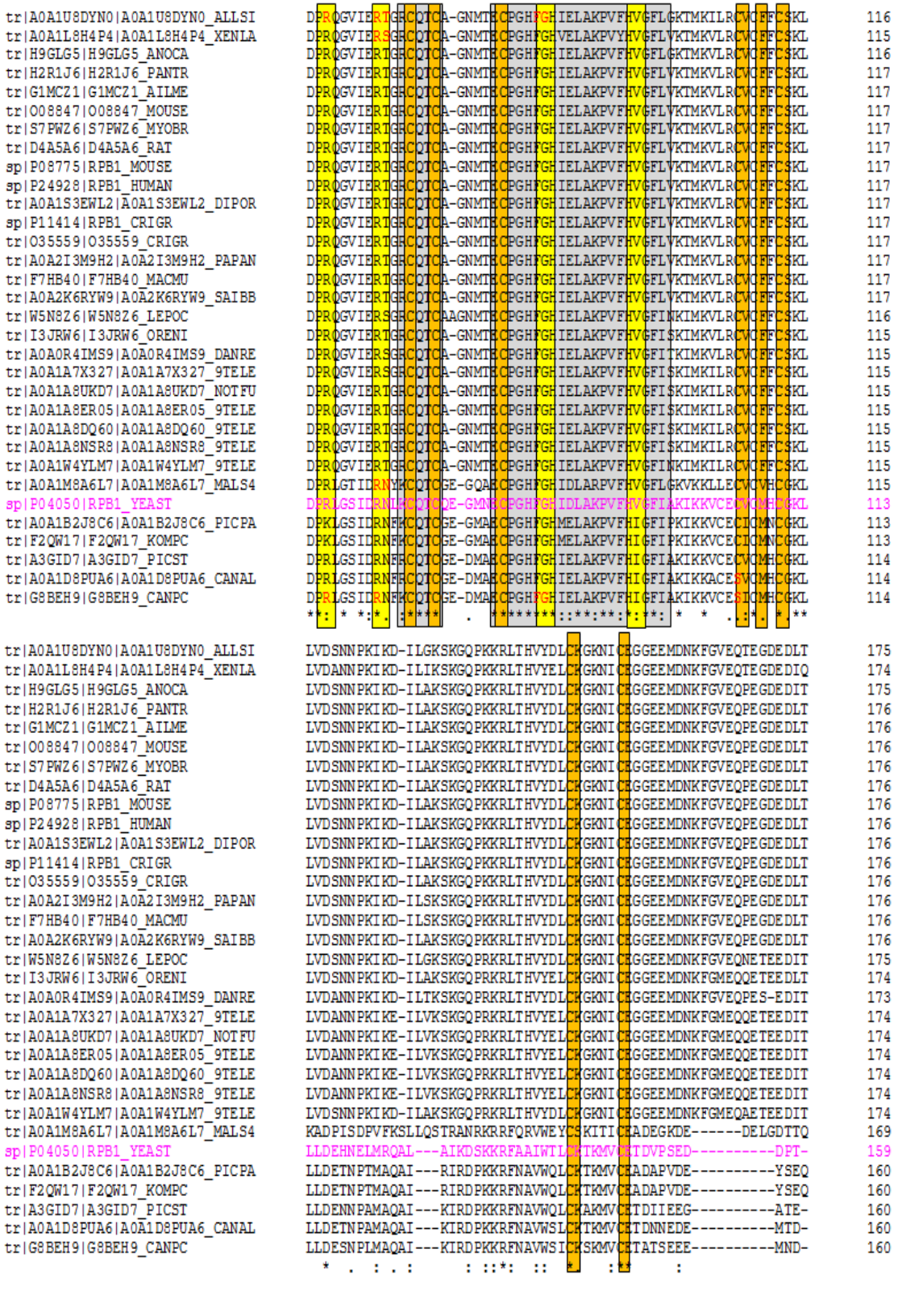

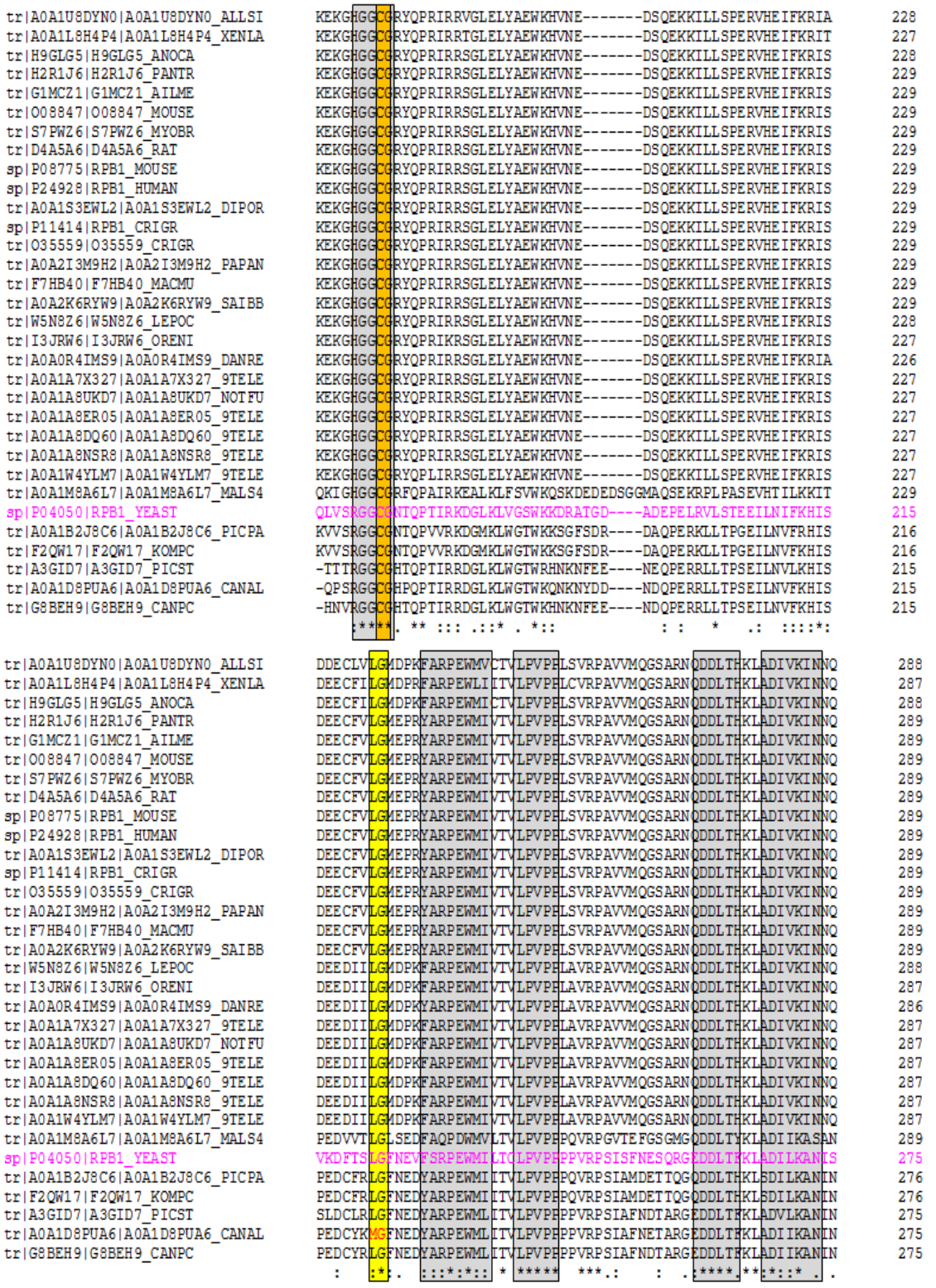
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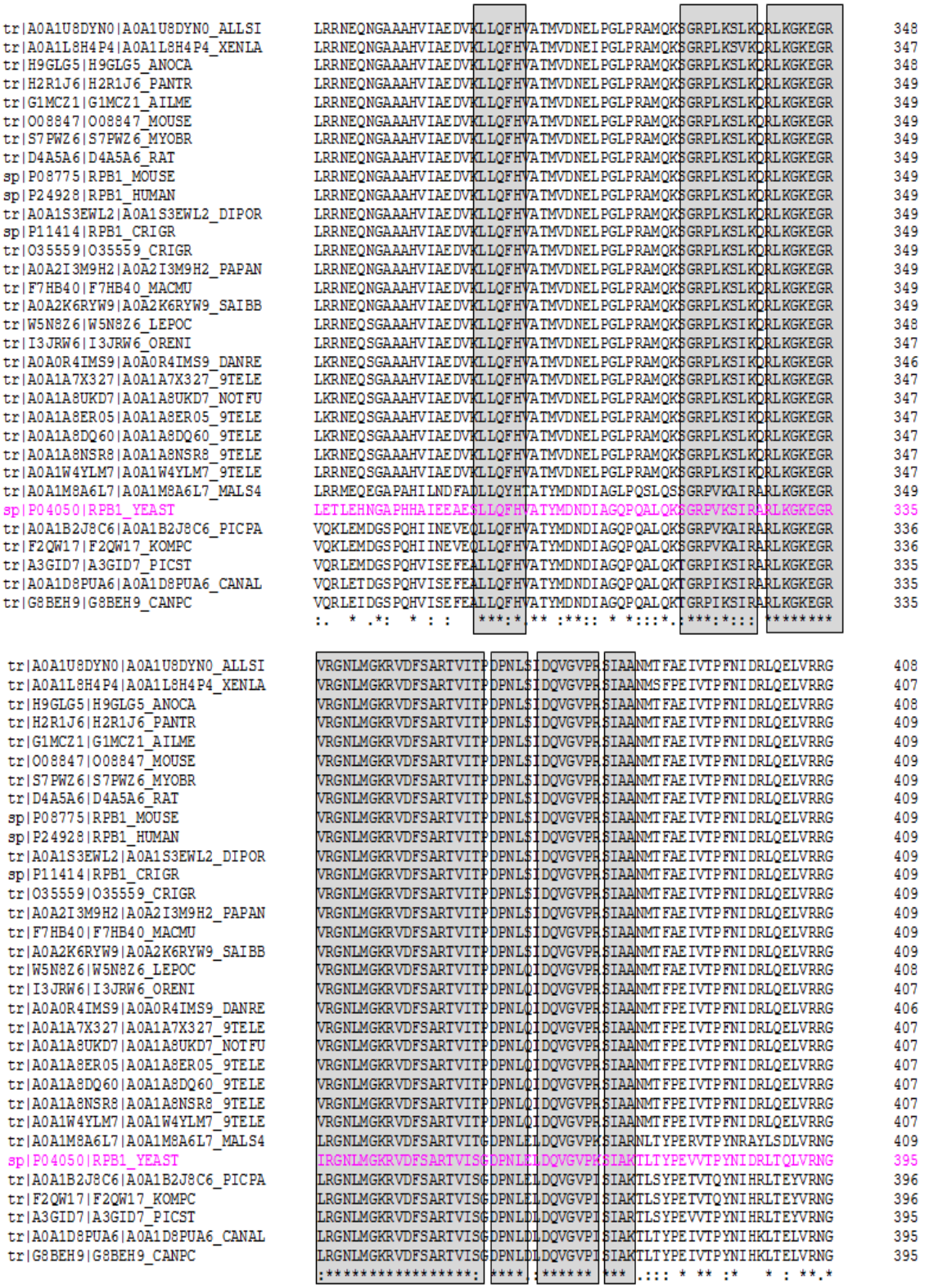
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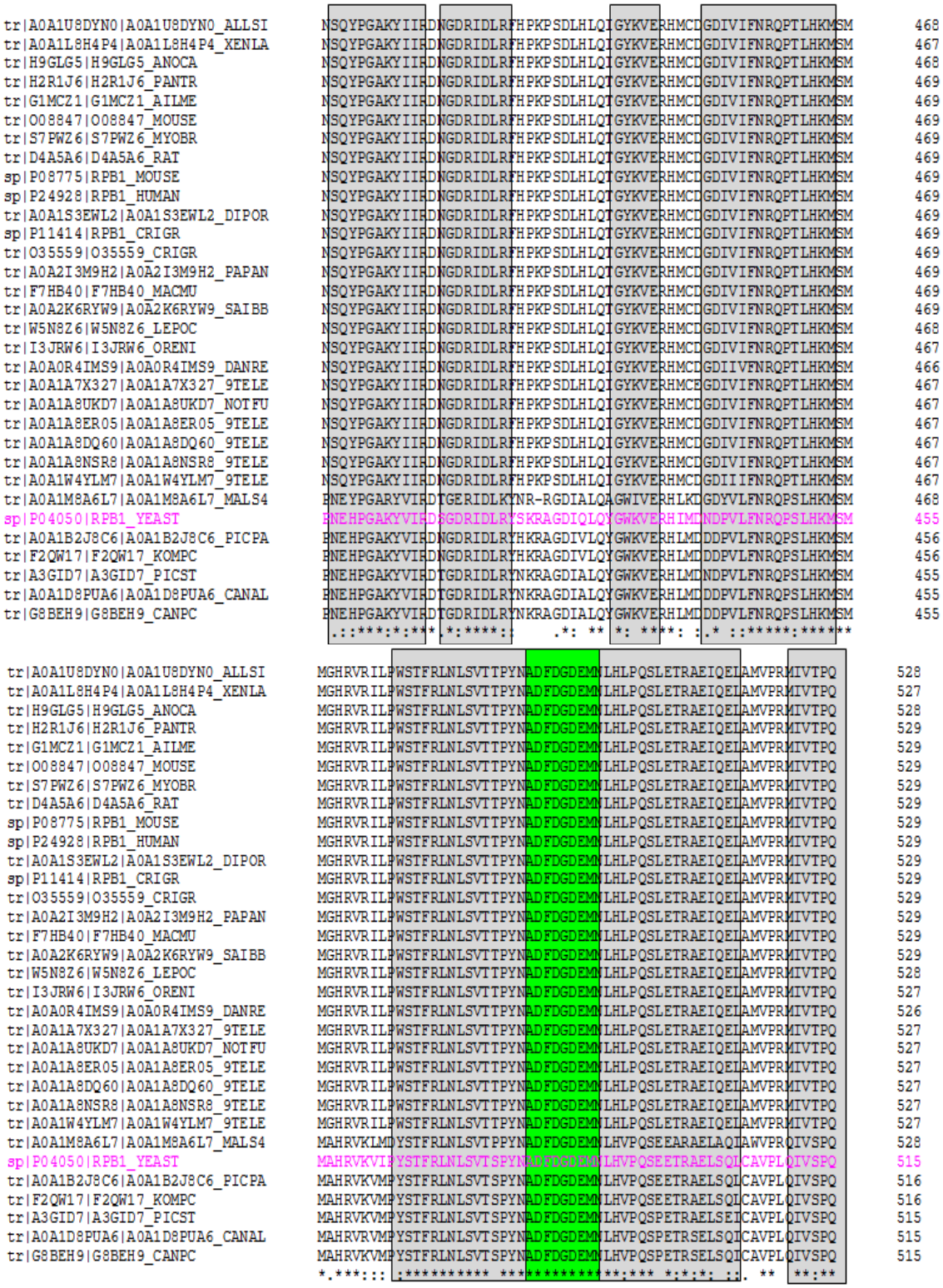

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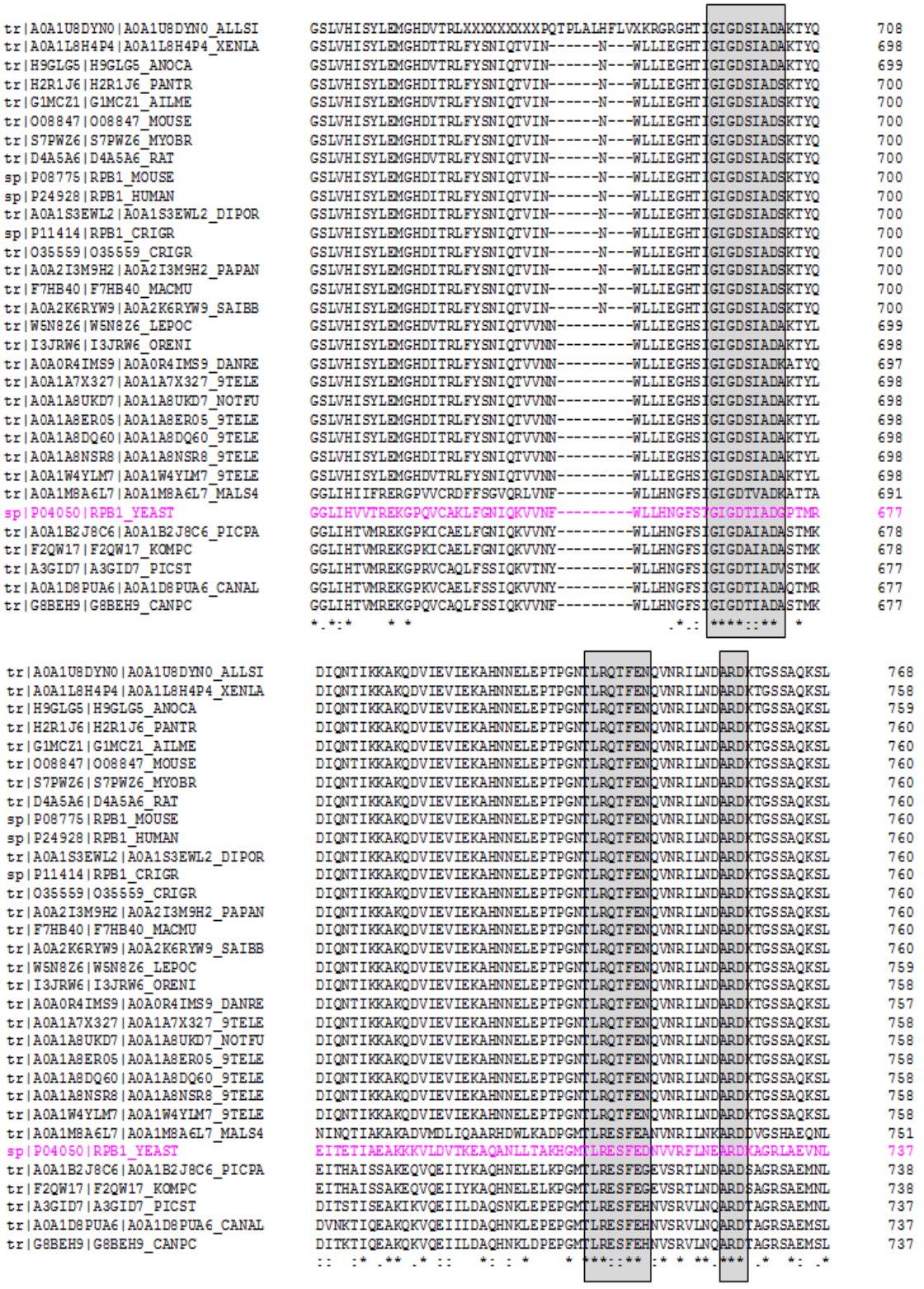
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tr|G1MCZ1|G1MCZ1_AILME DIQNTIKKAKQDVIEVIEKAHNNELEPTPGNTLRQTFENQVNRILNDARDKTGSSAQKSL 760
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tr|A0A1D8PUA6|A0A1D8PUA6_CANAL DVNKTIQEAKQKVQEIIIDAQHNKLEPEPGMTLRESFEHNVSRVLNQARDTAGRSAEMSL 737
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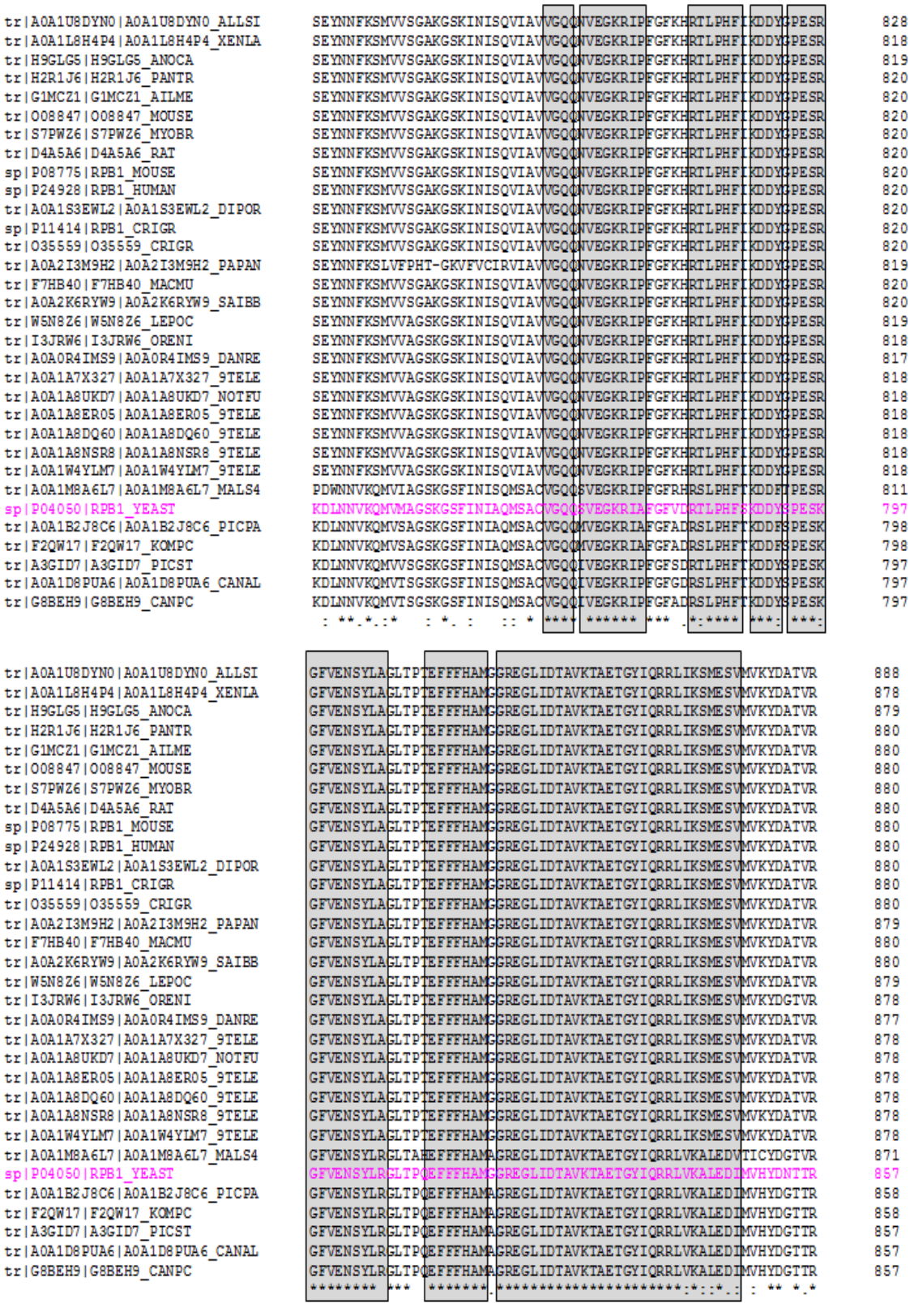
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tr|A0A1L8H4P4|A0A1L8H4P4_XENLA SEYNNFKSMVVSGAKGSKINISQVIAVVGQQNVEGKRIPFGFKHRTLPHFIKDDYGPESR 818
tr|H9GLG5|H9GLG5_ANOCA SEYNNFKSMVVSGAKGSKINISQVIAVVGQQNVEGKRIPFGFKHRTLPHFIKDDYGPESR 819
tr|H2R1J6|H2R1J6_PANTR SEYNNFKSMVVSGAKGSKINISQVIAVVGQQNVEGKRIPFGFKHRTLPHFIKDDYGPESR 820
tr|G1MCZ1|G1MCZ1_AILME SEYNNFKSMVVSGAKGSKINISQVIAVVGQQNVEGKRIPFGFKHRTLPHFIKDDYGPESR 820
tr|O08847|O08847_MOUSE SEYNNFKSMVVSGAKGSKINISQVIAVVGQQNVEGKRIPFGFKHRTLPHFIKDDYGPESR 820
tr|S7PWZ6|S7PWZ6_MYOBR SEYNNFKSMVVSGAKGSKINISQVIAVVGQQNVEGKRIPFGFKHRTLPHFIKDDYGPESR 820
tr|D4A5A6|D4A5A6_RAT SEYNNFKSMVVSGAKGSKINISQVIAVVGQQNVEGKRIPFGFKHRTLPHFIKDDYGPESR 820
sp|P08775|RPB1_MOUSE SEYNNFKSMVVSGAKGSKINISQVIAVVGQQNVEGKRIPFGFKHRTLPHFIKDDYGPESR 820
sp|P24928|RPB1_HUMAN SEYNNFKSMVVSGAKGSKINISQVIAVVGQQNVEGKRIPFGFKHRTLPHFIKDDYGPESR 820
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tr|A0A1A8UKD7|A0A1A8UKD7_NOTFU SEYNNFKSMVVAGSKGSKINISQVIAVVGQQNVEGKRIPFGFKHRTLPHFIKDDYGPESR 818
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tr|G8BEH9|G8BEH9_CANPC              NSLGDIIQFIYGEDGIDATQVEKQSVDTIPGSDASFERRYRIDLLEKNGSISESLLESGK      917
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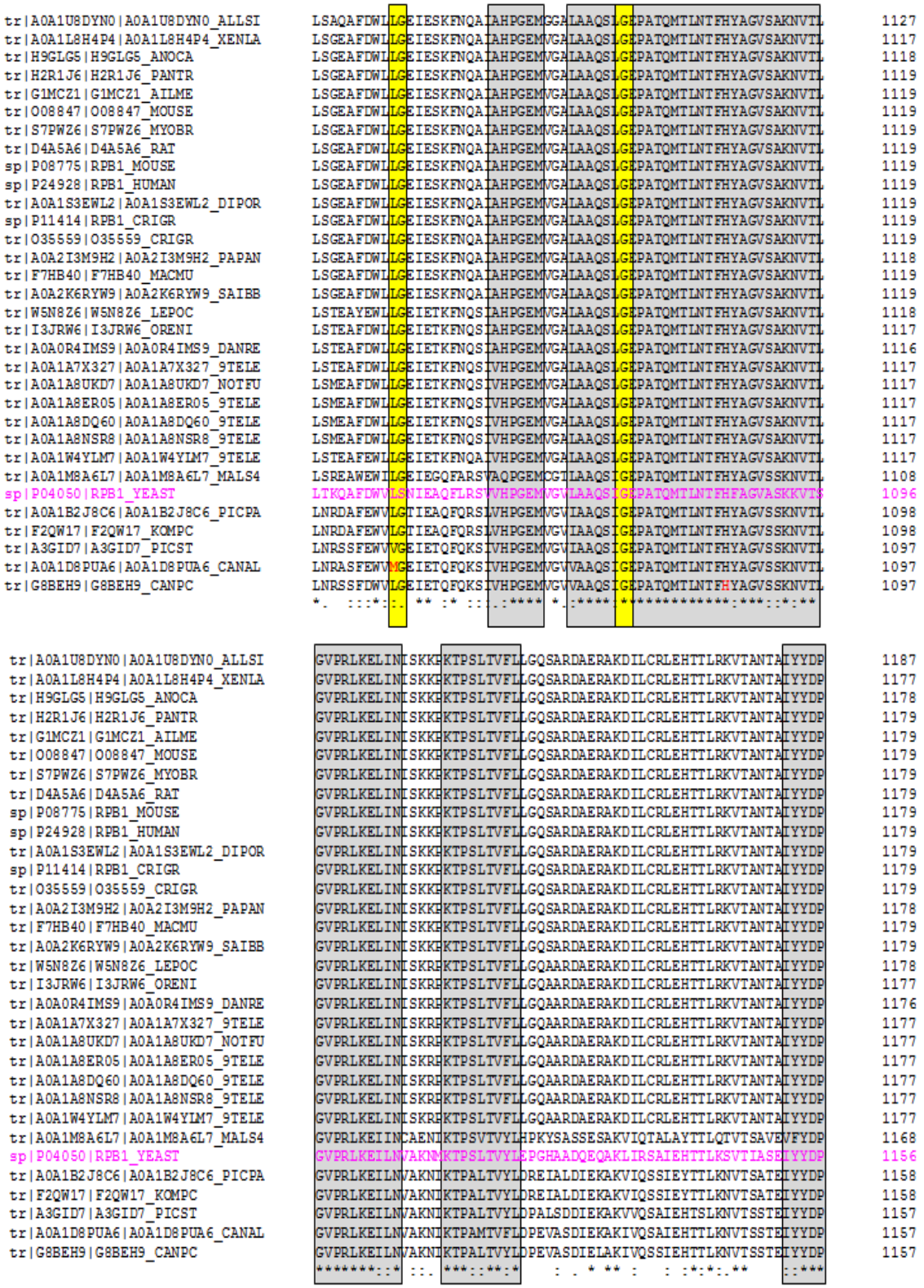
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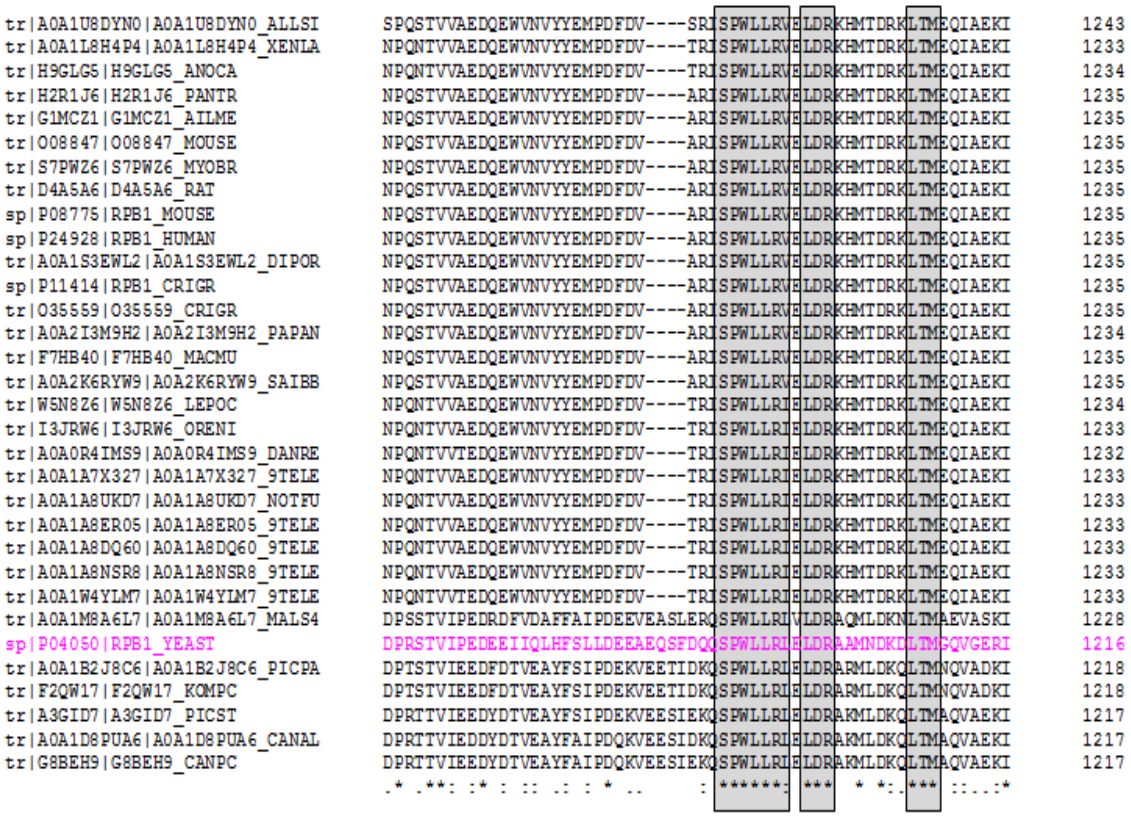
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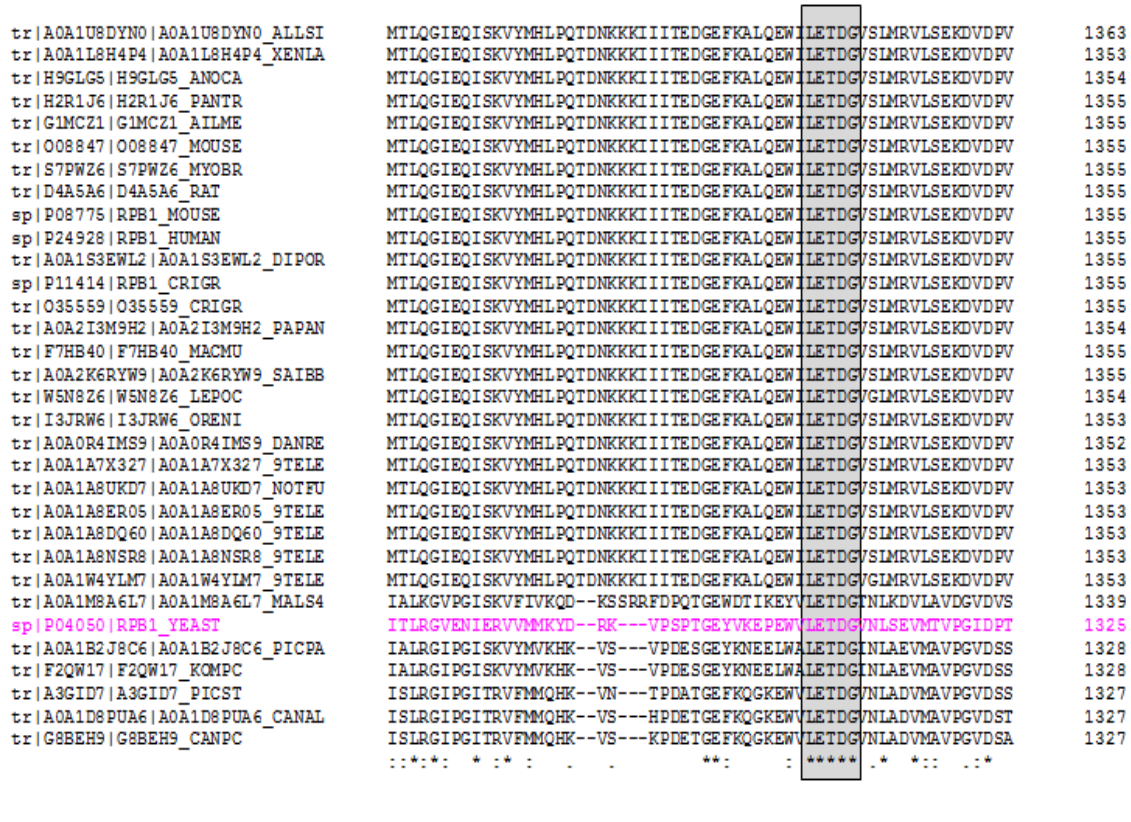
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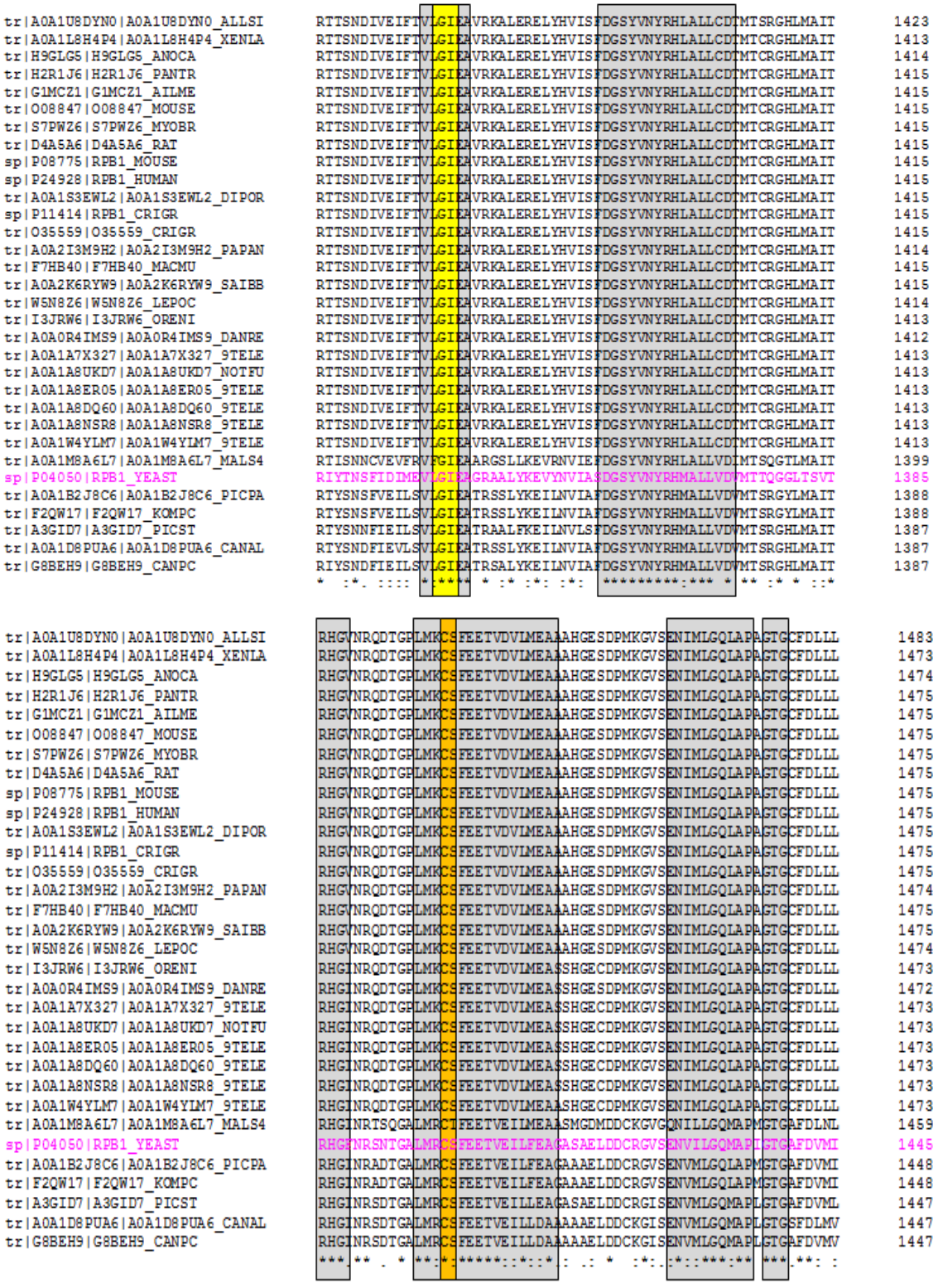
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tr|H9GLG5|H9GLG5_ANOCA RHGVNRQDTGPLMKCSFEETVDVLMEAAAHGESDPMKGVSENIMLGQLAPAGTGCFDLLL 1474
tr|H2R1J6|H2R1J6_PANTR RHGVNRQDTGPLMKCSFEETVDVLMEAAAHGESDPMKGVSENIMLGQLAPAGTGCFDLLL 1475
tr|G1MCZ1|G1MCZ1_AILME RHGVNRQDTGPLMKCSFEETVDVLMEAAAHGESDPMKGVSENIMLGQLAPAGTGCFDLLL 1475
tr|O08847|O08847_MOUSE RHGVNRQDTGPLMKCSFEETVDVLMEAAAHGESDPMKGVSENIMLGQLAPAGTGCFDLLL 1475
tr|S7PWZ6|S7PWZ6_MYOBR RHGVNRQDTGPLMKCSFEETVDVLMEAAAHGESDPMKGVSENIMLGQLAPAGTGCFDLLL 1475
tr|D4A5A6|D4A5A6_RAT RHGVNRQDTGPLMKCSFEETVDVLMEAAAHGESDPMKGVSENIMLGQLAPAGTGCFDLLL 1475
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sp|P24928|RPB1_HUMAN RHGVNRQDTGPLMKCSFEETVDVLMEAAAHGESDPMKGVSENIMLGQLAPAGTGCFDLLL 1475
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tr|A0A2I3M9H2|A0A2I3M9H2_PAPAN RHGVNRQDTGPLMKCSFEETVDVLMEAAAHGESDPMKGVSENIMLGQLAPAGTGCFDLLL 1474
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tr|F2QW17|F2QW17_KOMPC RHGINRADTGALMRCSFEETVEILFEAGAAAELDDCRGVSENVMLGQLAPMGTGAFDVMI 1448
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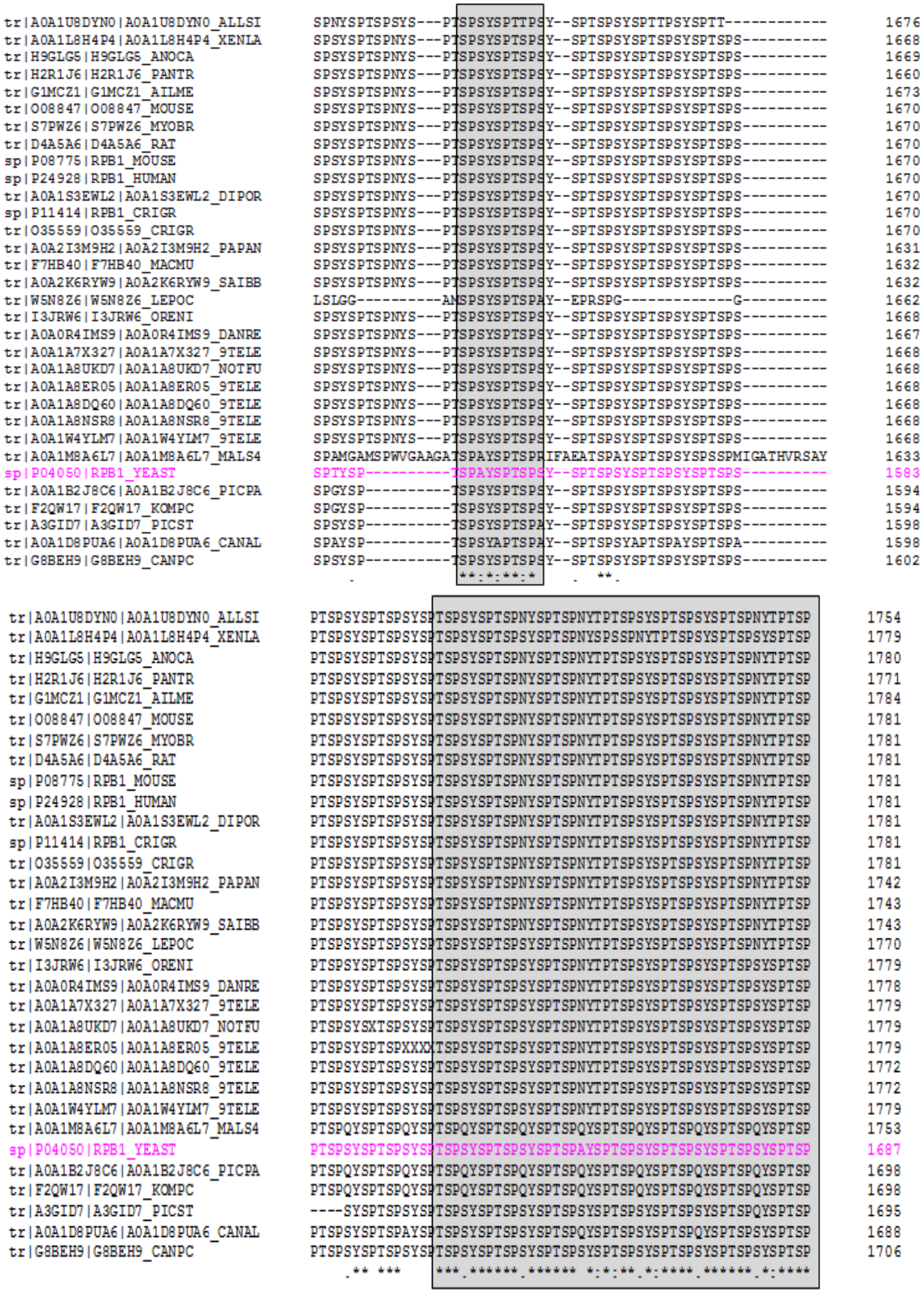
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tr|H9GLG5|H9GLG5_ANOCA SPSYSPTSPNYS---PTSPSYSPTSPSY--SPTSPSYSPTSPSYSPTSPS---------- 1669
tr|H2R1J6|H2R1J6_PANTR SPSYSPTSPNYS---PTSPSYSPTSPSY--SPTSPSYSPTSPSYSPTSPS---------- 1660
tr|G1MCZ1|G1MCZ1_AILME SPSYSPTSPNYS---PTSPSYSPTSPSY--SPTSPSYSPTSPSYSPTSPS---------- 1673
tr|O08847|O08847_MOUSE SPSYSPTSPNYS---PTSPSYSPTSPSY--SPTSPSYSPTSPSYSPTSPS---------- 1670
tr|S7PWZ6|S7PWZ6_MYOBR SPSYSPTSPNYS---PTSPSYSPTSPSY--SPTSPSYSPTSPSYSPTSPS---------- 1670
tr|D4A5A6|D4A5A6_RAT SPSYSPTSPNYS---PTSPSYSPTSPSY--SPTSPSYSPTSPSYSPTSPS---------- 1670
sp|P08775|RPB1_MOUSE SPSYSPTSPNYS---PTSPSYSPTSPSY--SPTSPSYSPTSPSYSPTSPS---------- 1670
sp|P24928|RPB1_HUMAN SPSYSPTSPNYS---PTSPSYSPTSPSY--SPTSPSYSPTSPSYSPTSPS---------- 1670
tr|A0A1S3EWL2|A0A1S3EWL2_DIPOR SPSYSPTSPNYS---PTSPSYSPTSPSY--SPTSPSYSPTSPSYSPTSPS---------- 1670
sp|P11414|RPB1_CRIGR SPSYSPTSPNYS---PTSPSYSPTSPSY--SPTSPSYSPTSPSYSPTSPS---------- 1670
tr|O35559|O35559_CRIGR SPSYSPTSPNYS---PTSPSYSPTSPSY--SPTSPSYSPTSPSYSPTSPS---------- 1670
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tr|A0A2K6RYW9|A0A2K6RYW9_SAIBB SPSYSPTSPNYS---PTSPSYSPTSPSY--SPTSPSYSPTSPSYSPTSPS---------- 1632
tr|W5N8Z6|W5N8Z6_LEPOC LSLGG----------AMSPSYSPTSPAY--EPRSPG----------G---------- 1662
tr|I3JRW6|I3JRW6_ORENI SPSYSPTSPNYS---PTSPSYSPTSPSY--SPTSPSYSPTSPSYSPTSPS---------- 1668
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tr|H2R1J6|H2R1J6_PANTR PTSPSYSPTSPSYSPTSPSYSPTSPNYSPTSPNYTPTSPSYSPTSPSYSPTSPNYTPTSP 1771
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tr|O08847|O08847_MOUSE PTSPSYSPTSPSYSPTSPSYSPTSPNYSPTSPNYTPTSPSYSPTSPSYSPTSPNYTPTSP 1781
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tr|D4A5A6|D4A5A6_RAT PTSPSYSPTSPSYSPTSPSYSPTSPNYSPTSPNYTPTSPSYSPTSPSYSPTSPNYTPTSP 1781
sp|P08775|RPB1_MOUSE PTSPSYSPTSPSYSPTSPSYSPTSPNYSPTSPNYTPTSPSYSPTSPSYSPTSPNYTPTSP 1781
sp|P24928|RPB1_HUMAN PTSPSYSPTSPSYSPTSPSYSPTSPNYSPTSPNYTPTSPSYSPTSPSYSPTSPNYTPTSP 1781
tr|A0A1S3EWL2|A0A1S3EWL2_DIPOR PTSPSYSPTSPSYSPTSPSYSPTSPNYSPTSPNYTPTSPSYSPTSPSYSPTSPNYTPTSP 1781
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tr|G8BEH9|G8BEH9_CANPC PTSPSYSPTSPSYSPTSPSYSPTSPSYSPTSPSYSPTSPSYSPTSPSYSPTSP 1706

Fig. 4 MSA of the Rpb1, the elongation subunits of eukaryotic RNAP II

A0A1U8DYN0 _ALLSI *Alligator sinensis*
A0A1L8H4P4 _XENLA *Xenopus laevis*
H9GLG5 _ANOCA *Anolis carolinensis*
H2R1J6 _PANTR *Pan troglodytes*
G1MCZ1 _AILME *Ailuropoda melanoleuca*
O08847 _MOUSE *Mus musculus*
S7PWZ6 _MYOBR *Myotis brandtii*
D4A5A6 _RAT *Rattus norvegicus*
P08775 _MOUSE *Mus musculus*
P24928|RPB1_HUMAN *Homo sapiens*
A0A1S3EWL2 _DIPOR *Dipodomys ordii*
P11414 _CRIGR *Cricetulus griseus*
O35559 _CRIGR *Cricetulus griseus*
A0A2I3M9H2 _PAPAN *Papio Anubis*
F7HB40| _MACMU *Macaca mulatta*
A0A2K6RYW9 _SAIBB *Saimiri boliviensis*
W5N8Z6 _LEPOC *Lepisosteus oculatus*
I3JRW6 _ORENI *Oreochromis niloticus*
A0A0R4IMS9 _DANRE *Danio rerio*
A0A1A7X327 _9TELE *Aphyosemion striatum*
A0A1A8UKD7 _NOTFU *Nothobranchius furzeri*
A0A1A8ER05 _9TELE *Nothobranchius korthausae*
A0A1A8DQ60 _9TELE *Nothobranchius kadleci*
A0A1A8NSR8 _9TELE *Nothobranchius rachovii*
A0A1W4YLM7 _9TELE *Scleropages formosus*
A0A1M8A6L7 _MALS4 *Malassezia sympodialis*
P04050|RPB1_YEAST *Saccharomyces cerevisiae*
A0A1B2J8C6 _PICPA *Komagataella pastoris*
F2QW17 _KOMPC *Komagataella phaffii*
A3GID7 _PICST *Scheffersomyces stipitis*
A0A1D8PUA6 _CANAL *Candida albicans*
G8BEH9 _CANPC *Candida parapsilosis*

7. MIX AND MATCH ANALYSIS OF EUBACTERIAL AND EUKARYOTIC INITIATION AND ELONGATION SUBUNITS

For this analysis a small number of initiation and elongation subunits of eubacterial and eukaryotic MSU RNAPs were subjected to MSA with ClustalW Omega programme and presented in Figs. 5 and 6. For eubacteria, *E. coli* MSU RNAP and for eukaryotes, *S. cerevisiae* MSU RNAP II sequences were used as standards. Only highly conserved regions are shown in the figures.

7.1 Mix and Match Analysis of the *E. coli* (β) and *S. cerevisiae* (Rpb2) Initiation Subunits

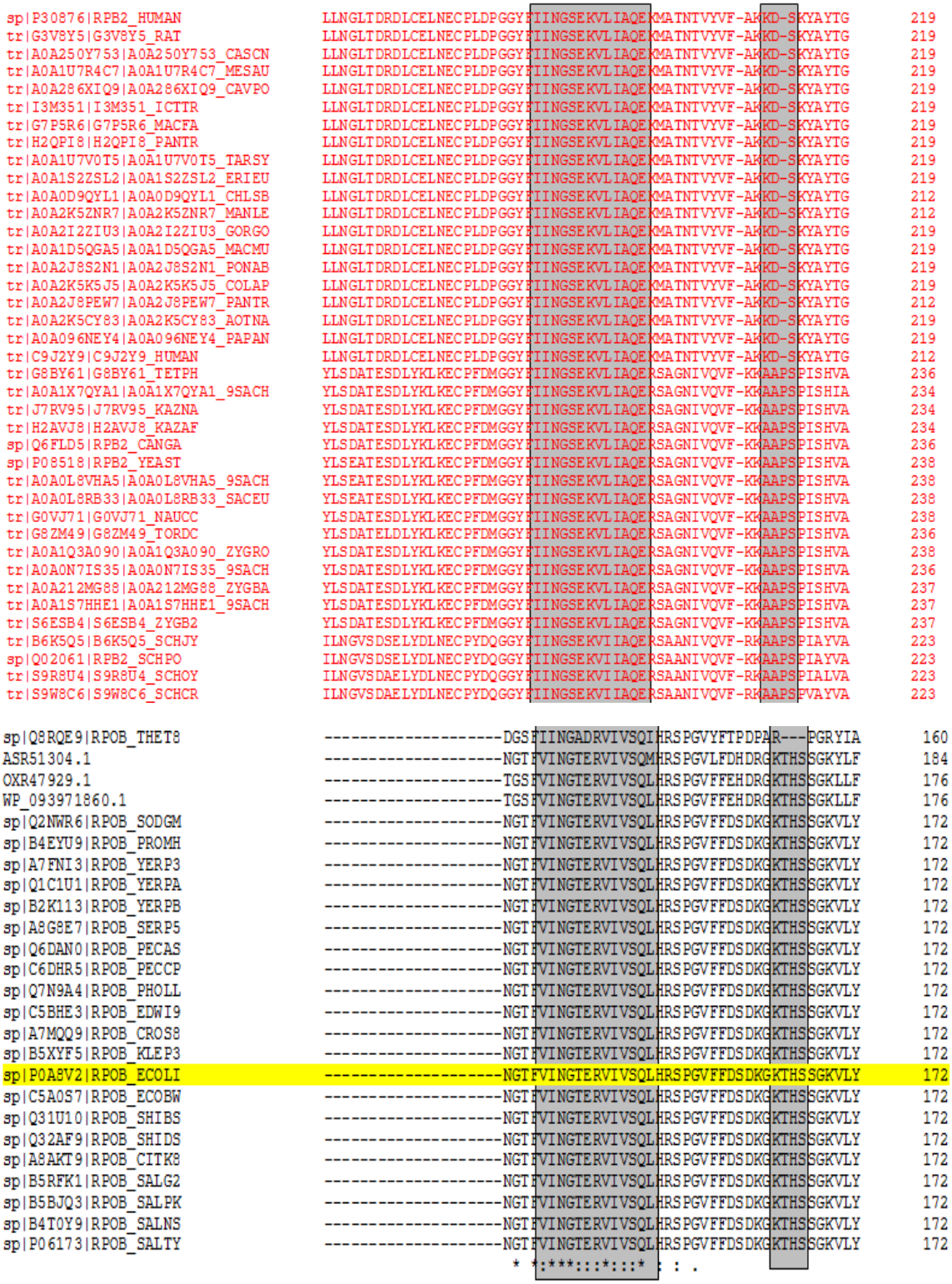
Fig. 5 shows the mix and match analysis of the initiation subunits from pro- and eukaryotic MSU RNAPs. The eukaryotic sequences are shown in red. The active site regions are highlighted in yellow the representative sequences are highlighted in yellow. There are a good number of sequences aligning in both. Significant among them are -FI/VINGS/TEK/RVL/II/VA/SQ- (~200), IETPE (~500) preceding this sequence a WG in eukaryotic and YG in prokaryotic sequences, -ASI/LIPF-, the metal ion binding regions -GYNQ/FEDS- (~800), -LDD/ED/SGL/I- (~850); -GDKF/MAS/GRHGXKG- (~1000), HLVDDKI/MHAR (~1050), RFGEME (~1100). The catalytic regions are matching but among themselves only and there is no complete consensus among them, i.e., they are located at different regions. However, the metal binding motifs are aligning in both the initiation subunits suggesting the metal binding regions are preserved as a domain and did not diverge much during evolution. The prokaryotic active site region is placed around 540-555/1342 amino acids whereas eukaryotic active site region is placed around 851-866/1224 amino acids. The notable difference in the eukaryotic template binding pair sis KG in lower eukaryotes like human and in lower eukaryotes it uses YG like yeasts. The eukaryotes follow two very similar ending sequences at the C- terminal end as –ACKLLFQELMSMSIAPRMMSV- (~1150) and AAKLLFQELMAMNITPRLYT- (~1200) (deviating amino acids are shown in red) and the prokaryotes follow an altogether different consensus end sequence as –SFNVLLKEIRSL- (~1280). Thus, the eukaryotic and prokaryotic ending sequences are different and their significance is not clear now.

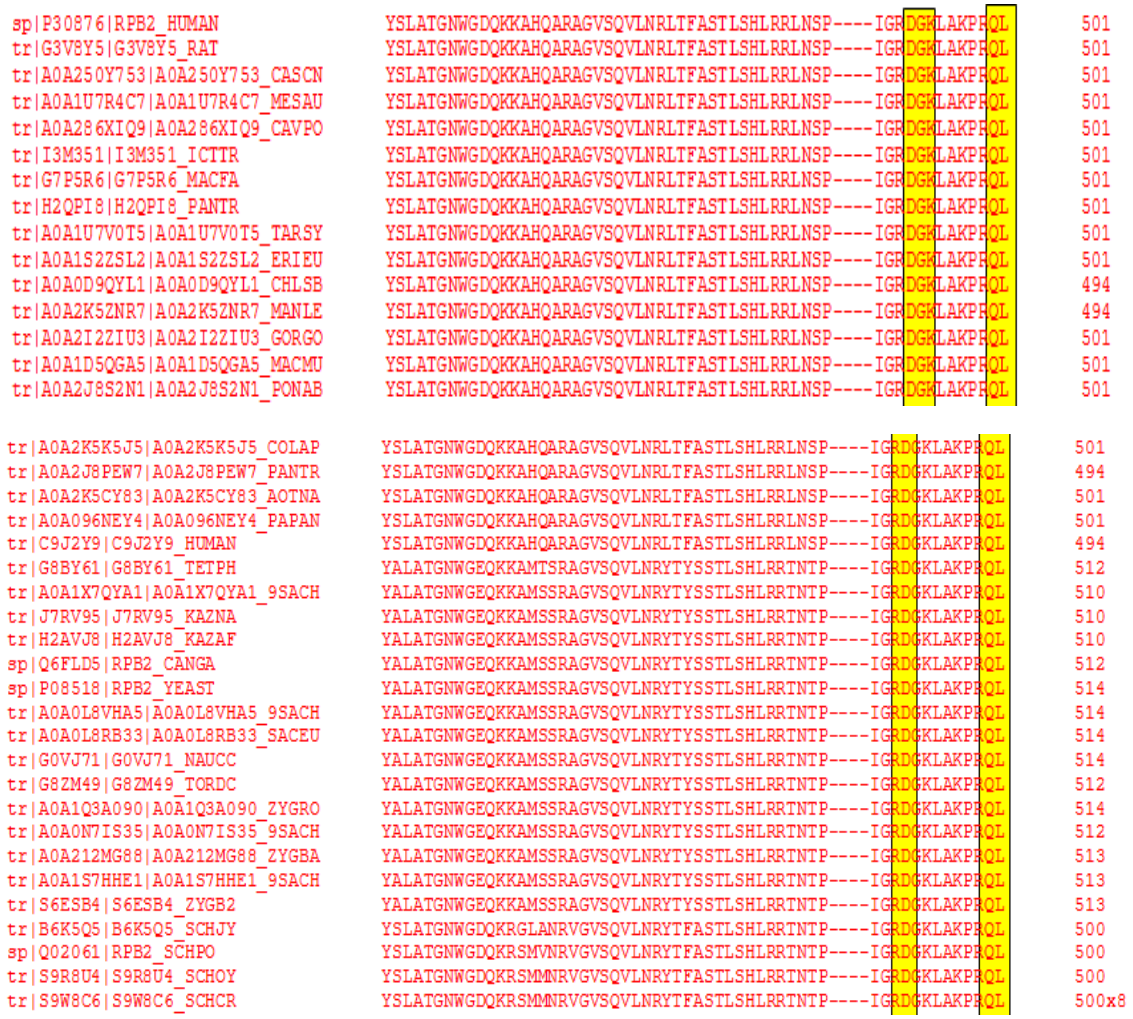
Table 4 Amino acids around the catalytic amino acid K/R and the YG/FG pair in DNA polymerases, DNA dependent SSU and MSU RNAPs

Polymerase Type	Catalytic Region
SSU RNAP family	
Viral SSU RNA pol (T7, T3, SP6)	-TR^{-4}VTKR^{1}SVMTLAY^{8}GS-
Mitochondrial SSU RNA pol (Yeast)	-TR^{-4}KVVKQ^{1}TVMTNVY^{8}GV--
Chloroplast SSU pol (ARATH)	-DR^{-4}KLVKQ^{1}TVMTSVY^{8}GV-
DNA polymerase family	
E. coli DNA pol I	-QR^{-4}RSAKA^{1}INFGLIY^{8}GM-
MSU RNAP family (Initiation subunits)	
E. coli MSU RNAP β subunit	-^{539}TR^{-8}ERAGFEVRD^{1}VHPTHY^{7}G^{8}RV^{558}-
S. cerevisiae MSU RNAP II Rpb2 subunit	-^{851}FR^{-5}SLFFRS^{1}YMDQEKKY^{9}GMSI^{870}-
Human MSU RNAP II Rpb2 subunit	-^{806}FR^{-5}SVFYRS^{1}YKEQESKK^{9}GFDQ^{825}-
MSU RNAP family (Elongation subunits)	
E. coli MSU RNAP β' subunit	-^{833}NSV^{-} ^{6}DAVKVRS^{1}VVSC^{5}DTDFGVC^{12}AHC^{15}Y^{16}G^{17}RDL^{861}-
*S.cerevisiae*MSURNAPIIRpb1 subunit	-^{55}DPR^{-6}LGSIDRN^{1}LKC^{4}QTC^{7}QEGMNEC^{14}PGHF^{18}G^{19}HI^{84}-
HumanMSURNAPIIRpb1subunit	-^{59}DPR^{-6}QGVIERT^{1}GRC^{4}QTC^{7}AGNMTEC^{14}PGHF^{18}G^{19}HI^{88}-

NB: MSU RNA polymerases which use R in the catalytic site is shown in bold. The invariant R, at -6/-7 is not found in β' subunits of eubacteria; The eukaryotic elongation subunits use an FG instead of a YG

CLUSTAL O (1.2.4): Mix and Match analysis of eukaryotic Rpb2 and eubacterial β initiation subunits 5

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tr|A0A250Y753|A0A250Y753_CASCN YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|A0A1U7R4C7|A0A1U7R4C7_MESAU YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|A0A286XIQ9|A0A286XIQ9_CAVPO YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|I3M351|I3M351_ICTTR YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|G7P5R6|G7P5R6_MACFA YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|H2QPI8|H2QPI8_PANTR YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|A0A1U7V0T5|A0A1U7V0T5_TARSY YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|A0A1S2ZSL2|A0A1S2ZSL2_ERIEU YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|A0A0D9QYL1|A0A0D9QYL1_CHLSB YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 494
tr|A0A2K5ZNR7|A0A2K5ZNR7_MANLE YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 494
tr|A0A2I2ZIU3|A0A2I2ZIU3_GORGO YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|A0A1D5QGA5|A0A1D5QGA5_MACMU YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|A0A2J8S2N1|A0A2J8S2N1_PONAB YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|A0A2K5K5J5|A0A2K5K5J5_COLAP YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|A0A2J8PEW7|A0A2J8PEW7_PANTR YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 494
tr|A0A2K5CY83|A0A2K5CY83_AOTNA YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|A0A096NEY4|A0A096NEY4_PAPAN YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 501
tr|C9J2Y9|C9J2Y9_HUMAN YSLATGNWGDQKKAHQARAGVSQVLNRLTFASTLSHLRRLNSP----IGRDGKLAKPRQL 494
tr|G8BY61|G8BY61_TETPH YALATGNWGEQKKAMTSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 512
tr|A0A1X7QYA1|A0A1X7QYA1_9SACH YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 510
tr|J7RV95|J7RV95_KAZNA YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 510
tr|H2AVJ8|H2AVJ8_KAZAF YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 510
sp|Q6FLD5|RPB2_CANGA YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 512
sp|P08518|RPB2_YEAST YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 514
tr|A0A0L8VHA5|A0A0L8VHA5_9SACH YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 514
tr|A0A0L8RB33|A0A0L8RB33_SACEU YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 514
tr|G0VJ71|G0VJ71_NAUCC YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 514
tr|G8ZM49|G8ZM49_TORDC YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 512
tr|A0A1Q3A090|A0A1Q3A090_ZYGRO YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 514
tr|A0A0N7IS35|A0A0N7IS35_9SACH YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 512
tr|A0A212MG88|A0A212MG88_ZYGBA YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 513
tr|A0A1S7HHE1|A0A1S7HHE1_9SACH YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 513
tr|S6ESB4|S6ESB4_ZYGB2 YALATGNWGEQKKAMSSRAGVSQVLNRYTYSSTLSHLRRTNTP----IGRDGKLAKPRQL 513
tr|B6K5Q5|B6K5Q5_SCHJY YSLATGNWGDQKRGLANRVGVSQVLNRYTFASTLSHLRRTNTP----IGRDGKLAKPRQL 500
sp|Q02061|RPB2_SCHPO YSLATGNWGDQKRSMVNRVGVSQVLNRYTFASTLSHLRRTNTP----IGRDGKLAKPRQL 500
tr|S9R8U4|S9R8U4_SCHOY YSLATGNWGDQKRSMMNRVGVSQVLNRYTFASTLSHLRRTNTP----IGRDGKLAKPRQL 500
tr|S9W8C6|S9W8C6_SCHCR YSLATGNWGDQKRSMMNRVGVSQVLNRYTFASTLSHLRRTNTP----IGRDGKLAKPRQL 500x8
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OXR47929.1 ----------EFFGSSQLSQFMDQTNPLSEITHKRRVSALGPGGLTRERAGFEVRDV 556
WP_093971860.1 ----------EFFGSSQLSQFMDQTNPLSEITHKRRVSALGPGGLTRERAGFEVRDV 556
sp|Q2NWR6|RPOB_SODGM ----------EFFGSSQLSQFMDQNNPLSEITHKRRISALGPGGLTRERAGFEVRDV 550
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sp|A7FNI3|RPOB_YERP3 ----------EFFGSSQLSQFMDQNNPLSEITHKRRISALGPGGLTRERAGFEVRDV 550
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sp|B2K113|RPOB_YERPB ----------EFFGSSQLSQFMDQNNPLSEITHKRRISALGPGGLTRERAGFEVRDV 550
sp|A8G8E7|RPOB_SERP5 ----------EFFGSSQLSQFMDQNNPLSEITHKRRISALGPGGLTRERAGFEVRDV 550
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sp|C5BHE3|RPOB_EDWI9 ----------EFFGSSQLSQFMDQNNPLSEITHKRRISALGPGGLTRERAGFEVRDV 550
sp|A7MQQ9|RPOB_CROS8 ----------EFFGSSQLSQFMDQNNPLSEITHKRRISALGPGGLTRERAGFEVRDV 550
sp|B5XYF5|RPOB_KLEP3 ----------EFFGSSQLSQFMDQNNPLSEITHKRRISALGPGGLTRERAGFEVRDV 550
sp|P0A8V2|RPOB_ECOLI ----------EFFGSSQLSQFMDQNNPLSEITHKRRISALGPGGLTRERAGFEVRDV 550
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sp|A8AKT9|RPOB_CITK8 ----------EFFGSSQLSQFMDQNNPLSEITHKRRISALGPGGLTRERAGFEVRDV 550
sp|B5RFK1|RPOB_SALG2 ----------EFFGSSQLSQFMDQNNPLSEITHKRRISALGPGGLTRERAGFEVRDV 550
sp|B5BJQ3|RPOB_SALPK ----------EFFGSSQLSQFMDQNNPLSEITHKRRISALGPGGLTRERAGFEVRDV 550
sp|B4T0Y9|RPOB_SALNS ----------EFFGSSQLSQFMDQNNPLSEITHKRRISALGPGGLTRERAGFEVRDV 550
sp|P06173|RPOB_SALTY ----------EFFGSSQLSQFMDQNNPLSEITHKRRISALGPGGLTRERAGFEVRDV 550


sp|P30876|RPB2_HUMAN HNTLWGMVCPAETPEGHAVGLVKNLALMAYISVGSQPSPILEFLEEWSMENLEEISPAAI 561
tr|G3V8Y5|G3V8Y5_RAT HNTLWGMVCPAETPEGHAVGLVKNLALMAYISVGSQPSPILEFLEEWSMENLEEISPAAI 561
tr|A0A250Y753|A0A250Y753_CASCN HNTLWGMVCPAETPEGHAVGLVKNLALMAYISVGSQPSPILEFLEEWSMENLEEISPAAI 561
tr|A0A1U7R4C7|A0A1U7R4C7_MESAU HNTLWGMVCPAETPEGHAVGLVKNLALMAYISVGSQPSPILEFLEEWSMENLEEISPAAI 561
tr|A0A286XIQ9|A0A286XIQ9_CAVPO HNTLWGMVCPAETPEGHAVGLVKNLALMAYISVGSQPSPILEFLEEWSMENLEEISPAAI 561
tr|I3M351|I3M351_ICTTR HNTLWGMVCPAETPEGHAVGLVKNLALMAYISVGSQPSPILEFLEEWSMENLEEISPAAI 561
tr|G7P5R6|G7P5R6_MACFA HNTLWGMVCPAETPEGHAVGLVKNLALMAYISVGSQPSPILEFLEEWSMENLEEISPAAI 561
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tr|A0A1S2ZSL2|A0A1S2ZSL2_ERIEU HNTLWGMVCPAETPEGHAVGLVKNLALMAYISVGSQPSPILEFLEEWSMENLEEISPAAI 561
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tr|A0A2K5CY83|A0A2K5CY83_AOTNA HNTLWGMVCPAETPEGHAVGLVKNLALMAYISVGSQPSPILEFLEEWSMENLEEISPAAI 561
tr|A0A096NEY4|A0A096NEY4_PAPAN HNTLWGMVCPAETPEGHAVGLVKNLALMAYISVGSQPSPILEFLEEWSMENLEEISPAAI 561
tr|C9J2Y9|C9J2Y9_HUMAN HNTLWGMVCPAETPEGHAVGLVKNLALMAYISVGSQPSPILEFLEEWSMENLEEISPAAI 554
tr|G8BY61|G8BY61_TETPH HNTHWGLVCPAETPEGQACGLVKNLSLMSCISVGTDPMPIITFLSEWGMEPLEDYVPHQS 572
tr|A0A1X7QYA1|A0A1X7QYA1_9SACH HNTHWGLVCPAETPEGQACGLVKNLSLMSCISVGTDPTPIITFLSEWGMEPLEDYVPHQS 570
tr|J7RV95|J7RV95_KAZNA HNTHWGLVCPAETPEGQACGLVKNLSLMSSISVGTDPMPIITFLSEWGLEPLEDYVPHQS 570
tr|H2AVJ8|H2AVJ8_KAZAF HNTHWGLVCPAETPEGQACGLVKNLSLMSCISVGTDPMPIITFLSEWGMEPLEDYIPHQS 570
sp|Q6FLD5|RPB2_CANGA HNTHWGLVCPAETPEGQACGLVKNLSLMSCISVGADPMPIITFLSEWGMEPLEDYVPHQS 572
sp|P08518|RPB2_YEAST HNTHWGLVCPAETPEGQACGLVKNLSLMSCISVGTDPMPIITFLSEWGMEPLEDYVPHQS 574
tr|A0A0L8VHA5|A0A0L8VHA5_9SACH HNTHWGLVCPAETPEGQACGLVKNLSLMSCISVGTDPMPIITFLSEWGMEPLEDYVPHQS 574
tr|A0A0L8RB33|A0A0L8RB33_SACEU HNTHWGLVCPAETPEGQACGLVKNLSLMSCISVGTDPMPIITFLSEWGMEPLEDYVPHQS 574
tr|G0VJ71|G0VJ71_NAUCC HNTHWGLVCPAETPEGQACGLVKNLSLMSCISVGTDPMPIITFLSEWGMEPLEDYVPHQS 574
tr|G8ZM49|G8ZM49_TORDC HNTHWGLVCPAETPEGQACGLVKNLSLMSCISVGTDPMPIITFLSEWGMEPLEDYVPHQS 572
tr|A0A1Q3A090|A0A1Q3A090_ZYGRO HNTHWGLVCPAETPEGQACGLVKNLSLMSCISVGTDPMPIITFLSEWGMEPLEDYIPHQS 574
tr|A0A0N7IS35|A0A0N7IS35_9SACH HNTHWGLVCPAETPEGQACGLVKNLSLMSCISVGTDPMPIITFLSEWGMEPLEDYVPHQS 572
tr|A0A212MG88|A0A212MG88_ZYGBA HNTHWGLVCPAETPEGQACGLVKNLSLMSCISVGTDPMPIITFLSEWGMEPLEDYVPHQS 573
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tr|S6ESB4|S6ESB4_ZYGB2 HNTHWGLVCPAETPEGQACGLVKNLSLMSCISVGTDAMPIITFLSEWGMEPLEDYVPHQS 573
tr|B6K5Q5|B6K5Q5_SCHJY HNTHWGMVCPAETPEGQACGLVKNLSLMSYVSVGSPSAPIIEFLEEWGMESLEDYNPSAS 560
sp|Q02061|RPB2_SCHPO HNTHWGMVCPAETPEGQACGLVKNLSLMSYVSVGSPSAPIIEFLEEWGLETLEDYNPSAS 560
tr|S9R8U4|S9R8U4_SCHOY HNTHWGMVCPAETPEGQACGLVKNLALMSYVSVGSPAAPIIEFLEEWGLESLEDFNPSAS 560
tr|S9W8C6|S9W8C6_SCHCR HNTHWGMVCPAETPEGQACGLVKNLALMSYVSVGSPAAPIIEFLEEWGLESLEDYNPSAS 560
sp|Q8RQE9|RPOB_THET8 HRTHYGRICPVETPEGANIGLITSLAAYARVD----------ELGFI---------- 4677
ASR51304.1 HPTHYGRICPIETPEGPNIGLINSLASFSRVN----------KYGFI---------- 601
OXR47929.1 HPTHYGRVCPIETPEGPNIGLINSMALYARLN----------EYGFL---------- 593
WP_093971860.1 HPTHYGRVCPIETPEGPNIGLINSMALYARLN----------EYGFL---------- 593
sp|Q2NWR6|RPOB_SODGM HPTHYGRVCPIETPEGPNIGLINSLSVYAQTN----------EYGFL---------- 587
sp|B4EYU9|RPOB_PROMH HPTHYGRVCPIETPEGPNIGLINSLSVYAQTN----------EYGFL---------- 587
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sp|B4T0Y9|RPOB_SALNS HPTHYGRVCPIETPEGPNIGLINSLSVYAQTN----------EYGFL---------- 587
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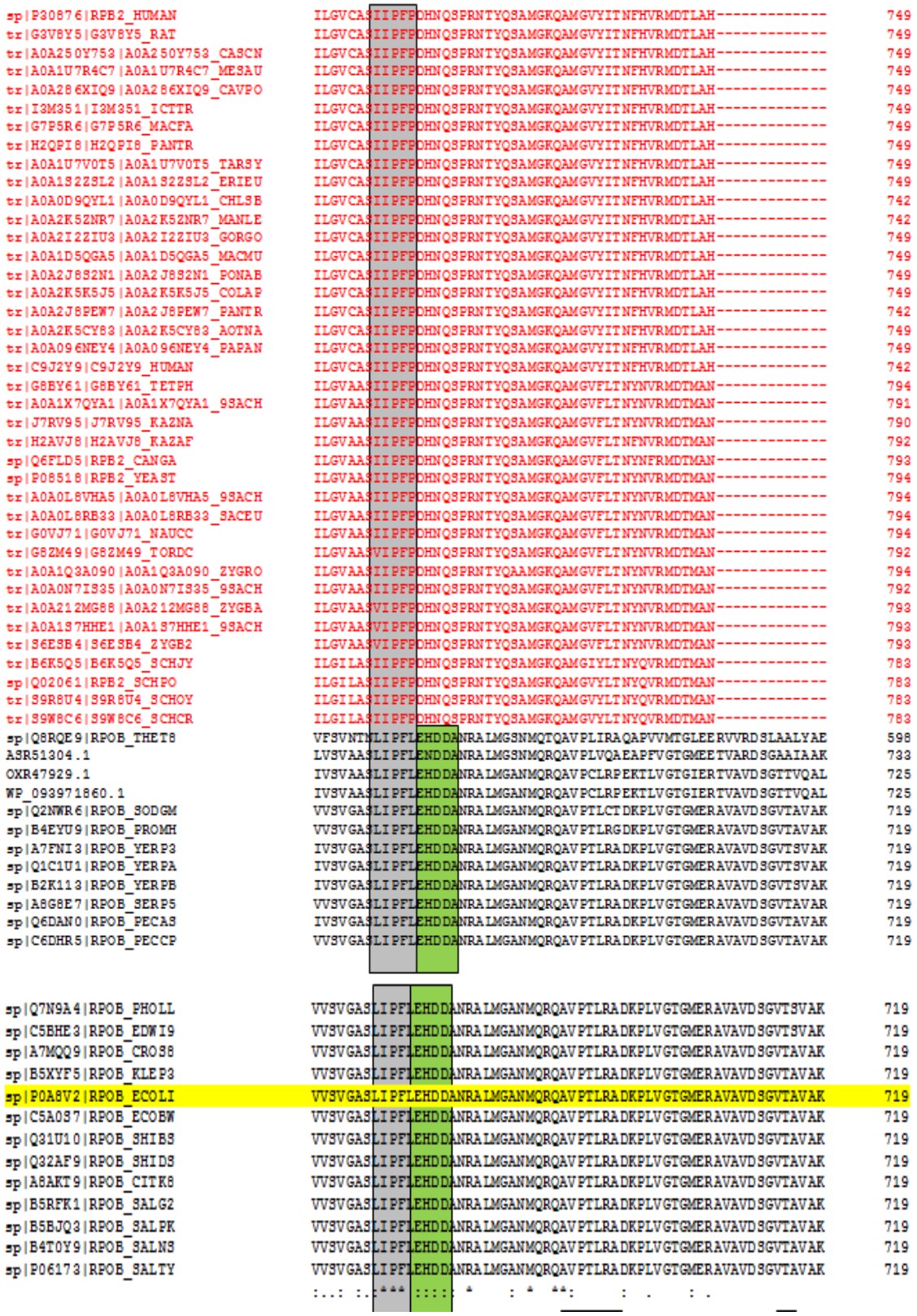
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tr|G3V8Y5|G3V8Y5_RAT ILGVCASIIPFDHNQSPRNTYQSAMGKQAMGVYITNFHVRMDTLAH---------- 749
tr|A0A250Y753|A0A250Y753_CASCN ILGVCASIIPFDHNQSPRNTYQSAMGKQAMGVYITNFHVRMDTLAH---------- 749
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tr|A0A286XIQ9|A0A286XIQ9_CAVPO ILGVCASIIPFDHNQSPRNTYQSAMGKQAMGVYITNFHVRMDTLAH---------- 749
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tr|G7P5R6|G7P5R6_MACFA ILGVCASIIPFDHNQSPRNTYQSAMGKQAMGVYITNFHVRMDTLAH---------- 749
tr|H2QPI8|H2QPI8_PANTR ILGVCASIIPFDHNQSPRNTYQSAMGKQAMGVYITNFHVRMDTLAH---------- 749
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tr|A0A096NEY4|A0A096NEY4_PAPAN ILGVCASIIPFDHNQSPRNTYQSAMGKQAMGVYITNFHVRMDTLAH---------- 749
tr|C9J2Y9|C9J2Y9_HUMAN ILGVCASIIPFDHNQSPRNTYQSAMGKQAMGVYITNFHVRMDTLAH---------- 742
tr|G8BY61|G8BY61_TETPH ILGVAASIIPFDHNQSPRNTYQSAMGKQAMGVFLTNYNVRMDTMAN---------- 794
tr|A0A1X7QYA1|A0A1X7QYA1_9SACH ILGVAASIIPFDHNQSPRNTYQSAMGKQAMGVFLTNYNVRMDTMAN---------- 791
tr|J7RV95|J7RV95_KAZNA ILGVAASIIPFDHNQSPRNTYQSAMGKQAMGVFLTNYNVRMDTMAN---------- 790
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tr|A0A0L8RB33|A0A0L8RB33_SACEU ILGVAASIIPFDHNQSPRNTYQSAMGKQAMGVFLTNYNVRMDTMAN---------- 794
tr|G0VJ71|G0VJ71_NAUCC ILGVAASIIPFDHNQSPRNTYQSAMGKQAMGVFLTNYNVRMDTMAN---------- 794
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tr|A0A1Q3A090|A0A1Q3A090_ZYGRO ILGVAASIIPFDHNQSPRNTYQAAMGKQAMGVFLTNYNVRMDTMAN---------- 794
tr|A0A0N7IS35|A0A0N7IS35_9SACH ILGVAASIIPFDHNQSPRNTYQSAMGKQAMGVFLTNYNVRMDTMAN---------- 792
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tr|S6ESB4|S6ESB4_ZYGB2 ILGVAASVIPFDHNQSPRNTYQSAMGKQAMGVFLTNYNVRMDTMAN---------- 793
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sp|B4EYU9|RPOB_PROMH VVSVGASLIPFLEHDDANRALMGANMQRQAVPTLRGDKPLVGTGMERAVAVDSGVTAVAK 719
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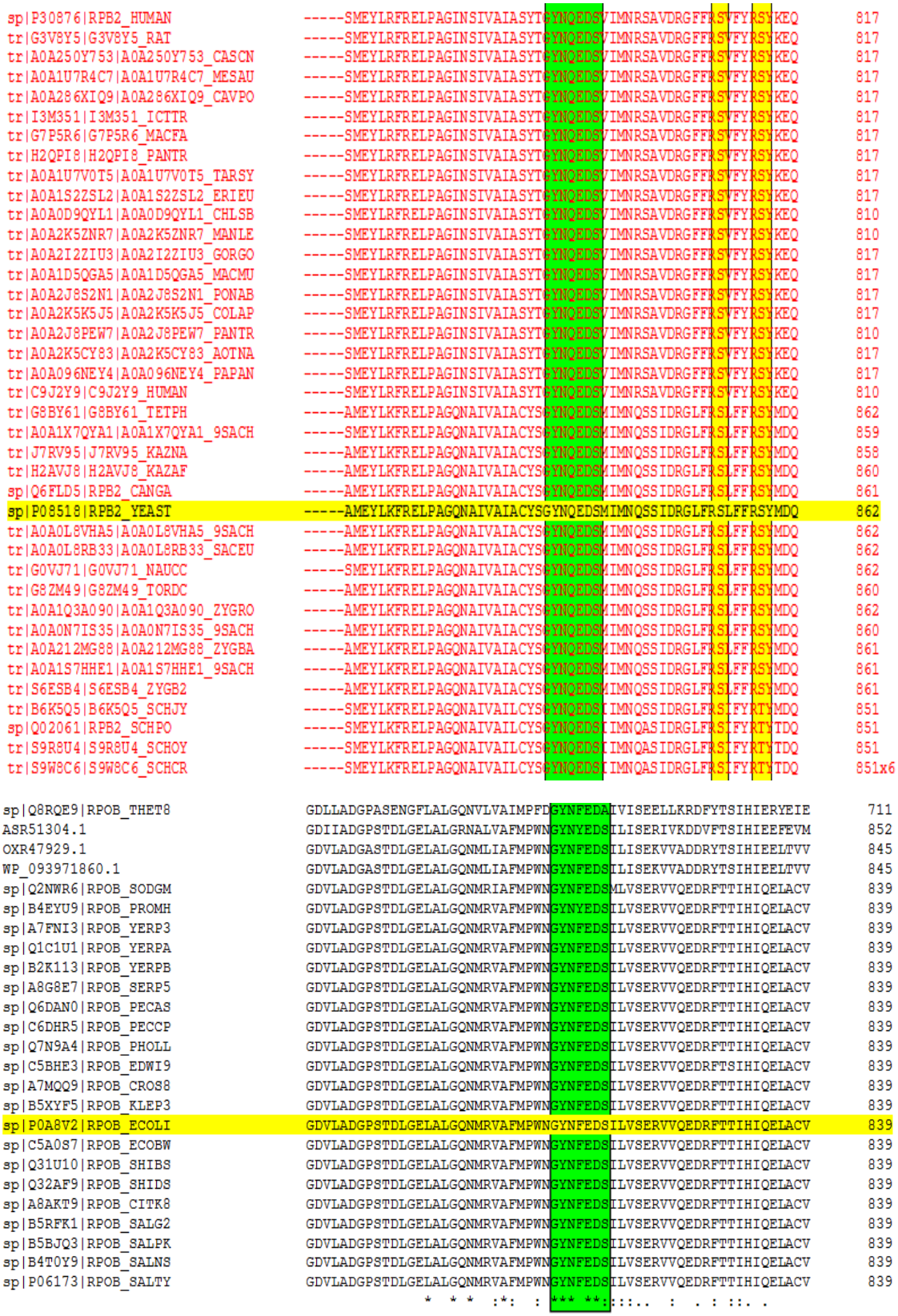
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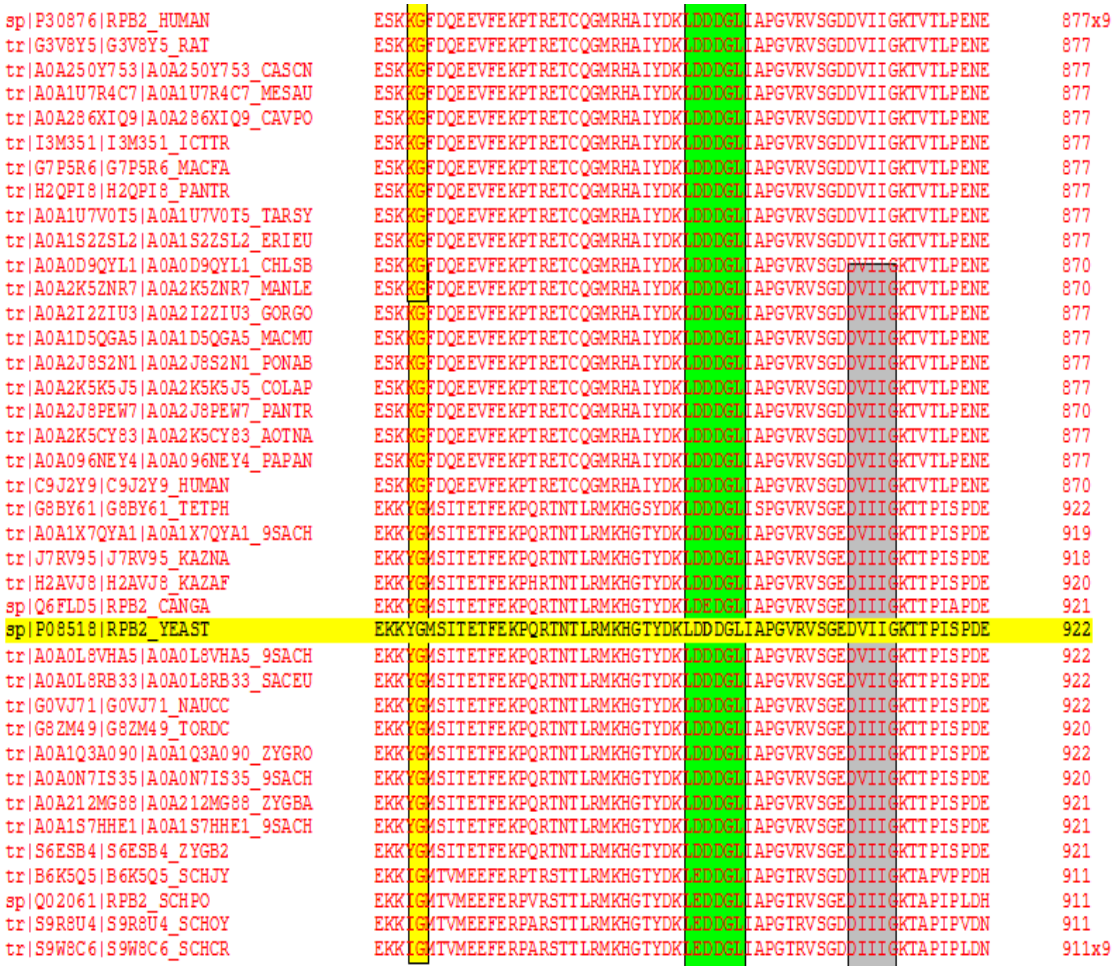
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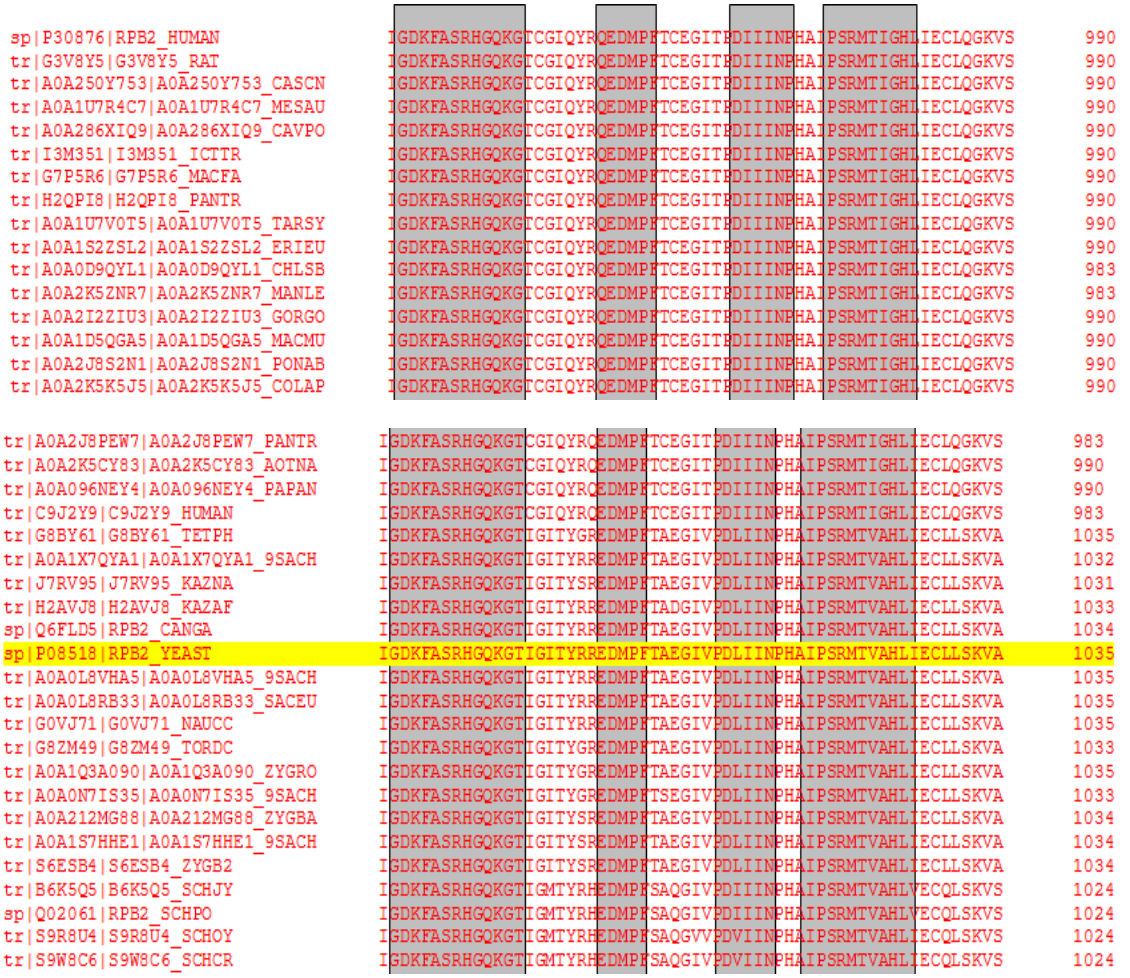
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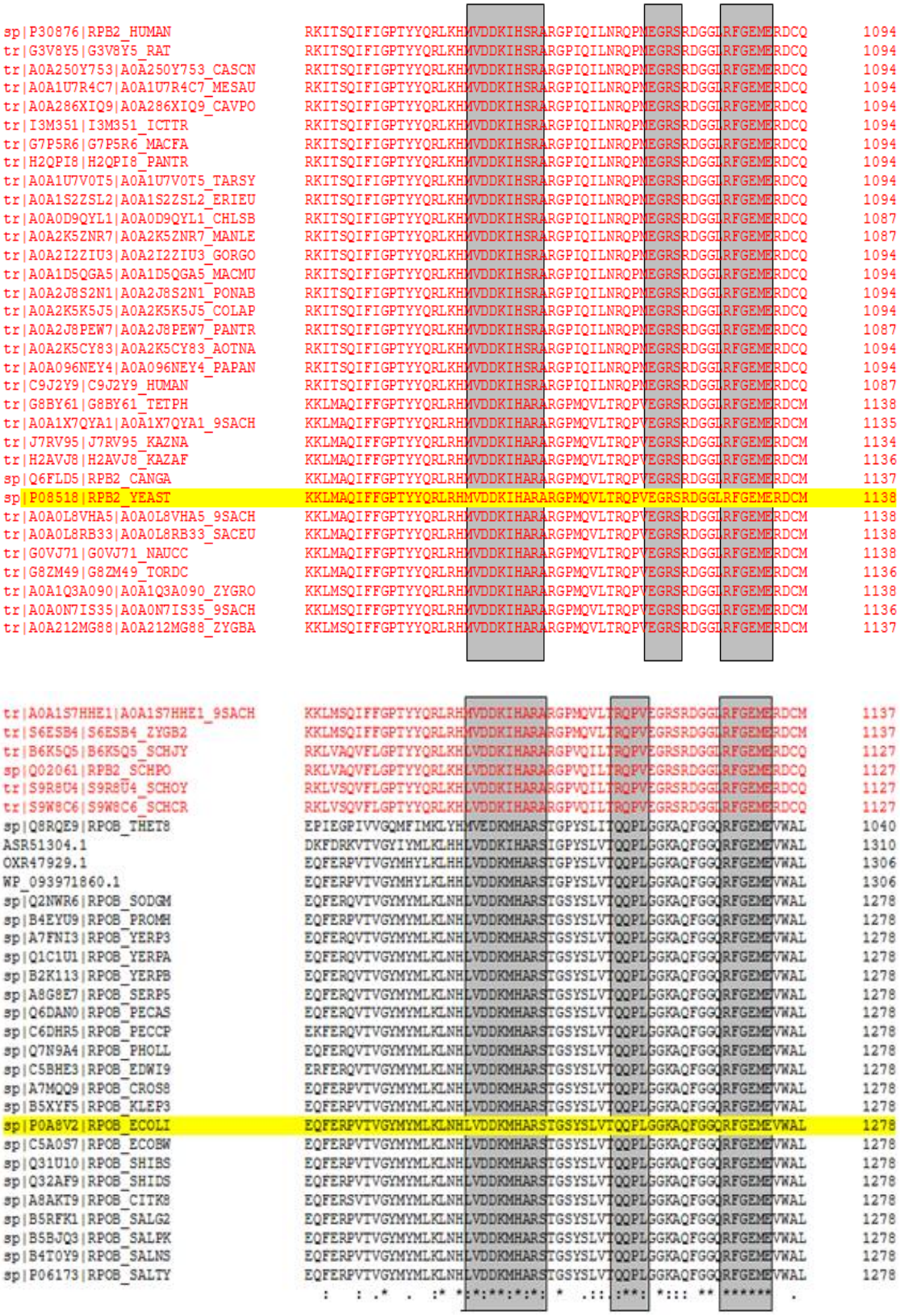
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sp|B5XYF5|RPOB_KLEP3 EQFERPVTVGYMYMLKLNHLVDDKMHARSTGSYSLVTQQPLGGKAQFGGQRFGEMEVWAL 1278
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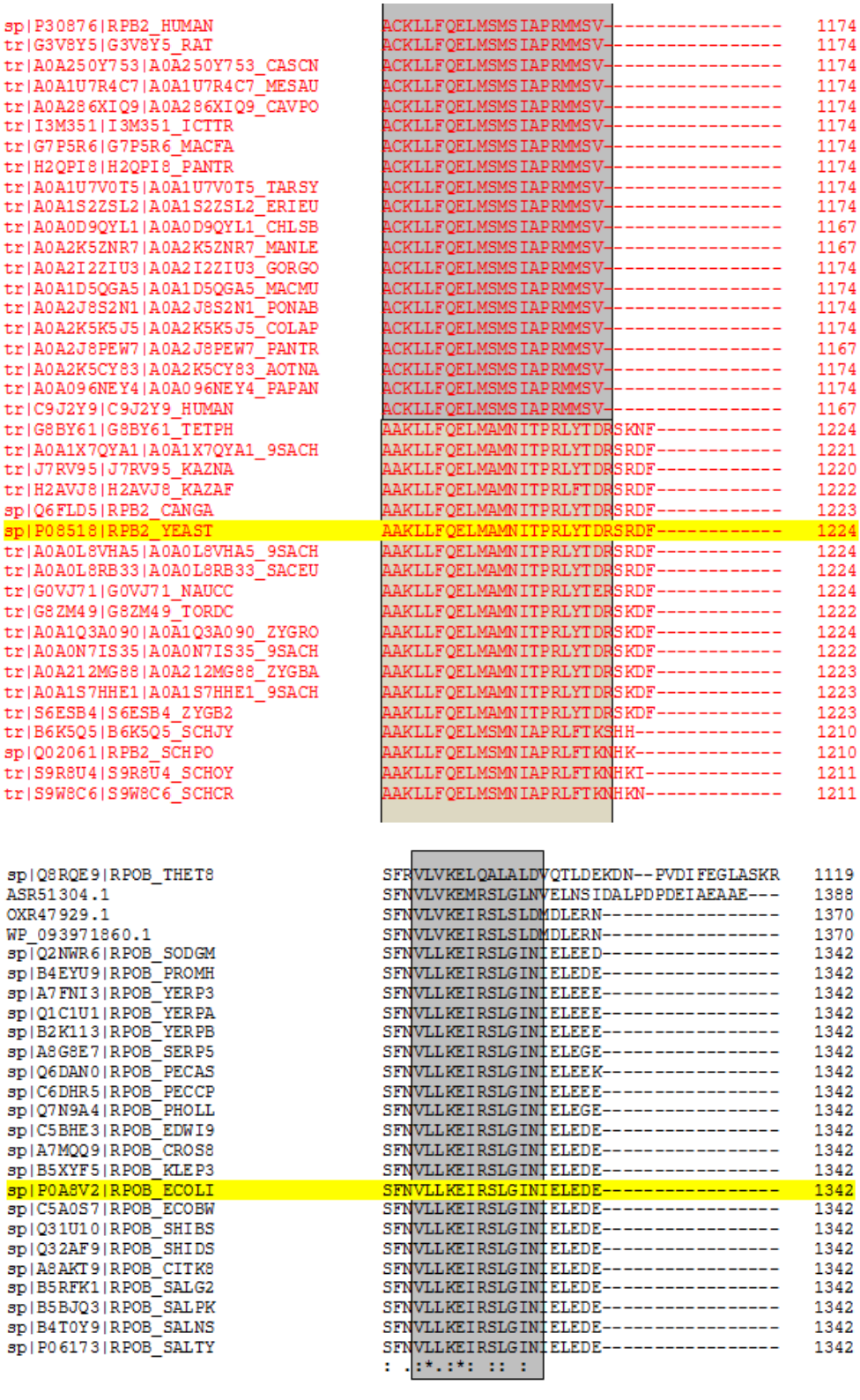

Fig. 5 Mix and match analysis of the initiation subunits β of *E. coli* and Rpb2 of yeast RNAP II
For figure legends, refer to Figs. 3 and 4

CLUSTAL O (1.2.4): MSA of eubacterial β' and eukaryotic Rpb1 subunits 6


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sp|P0A8T7|RPOC_ECOLI DALLDNGRRGRAITG-SNKRPLKSLADMIKGKQGRFRQNLLGKRVDYSGRSVITVGPYLR 362
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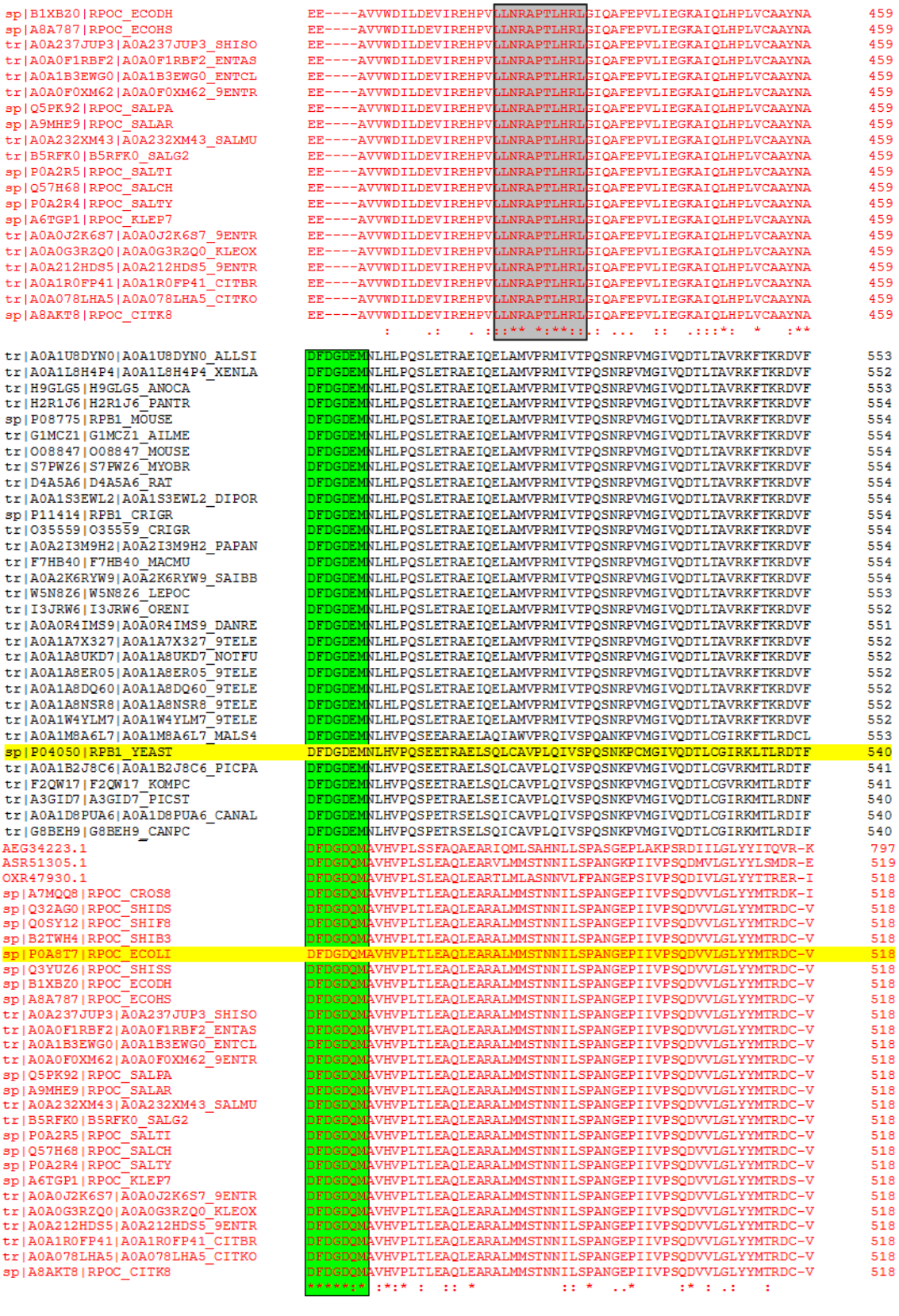
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tr|F2QW17|F2QW17_KOMPC DFDGDEMNLHVPQSEETRAELSQLCAVPLQIVSPQSNKPVMGIVQDTLCGVRKMTLRDTF 541
tr|A3GID7|A3GID7_PICST DFDGDEMNLHVPQSPETRAELSEICAVPLQIVSPQSNKPVMGIVQDTLCGIRKMTLRDNF 540
tr|A0A1D8PUA6|A0A1D8PUA6_CANAL DFDGDEMNLHVPQSPETRSELSQICAVPLQIVSPQSNKPVMGIVQDTLCGIRKMTLRDIF 540
tr|G8BEH9|G8BEH9_CANPC DFDGDEMNLHVPQSPETRSELSQICAVPLQIVSPQSNKPVMGIVQDTLCGIRKMTLRDIF 540
AEG34223.1 DFDGDQMAVHVPLSSFAQAEARIQMLSAHNLLSPASGEPLAKPSRDIILGLYYITQVR-K 797
ASR51305.1 DFDGDQMAVHVPLSLEAQLEARVLMMSTNNILSPANGKPIIVPSQDMVLGLYYLSMDR-E 519
OXR47930.1 DFDGDQMAVHVPLSLEAQLEARTLMLASNNVLFPANGEPSIVPSQDIVLGLYYTTRER-I 518
sp|A7MQQ8|RPOC_CROS8 DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDK-I 518
sp|Q32AG0|RPOC_SHIDS DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518
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sp|A8A787|RPOC_ECOHS DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518
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sp|Q5PK92|RPOC_SALPA DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518
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tr|A0A232XM43|A0A232XM43_SALMU DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518
tr|B5RFK0|B5RFK0_SALG2 DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518
sp|P0A2R5|RPOC_SALTI DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518
sp|Q57H68|RPOC_SALCH DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518
sp|P0A2R4|RPOC_SALTY DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518
sp|A6TGP1|RPOC_KLEP7 DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDS-V 518
tr|A0A0J2K6S7|A0A0J2K6S7_9ENTR DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518
tr|A0A0G3RZQ0|A0A0G3RZQ0_KLEOX DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518
tr|A0A212HDS5|A0A212HDS5_9ENTR DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518
tr|A0A1R0FP41|A0A1R0FP41_CITBR DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518
tr|A0A078LHA5|A0A078LHA5_CITKO DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518
sp|A8AKT8|RPOC_CITK8 DFDGDQMAVHVPLTLEAQLEARALMMSTNNILSPANGEPIIVPSQDVVLGLYYMTRDC-V 518

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tr|O35559|O35559_CRIGR              REGLIDTAVKTAETGYIQRRLIKSMESVMVKYDATVRNSINQVVQLRYGEDGLAGESVEF       903
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OXR47930.1                          RKGLADTALKTANSGYLTRRLVDVTQDLVITETDCGTTSGYTMKALVEGGEVI-------      832
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tr|A0A237JUP3|A0A237JUP3_SHISO      RKGLADTALKTANSGYLTRRLVDVAQDLVVTEDDCGTHEGIMMTPVIEGGDVK-------      832
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tr|A0A0G3RZQ0|A0A0G3RZQ0_KLEOX      RKGLADTALKTANSGYLTRRLVDVAQDLVVTEDDCGTLEGITMTPVIEGGDVK-------      832
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tr|A0A1R0FP41|A0A1R0FP41_CITBR      RKGLADTALKTANSGYLTRRLVDVAQDLVVTEDDCGTLEGITMTPVIEGGDVK-------      832
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                                    *:*  ***::**::**: *:*:.  ..  :       .   :  .    .

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tr|H9GLG5|H9GLG5_ANOCA              VNGDDPLSKQAQENATLLFNIHLRSTLCSRRMIEEFRLSGEAFDWLLGEIESKFNQAIAH      1081
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sp|P08775|RPB1_MOUSE                VNGDDPLSRQAQENATLLFNIHLRSTLCSRRMAEEFRLSGEAFDWLLGEIESKFNQAIAH      1082
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sp|P11414|RPB1_CRIGR                VNGDDPLSRQAQENATLLFNIHLRSTLCSRRMAEEFRLSGEAFDWLLGEIESKFNQAIAH      1082
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tr|A0A1A8ER05|A0A1A8ER05_9TELE      VNGDDPLSRQAQENATLLFNIHLRSTLCSRRMTEEFRLSMEAFDWLLGEIETKFNQSIVH      1080
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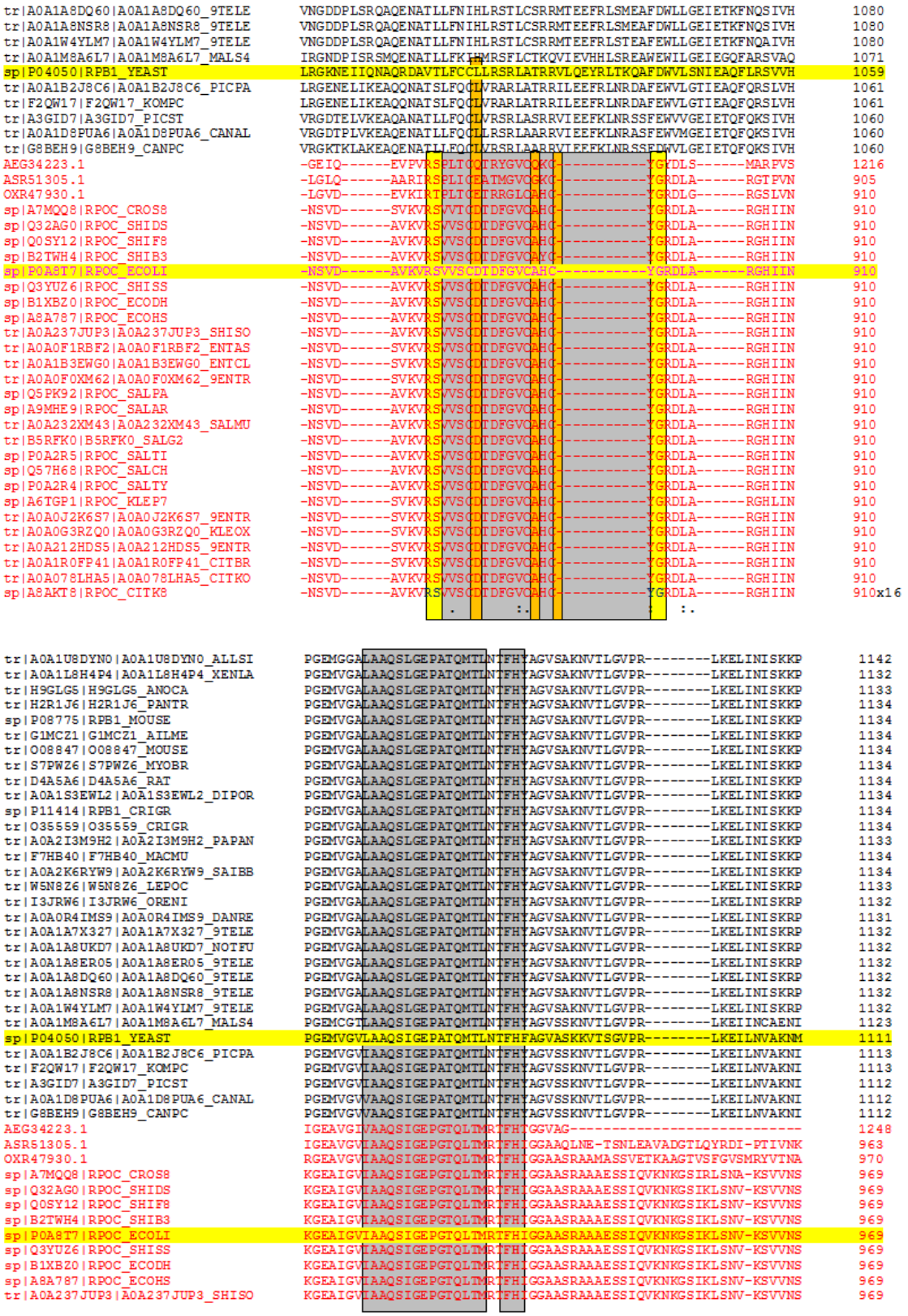
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sp|Q57H68|RPOC_SALCH -NSVD------AVKVRSVVSCDTDFGVQAHG----------YGRDLA------RGHIIN 910
sp|P0A2R4|RPOC_SALTY -NSVD------AVKVRSVVSCDTDFGVQAHG----------YGRDLA------RGHIIN 910
sp|A6TGP1|RPOC_KLEP7 -NSVD------SVKVRSVVSCDTDFGVQAHG----------YGRDLA------RGHLIN 910
tr|A0A0J2K6S7|A0A0J2K6S7_9ENTR -NSVD------SVKVRSVVSCDTDFGVQAHG----------YGRDLA------RGHIIN 910
tr|A0A0G3RZQ0|A0A0G3RZQ0_KLEOX -NSVD------SVKVRSVVSCDTDFGVQAHG----------YGRDLA------RGHIIN 910
tr|A0A212HDS5|A0A212HDS5_9ENTR -NSVD------SVKVRSVVSCDTDFGVQAHG----------YGRDLA------RGHIIN 910
tr|A0A1R0FP41|A0A1R0FP41_CITBR -NSVD------SVKVRSVVSCDTDFGVQAHG----------YGRDLA------RGHIIN 910
tr|A0A078LHA5|A0A078LHA5_CITKO -NSVD------AVKVRSVVSCDTDFGVQAHG----------YGRDLA------RGHIIN 910
sp|A8AKT8|RPOC_CITK8 -NSVD------AVKVRSVVSCDTDFGVQAHG----------YGRDLA------RGHIIN 910x16
tr|A0A1U8DYN0|A0A1U8DYN0_ALLSI PGEMGGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1142
tr|A0A1L8H4P4|A0A1L8H4P4_XENLA PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1132
tr|H9GLG5|H9GLG5_ANOCA PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1133
tr|H2R1J6|H2R1J6_PANTR PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1134
sp|P08775|RPB1_MOUSE PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1134
tr|G1MCZ1|G1MCZ1_AILME PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1134
tr|O08847|O08847_MOUSE PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1134
tr|S7PWZ6|S7PWZ6_MYOBR PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1134
tr|D4A5A6|D4A5A6_RAT PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1134
tr|A0A1S3EWL2|A0A1S3EWL2_DIPOR PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1134
sp|P11414|RPB1_CRIGR PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1134
tr|O35559|O35559_CRIGR PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1134
tr|A0A2I3M9H2|A0A2I3M9H2_PAPAN PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1133
tr|F7HB40|F7HB40_MACMU PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKKP 1134
tr|A0A2K6RYW9|A0A2K6RYW9_SAIBB PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKRP 1134
tr|W5N8Z6|W5N8Z6_LEPOC PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKRP 1133
tr|I3JRW6|I3JRW6_ORENI PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKRP 1132
tr|A0A0R4IMS9|A0A0R4IMS9_DANRE PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKRP 1131
tr|A0A1A7X327|A0A1A7X327_9TELE PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKRP 1132
tr|A0A1A8UKD7|A0A1A8UKD7_NOTFU PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKRP 1132
tr|A0A1A8ER05|A0A1A8ER05_9TELE PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKRP 1132
tr|A0A1A8DQ60|A0A1A8DQ60_9TELE PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKRP 1132
tr|A0A1A8NSR8|A0A1A8NSR8_9TELE PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKRP 1132
tr|A0A1W4YLM7|A0A1W4YLM7_9TELE PGEMVGALAAQSLGEPATQMTLNTFHYAGVSAKNVTLGVPR--------LKELINISKRP 1132
tr|A0A1M8A6L7|A0A1M8A6L7_MALS4 PGEMCGTLAAQSIGEPATQMTLNTFHYAGVSSKNVTLGVPR--------LKEIINCAENI 1123
sp|P04050|RPB1_YEAST PGEMVGVLAAQSIGEPATQMTLNTFHFAGVASKKVTSGVPR--------LKEILNVAKNM 1111
tr|A0A1B2J8C6|A0A1B2J8C6_PICPA PGEMVGVIAAQSIGEPATQMTLNTFHYAGVSSKNVTLGVPR--------LKEILNVAKNI 1113
tr|F2QW17|F2QW17_KOMPC PGEMVGVIAAQSIGEPATQMTLNTFHYAGVSSKNVTLGVPR--------LKEILNVAKNI 1113
tr|A3GID7|A3GID7_PICST PGEMVGVIAAQSIGEPATQMTLNTFHYAGVSSKNVTLGVPR--------LKEILNVAKNI 1112
tr|A0A1D8PUA6|A0A1D8PUA6_CANAL PGEMVGVVAAQSIGEPATQMTLNTFHYAGVSSKNVTLGVPR--------LKEILNVAKNI 1112
tr|G8BEH9|G8BEH9_CANPC PGEMVGVVAAQSIGEPATQMTLNTFHYAGVSSKNVTLGVPR--------LKEILNVAKNI 1112
AEG34223.1 IGEAVGIVAAQSIGEPGTQLTMRTFHTGGVAG---------------------------- 1248
ASR51305.1 IGEAVGVIAAQSIGEPGTQLTMRTFHIGGAAQLNE-TSNLEAVADGTIQYRDI-PTIVNK 963
OXR47930.1 RGEAVGVIAAQSIGEPGTQLTMRTFHIGGAASRAAMASSVETKAAGTVSFGVSMRYVTNA 970
sp|A7MQQ8|RPOC_CROS8 KGEAIGVIAAQSIGEPGTQLTMRTFHIGGAASRAAAESSIQVKNKGSIRLSNA-KSVVNS 969
sp|Q32AG0|RPOC_SHIDS KGEAIGVIAAQSIGEPGTQLTMRTFHIGGAASRAAAESSIQVKNKGSIKLSNV-KSVVNS 969
sp|Q0SY12|RPOC_SHIF8 KGEAIGVIAAQSIGEPGTQLTMRTFHIGGAASRAAAESSIQVKNKGSIKLSNV-KSVVNS 969
sp|B2TWH4|RPOC_SHIB3 KGEAIGVIAAQSIGEPGTQLTMRTFHIGGAASRAAAESSIQVKNKGSIKLSNV-KSVVNS 969
sp|P0A8T7|RPOC_ECOLI KGEAIGVIAAQSIGEPGTQLTMRTFHIGGAASRAAAESSIQVKNKGSIKLSNV-KSVVNS 969
sp|Q3YUZ6|RPOC_SHISS KGEAIGVIAAQSIGEPGTQLTMRTFHIGGAASRAAAESSIQVKNKGSIKLSNV-KSVVNS 969
sp|B1XBZ0|RPOC_ECODH KGEAIGVIAAQSIGEPGTQLTMRTFHIGGAASRAAAESSIQVKNKGSIKLSNV-KSVVNS 969
sp|A8A787|RPOC_ECOHS KGEAIGVIAAQSIGEPGTQLTMRTFHIGGAASRAAAESSIQVKNKGSIKLSNV-KSVVNS 969
tr|A0A237JUP3|A0A237JUP3_SHISO KGEAIGVIAAQSIGEPGTQLTMRTFHIGGAASRAAAESSIQVKNKGSIKLSNV-KSVVNS 969

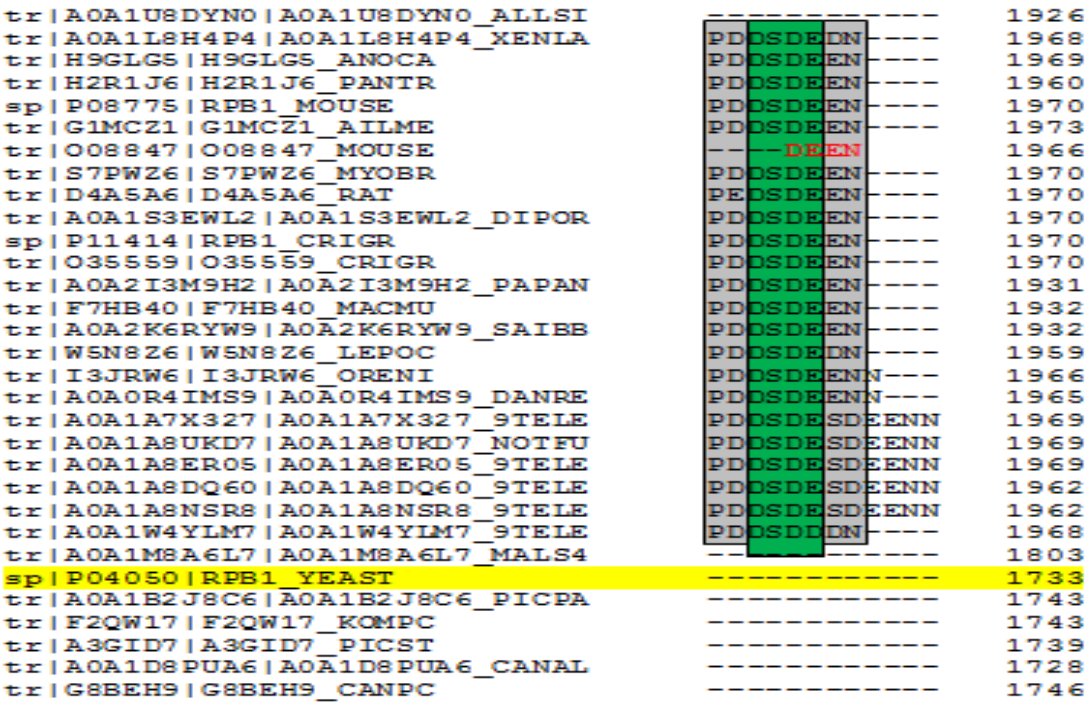

Fig. 6 Mix and Match analysis of the elongation subunits β' of *E. coli* and Rpb1 of yeast RNAP II. For figure legends, refer to Figs. 3 and 4

Fig. 6 shows the mix and match analysis of the elongation subunits from pro- and eukaryotes MSU RNAPs. The active site regions are highlighted in yellow and the representative sequences are highlighted in yellow. In eukaryotic elongation subunits, the catalytic region is brought to the N-terminal region whereas it is found very close to the C-terminal region. There are 4 Cs at the N-terminal region in prokaryotic elongation subunits (out of which 2 are aligning in both) suggesting a possible additional Zn binding region. There are a very few motifs aligning in both. Significant among them are –GHIELA-, -NLM/LGKRVDF/YS-, possible metal binding region -DFDGDE/QM-, -DTAV/LKTAE/NT/SGYI/L-, -L/V/IAAQSIGEPA/GTQM/LTL/MXTFH-. The metal binding region -NADFDGD- is aligning in both and placed in the middle of the enzyme. The C-terminal ends in eukaryotes usually end in -PDDSDE/DE/DN- (except in yeasts and Alligator) and -GSDNE/D- in prokaryotes, suggesting a possible metal binding site (DxD) at the ends. It is interesting to note that the prokaryotic active site is placed at the C-terminal region (~900 amino acids) whereas the eukaryotic active site is placed at the N-terminal region (~90 amino acids) with their built-in Zn binding motifs.

8. ACTIVE SITE ANALYSIS OF THE *S. cerevisiae* MSU RNAP- II

8.1 Catalytic Region

It has been found that almost all DNA polymerases and SSU RNAPs use an invariant K for catalysis, i.e., in the initial proton transfer reactions [34,29]. However, in all MSU RNAPs analyzed, no K was found at the expected distance from the template binding YG/FG pair but an equivalent invariant R (Table 4). However, a detailed analysis has shown that all prokaryotic DNA polymerases II also use an invariant R in catalysis with similar distance conservations [34, 4] instead of a usual K; interestingly, an enzyme also possesses primase activity and along with associated 3′→5′ exonuclease activity.

Table 4 shows the invariant template binding YG pair with its catalytic R in the initiation (β and Rpb2) and in the elongation subunits (β' and Rpb1) of eubacterial and eukaryotic MSU RNAPs, respectively (Figs. 3-7). The catalytic R in both in the initiation and elongation subunits of the MSU RNAPs will serve as a proton abstractor for initiating the catalysis as explained by Palanivelu

[4]. Table 4 shows the invariant YG/FG pair and its catalytic R in the initiation and elongation subunits of eubacterial and eukaryotic MSU RNAPs.

It is interesting to note that the YG pair appears to be specific for polymerases using DNA as the template (including the prokaryotic and eukaryotic MSU RNAPs, data not shown) as it is not reported in RNA dependent RNAPs where they use RNA as the template [35]. In fact, Kotsyuk et al. [37] have shown that the DNA dependent T7 RNAP requires both the strands for activity and uses two YG pairs and there was no activity when single-stranded DNA was used as the substrate. However, the eukaryotic initiation subunit Rpb2 uses a functional equivalent FG and the initiation subunit from higher eukaryotes including human uses a completely different pair, KG but followed by an F. The elongation subunits in all eukaryotes use a functionally equivalent FG pair. However, it is interesting to note the catalytic amino acid is R and is completely conserved in all MSU RNAPs II. Three invariant Cs between catalytic R and YG/FG pair in the elongation subunits (β' and Rpb1) are highly conserved in both pro- and eukaryotes but the three Cs are placed at a different distances as 5+12+15 and 4+7+14 with an 11 amino acids span in both the cases (Table 4). These completely conserved Cs are implicated in Zn binding in the bacterial elongation subunits by crystallographic analysis [36].

8.2 Mechanism of NTP and dNTP Discrimination in Eukaryotic MSU RNA Polymerases

NTP and dNTP discrimination in nucleic acid polymerases is usually achieved by base pairing, base stacking, hydrogen bonding and also by specific interaction(s) of completely conserved amino acid(s) in the nucleotide interacting domains**.** A completely conserved R at -5 in the Rpb2 and -6 in Rpb1 is known to participate in the nucleotide discrimination and select only NTPs in the polymerization site (Table 4). Similar absolute conservation is seen in SSU RNAPs from viruses, mitochondria and chloroplasts and DNA polymerases too. A conspicuous absence of an invariant R at the expected distance at -6 in the elongation subunit β' of eubacterial MSU RNAPs (Table 4) raises the question of how they discriminate the NTPs from dNTPs. Modelling of the substrate NTP bound to the *T. thermophilus* RNAP active site suggests that N^{458} (numbering from *E. coli* RNA polymerase) within a highly conserved sequence motif ^{458}NADFDGD^{464} that includes the catalytic Asp triad (D460, D462, D464) could mediate specific recognition of the O2 ribose atom [39,36]. Functional *in vitro* analysis demonstrated that the substitutions of the corresponding β′ N^{458} residue led to the loss of discrimination between NTP and dNTP substrates as well as to defects in RNA chain extension [39]. It is interesting to note that substitution of the corresponding amino acid in yeast Rpb1 (N479Y) is lethal in the same sequence motif ^{478}YNADFDGD in eukaryotes [40]. The absolutely conserved N in both the cases could discriminate the NTP from dNTP by recognizing the 2'-OH of the ribose and suggested that the crucial N could interact with both the 2'-OH as well 3'-OH [40].

The highly conserved S/T adjacent (N in *S. cerevisiae*) to the catalytic R in the initiation and elongation subunits likely recognizes the 2'-OH in the NTPs and possibly makes a hydrogen bond and discriminate dNTPs, which lack a 2'-OH (the yeast elongation subunit, Rpb1 could also use the invariant N^{479} to make the necessary H bond with the 2'-OH a well as 3'-OH as shown in elongation subunit β' of eubacterial MSU RNAPs [4]. Kaplan et al. [41] have shown by SDM experiments that the completely conserved His1085 both in prokaryotes (β') and eukaryotes Rpb1 might involve in NTP selection and substitution of Ala or Phe resulted in inviability. This H1085 in the trigger loop (amino acids from 1060 to 1101) was shown to make a contact with the β phosphate either through H-bond or salt bridge and the L1081 was located at the 3' end of the RNA [42]. Mix and match analysis also shows and that particular His is completely conserved in both prokaryotes and eukaryotes in highly conserved stretch (Fig. 6). Another amino acid Q1078 in the same block is also shown to be essential and replacing Q1078 in Rpb1 to either N or S is lethal in yeast [41], consistent with a key role of these residues in NTP/dNTP discrimination.

9. THE INITIATION AND ELONGATION SUBUNITS WORK IN TANDEM DURING TRANSCRIPTION CYCLES IN EUKARYOTIC MSU RNAP II

A close similarity is observed between the prokaryotic and eukaryotic transcription cycles. For example, it has been shown in prokaryotes (*E. coli)* that the initiation of transcription by the β subunit is not smooth and it makes many aborted

transcripts of sizes 2-7 nts before the elongation step is taken over by the β' subunit [43]. It was found that RNA/DNA hybrids of less than 8-bp display markedly less stability than those that are 8 bp or longer. In fact, the *E. coli* MSU RNAPs use these short RNA/DNA hybrids of 8 bp or longer for the ternary elongation complex (TEC) formation and further processivity [44]. Furthermore, Zaychikov et al. [45] have shown that an ~17 bp region of the DNA called the 'transcription bubble' was melted to expose the template strand for transcription in *E. coli*. MSA analysis agreed with these findings with the 7 amino acid gap between the catalytic R and the template binding YG pair in the initiation subunit β and 17 amino acid gap ('transcription bubble') between the catalytic R and the template binding YG pair in the elongation subunit β' (Table 5) [4].

A similar observation of abortive initiations in eukaryotic Rpb2 was also reported by Pal and Luse [32]. In addition to, as in prokaryotes, in eukaryotes also a 9 bp DNA-RNA stable hybrid is formed which extends from the active centre at nearly right angles to the entering DNA during the elongation cycle [16,33]. Fiedler and Timmers [33] results further support the MSA findings where the transition from abortive to productive elongation cycle occurred once the RNAP register +10 nts (Table 5). These observations are further supported by Luse who have shown that the promoter clearance was complete with ~10 nts [46]. Pal et al on analyzing the 'transcription bubble' have found that regardless of promoter spacing, the upstream edge of the 'transcription bubble' formed 20 bp from TATA which is in close agreement with MSA analysis data [47]. A similar finding was reported by Giardina and Lis [48]. Furthermore, Holstege et al analyzed the transcription initiation by the yeast RNAP II in a highly efficient *in vitro* transcription system composed of essentially homogeneous protein preparations and found that the downstream part of the 'transcription bubble' expands in a continuous motion, but the initially opened region on the non-template strand reclosed abruptly when transcription reached 11, which was accompanied by a switch from abortive initiations to productive mRNA synthesis (elongation) [49]. Similar findings were also reported by Barnes et al by analyzing the crystal structure of the transcribing RNAP II complex. The transcription bubble was unwound ~18-25 bases and transcripts of 10 nts or more resulted in promoter escape with stabilization of a mature bubble [50].

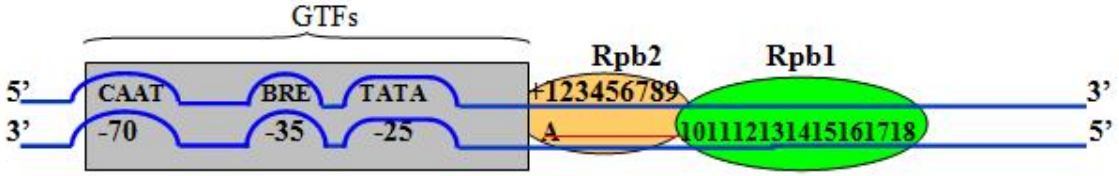

Fig. 7 A consensus model showing pre-initiation, initiation and elongation events by GTFs, Rpb2 and Rpb1 subunits of MSU RNAP- II of *S. cerevisiae*

NB: Thick lines indicate DNA strands and the thin line indicates the mRNA transcript
A is shown as the first nucleotide at the +1 TSS
GTFs, General Transcription Factors (TFII-D, -A, -B, -F, -E, -H)
BRE, TFII-B Recognition Element (G/C-G/C-G/A-C-G-C-C)

Table 5. Metal-binding sites in prokaryotic and eukaryotic MSU RNAPs

Subunit (Organism)	Metal-biding sites	Method and Reference
β eubacteria (*E. coli*)	-^{671}LEHDDA/ -^{809}GYNFEDS* - (Mg^{2+})	MSA (This communication)
β' eubacteria (*E. coli*)	-^{458}**YNADFDGDQM - (Mg^{2+})**	X-ray crystallographic data
	-^{883}**RS^{1}VVSC^{5}DTDFGVC^{12}AHC^{15}Y^{16}GR^{901}-(Zn^{2+})***	[36]
Rpb2 eukaryote (*Sc*)	-^{893}LDDDG^{897}- -^{832}GYNQED*S^{838}-(Mg^{2+})	MSA (This communication)
Rpb1 eukaryote (*Sc*)	–^{478}**YNAD*FD*GDEM^{487}- (Mg^{2+})**	MSA (This communication)
	-^{56}**PR^{-6}LGSIDRN^{1}LKC^{4}QTC^{7}QEGMNEC^{14}PGHF^{18}GH^{83}-(Zn^{2+})**	,,

Possible metal binding sites arrived at by MSA and SDM

NB: The β' and RpB1 elongation subunits of eubacteria and eukaryotes contain both the Mg^{2+}\ and Zn^{2+} binding sites. In both the cases, the Zn^{2+} binding site is built in the catalytic region with the 3 invariant Cs which coordinates the Zn atom. Sc, S. cerevisiae

In contrast to prokaryotes, in eukaryotes, it has been found that an A is inserted (and not a usual G, as in prokaryotes) in the initiation site as it invariably uses a G for capping enzyme which is also associated with the RNAP II.

MSA analysis agrees with these findings with the 9 amino acid gap between the catalytic R and the template binding YG pair in the initiation subunit Rpb2 and 19 amino acid gap ('transcription bubble') between the catalytic R and the template binding FG pair in the elongation subunit Rpb1. Furthermore, Gnatt et al found that the contacts to the downstream and upstream parts of the hybrid are made by Rpb1 and Rpb2, respectively, which further supports the tandem arrangement of the initiation and elongation subunits as proposed in this model [16].

Fig. 7 shows a consensus model of the yeast MSU RNAP II subunits, from promoter recognition to initiation and elongation events during the transcription process. This has been confirmed that the RNAP II undergoes abortive initiations until it reached a position beyond +9 (i.e., the distance between the template binding FG pair and the catalytic R), at which stage the RNAP II was released from its promoter contacts and an elongation complex (TEC) is formed and a 20 bp "transcription bubble' formed from the TATA box [47]. A modular structure is proposed for the initiation and elongation subunits' function in eukaryotes also as suggested by in prokaryotes [51].

10. METAL- BINDING SITES

The metal-binding sites of *S. cerevisiae* MSU RNAP II is arrived at from the data obtained by the MSA (this work) and X-ray crystallographic analyses [36] and SDM experiments [39] on eubacterial MSU RNAPs. The eukaryotic Rpb2 and Rpb1 subunits show many possible metal binding sites (highlighted in green). A Mg^{2+} ion binding site is found in the mRNA initiation subunit, Rpb2, from all eukaryotes. Similarly, a Mg^{2+} and a Zn^{2+} binding motifs are also found in the elongation subunits, Rpb1, of all eukaryotic RNAPs II. Crystallographic analysis of the *T. aquaticus* RNAP by Zhang et al have shown that the Mg atom is chelated at an absolutely conserved –NADFDGD- motif in the β' elongation subunit and surprisingly the same invariant motif is found by MSA in all eukaryotic elongation subunits as well [36]. Moreover, this is one of the regions that align in both the pro- and eukaryotes by mix and match analysis (Fig. 6). Interestingly, substitution of these Ds by A (D→A) gave rise to a dominant lethal phenotype and showed no detectable enzyme activity [45]. In addition to that, a Zn binding motif is also recognized in the eubacterial and eukaryotic elongation subunits with three conserved Cs. However, their distance arrangements between the three Cs are found to be different (Table 5). Another distinguishing feature between the eukaryotic and eubacterial elongation subunits is the catalytic and Zn binding regions, i.e., in *E. coli* β' subunit, the amino acids 888, 895 and 898 are shown to be involved in Zn binding (Table 5) but in eukaryotic elongation subunits it is placed at the very beginning of the N-terminal and covers the amino acids region 57-82 (Table 5). The Zn binding motif that is located in Rpb1 subunits may play a similar role in the Zn mediated proof-reading function as proposed for DNA polymerases and MSU RNAPs from eubacteria [4,29].

11. MECHANISM OF ACTION OF THE MSU RNAP II of *S. cerevisiae*

A minimal number of steps involved in the catalytic cycle of RNAPs consist of NTP selection, Watson-Crick base pairing with the complementary nucleotide to the template, catalysis, pyrophosphate release and translo-cation. As the catalytic regions are found to be similar in both the initiation and elongation subunits, the polymerization mechanism could be also similar in both the initiation and elongation reactions. Figs. 8 and 9 describe the reactions involved in the initiation and elongation cycles during transcription in *S. cerevisiae.* (all participating amino acids are not shown in the figures).

11.1 Mechanism of Initiation by Rpb2 Subunit of the MSU RNAP II from *S. cerevisiae*

Step 1: Enzyme and the NTP at the Entry Site: Template binding pair (Tyr-Gly) and nucleotide discrimination by the invariant amino acids, Watson-Crick base pairing of the incoming NTP with the template DNA. The catalytic site amino acid Arg in positioned for proton abstraction. ATP is the initiating nucleotide.

Step 2: Proton abstraction and nucleophilic attack of the α-phosphate of NTP: Electronic transition at the active site for proton abstraction by the active site Arg and an electrophilic and nucleophilic attack of the incoming NTPs on the 3'-OH.

Step 3: Phosphodiester bond formation: Proton abstraction by the active site amino acid Arg with simultaneous formation of 3'→5' phosphodiester bond with the incoming NTPs.

Step 4: Inorganic pyrophosphate formation and translocation of the enzyme to next nucleotide: Proton transfer from the active site amino acid Arg, formation of inorganic pyrophosphate, active site restoration and translocation of the enzyme to the next nucleotide (Fig. 8).

11.2 Mechanism of elongation by Rpb1 subunit of the MSU RNAP II from *S. cerevisiae*

Step1: Enzyme and the NTP at the Entry Site: Template binding by the template binding amino acids (Phe-Gly) and nucleotide discrimination by the invariant amino acids, Watson-Crick base pairing of the incoming NTP with the template DNA. The catalytic site amino acid Arg in positioned for proton abstraction.

Step 2: Proton abstraction and nucleophilic attack of α-phosphate of NTP: Electronic transition at the active site for proton abstraction by the active site Arg and an electrophilic and nucleophilic attack of the incoming NTPs on the 3'-OH.

Step 3: Phosphodiester bond formation: Proton abstraction by the active site amino acid Arg with simultaneous formation of 3'→5' phosphodiester bond with the incoming NTPs.

Step 4: Inorganic pyrophosphate formation and translocation of the enzyme to next nucleotide: Proton transfer from the active site amino acid Arg, formation of inorganic pyrophosphate, active site restoration and translocation of the enzyme to the next nucleotide (Fig. 9).

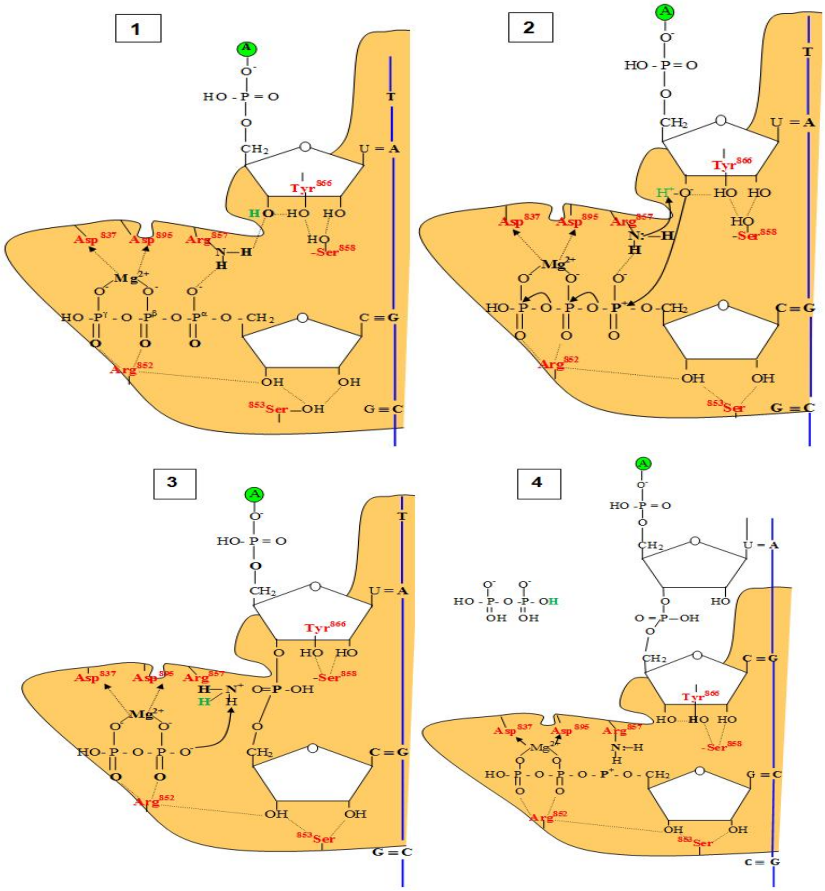

Fig. 8 Steps (1-4) proposed for the polymerization reactions during initiation of transcription by the yeast initiation subunit Rpb2 of the MSU RANP II

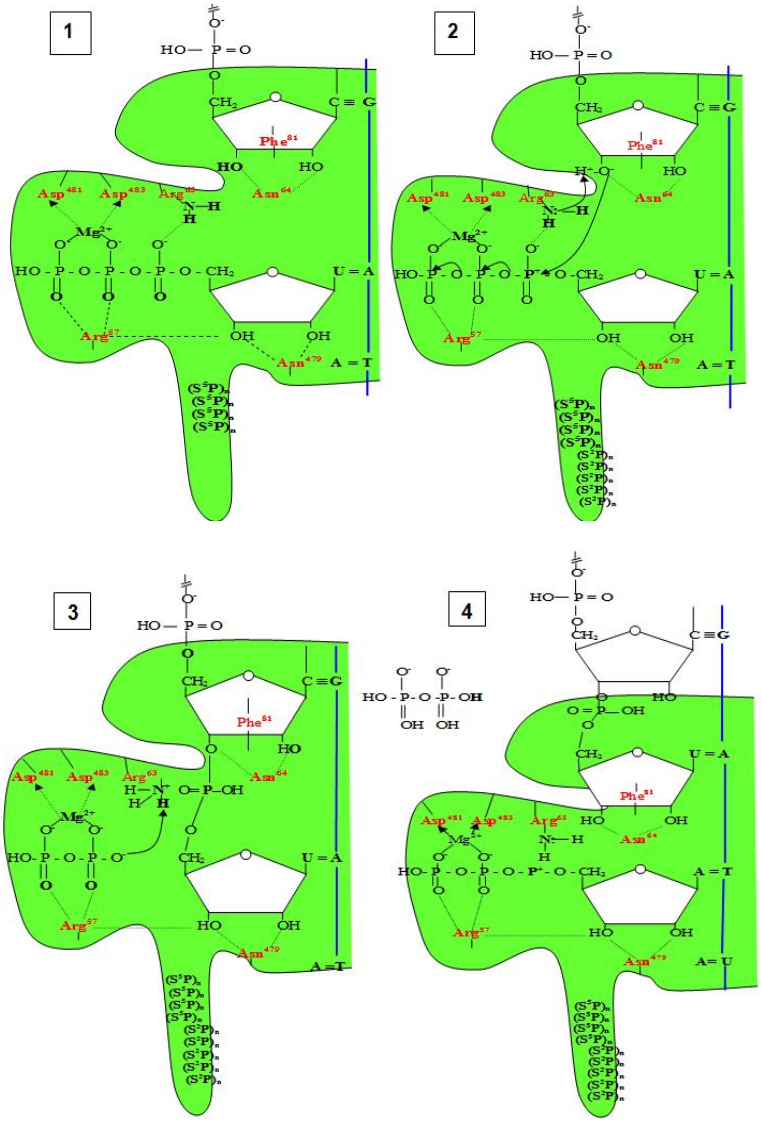

Fig. 9 Steps (1-4) proposed for the polymerization reactions during elongation of transcription by the yeast elongation subunit Rpb1 of the MSU RNAP II

12. PROOF-READING MECHANISM AND TRANSCRIPTION TERMINATION IN *S. cerevisiae* MSU RNAP II

Maintaining high fidelity during transcription is essential for the accurate transfer of genetic information from DNA to RNA as the first step in gene expression. The proof-reading mechanism is well established in DNA polymerases [34]. However, it is poorly understood in RNAPs. Transcription accuracy is relatively high, as RNAPs generally misincorporate one wrong nucleotide/~100000 bases. As RNAPs are also Zn metalloenzymes the Zn-mediated deletion of the misincorporated NTP could be a possible mechanism as explained for DNA polymerases and eubacterial MSU RNAPs as both use DNA template to produce a complementary DNA/RNA strand [34,4,29,30]. There is no distinct proof-reading domain or separate proof-reading subunit as reported in DNA polymerases. However, in eubacterial and eukaryotic elongation subunits of the MSU RNAPs a highly conserved Zn binding motif built into the catalytic region itself might involve in the proof-reading function [4]. Presence of two metal ions at the active site is supported by a 2.8 Å difference Fourier map, one persistently bound and the

other possibly exchangeable during RNA synthesis [28]. Unlike the DNA polymerases, the RNAPs could move forward (when correct NTP is bound) and backtrack (when wrong NTP is bound and secondary structures) [42]. When the enzyme stalls due to secondary structures and/or misincorporation, the proof-reading begins with fraying of the misincorporated nucleotide away from the DNA template and subsequent backtracking of RNAP by one position followed by nucleolytic cleavage of a dinucleotide that contains the misincorporated nucleotide [52]. Sydow and Cramer [52] have also proposed that the exo- or endonucleolytic cleavage occurs at the same active site that is used for polymerization, which is further confirmed by X-ray crystallographic analysis of the *E. coli* and *T. thermophilus* MSU RNAPs suggesting a possible Zn mediated cleavage [36]. The complete conservation of the active sites and Zn binding motif in all prokaryotic and eukaryotic elongation subunits, found by MSA analysis also further proves this point. The proof-reading mechanism may not be that much important during initiation events by the Rpb1 subunits, as they transcribe only very small regions, i.e., only ~ 10 nts and again such transcripts are well within the 5' untranslated regions of the RNA; so any error it makes may not be deleterious. Furthermore, a Zn binding motif is not found in the active site region of the initiation subunits. However, proof-reading is very important for the elongation subunit, viz., Rpb1 to produce an error–free transcript, as they are going to be translated into active proteins. Therefore, when the enzyme stalls at the wrong nucleotide, it could backtrack and make an endonucleolytic cleavage or simply remove the wrong nucleotide by exonuclease action [53, 34]. Unlike in DNA-dependent RNA polymerases, where the polymerization and proofreading functions are separated, in RNAPs, synthesis and degradation are performed by the same active centre [54]. In support of this, Liu et al have shown that following the initiation, RNAP II alone was capable of RNA transcript elongation and of proofreading [55]. Thus, the fidelity in the transcription is ensured by two mechanisms in MSU RNAPs, viz. by the selection of correct NTPs at the entry site and an efficient Zn mediated proof-reading mechanism.

The enzyme could use the same strategy for transcription terminations (intrinsic types) at TTSs. That is, when the enzyme stalls due to the stem-loop structures commonly found at the TTSs, it could backtrack and make an endo- or exonucleolytic cleavage and release the RNA transcript, using the same active site by Zn mediated reaction.

13. OTHER CONSERVED REGIONS AND AMINO ACID(s) IN THE MSU RNAP II

The above analysis to find out the conserved motifs, active sites and invariant amino acids, with respect to the substrate binding and catalytic region, form only a small region of the MSU RNAPs. Apart from these, there are a large number of single amino acid conservations like Ys, Ws, Cs, Ps and Gs, diads, triads and long stretches of conserved amino acids in all these polymerases (Figs. 4 – 6). The highly conserved stretches of amino acids may represent the different conserved structural motifs such as loops, rudders, jaws, bridge helix, exit/entry points for DNA/RNA, etc. Thus, they could form small functional domains. A good number of completely conserved Ps in these polymerases is implicated in making the necessary bents on the enzyme's structure during unique folding, substrate and template binding. The completely conserved Cs other than the catalytic region may play a role in the formation of disulphide bridges to make the enzyme more compact and stable.

14. CONCLUSIONS

Unlike reported for the DNA polymerases and SSU RNA polymerases, the MSU enzymes of eukaryotic MSU RNAPs are similar to the prokaryotic ones and use an R as the catalytic amino acid. However, they maintain a different distance conservation in the initiation and elongation subunits. An invariant Zn^{2+} binding motif found in the Rpb1 elongation subunits, is proposed to participate in the proof-reading function. Therefore, it is clear from this communication that even though the transcription machinery of eukaryotes is much more complex than that of prokaryotes, the general principals of transcription and its regulation are found to be highly preserved. Hence, it is proposed that the MSU RNAP II of eukaryotes may also follow very similar polymerization and proof-reading mechanisms like their counterparts in eubacteria. MSA data and the available experimental data show that both the eubacterial and eukaryotic MSU RNAPs would have evolved from a common ancestor.

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COMPETING INTERESTS

The author has declared that no competing interests exist.

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