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The SDR (Short-Chain Dehydrogenase/Reductase and Related Enzymes) Nomenclature Initiative

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Summary

Short-chain dehydrogenases/reductases (SDR) constitute one of the largest enzyme superfamilies with presently over 46 000 members. In phylogenetic comparisons, members of this superfamily

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show early divergence where the majority have only low pair-wise sequence identity, although sharing common structural properties. The SDR enzymes are present in virtually all genomes investigated, and in humans over 70 SDR genes have been identified. In humans, these enzymes are involved in the metabolism of a large variety of compounds, including steroid hormones, prostaglandins, retinoids, lipids and xenobiotics. It is now clear that SDRs represent one of the oldest protein families and contribute to essential functions and interactions of all forms of life. As this field continues to grow rapidly, a systematic nomenclature is essential for future annotation and reference purposes. A functional subdivision of the SDR superfamily into at least 200 SDR families based upon hidden Markov models forms a suitable foundation for such a nomenclature system, which we present in this paper using human SDRs as examples.

Keywords

SDR; enzymes; nomenclature; bioinformatics; hidden Markov models

Introduction

One of the largest protein superfamilies is that of short-chain dehydrogenases/reductases (SDR) and other enzymes [1], with over 46,000 members in sequence databases and over 300 crystal structures deposited in PDB today. The SDR superfamily encompasses a “classical” type (corresponding to Pfam [2] entry PF00106) and an “extended” type (including epimerases and dehydratases; Pfam PF01073 and PF01370) [3,4]. In addition, transcriptional regulators such as fungal NmrA (Pfam PF05368) were shown to be structurally related to the SDR family and constitute a separate branch which we refer to as “atypical” SDRs [5,6]. These enzymes were established as a separate and new group of oxidoreductase in the 1970/80's [7,8], and the term SDR was coined in 1991 [9]. The enzyme family is present in all domains of life, from simple organisms to higher eukaryotes [10], emphasising their versatility and fundamental importance for metabolic processes. A recent survey shows that about 25% of all dehydrogenases belong to the SDR family [1]. SDR enzymes are NAD(P)(H)-dependent oxidoreductases which are distinct from the medium-chain dehydrogenase (MDR) and aldo-keto reductase (AKR) superfamilies [3,4].

Members of the SDR superfamily show early divergence and have only low pairwise sequence identity, but share common sequence motifs that define the cofactor binding site (TGxxxGxG) and the catalytic tetrad (N-S-Y-K), even though variations on this general theme also exist [11,12]. The three-dimensional SDR structures are clearly homologous with a common α/β -folding pattern characterised by a central β -sheet typical of a Rossmann-fold with helices on either side [4].

In humans over 70 SDR genes exist [13,14]. Human SDRs have physiological roles in steroid hormone, prostaglandin and retinoid metabolism, and hence signalling [14], or metabolise lipids and xenobiotics [15]. A growing number of single-nucleotide polymorphisms have been identified in SDR genes, and a variety of inherited metabolic diseases have as underlying cause genetic defects in SDR genes [16].

As the number of SDR sequences grows at an unprecedented pace, a systematic nomenclature is essential for annotation and reference purposes. For example, a recent metagenome analysis showed that classical and extended SDRs combined constitute at present by far the largest protein family [17]. Given this large amount of sequence data, a nomenclature system would prevent either the same protein or gene being given multiple names or the same name being given to multiple proteins or genes. Recently, a functional subdivision of the SDR superfamily into at least 200 SDR families has been reported based on Hidden Markov Models (HMMs),

using an iterative approach delineating a set of stable families, described in detail elsewhere [18]. These SDR families form a suitable foundation for the nomenclature system that is presented in this work.

Results and Discussion

SDR family identification using Hidden Markov Models (HMMs)

SDR proteins were extracted from the Uniprot database [19] and from Refseq [20], using a previously developed HMM [21] and the Pfam [2] profiles PF00106, PF01073, PF01370 and PF05368. SDR families were identified using a hidden Markov model approach. Initial HMMs were created based upon SDR clusters aligned using ClustalW [22]. These HMMs were iteratively refined to achieve stable and specific models that could be used for classification and functional assignments of SDR members [18]. In order to avoid bias of the models towards closely related proteins, the alignments were made non-redundant, so that no pair of sequences had more than 80% sequence identity. The iterative clustering process was automated using a series of shell scripts and programs developed in C. Elements of the large-scale computer analysis were carried out on the 805-node Hewlett-Packard DL140 cluster Neolith at the National Supercomputer Centre (Linköping, Sweden). Further details regarding this methodology is described elsewhere [18]. The HMMs will be made available for inclusion in the Pfam [2] and/or InterPro [23] databases.

A sustainable and expandable nomenclature scheme

In the nomenclature scheme, each SDR family has been given a unique number from 1 upwards. The 48 known human SDR families have been allocated numbers from 1 to 48..... of hitherto identified members. Thus, the SDR families found in human and the most common families get the lowest numbers. At present, there are 48 human SDR families detected which are listed in Table 1.

After numbering of all human families, priority was given to SDR families having mammalian or other eukaryotic members. Here, families present in all kingdoms were given lower numbers than those present in only two and one kingdom. Next, SDR families that were present in both bacteria and archaea were numbered, according to decreasing size of the family. Finally, SDR families present in bacteria were numbered, also according to family size, beginning with the largest. There is no single family with only archaeal members. All non-human SDR families are listed on the SDR web page <http://www.sdr-enzymes.org>.

Since sequences of newly characterised genomes are reported every month, and the number of completed genomes is expected to grow considerably over the coming years, thanks to the advances in sequencing technologies, it is likely that the current SDR families will grow and that more SDR families will be identified over time. Thus, new SDR family numbers will be added in the future, and the nomenclature will need to be continuously updated. As a continuous source and service to the scientific community we will update and make the data available through the website indicated above.

We are well aware that even if the majority of the protein-coding regions of the human genome are now known, there might be new hitherto unknown SDR forms identified, which might lead to a higher number. However, this is an inevitable consequence of any nomenclature system and should not preclude the launch of a system that covers the majority of known proteins based on current knowledge.

SDR types

There are two types of SDR enzymes with many members, and at least four types with fewer members. The two major types are denoted “Classical” and “Extended” [21] and these are clearly distinguished by subunit size and sequence patterns at the coenzyme binding site and at a segment N-terminally of the active site region. The currently four minor SDR types are denoted “Intermediate”, “Divergent”, “Complex” [21], and “Atypical”. The latter has SDR topology but no known enzymatic activity. Each of these types is characterised by type-specific sequence patterns at the coenzyme-binding site and/or the active site. In the nomenclature scheme, the family number is followed by one letter designating the SDR type, thus making it clear from a quick glance at the family designation to which type the SDR family belongs to, *e.g.* SDR1E represents an SDR of the extended type. The letters used in this scheme are shown in Table 2.

Optional numbering of individual family members

The nomenclature scheme is extended by adding a number after the type letter, so that each member of every SDR family is given an individual designation, *e.g.* SDR1E1. This is essential for tracking individual SDR members, since considerable confusion exists in the literature with multiple designations, aliases, names and abbreviations. Such individual numbering of enzyme members have since long been successfully implemented for other enzyme families, *e.g.* aldo-keto reductases (AKRs) [24] and cytochrome P450s [25], and has been recognised as a key to unambiguous referencing. The numbering for the human SDR enzymes is given in Table 1. SDR forms with neighbouring gene locations were given adjacent numbers, *e.g.* SDR16C2 and SDR16C3. An additional P after the number denotes a pseudogene, *e.g.* SDR14E1P.

Gene-oriented nomenclature

The new SDR nomenclature is gene based. Thus, all splice variants derived from the same gene hold the same main number, but each splice variant is distinguished by a sub-number, separated from the main number by a dash, *e.g.* SDR15C1-1, SDR15C1-2. Similarly, polymorphic variants and SNPs are assigned using an asterisk, resulting in a nomenclature such as SDR11E1*1, SDR11E1*2, SDR11E1*3. These are numbered according to the order of the corresponding refSNP (rs) numbers. A continuously updated list of these variants will be available at the SDR web page.

Hierarchical system

The new nomenclature system is strictly hierarchical so that the designations can be shortened at various stages, but still is clearly informative.

Example:

SDR15C1-1	one splice variant of a particular SDR member from one species
SDR15C1	a particular SDR member from one species
SDR15C	one specific SDR family of the classical type

Web page and continuous updates

The nomenclature scheme outlined in this paper is part of an international effort to systematise and to facilitate all aspects of SDR related research. This will be described in detail on the web page <http://www.sdr-enzymes.org>, where continuous updates will be available. In addition, various search functions will also be available here, *e.g.* to find the SDR name using an amino acid sequence as input or vice versa. This nomenclature system has been presented, discussed and endorsed on the occasions of the VII European Symposium of The Protein Society 2007,

the Endocrine Society meeting (ENDO 2007) and the 14th Carbonyl Metabolism meeting (2008).

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Table 1

SDR families with human members. Uniprot identifiers are given for all human SDRs (one representative per corresponding gene).

Family designation	Family name	Uniprot identifier	Accession number	Protein designation	Description
SDR1E	UDP-glucose 4-epimerase	GALE_HUMAN	Q14376	SDR1E1	UDP-glucose 4-epimerase
SDR2E	dTDP-D-glucose 4,6-dehydratase	TGDS_HUMAN	O95455	SDR2E1	dTDP-D-glucose 4,6-dehydratase/ Growth-inhibiting protein 21
SDR3E	GDP-mannose 4,6 dehydratase	GMDS_HUMAN	O60547	SDR3E1	GDP-mannose 4,6 dehydratase
SDR4E	GDP-L-fucose synthetase	FCL_HUMAN	Q13630	SDR4E1	GDP-L-fucose synthetase
SDR5C	3-hydroxyacyl-CoA dehydrogenase	HCD2_HUMAN	Q99714	SDR5C1	3-hydroxyacyl-CoA dehydrogenase type-2
SDR6E	UDP-glucuronic acid decarboxylase	UXS1_HUMAN	Q8NBZ7	SDR6E1	UDP-glucuronic acid decarboxylase 1
SDR7C	Retinol dehydrogenase	RDH11_HUMAN	Q8TC12	SDR7C1	Retinol dehydrogenase 11
		RDH12_HUMAN	Q96NR8	SDR7C2	Retinol dehydrogenase 12
		RDH13_HUMAN	Q8NBN7	SDR7C3	Retinol dehydrogenase 13
		RDH14_HUMAN	Q9HBH5	SDR7C4	Retinol dehydrogenase 14
		DHR13_HUMAN	Q6UX07	SDR7C5	EALL419
SDR8C	Peroxisomal multifunctional enzyme	DHB4_HUMAN	P51659	SDR8C1	Peroxisomal multifunctional enzyme type 2
SDR9C	Steroid and retinol dehydrogenase	BDH_HUMAN	Q02338	SDR9C1	D-beta-hydroxybutyrate dehydrogenase
		DHB2_HUMAN	F37059	SDR9C2	17-beta-hydroxysteroid dehydrogenase type 2
		DHI2_HUMAN	P80365	SDR9C3	Corticosteroid 11-beta-dehydrogenase isozyme 2
		DHRS9_HUMAN	Q9BPW9	SDR9C4	3-alpha hydroxysteroid dehydrogenase
		RDH1_HUMAN	Q92781	SDR9C5	11-cis retinol dehydrogenase
		HI7B6_HUMAN	O14756	SDR9C6	Oxidoreductase
		SDRO_HUMAN	Q8NEX9	SDR9C7	Retinol dehydrogenase similar protein
		RDH16_HUMAN	O75452	SDR9C8	Retinol dehydrogenase
SDR10E	Fatty acyl-CoA reductase	FACR1_HUMAN	Q8WVX9	SDR10E1	Hypothetical protein DKFZp686A0370
		FACR2_HUMAN	Q96K12	SDR10E2	Fatty acyl-CoA reductase 2
SDR11E	3 beta-hydroxysteroid dehydrogenase	3BHS1_HUMAN	P14060	SDR11E1	3 beta-hydroxysteroid dehydrogenase/Delta 5->4-isomerase type 1

Family designation	Family name	Uniprot identifier	Accession number	Protein designation	Description
		3BHS2_HUMAN	P26439	SDR11E2	3 beta-hydroxysteroid dehydrogenase/Delta 5-->4-isomerase type II
		3BHS7_HUMAN	Q9HF23	SDR11E3	3 beta-hydroxysteroid dehydrogenase type 7
SDR12C	Estradiol 17-beta-dehydrogenase	DHB12_HUMAN	Q53GQ0	SDR12C1	Estradiol 17-beta-dehydrogenase 12
		DHB3_HUMAN	P37058	SDR12C2	Estradiol 17-beta-dehydrogenase 3
		HSDL1_HUMAN	Q3SXM5	SDR12C3	Hydroxysteroid dehydrogenase like 1
SDR13C	Hydroxysteroid dehydrogenase-like	HSDL2_HUMAN	Q6YN16	SDR13C1	Hydroxysteroid dehydrogenase-like protein
SDR14E	L-threonine dehydrogenase	Q96KTI_HUMAN	Q96KTI	SDR14E1P	L-threonine dehydrogenase
SDR15C	3-hydroxybutyrate dehydrogenase	BDH2_HUMAN	Q9BUT1	SDR15C1	3-hydroxybutyrate dehydrogenase type 2
SDR16C	Steroid and retinol dehydrogenase	DHRS3_HUMAN	O75911	SDR16C1	Short-chain dehydrogenase/reductase 3
		DHB11_HUMAN	Q8NBQ5	SDR16C2	Dehydrogenase/reductase SDR family member 8
		DHB13_HUMAN	Q7Z5P4	SDR16C3	17-beta hydroxysteroid dehydrogenase 13
		RDH10_HUMAN	Q8IZV5	SDR16C4	Retinol dehydrogenase 10
		RDHE2_HUMAN	Q8N3Y7	SDR16C5	Retinal short chain dehydrogenase reductase isoform 1
		XP_498284		SDR16C6	PREDICTED: similar to RIKEN cDNA 4833413O15 gene
SDR17C	Peroxisomal 2,4-dienoyl-CoA reductase	DECR2_HUMAN	Q9NUJ1	SDR17C1	Peroxisomal 2,4-dienoyl-CoA reductase
SDR18C	2,4-dienoyl-CoA reductase	DECR_HUMAN	Q16698	SDR18C1	2,4-dienoyl-CoA reductase
SDR19C	Dehydrogenase/reductase SDR family	DHRS1_HUMAN	Q96LJ7	SDR19C1	Dehydrogenase/reductase SDR family member 1
SDR20C	L-xylulose reductase	DCXR_HUMAN	Q7ZAW1	SDR20C1	L-xylulose reductase
SDR21C	Carbonyl reductase	CBR1_HUMAN	P16152	SDR21C1	Carbonyl reductase 1
		CBR3_HUMAN	O75828	SDR21C2	Carbonyl reductase 3
SDR22E	NADH dehydrogenase	NDUA9_HUMAN	Q16795	SDR22E1	NADH dehydrogenase [ubiquinone]
SDR23E	Methionine adenosyltransferase	MAT2B_HUMAN	Q9NZL9	SDR23E1	Methionine adenosyltransferase 2 subunit beta
SDR24C	Dehydrogenase/reductase SDR family	DHR11_HUMAN	Q6UWP2	SDR24C1	Dehydrogenase/reductase SDR family member 11
SDR25C	Dehydrogenase/reductase SDR family	DHRS2_HUMAN	Q13268	SDR25C1	Dehydrogenase/reductase SDR family member 2

Family designation	Family name	Uniprot identifier	Accession number	Protein designation	Description
SDR26C	Corticosteroid 11-beta-dehydrogenase	DHRS4_HUMAN NP_001075957	Q9BTZ2	SDR25C2 SDR25C3	Dehydrogenase/reductase SDR family member 4 Similar to peroxisomal short-chain alcohol dehydrogenase
SDR27X	Fatty acid synthase	FAS_HUMAN	P49327	SDR27X1	Fatty acid synthase
SDR28C	17 beta-hydroxysteroid dehydrogenase	DHB1_HUMAN RDH8_HUMAN	P28845 Q9NYR8	SDR28C1 SDR28C2	17-beta-hydroxysteroid dehydrogenase type 1 Photoreceptor outer segment all-trans retinol dehydrogenase
SDR29C	Peroxisomal trans-2-enoyl-CoA reductase	PECR_HUMAN	Q9BY49	SDR29C1	Peroxisomal trans-2-enoyl-CoA reductase
SDR30C	Estradiol 17-beta-dehydrogenase	DHB8_HUMAN	Q92506	SDR30C1	Estradiol 17-beta-dehydrogenase 8
SDR31E	Sterol-4-alpha-carboxylate 3-dehydrogenase	NSDHL_HUMAN	Q15738	SDR31E1	Sterol-4-alpha-carboxylate 3-dehydrogenase
SDR32C	Dehydrogenase/reductase (SDR family) member 7B	DRS7B_HUMAN	Q6IAN0	SDR32C1	Dehydrogenase/reductase (SDR family) member 7B
SDR33C	Dihydropteridine reductase	DRS7C_HUMAN	A6NNS2	SDR32C2	Dehydrogenase/reductase SDR family member 7C precursor
SDR34C	Dehydrogenase/reductase SDR family	DHPR_HUMAN	P09417	SDR33C1	Dihydropteridine reductase
SDR35C	3-ketodihydrospingosine reductase	DHR57_HUMAN	Q9Y394	SDR34C1	Dehydrogenase/reductase SDR family member 7
SDR36C	15-hydroxyprostaglandin dehydrogenase	KDSR_HUMAN	Q06136	SDR35C1	3-ketodihydrospingosine reductase precursor
SDR37C	3-keto-steroid reductase	PGDH_HUMAN	P15428	SDR36C1	15-hydroxyprostaglandin dehydrogenase
SDR38C	Sepiapterin reductase	DHB7_HUMAN	P56937	SDR37C1	3-keto-steroid reductase
SDR39U	C14orf124 protein	SPRE_HUMAN	P35270	SDR38C1	Sepiapterin reductase
SDR40C	Dehydrogenase/reductase (SDR family)	CN124_HUMAN	Q9NRG7	SDR39U1	C14orf124 protein
SDR41C	WW domain-containing oxidoreductase	DHR12_HUMAN	A0PJE2	SDR40C1	Dehydrogenase/reductase (SDR family) member 12
		WWOX_HUMAN	Q9NZC7	SDR41C1	WW domain-containing oxidoreductase

Family designation	Family name	Uniprot identifier	Accession number	Protein designation	Description
SDR42E	3-beta-HSD family protein HSPC105	YP022_HUMAN	Q8WUS8	SDR42E1	3-beta-HSD family protein HSPC105
		YP030_HUMAN	A6NKP2	SDR42E2	Putative 3-beta-HSD family protein ENSP00000330812
SDR43U	Biliverdin reductase B	BLVRB_HUMAN	P30043	SDR43U1	Biliverdin reductase B
SDR44U	Oxidoreductase HTATIP2	HTAI2_HUMAN	Q9BUP3	SDR44U1	Oxidoreductase HTATIP2
SDR45C	Carbonyl reductase	CBR4_HUMAN	Q8N4T8	SDR45C1	Carbonyl reductase 4
SDR46C	Dehydrogenase/reductase SDR family	DHRXS_HUMAN	Q8N5I4	SDR46C1	Dehydrogenase/reductase SDR family member on chromosome X precursor
SDR47C	Dehydrogenase/reductase SDR family	DHB14_HUMAN	Q9BPX1	SDR47C1	Dehydrogenase/reductase SDR family member 10
SDR48A	NmrA-like family domain-containing	NMRL1_HUMAN	Q9HBL8	SDR48A1	NmrA-like family domain-containing protein 1

Table 2

SDR types and their designations.

Type	Designation
Classical	C
Extended	E
Atypical	A
Intermediate	I
Divergent	D
Complex	X
Unknown	U