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STAMPing at the crossroads of normal physiology and disease states

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ABSTRACT

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Keywords: STAMP STEAP Ironreductase Prostate cancer Metabolism Inflammation The six transmembrane protein of prostate (STAMP) proteins, also known as six transmembrane epithelial antigen of prostate (STEAPs), comprises three members: STAMP1-3. Their expression is regulated by a variety of stimuli, including hormones and cytokines, in varied settings and tissues with important roles in secretion and cell differentiation. In addition, they are implicated in metabolic and inflammatory diseases and cancer. Here, we review the current knowledge on the role of STAMPs in both physiological and pathological states.

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1. Discovery of the STAMP family

The six transmembrane protein of prostate (STAMP) proteins, also known as six transmembrane epithelial antigen of the prostate (STEAPs), consists of three members (STAMP1-3) (Fig. 1). STAMPs were characterized independently in different organisms within a short time period: *STAMP1* (*STEAP2*) was identified as a human gene that is highly expressed in the prostate (Korkmaz et al., 2002; Porkka et al., 2002). *STAMP2* (*STEAP4*) was then identified due to its sequence similarity to *STAMP1* (Korkmaz et al., 2005). The murine *Stamp2*, first called tumor necrosis factor- α -induced adipose-related protein (Tiarp) was cloned in 3T3-L1 adipocytes (Moldes et al., 2001). *Stamp3* (*Steap3*), also known as tumor suppressor activated pathway 6 (*Tsap6*), was first identified in murine myeloid M1 cells (Amson et al., 1996), and later cloned by the same group (Passer et al., 2003). The rat ortholog, pHyde, was independently discovered and cloned (Rinaldy et al., 2000).

STAMP proteins share high sequence similarity (Korkmaz et al., 2005, 2002; Moldes et al., 2001; Ohgami et al., 2005b; Porkka et al., 2002). As the name indicates, STAMPs contain a six α -helical transmembrane domain in the C-terminal half and an N-terminal

domain that shares similarity to the prokaryotic F_{420} :NADP⁺ Oxidoreductase (FNO) (Warkentin et al., 2001). The C-terminal transmembrane domain has distant homologies to yeast ferric reductases (FRE) and to mammalian NADPH oxidase (NOX). Since STAMPs also have metalloreductase activity, they are now placed along with NOX and FRE families within the ferric reductase domain (FRD) superfamily (Zhang et al., 2013). STEAP1 encodes a significantly truncated protein compared to STAMP1-3 that was first cloned as a gene predominantly expressed in human prostate and overexpressed in prostate cancer (PCa) (Hubert et al., 1999). Unlike STAMPs, STEAP1 lacks the N-terminal cytosolic domain that contains the essential motifs for oxidoreductase activity, and thus cannot reduce iron (Ohgami et al., 2006). Since this review mainly focuses on STAMP functions in which the iron reductase activity is involved, discussion of STEAP1 biology is not included herein. Detailed information about STEAP1 has been provided in previous reviews (Gomes et al., 2012; Grunewald et al., 2012).

2. Regulation of STAMP expression

STAMP expression has been found in multiple tissues and is regulated by a number of different stimuli (Table 1A, B, andC). This indicates the potential roles of the STAMP family in various physiological processes, tissues, and disease states. These data are summarized below.







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A		10	20	30	40	50	εo 70	80	90	100	110 1	20 130	140	150	160
	hSTAMP1	1 MESISMMGSPKSL	SETFLPNGING	IKDARKVTVGVI	DFAKSLTIRI	IRCGYHVVIG	SPNPKFASEFFP1	IVVDVTHHEDAI	TKTNIIFVAIH	REHYTSLWDLRHI	LLVGKILIDV <mark>SN</mark> NM	RINQYPESNAE	LASLFPDSLIVK	GFNVVSAWALO	LGPKDAS 162
	mStamp1	1 MESISMMGSPKSL	-ETFLPNGING	IKDARQVTVGVI	SEDFAKSLTIRI	IRCGYHVVIG	SPNPKFASEFFP1	IVVDVTHHEDAL	TKTNIIFVAIH	REHYTSLWDLRHI	LLVGKILIDV <mark>SN</mark> NM	RVNQYPESNAE	LASLFPDSLIVK	GFUVISAWALO	LGPKDAS 161
	hSTAMP2	1MEKTCID.	ALPLTM	NSSEKQETVCIF	TEDFGRSLGLKI	LQCGYSVVFG	SPNPQKT-TLLP:	GAEVLSYSEA	KKSGIIIIAIH	REHYDFLTELTEN	VLNGKILVDI <mark>SN</mark> NL	KINQYPESNAEY	LAHLVPGAHVVK	AFTISAWALQ	GALDAS 150
	mStamp2	1MEKAHAD	EFPLTT	DSSEKQGVVCIF	TEDFGKSLGLKI	LQCGYSIVFG	SPNPQVS-SLLPI	GAEVLSYSEA	SKSDIIILAMH	REHYDSLTELVDY	YLKGKVLVDV <mark>SN</mark> NR:	KINQYPESNAE	LAQLEPGAHVVK	AFTI AWALQ	GTLDAS 150
	hSTAMP3	1 MPEEMDKPLIS	LHLVDSDSSLA	KVPDEAPKVGIL	SUPARSLATE	VGSGFKVVVG	SPNPKRTARLFP:	SAAQVTFQEEA	SSPEVIEVAVE	REHYSSLCSLSD	QLAGKILVDV <mark>SN</mark> PT	EQEHLQHRESNAE	LASLFPTCTVVK	AFNV ISAWTLO	AGPRDGN 162
	mStamp3	1MSGEMDKPLIS	RRLVDSDGSLA	EVPKEAPKVGIL	SEDFARSLATRI	VGSGFSVVVG	SPNPKRTAGLFP:	SLAQVTFQEEA	SSPEVIEVAVE	REHYSSLCSLAD	QLAGKILVDV <mark>SN</mark> PT	EKEHLQHRQSNAEN	LASLFPACTVVK	AFWVISAWALO	AGPRDGN 162
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		* 456453	0365663	33537424*998*	9***+9**7699	9947*949*7*	****737-388*4	1787*63669*1	755749*89*87	****75*66*35	5*3**9*9*9**84	747*858****	**4*3*5739**	+**79***7**	5*65*+9
		170	180	190 20	00 210	220	230	240	250	260 27	70 280	290	300 3	10 320)
	hSTAMP1	163 ROVVICSNNIQAR	QQVIELARQLN	PIPIDLGSLSSAF	EIENLPLRLFT	WRGPVVVAIS	LATFFFLUSFVRI	VIHPYARNQQ	DFYKIPIEIVN	KTLPIVAITLLSI	LVYLAGLLAAAYQL	YYGTKYRRFP PWL E	TWLOCRHOLGLL	SFFFAMVHVAN	SLCLPMR 326
	mStamp1	162 ROVVICSNNIQAR	QQVIELARQLN	PIPVDLGSLSSAN	EIENLPLELFT	WRGPVVVAIS	LATFFFL ^M SFVRI	VIHPYARNQQ	DFYKIPIEIVN	KTLPIVAITLLSI	LVYLAGLLAAAYQL	YGTKYRRFFPWLI	TWLOCREOLGLL	SFFFAVVHVAT	SLCLPMR 325
	hSTAMP2	151 ROVEVCGNDSKAK	QRVMDIVRNLG	LTPMDQGSLMAAH	EIEKYPLQLFPN	WRFPFYLSAV	LCVFLFF <mark>_</mark> CVIRI	VIYPYVYEKK	NTFRMAISIPN	RIFPITALTLLAI	LVYLPGVIAAILQL	TR GTKYRRFP DWLI	HWMLCREQLGLV	ALGFAFLHVLY	TLVIPIR 314
	mStamp2	151 ROVEVCGNDSKAK	QRVMDIARTLG	LTPLDQGSLMAAS	EIENYPLOLFPN	WRFPFYLSSV	LCVFFFV	VIYPYVNGKT	ATYRLAISIPN	RVFPITALILLAI	LVYLPGILAAILQL	TR GTKYRRFP NWLI	HWMLCRROLGLV	ALGFAFLHVI	TLVIPIR 314
	hSTAMP3	163 ROVPICGDOPEAK	RAVSEMALAMG	PMPVDMGSLASAV	VEVEAMPLRLLP/	WKVPTLLALG	LFVCFYA <mark>N</mark> NFVRI	VLQPYVQESQ	IKFFKLPVSVVN	TTLPCVAYVLLSI	LVYLPGVLAAALQL	RRGTKYQRFFDWLI	HWLQHREQIGLL	SFFCAALHALM	SFCLPLR 326
	mStamp3	163 ROVLICSDOPEAK	RTISEMARAMG	TPLDMGSLASAR	EVEAIPLELPS	WKVPTLLALG	LFVCFYT	VLQPYIRKDE	KFYKMPLSVVN	TTLPCVAYVLLSI	LVYLPGVLAAALQL	RR <u>GTKYORFP</u> DWLI	HWLQH <mark>RR</mark> QIGLL	SFFFAMLHAL	SFCLPLR 326
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		330 34	0 320	360	370	380	390 4	100 4:	10 420	430	440	450 460	470	480	490
	hSTAMP1	327 RSERYLFLNMAYQ	QVHANIENSWN	EEEVWRIEMYISE	GIMSLGLLSLL	VTSIPSVSNA	LINNEEFSFICSTI	GYVALLISTF	VLIYGWKRAFE	EEYYRFYTPPNF\	VLALVLPSIVILGK	ILFLPCISRKLK	RIKKGWEKSQFLE	EGMGGTIPHVS	PERVTVM 490
	mStamp1	326 RSERYLFLNMAYQ	QVHANIENAWN	EEEVWRIEMYISE	GIMSLGLLSLL	VTSIPSVSNA	LINN REFSFICSTI	LGYVALL ITTF	VLIYGWKRAFA	EEYYRFYTPPNFV	VLALVLPSIVILGK	MILLLPCISRKLKE	RIKKGWEKSQFLD	EGMGGAVPHLS	PERVTVM 489
	-														



Fig. 1. The STAMP family - overview of the domains and functional motifs. A) A multiple sequence alignment of the members of the human and murine STAMP family (hSTAMP1, NP_001035755.1; mStamp1, NP_083010.2; hSTAMP2, NP_078912.2; mStamp2, NP_473439.2; hSTAMP3, NP_060704.2; mStamp3, NP_573449.2) constructed using Clustal Omega (Sievers et al., 2011). Brown to yellow numbers and bars below is similarity scores using AMAS method of multiple sequence alignment analysis built in Jalview (Livingstone and Barton, 1993; Waterhouse et al., 2009). Colored regions are highly conserved residues that are important for STAMP catalytic activity (Gauss et al., 2013; Kleven et al., 2015). These residues have been verified through resolving of crystal structures and/or mutagenesis studies (Gauss et al., 2013; Kleven et al., 2009; Sendamarai et al., 2008). The color-coding corresponds to the structural overview built with Illustrator for Biological Sequences (IBS). B) Different domains/sites in STAMP proteins (using tools as described in (Liu et al., 2015)). NADPH interaction (blue), FAD interaction (red), iron interaction (brown), heme-group interaction (purple), endosomal targeting motif (green). Question mark indicates conserved, but putative sites of interaction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1A

B

Regulation of STAMP1. Overview of expression levels of STAMP1 in tissues and the disease states. Also shown are cellular events that STAMP1 are involved in, or stimuli that can regulate its expression in various tissues/cell lines.

STAMP1 (STEAP2	2)	Tissue/cell line	Reference				
High expression	ion	Human: Prostate Human: Brain Pancreas Fetal Liver, Ovary	(Korkmaz et al., 2002; Ohgami et al., 2006; Porkka et al., 2002) (Korkmaz et al., 2002; Ohgami et al., 2006; Porkka et al., 2002)				
Low expression	1011	Human: Heart, Lung, Kidney, Liver, Bone Marrow, Colon, Small Intestine; Stomach, Thymus	(Korkmaz et al., 2002; Ohgami et al., 2006; Porkka et al., 2002) (Korkmaz et al., 2002; Ohgami et al., 2006; Porkka et al., 2002)				
Regulated express Stimuli/event/	ssion Effect						
disease Cancer progression	Increase	Prostate Cancer	(Korkmaz et al., 2002; Porkka et al., 2002; Wang et al., 2010a; Whiteland et al., 2014)				
Adipogenesis TNFa AR dependency	Decrease Decrease Maintenance	3T3-L1 murine preadipocytes, murine mesenchymal stem cell LNCaP human PCa cell line e Human PCa cell lines	(Sikkeland and Saatcioglu, 2013; Vaghjiani et al., 2009) (Gonen-Korkmaz et al., 2014) (Korkmaz et al., 2005; Korkmaz et al., 2002; Porkka et al., 2002)				

2.1. STAMP1

The expression of *STAMP1* mRNA is highly prostate-enriched, but is also detectable at low levels in several other tissues such as

heart, brain, kidney, pancreas, and ovary. *STAMP1* is highly expressed in the androgen-responsive PCa cell line LNCaP, but not the AR-negative cell lines PC3 and DU145 (Korkmaz et al., 2002; Porkka et al., 2002). Interestingly, STAMP1 expression is not

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