

Guidelines for the nomenclature of the human heat shock proteins

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Abstract The expanding number of members in the various human heat shock protein (HSP) families and the inconsistencies in their nomenclature have often led to confusion. Here, we propose new guidelines for the nomenclature of the human HSP families, HSPH (HSP110), HSPC (HSP90), HSPA (HSP70), DNAJ (HSP40), and HSPB (small HSP) as well as for the human chaperonin families HSPD/E (HSP60/HSP10) and CCT (TRiC). The nomenclature is based largely on the more consistent nomenclature assigned by the HUGO Gene Nomenclature Committee and used in the National Center of Biotechnology Information Entrez Gene database for the heat shock genes. In addition to this nomenclature, we provide a list of the human Entrez Gene IDs and the corresponding Entrez Gene IDs for the mouse orthologs.

Keywords Nomenclature · Human heat shock proteins

Introduction

Human heat shock proteins (HSPs) were originally identified as stress-responsive proteins required to deal with thermal and other proteotoxic stresses. It became clear shortly thereafter that all HSP families also encode constitutively expressed members like Hsc70 (HSPA8) in the HSP70 family. The heat shock genes (and the protein family members that they encode) that have been most extensively studied are those that are heat inducible, such as HSP70i (HSPA1A/B), HSP40 (DNAJB1), and HSP27 (HSPB1). With the sequencing of the human genome and

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the computational annotation of its genes, it became apparent that most HSP families contain additional members. The number of genes coding for the diverse HSP family members varies widely in different organisms. For example, in the HSPA (HSP70) family, the number of members varies from three in *Escherichia coli* to 13 in humans. Gene duplication during evolution likely satisfied the need for additional members in different intracellular compartments as well as for tissue specific or developmental expression. Moreover, gene duplication provides functional diversity for client specificity and/or processing.

Since the annotation of the human genome, the names used for the human family members in the literature have become rather chaotic and up to ten different names can be found for the same gene product. In addition, almost identical names have been used to refer to different gene products. For example, HSPA1B has been called HSP70-2, whereas HSP70.2 refers to the testis specific HSPA2 member. This has greatly hampered studies that involve comparisons of regulation and function between these members. The first attempt to clarify the nomenclature of the HSPA family was published in 1996 (Tavaria et al. 1996) but now requires modification and expansion. Here, we provide updated guidelines for the nomenclature of human HSPA (HSP70) as well as for the HSPH (HSP110), HSPC (HSP90), DNAJ (HSP40), and HSPB (small HSP) families and for the human chaperonin families (HSP60 and

CCT). This nomenclature is based on the systematic gene symbols that have been assigned by the HUGO Gene Nomenclature Committee (HGNC) and are used as the primary identifiers in databases such as Entrez Gene and Ensemble. For HSP gene retrieval, we used Entrez Gene (Wheeler et al. 2008). Mouse orthologs were identified using National Center of Biotechnology Information (NCBI) Homologene (Wheeler et al. 2008).

The HSPA (HSP70) and HSPH (HSP110) families

The human genome encodes 13 members of the HSPA family (Table 1), excluding the many pseudogenes (Brocchieri et al. 2008). The most studied genes are HSPA1A and HSPA1B, the products of which only differ by two amino acids and which are believed to be fully interchangeable proteins. Together with HSPA6, these are the most heat-inducible family members. *HSPA7* has long been considered to be a pseudogene, but recent analyses (Brocchieri et al. 2008) suggest that it might be a true gene that is highly homologous to *HSPA6*. HSPA8 is the cognate HSPA and was designated previously as Hsc70 (or HSP73). It is an essential “house-keeping” HSPA member and is involved in cotranslational folding and protein translocation across intracellular membranes. HSPA1L and HSPA2 are two cytosolic family members

Table 1 HSP70 superfamily: HSPA (HSP70) and HSPH (HSP110) families

	Gene name	Protein name	Old names	Human gene ID	Mouse ortholog ID
HSP A					
1	<i>HSPA1A</i>	HSPA1A	HSP70-1; HSP72; HSPA1	3303	193740
2	<i>HSPA1B</i>	HSPA1B	HSP70-2	3304	15511
3	<i>HSPA1L</i>	HSPA1L	hum70t; hum70t; Hsp-hom	3305	15482
4	<i>HSPA2</i>	HSPA2	Heat-shock 70kD protein-2	3306	15512
5	<i>HSPA5</i>	HSPA5	BIP; GRP78; MIF2	3309	14828
6	<i>HSPA6</i>	HSPA6	Heat shock 70kD protein 6 (HSP70B')	3310	X
7	<i>HSPA7^a</i>	HSPA7	Heat shock 70kD protein 7	3311	X
8	<i>HSPA8</i>	HSPA8	HSC70; HSC71; HSP71; HSP73	3312	15481
9	<i>HSPA9</i>	HSPA9	GRP75; HSPA9B; MOT; MOT2; PBP74; mot-2	3313	15526
10	<i>HSPA12A</i>	HSPA12A	FLJ13874; KIAA0417	259217	73442
11	<i>HSPA12B</i>	HSPA12B	RP23-32L15.1; 2700081N06Rik	116835	72630
12	<i>HSPA13^b</i>	HSPA13	Stch	6782	110920
13	<i>HSPA14</i>	HSPA14	HSP70-4; HSP70L1; MGC131990	51182	50497
HSP H					
1	<i>HSPH1</i>	HSPH1	HSP105	10808	15505
2	<i>HSPH2^b</i>	HSPH2	HSPA4; APG-2; HSP110	3308	15525
3	<i>HSPH3^b</i>	HSPH3	HSPA4L; APG-1	22824	18415
4	<i>HSPH4^b</i>	HSPH4	HYOU1/Grp170; ORP150; HSP12A	10525	12282

^a Annotated as pseudogene, but possibly a true gene

^b Under consultation with HGNC and the scientific community

Table 2 The DNAJ (HSP40) family

	Gene name	Protein name	Old names	Human gene ID	Mouse ortholog ID
DnaJA					
1	<i>DNAJA1</i>	DNAJA1	DJ-2; DjA1; HDJ2; HSDJ; HSJ2; HSPF4; hDJ-2	3301	15502
2	<i>DNAJA2</i>	DNAJA2	DNJ3; mDj3; Dnaj3; HIRIP4	10294	56445
3	<i>DNAJA3</i>	DNAJA3	Tid-1; Tid11	9093	83945
4	<i>DNAJA4</i>	DNAJA4	Dj4; Hsj4	55466	58233
DnaJB					
5	<i>DNAJB1</i>	DNAJB1	HSPF1; HSP40	3337	81489
6	<i>DNAJB2</i>	DNAJB2	HSJ1; HSPF3; Dnajb10; MDJ8	3300	56812
7	<i>DNAJB3</i>	DNAJB3	Hsj3; Msj1; MSJ-1; Hcg3 ^a	414061 ^a	15504
8	<i>DNAJB4</i>	DNAJB4	Hsc40	11080	67035
9	<i>DNAJB5</i>	DNAJB5	Hsc40; HSP40-3	25822	56323
10	<i>DNAJB6</i>	DNAJB6	Mrj; mDj4	10049	23950
11	<i>DNAJB7</i>	DNAJB7	Dj5; mDj5	150353	57755
12	<i>DNAJB8</i>	DNAJB8	mDj6	165721	56691
13	<i>DNAJB9</i>	DNAJB9	Mdg1; mDj7; ERdj4	4189	27362
14	<i>DNAJB11</i>	DNAJB11	Dj9; ABBP-2; Erdj3	51726	67838
15	<i>DNAJB12</i>	DNAJB12	Dj10; mDj10	54788	56709
16	<i>DNAJB13</i>	DNAJB13	Tsarg6; Tsarg 3 protein	374407	69387
17	<i>DNAJB14</i>	DNAJB14	EGNR9427; FLJ14281	79982	70604
DnaJC					
19	<i>DNAJC1</i>	DNAJC1	MTJ1; ERdj1; ERj1p; Dnaj1	64215	13418
20	<i>DNAJC2^b</i>	DNAJC2	Zrf1; Zrf2; MIDA1; M-phase phosphatase protein 11; MPP11; zuotin; ZUO1	27000	22791
21	<i>DNAJC3</i>	DNAJC3	p58; mp58; Prkri; Dnajc3; p58IPK; Dnajc3b	5611	100037258
22	<i>DNAJC4</i>	DNAJC4	HSPf2; Mcg18	3338	57431
23	<i>DNAJC5</i>	DNAJC5	Csp	80331	13002
24	<i>DNAJC5B</i>	DNAJC5B	CSP-beta	85479	66326
25	<i>DNAJC5G</i>	DNAJC5G	MGC107182; gamma-CSP	285126	231098
26	<i>DNAJC6</i>	DNAJC6	mKIAA0473; auxilin	9829	72685
27	<i>DNAJC7</i>	DNAJC7	Ttc2; mDj11; mTpr2	7266	56354
28	<i>DNAJC8</i>	DNAJC8	AL024084; AU019262; splicing protein (spf31)	22826	68598
29	<i>DNAJC9</i>	DNAJC9	AU020082; RcDNAJ9	23234	108671
30	<i>DNAJC10</i>	DNAJC10	JPDI; ERdj5; macrothioredoxin	54431	66861
31	<i>DNAJC11</i>	DNAJC11	FLJ10737; dJ126A5.1	55735	230935
32	<i>DNAJC12</i>	DNAJC12	Jdp1; mJDP1	56521	30045
33	<i>DNAJC13</i>	DNAJC13	Rme8; RME-8; Gm1124	23317	235567
34	<i>DNAJC14</i>	DNAJC14	HDJ3; LIP6; DRIP78	85406	74330
35	<i>DNAJC15</i>	DNAJC15	Dnajd1; MCJ; Cell growth-inhibiting 22 protein	29103	66148
36	<i>DNAJC16</i>	DNAJC16	mKIAA0962	23341	214063
37	<i>DNAJC17</i>	DNAJC17	C87112	55192	69408
38	<i>DNAJC18</i>	DNAJC18	MGC29463	202052	76594
39	<i>DNAJC19</i>	DNAJC19	TIM14; TIMM14	131118	67713
40	<i>DNAJC20^b</i>	DNAJC20	JAC1; HSC20; HscB	150274	100900
41	<i>DNAJC21</i>	DNAJC21	GS3; JJJ1; DNAJA5	134218	78244
42	<i>DNAJC22</i>	DNAJC22	FLJ13236; Wurst	79962	72778
43	<i>DNAJC23^b</i>	DNAJC23	Sec63; AI649014	11231	140740
44	<i>DNAJC24^b</i>	DNAJC24	DPH4; zinc finger, CSL-type containing 3	120526	99349
45	<i>DNAJC25</i>	DNAJC25	bA16L21.2.1; DnaJ-like protein; AAH48318; LOC552891; G-protein gamma 10	548645	72429
46	<i>DNAJC26</i>	DNAJC26	GAK; cyclin G associated kinase; auxilin-2	2580	231580
47	<i>DNAJC27^b</i>	DNAJC27	RBJ; RabJ	51277	217378
48	<i>DNAJC28</i>	DNAJC28	Orf28 open reading frame 28; C21orf55; oculomedin	54943	246738
49	<i>DNAJC29^b</i>	DNAJC29	Sacsin; SACS	26278	50720
50	<i>DNAJC30</i>	DNAJC30	WBSCR18; Williams–Beuren syndrome chromosome region 18 homolog (human)	84277	66114

^a Hcg3 is the closest human homologue of, and is syntenic with, MSJ-1 which encodes both N- and C-terminal domains in the same transcript but there is a reported frame shift between these domains

^b Under consultation with HGNC and the scientific community

Table 3 The HSPB family (small heat shock proteins)

	Gene name	Protein name	Old names	Human gene ID	Mouse ortholog ID
1	<i>HSPB1</i>	HSPB1	CMT2F; HMN2B; HSP27; HSP28; HSP25; HS.76067; DKFZp586P1322	3315	15507
2	<i>HSPB2</i>	HSPB2	MKBP; HSP27; Hs.78846; LOH11CR1K; MGC133245	3316	69253
3	<i>HSPB3</i>	HSPB3	HSPL27	8988	56534
4	<i>HSPB4^a</i>	HSPB4	crystallin alpha A; CRYAA, CRYA1	1409	12954
5	<i>HSPB5^a</i>	HSPB5	crystallin alpha B, CRYAB; CRYA2	1410	12955
6	<i>HSPB6</i>	HSPB6	HSP20; FLJ32389	126393	243912
7	<i>HSPB7</i>	HSPB7	cvHSP; FLJ32733; DKFZp779D0968	27129	29818
8	<i>HSPB8</i>	HSPB8	H11; HMN2; CMT2L; DHMN2; E2IG1; HMN2A; HSP22	26353	80888
9	<i>HSPB9</i>	HSPB9	FLJ27437	94086	75482
10	<i>HSPB10^a</i>	HSPB10	ODF1; ODF; RT7; ODF2; ODFP; SODF; ODF27; ODFPG; ODFPGA; ODFPGB; MGC129928; MGC129929	4956	18285
11	<i>HSPB11</i>	HSPB11	HSP16.2; C1orf41; PP25	51668	72938

^aUnder consultation with HGNC and the scientific community

with high expression in the testis. HSPA9 is the mitochondrial housekeeping HSPA member (HSPA9 is also known as mortalin/mtHSP70/GRP75/PBP74). We also note that there are two murine mortalins, mot-1 and mot-2. HSPA5 is the ER localized HSPA chaperone (BiP). Stch (which we propose to be called HSPA13) is found in microsomes and may yet be another compartment-specific HSPA member with housekeeping functions. HSPA12A, HSPA12B, and HSPA14 are more distantly related members about which very few data are available.

The human genome also encodes four HSP110 (HSPH; Table 1) genes which encode a family of HSPs with high homology to HSPA members except for the existence of a longer linker domain between the N-terminal ATPase domain and the C-terminal peptide binding domain. In fact, two members, HSPA4 (HSPH2) and HSPA4L (HSPH3), were previously named as HSPA members in the Entrez Gene database. Besides the three cytosolic members, one compartment-specific HSPH member (HYOU1/Grp170) is present in the ER, and we propose to name it HSPH4 to be consistent with the rest of the HSP110 family. Recent evidence shows that HSPH members are

nucleotide exchange factors for the HSPA family (Dragovic et al. 2006; Raviol et al. 2006).

The DNAJ (HSP40) family

A first attempt to standardize the HSP40 family nomenclature was published previously (Ohtsuka and Hata 2000) and parts of this system have been preserved herein. The DNAJ (HSP40) family is probably the largest HSP family in humans (Table 2) and is identified by the presence of a conserved J-domain known to be responsible for HSPA recruitment and stimulation of the HSPA ATPase activity. Cheetham and co-workers (Hennessy et al. 2005) divided this family into three subfamilies based on their homology to the DnaJ protein from *E. coli*. The human genome encodes four type A proteins (Table 2) that show homology to the *E. coli* DnaJ and contain an N-terminal J-domain (potentially following a signal sequence), a glycine/phenylalanine-rich region, a cysteine-rich region, and a variable C-terminal domain. To date, there are 14 type B proteins that contain an N-terminal J-domain and

Table 4 The HSP90/HSPC family

	Gene name	Protein name	Old names	Human gene ID	Mouse ortholog ID
1	<i>HSPC1^a</i>	HSPC1	HSP90AA1; HSPN; LAP2; HSP86; HSPC1; HSPCA; HSP89; HSP90; HSP90A; HSP90N; HSPCAL1; HSPCAL4; FLJ31884	3320	15519
2	<i>HSPC2^a</i>	HSPC2	HSP90AA2; HSPCA; HSPCAL3; HSP90ALPHA;	3324	X
3	<i>HSPC3^a</i>	HSPC3	HSP90AB1; HSPC2; HSPCB; D6S182; HSP90B; FLJ26984; HSP90-BETA	3326	15516
4	<i>HSPC4^a</i>	HSPC4	HSP90B1; ECGP; GP96; TRA1; GRP94; endoplasmic	7184	22027
5	<i>HSPC5^a</i>	HSPC5	TRAP1; HSP75; HSP90L	10131	68015

^aUnder consultation with HGNC and the scientific community

adjacent glycine/phenylalanine-rich region. This subfamily contains the most widely expressed and most heat-inducible human DNAJ member, DNAJB1. In addition, humans have 22 type C DNAJ proteins that only contain the J-domain but not necessarily positioned at the N terminus. It has been suggested that these members recruit HSPA members to specific subcompartments and/or functions. Finally, a number of other J-domain containing proteins are found in the NCBI and InterPro databases which have not yet been annotated as DNAJC members. They currently are listed in Table 2 as DNAJC23–DNAJC30. In addition, many *DNAJ* pseudogenes, which are not listed here, are scattered throughout the genome. Many of these pseudogenes show homology to only part of the J-protein but lack large parts of the protein, in some cases even the entire J-domain. A closely related family of proteins with imperfect HPD motifs has been described as ‘J-like’ proteins (Walsh et al. 2004). Only one annotated J-protein with an imperfect HPD motif is currently included—DNAJB13—which has an HPL instead that is conserved in the mouse ortholog. The gene previously named as *Dnajb10* is actually the mouse ortholog of human DNAJB2 and, hence, at our request has been renamed by the Mouse Genomic Nomenclature Committee as *Dnajb2*. *Hcg3* is the closest human homologue of DNAJB3/MSJ-1 and it encodes both N- and C-terminal domains in the same transcript but there is a reported frame shift between them, which, if true, results in a truncated protein of 145 amino acids.

The HSPB (small HSP) family

The family of small HSPs consists presently of 11 members (Table 3) that are characterized by a signature conserved crystallin domain flanked by variable N- and C-termini. The best studied members are HSPB1 (HSP27), HSPB4 (α A crystallin), and HSPB5 (α B crystallin). The small HSPs are often found in oligomeric complexes involving one or more family members and as such may provide the cell with a large diversity in chaperone specificity. Interestingly, many members show high and sometimes even exclusive expression in skeletal and cardiac muscle, but high expression is also found in many other tissues.

The HSPC (HSP90) family

This HSP family encodes five members (Table 4) with the exception of the so-called new member *Hsp89-alpha-delta-N* (*HSP90N*) (Schweinfest et al. 1998), which was found to be a chimera of two genes with its main part identical to *HSPC1* (Chen et al. 2005). The genes encoding these family members were initially annotated as *HSPC* members in Locuslink (the forerunner of the current Entrez Gene database). Based on the analysis of human and an additional 31 genomes across all kingdoms of organisms, Chen et al. (2005, 2006) built a nomenclature system for the family to indicate the homologues of different genes. To be consistent with the rest of the HSP family members, we

Table 5 Chaperonins and related genes

	Gene name	Protein name	Old names	Human gene ID	Mouse ortholog ID
HSPD					
1	<i>HSPD1</i>	HSPD1	HSP60; GroEL	3329	15510
HSPE					
1	<i>HSPE1</i>	HSPE1	HSP10; chaperonin 10; GroES	3336	15528
CCT					
1	<i>CCT1</i> ^a	CCT1	TCP1; CCTA; CCT-alpha; TCP-1-alpha	6950	21454
2	<i>CCT2</i>	CCT2	CCTB; CCT-beta; TCP-1-beta	10576	12461
3	<i>CCT3</i>	CCT3	CCTG; CCT-gamma; TCP-1-gamma; TRiC-P5	7203	12462
4	<i>CCT4</i>	CCT4	CCTD; CCT-delta; TCP-1-delta; SRB	10575	12464
5	<i>CCT5</i>	CCT5	CCTE; CCT-epsilon; TCP-1-epsilon	22948	12465
6	<i>CCT6A</i>	CCT6A	CCT6; CCTZ; CCT-zeta; CCT-zeta1; TCP-1-zeta; HTR3; TCP20	908	12466
7	<i>CCT6B</i>	CCT6B	CCTZ2; CCT-zeta2; TSA303	10693	12467
8	<i>CCT7</i>	CCT7	CCTH; CCT-eta; TCP-1-eta	10574	12468
9	<i>CCT8</i>	CCT8	CCTQ; CCT-theta; TCP-1-theta; KIAA002	10694	12469
Other chaperonin-like					
1	<i>MKKS</i>	MKKS	McKusick–Kaufman syndrome; MKS; Bardet–Biedl syndrome 6; BBS6	8195	59030
2	<i>BBS10</i>	BBS10	Bardet–Biedl syndrome 10	79738	71769
3	<i>BBS12</i>	BBS12	Bardet–Biedl syndrome 12	166379	241950

^aUnder consultation with HGNC and the scientific community

have chosen to use HSPC as the approved designation. However, we recognize that there will be occasions when it will be useful to link the human gene and protein names to earlier systems of nomenclature such as the one developed by Chen and colleagues. This nomenclature system provides an example of how nomenclature equivalence statements can be used to advantage, such as HSPC1/HSP90AA1, particularly when an author wants to link to an established phylogeny-based nomenclature to discuss homologues of the human HSPC genes in other organisms. We recommend that future phylogeny-based nomenclatures that include human homologues also include the root human designation such as HSPC as the beginning of the name of the gene in the other species.

The human chaperonin families (HSPD/E and CCT)

In the mitochondria, single human orthologs of the *E. coli* GroEL (HSP60) and GroES (HSP10) are expressed and are annotated as HSPD and HSPE, respectively (Table 5). In the cytosol of human cells CCT (TRiC), a hetero-oligomeric chaperonin complex composed of eight different subunits, plays an essential role in folding newly synthesized cytosolic proteins and preventing protein aggregation. These subunits are encoded by separate genes and share approximately 30% amino acid sequence identity (approximately 15–20% identity to GroEL). There are two genes encoding CCT6 (zeta subunit): CCT6A (zeta-1) is constitutively expressed while CCT6B (zeta-2) is expressed in a testis-specific manner. None of them has been shown to be heat inducible. Eight genes of this family are annotated in the NCBI database as *CCT2-CCT5*, *CCT6A*, *CCT6B*, *CCT7*, and *CCT8*. Although the human gene encoding the alpha subunit of CCT is not currently named as CCT1 by the HGNC (current symbol is TCP1), we think that the symbol CCT1 would be clearer because then it is obviously denoted as a subunit of CCT. In addition, three chaperonin-like genes, *MKKS/BBS6*, *BBS10*, and *BBS12*, have been identified in the human genome. Mutations in these genes cause McKusick–Kaufman syndrome and/or Bardet–Biedl syndrome (Stoetzel et al. 2006, 2007). Products of these three genes are unlikely to be CCT subunits and may be related to cilia and centrosome/basal body functions.

Other heat-inducible protein families and chaperones

There are proteins in other families that are heat inducible and that have chaperone-like functions. Some of these have also been named heat shock proteins, e.g., HSP47 (Nagai et al. 1999). This ER-resident protein functions as a collagen-specific chaperone. However, it has full length homology to

the serine peptidase inhibitor (serpin) protein family. So far, none of the other serpin paralogs has been demonstrated to be heat inducible or to have chaperone-like activities. Therefore, this gene has been named as *SERPINH1* by the HGNC and has not been listed as an Hsp here.

Concluding remarks

This is a first attempt to arrive at a consistent and clear nomenclature for the *HSP* and related chaperone genes in the human database. We realize that future modifications will be necessary and we plan to update the tables provided here at regular intervals. This nomenclature has been reviewed and approved by the editors of *Cell Stress & Chaperones* and all proposed modifications to the current HGNC nomenclature are currently under review by the HGNC. It has been adopted by this, the official journal of the Cell Stress Society International, as the accepted nomenclature of human heat shock genes and proteins.

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