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Short Communication

The human *DDX* and *DHX* gene families of putative RNA helicases

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Abstract

Nucleic acid helicases are characterized by the presence of the helicase domain containing eight motifs. The sequence of the helicase domain is used to classify helicases into families. To identify members of the DEAD and DEAH families of human RNA helicases, we used the helicase domain sequences to search the nonredundant peptide sequence database. We report the identification of 36 and 14 members of the DEAD and DEAH families of putative RNA helicases, including several novel genes. The gene symbol *DDX* had been used previously for both DEAD- and DEAH-box families. We have now adopted *DDX* and *DHX* symbols to denote DEAD- and DEAH-box families, respectively. Members of human *DDX* and *DHX* families of putative RNA helicases play roles in differentiation and carcinogenesis.

Nucleic acid helicases are characterized by the presence of the helicase domain, which consists of eight conserved motifs (I, Ia, Ib, and II-VI). The helicase domain contains the amino acids required for ATP binding, hydrolysis, and nucleic acid binding and unwinding [1]. Helicases are classified into DNA and RNA helicases, depending on their substrate specificity [2]. The majority of putative RNA helicases fall into two families, DEAD-box and DEAH-box, which are named after the single-letter designation of the amino acid sequence of motif II. However, the helicase domain shows differences in other motifs as well [3]. Human putative RNA helicases have been given the gene family symbol *DDX*, which does not distinguish between DEAD- and DEAH-box families. The exact number and functions of human DEAD-box and DEAH-box proteins are unknown. To identify human members of both families, we used the sequence of the helicase domain of a representative helicase that contains the consensus sequence of each family to search the nonredundant (nr) peptide sequence database by using the PSI-protein BLAST program [4] at the National Center for Biotechnology Information (NCBI) (http://www.ncbi.nlm.nih.gov/BLAST/). Thus, 292 amino acids encompassing the helicase domain of *DDX2A* (EIF4A) were used to detect members of the DEAD-box, and 306 amino acids encompassing the helicase domain of *DDX8* (HRH1) were used to detect members of the DEAH-box domain. The nr peptide sequence database at NCBI was searched using the limitation of *Homo sapiens* [ORGN]. Results with a bit score >40 were analyzed. Sequences showing a significant substitution of amino acids in the consensus sequence are excluded, such as *DDX32* (LocusLink 55760) and *DQX1* (LocusLink 165545) (DEAH-box). Also excluded were very closely related sequences that might represent alternatively spliced isoforms, or sequencing differences and putative RNA helicases with consensus sequence similar to members of the Ski2p family of yeast helicases, such as *DDX13* (LocusLink 6499), *DDX22*, and KIAA0052 (LocusLink 23517). Finally, we also excluded genes with homology to xeroderma pigmentosum genes, which were given the *DDX* designations, *DDX11* (LocusLink 1663) and *DDX12* (LocusLink 1664).

To allow easy distinction between the DEAD-box and DEAH-box families, human *DDX* and *DHX* and mouse *Ddx* and *Dhx* gene symbols were approved by both human and mouse nomenclature committees, respectively. Table 1 lists

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Table 1
Summary of the features of the members of the human family of putative RNA helicases of the DEAD-box (*DDX*) and DEAH-box (*DHX*) families

Gene Symbol	Aliases	LocusLink	Location	Function (proven or suggested) and/or other features	Reference	Yeast Homologue	% identity
DEAD-box family							
DDX1	*DBP-RB*	1653	2p24	Over-expressed in neuroblastoma and retinoblastoma, pre-mRNA processing	6,7	Dbp2p	32 over 344 aa
DDX2A	EIF4A, EIF-4A	1973	17p13	Translation initiation	8,9	Tif2p	66 over 387 aa
DDX2B	BM-010, EIF4A2	1974	3q28	Translation initiation	9, 10	Tif2p	65 over 384 aa
DDX3Y	*DBY*	8653	Yq11	Spermatogenesis	11	Dbp1p	48 over 667 aa
DDX3X	*DDX14, DBX, HLP2*	1654	Xp11.3-p11.23	Translation	12	Dbp1p	49 over 657 aa
DDX4	VASA Protein	54514	5p15.2-p13.1	Germ cell development	13	Dbp1p	45 over 494 aa
DDX5	p68, *HLR1*, G17P1, HUMp68	1655	17q21	Rearrangement of RNA secondary structure, organ differentiation, over-expressed in colorectal cancer	14, 15, 16	Dbp2p	58 over 473 aa
DDX6	p54, *RCK, HLR2*	1656	11q23.3	Over-expressed in colorectal cancer, involved in t(11;14)(q23; q32) in lymphoma, role in mRNP assembly	17, 18, 19	Dhh1p	66 over 423 aa
DDX7	RNA Helicase, 52 kDa	1658	17q21.31	ND	20	Dhh1p	30 over 363 aa
DDX10	HRH-J8	1662	11q22-q23	Involved in Inv (11)(p15q22) in leukemia, function not determined	21	Hca4P	46 over 597 aa
DDX17	p72	10521	22q13.1	Related to p68, rearrangement of RNA secondary structure	14	Dbp2p	59 over 477 aa
DDX18	*MrDb*	8886	2q13	Target for transcription activation by Myc-Max heterodimers	22	Has1p	59 over 502 aa
DDX19	*DBP5*	11269	16q22	Nuclear export of mRNA	23	Dbp5p	46 over 476 aa
DDX20	*DP103, GEMIN3*	11218	1p21.1-p13.2	Transcription regulation	24	Dhh1p	36 over 396 aa
DDX21A	*GURDB, RH-II/GU*, Gu Protein	9188	10q21	Ribosome biogenesis, transcription co-factor	25, 26	Dbp1p	34 over 439 aa
DDX21B	GU2	79009	10q22.1	Ribosome biogenesis, transcription co-factor	25, 26	Prp28p	36 over 583 aa
DDX23	U5-100K, prp28	9416	12q13	Pre-mRNA splicing	27	Prp28p	36 over 583 aa
DDX24	CHL1-Like helicase	57062	14q32	ND	28	Mak5p	33 over 495 aa
DDX25	*GRTH*	29118	11q24	Spermatogenesis	29	Dbpp	47 over 369 aa
DDX27	dJ686N3.1	55661	20q13.13	ND		Rrp3p	34 over 524 aa
DDX28	MDDX28, FLJ11282	55794	16q22.1	ND	30	RRP3p	32 over 391 aa
DDX31	FLJ13633, FLJ14578, FLJ23349	64794	9q34.3	ND		Dbp7p	30 over 718 aa
DDX39	*DDXL, BAT1*	10212	19p13.13	RNA synthesis	31	Sub2p	62 over 439 aa
DDX41	DEAD-box protein abstrakt	51428	5q35	Visual system development	32	Ded1p	38 over 429 aa
DDX42	*RNAHP, RHELP*	11325	17q23	ND		Dpb2p	44 over 422 aa
DDX43	*HAGE*, DKFZp434H2114	55510	6q12-13	Over-expressed in several tumors, function not determined	33	Dpb2p	45 over 438 aa
DDX46	KIAA0801, FLJ25329	9879	5q31.1	ND		Dbp2p	45 over 425 aa
DDX47	hqp0256 protein	51202	12p13.2	ND		Prp3	56 over 404 aa
DDX48	KIAA0111	9775	17q25.3	ND		Fal1p	61 over 395 aa
DDX49	FLJ10432	54555	19p12	ND		Dbp8p	47 over 428 aa
DDX51	GI: 25455599	317781	ND	ND		Dbp6p	32 over 465 aa
DDX52	ROK1	11056	17q12.1	ND		ROK1	44 over 504 aa
DDX53		253636	Xp22	ND		Dbp2p	42 over 433 aa
DDX54	Apoptosis related protein 5	79039	12q24.11	ND		Dbp10p	36 over 830 aa
DDX55	KIAA1595	57696	12q24.13	ND		Spb4	39 over 569 aa
DDX56	NOH61	54606	7p15	ND		Dbp9p	42 over 580 aa
DEAH-box family							
DHX8	*HRH1*	1659	17q21	Nuclear export of spliced mRNA	34	Prp22p	49 over 986 aa
DHX9	RHA, NDHII	1660	1q25	Transcription, RNA metabolism, normal gastrulation	35, 36, 37	Y1r419wp	31 over 632 aa
DHX15	*HRH2, DBP1*	1665	4p15	Pre-mRNA splicing	38	PrPp43p	65 over 678 aa
DHX16	*DBP2*	8449	6p21	Pre-mRNA splicing	39	Prp22p	44 over 877 aa
DHX29		54505	5q11	ND		Y1r419wp	31 over 693 aa
DHX30	KIAA0890, FLJ11214	22907	3p21	ND		Y1r419wp	31 over 631 aa
DHX33	FLJ21972, DKFZp762F2011	56919	17p13	ND		Prp22p	43 over 637 aa
DHX34	KIAA0134	9704	19q13	Candidate tumor suppressor gene for gliomas, function not determined	40	Prp2	40 over 228 aa
DHX35	FLJ22759	60625	20q12	ND		Prp22p	47 over 666 aa
DHX36	MLEL1/KIAA1488	170506	3q25	ND		Y1r419wp	29 over 921 aa
DHX37	KIAA1517	57647	12q24	ND		DHR1	42 over 818 aa
DHX38	KIAA0224	9785	16Q22	PRE-mRNA splicing	41	Prp16p	49 over 782 aa
DHX40	ARG147, PAD	79665	17q22	ND		Prp22p	41 over 665 aa
DHX57	AAM73547	90957	2P22.3	ND		Y1r419wp	28 over 895 aa

Note. ND, not determined.

DEAD-box	I	Ia	Ib	II	III	IV	V	VI
DDX1	SKAPDGYI	PSRELAEQ	TPGR	DEAD	SAT	IIF	ARGID	YVHRIGRVGRAE
DDX2A	AQSGTGKT	PTRELAQQ	TPGR	DEAD	SAT	VIF	ARGID	YIHRIGRGGRFG
DDX2B	AQSGTGKT	PTRELAQQ	TPGR	DEAD	SAT	VIF	ARGID	YIHRIGRGGRFG
DDX3Y	AQTGSGKT	PTRELAVQ	TPGR	DEAD	SAT	LVF	ARGLD	YVHRIGRTGRVG
DDX3X	AQTGSGKT	PTRELAVQ	TPGR	DEAD	SAT	LVF	ARGLD	YVHRIGRTGRVG
DDX4	AQTGSGKT	PTRELVNQ	TPGR	DEAD	SAT	MVF	ARGLD	YVHRIGRTGRCG
DDX5	AQTGSGKT	PTRELAQQ	TPGR	DEAD	SAT	IVF	SRGLD	YIHRIGRTARST
DDX6	AKNGTGKS	PTRELALQ	TPGR	DEAD	SAT	IIF	TRGID	YLHRIGRSGRFG
DDX7	APTGTGKT	PSQELAMQ	TLGR	DEAD	SAT	LVF	ARGLD	YIHRAGRTGRMG
DDX10	AKTGSGKT	PTRELAYQ	TPGR	DEAD	SAT	IVF	ARGLD	YIHRAGRTARYK
DDX17	AQTGSGKT	PTRELAQQ	TPGR	DEAD	SAT	IIF	SRGLD	YVHRIGRTARST
DDX18	AKTGSGKT	PTRELAMQ	TPGR	DEAD	SAT	MVF	ARGLD	YIHRVGRTARGL
DDX19	SQSGTGKT	PTYELALQ	TPGT	DEAD	SAT	MIF	ARGID	YLHRIGRTGRFG
DDX20	AKSGTGKT	PTREIAVQ	SPGR	DEAD	SAT	LVF	SRGID	YMHRIGRAGRFG
DDX21A	ARTGTGKT	PTRELANQ	TPGR	DEVD	SAT	IIF	ARGLD	YIHRSGRTGRAG
DDX21B	ARTGTGKT	PTRELANQ	TPGR	DEVD	SAT	IIF	ARGLD	YIHRSGRTGRAG
DDX23	AETGSGKT	PTRELAQQ	TPGR	DEAD	TAT	IIF	GRGID	YIHRIGRTGRAG
DDX24	AETGSGKT	PTRELAVQ	TPGR	DEAD	SAT	LVF	ARGLD	YVHRSGRTARAT
DDX25	SQSGTGKT	PTYELALQ	TPGT	DEAD	SAT	IIF	ARGID	YLHRIGRTGRFG
DDX27	AATGTGKT	PTRELGIQ	TPGR	DEAD	SAT	MLF	ARGLD	YDHRVGRTARAG
DDX28	AETGSGKT	PSRELAQQ	TPGA	DEAD	GAT	LVF	SRGLD	YIHRAGRVGRVG
DDX31	SQTGSGKT	PTRELALQ	TPGR	DEAD	SAT	VVF	ARGLD	YIHRIGRTARIG
DDX39	AKSGMGKT	HTRELAFQ	TPGR	DECD	SAT	VIF	GRGMD	YLHRVARAGRFG
DDX41	AFTGSGKT	PSRELARQ	TPGR	DEAD	SAT	LIF	SKGLD	YVHRIGRTGRSG
DDX42	AKTGSGKT	PTRELCQQ	TPGR	DEAD	SAT	LLF	ARGLD	HTHRIGRTGRAG
DDX43	AQTGTGKT	PTRELALQ	TPGR	DEAD	SAT	IVF	SRGLD	YVHRIGRTGRAG
DDX46	AKTGSGKT	PTRELALQ	TPGR	DEAD	SAT	IIF	ARGLD	YVHRAGRTGRAG
DDX47	AETGSGKT	PTRELAFQ	TPGR	DEAD	SAT	MIF	SRGLD	YIHRVGRTARAG
DDX48	SQSGTGKT	PTRELAVQ	TPGR	DEAD	SAT	VIF	ARGLD	YIHRIGRSGRYG
DDX49	AKTGSGKT	PTRELAYQ	TPGR	DEAD	SAT	IIF	SRGLD	YIHRVGRTARAG
DDX51	APTGSGKT	PTKELARQ	TPGR	DEAD	SAT	LCF	ARGID	YVHRVGRTARAG
DDX52	APTGSGKT	PTRELASQ	TPNR	DESD	SAT	LVF	ARGID	YIHRIGRTGRAG
DDX53	AQTGTGKT	PTRELALH	TPGR	DEAD	SAT	IMF	ARGLD	YVHRVGYIGRTG
DDX54	ARTGSGKT	PTRELALQ	TPGR	DEAD	SAT	VVF	ARGLD	FLHRVGRVARAG
DDX55	AVTGSGKT	PTRELAI	TPGR	DEAD	SAT	VFF	ARGID	FVHRCGRTARIG
DDX56	ARTGSGKT	PTKELARQ	TPSR	DEAD	SAT	LLF	ARGID	YIHRAGRTARAN
Consensus	**AxxGxGKT**	**PTRELAxQ**	**TPGR**	**DEAD**	**SAT**	**xIF**	**ARGLD**	**YIHRxGRxGRxG**

DEAH-box	I	Ia	Ib	II	III	IV	V	VI
DHX8	GETGSGKTT	TQPRRV	TDGML	DEAH	SAT	FLTG	TNIAET	QRAGRAGR
DHX9	GATGCGKTT	TQPRRI	TVGVL	DEIH	SAT	FLPG	TNIAET	QRKGRAGR
DHX15	GETGSGKTT	TQPRRV	TDGML	DEAH	SAT	FLTG	TNIAET	QRAGRAGR
DHX16	GETGSGKTT	TQPRRV	TDGML	DEAH	SAT	FLTG	TNIAET	QRAGRAGR
DHX29	GETGSGKST	TQPRRI	TTGVL	DEVH	SAT	FLPG	TNIAET	QRQGRAGR
DHX30	GDTGCGKTT	TQPRRI	TVGIL	DEVH	SAT	FLPG	TNIAET	QRRGRAGR
DHX33	GETGSGKTT	TQPRRV	TDGML	DEAH	SAT	FLTG	TNIAET	QRTGRAGR
DHX34	GDTGCGKST	TQPRRI	TVGLL	DEVH	SAT		TNIAET	QRKGRAGR
DHX35	GETGCGKST	TQPRRV	TDGIL	DEAH	SAT	FLTG	TNVAET	QRAGRGGR
DHX36	GETGCGKTT	TQPRRI	TTGII	DEIH	SAT	FLPG	TNIAET	QRKGRAGR
DHX37	GETGSGKTT	TEPRRV	TDGVL	DEAH	SAT	FLTG	TNVAET	QRAGRAGR
DHX38	GETGSGKTT	TQPRRV	TDGML	DEAH	SAT	FMPG	TNIAET	QRSGRAGR
DHX40	GNTGSGKTT	TQPRKV	TDGCL	DEAH	SAT	FLTG	TNISAT	QRSGRAGR
DHX57	GMTGCGKTT	TQPRRI	TGVLL	DEVH	SAT	FLPG	TNIAET	QRKGRAGR
Consensus	**GETGSGKTT**	**TQPRRV**	**TDGxL**	**DEAH**	**SAT**	**FLTG**	**TNIAET**	**QRxGRAGR**

Fig. 1. The amino acid sequence of the eight helicase motifs constituting the helicase domain of *DDX* and *DHX* genes.

the human DEAD-box and DEAH-box members of putative RNA helicases. Fig. 1 shows the single-letter designation of the amino acid sequence of the eight motifs for each protein. Human DEAD-box and DEAH-box families include 36 and 14 members, respectively, compared to 27 and 7 in *Saccharomyces cerevisiae* [3]. The consensus sequence is similar to that of the yeast [3], an observation that is consistent with the evolutionary conservation of these gene families. For each human *DDX* and *DHX* gene, the most likely *S. cerevisiae* ortholog was identified using the BLATP program to search the yeast genomic nucleotide sequence database at NCBI. The results of this search are shown in Table 1.

Functional studies in yeast show that the two families appear to be involved in various steps of RNA metabolism. The majority of DEAD-box family members have demonstrated functions in ribosome biogenesis and translation

initiation. A few DEAD-box members such as the yeast *Prp5* and *Prp28* genes are involved in pre-mRNA splicing, in comparison to the majority of DEAH-box family members [3]. Table 1 lists the proven or suggested functions and/or other features of human *DDX* and *DHX* genes. Generally, DEAD-box members are involved in ribosome biogenesis (*DDX21A*, *DDX21B*), and translation initiation (*DDX2A*, *DDX2B*), whereas DEAH-box members are involved in pre-mRNA splicing (*DHX15*, *DHX16*, *DHX38*). In addition to a function in RNA metabolism, two other functional features appear to be present in these gene families. The first feature is dysregulation in cancer, which occurs in the form of involvement in recurrent chromosomal translocations (*DDX6*, *DDX10*), overexpression (*DDX1*, *DDX6*, *DDX43*), or identification as a candidate tumor suppressor gene (*DHX34*). This is not surprising, because genes encoding putative RNA helicases would be thought to have functions affecting the integrity of RNA machinery. Comparably, DNA helicase mutations are known to result in genetic disorders characterized by increased incidence of cancer such as xeroderma pigmentosum and Bloom syndrome [5].

The second feature is the involvement of *DDX* members in tissue-organ differentiation (*DDX4* in germ cell development, *DDX5* in organ differentiation, *DDX25* in spermatogenesis, and *DDX41* in visual system development) (Table 1). Therefore, putative RNA helicases may have a function in differentiation, possibly by their effect on the expression of critical differentiation genes.

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