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Update in Bioinformatics

PeroxiBase: The peroxidase database

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Abstract

Peroxidases (EC 1.11.1.x), which are encoded by small or large multigenic families, are involved in several important physiological and developmental processes. Analyzing their evolution and their distribution among various phyla could certainly help to elucidate the mystery of their extremely widespread and diversified presence in almost all living organisms. PeroxiBase was originally created for the exhaustive collection of class III peroxidase sequences from plants (Bakalovic, N., Passardi, F., et al., 2006. PeroxiBase: a class III plant peroxidase database. Phytochemistry 67, 534–539). The extension of the class III peroxidase database to all proteins capable to reduce peroxide molecules appears as a necessity. Our database contains haem and non-haem peroxidase sequences originated from annotated or not correctly annotated sequences deposited in the main repositories such as GenBank or UniProt KnowledgeBase. This new database will allow obtaining a global overview of the evolution the protein families and superfamilies capable of peroxidase reaction. In this rapidly growing field, there is a need for continual updates and corrections of the peroxidase protein sequences. Following the lack of unified nomenclature, we also introduced a unique abbreviation for each different family of peroxidases. This paper thus aims to report the evolution of the PeroxiBase database, which is freely accessible through a web server (http://peroxibase.isb-sib.ch). In addition to new categories of peroxidases, new specific tools have been created to facilitate query, classification and submission of peroxidase sequences.

Keywords: Database; Multigenic family; Peroxidase superfamily; Haem peroxidases; Non-haem peroxidases

1. Introduction

Peroxidases are enzymes that use various peroxides (ROOH) as electron acceptors to catalyse a number of oxidative reactions. These proteins can be found under the same enzyme classification number E.C.1.11.1.x, donor:hydrogen-peroxide oxidoreductase (Fleischmann et al., 2004). Currently, 15 different EC numbers have been ascribed to peroxidase: from EC 1.11.1.1 to EC 1.11.1.16 (the EC 1.11.1.4 was removed) (Table 1). Due to the presence of dual enzymatic domains, other peroxidase families were classified with the following numbers: EC 1.13.11.44, EC 1.14.99.1 and EC 1.6.3.1 and EC 4.1.1.44 (Table 1). To date, certain peroxidases do not possess an EC number (Pxd, Pxt, AnPOX, NAnPrx, DypPrx, APx-C*c*P and CII) and can only be classified in EC 1.11.1.7. Two particular cases are also observed for numbers EC 1.11.1.2 (NADPH peroxidase) and 1.11.1.3 (fatty acid peroxidase). Concerning EC 1.11.1.2, NADPH peroxidase activities have been

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Table 1
The international union of biochemistry classification of peroxidases

EC number	Recommended name	Abbreviation in PeroxiBase
EC 1.11.1.1	NADH peroxidase	NadPrx
EC 1.11.1.2	NADPH peroxidase	*No sequence available*
EC 1.11.1.3	Fatty acid peroxidase	*No sequence available* (aDox?)
EC 1.13.11.11 (previously EC 1.11.1.4)	Tryptophan 2,3-dioxygenase	*Not considered as a peroxidase any longer*
EC 1.11.1.5	Cytochrome-*c* peroxidase	C*c*P, DiHC*c*P
EC 1.11.1.6	Catalase	Kat, CP
EC 1.11.1.7	Peroxidase	Haem peroxidases
EC 1.11.1.8	Iodide peroxidase	TPO
EC 1.11.1.9	Glutathione peroxidase	GPx
EC 1.11.1.10	Chloride peroxidase	HalPrx, HalNPrx, HalVPrx
EC 1.11.1.11	L-ascorbate peroxidase	APx
EC 1.11.1.12	Phospholipid-hydroperoxide glutathione peroxidase	GPx
EC 1.11.1.13	Manganese peroxidase	MnP
EC 1.11.1.14	Lignin peroxidase	LiP
EC 1.11.1.15	Peroxiredoxin	1CysPrx, 2CysPrx, PrxII/V/PrxGrx, PrxQ/BCP
EC 1.11.1.16	Versatile peroxidase	VP
EC 1.13.11.44	Linoleate diol synthase	LDS
EC 1.14.99.1	Prostaglandin-endoperoxide synthase	PGHS
EC 1.6.3.1	NAD(P)H oxidase	DuOx
EC 4.1.1.44	4-Carboxymuconolactone decarboxylase	AhpD, CMD, CMDn, HCMD, HCMDn, DCMD, DCMDn, AlkyPrx, AlkyPrxn

Italicized values stand for EC numbers with no sequence (EC 1.11.1.2 and EC 1.11.1.3) or excluded (EC 1.11.1.4) from the peroxidase classification. Pxd, Pxt, AnPOX, NAnPrx, DypPrx, APx-C*c*P and CII do not possess an EC number. The two independent EC numbers (1.11.1.9 and 1.11.1.12) both correspond to GPx and are based on the electron acceptor (hydrogen peroxide or lipid peroxide, respectively).

observed in different studies (Conn et al., 1952; Hochman and Goldberg, 1991); however there is no known peroxidase sequence which has been assigned to this EC number, probably due to the fact that none of the peroxidases known so far have a predominant NADPH peroxidase activity. Regarding EC 1.11.1.3 (Martin and Stumpf, 1959), the orphan enzyme database (http://www.orenza.u-psud.fr) reports that this class is not represented by any protein sequence. However, we think that this class could include alpha-dioxygenases, which are known to have fatty acid peroxidase activity (Hamberg et al., 2005; Saffert et al., 2000), and which have currently no assigned EC number.

Genes encoding haem peroxidases can be found in almost all kingdoms of Life. They are grouped in two major superfamilies: one mainly found in bacteria, fungi and plants (Passardi et al., 2007b) and a second mainly found in animals, fungi and bacteria (Daiyasu and Toh, 2000; Furtmuller et al., 2006). Members of the superfamily of plant/fungal/bacterial peroxidases have been identified in the majority of the living organisms except animals. Only Metazoans (animals) and certain parasitic eukaryotes do not contain any sequence encoding for peroxidases of this superfamily. Three independent classes can be distinguished: class I, which includes ascorbate peroxidase (APx), cytochrome *c* peroxidase (C*c*P) and catalase peroxidase (CP); class II, which includes lignin peroxidases (LiP), manganese peroxidases (MnP), versatile peroxidase (VP) and finally, class III (Ruiz-Dueñas et al., 2001; Welinder, 1992).

The second superfamily described as "animal peroxidases" comprises a group of homologous proteins mainly found in animals and categorised as following: myeloperoxidase (MPO); eosinophil peroxidase (EPO); lactoperoxidase (LPO); thyroid peroxidase (TPO); prostaglandin H synthase (PGHS); peroxidasin (Pxd) and peroxinectin (Pxt). Homologous animal peroxidase sequences from the fungal kingdom can be also classified as PGHS. Two other groups of proteins which contain the typical ~600 amino acid long "animal" peroxidase domain have been also added to this widespread superfamily: the dual oxidase or thyroid NADPH oxidase (DuOx) and the alpha dioxygenase found in plants (aDox). Finally, a group of peroxidases that do not fall in the above defined groups was also introduced (AnPOX). According to structural and functional peculiarities independently of the origin, the "animal peroxidase" superfamily has been also denominated: "peroxidase-cyclooxygenase superfamily".

In addition to these two large superfamilies, smaller protein families are indexed as capable to reduce peroxide molecules (Fig. 1). Catalase (Kat) that can also oxidise hydrogen peroxide (unique feature), Di-haem cytochrome *C* peroxidases (DiHC*c*P), Dyp-type peroxidases (DypPrx), Haloperoxidases with (HalPrx) or without (HalNPrx, HalVPrx) haem, Alkylhydroperoxidase D-like superfamily (AhpD, CMD, HCMD, DCMD, and AlkyPrx), NADH peroxidase (NadPrx), Manganese Catalases (MnCat) and two families of Thiol peroxidases: Glutathione peroxidases (GPx) and Peroxiredoxins (1CysPrx, 2CysPrx, PrxII/PrxV/PrxGrx and PrxQ/BCP).

The numerous genome sequencing projects (according to the Genomes OnLine Database, roughly 1900 projects are ongoing while 525 genomes are complete and published, to date), the increasing number of short genomic sequences released (genome survey sequence (GSS)) and the automated clustering and assembly of EST sequences, led to the identification of a large number of sequences coding for peroxidases. We decided to enlarge the coverage of the PeroxiBase database by including all haem and non-haem peroxidase encoding sequences. As noticed during our work on the class III peroxidases, we still observed that the automated annotation processing produces a number of poor quality and/or misannotated sequences. Using existing profiles (from Interpro), or profiles specifically designed for each group of peroxidases (unpublished data), together with BLAST searches, data mining has been performed to identify novel peroxidase sequences.

We have redefined the goal of the PeroxiBase database, which is now to centralize all annotated and non-annotated

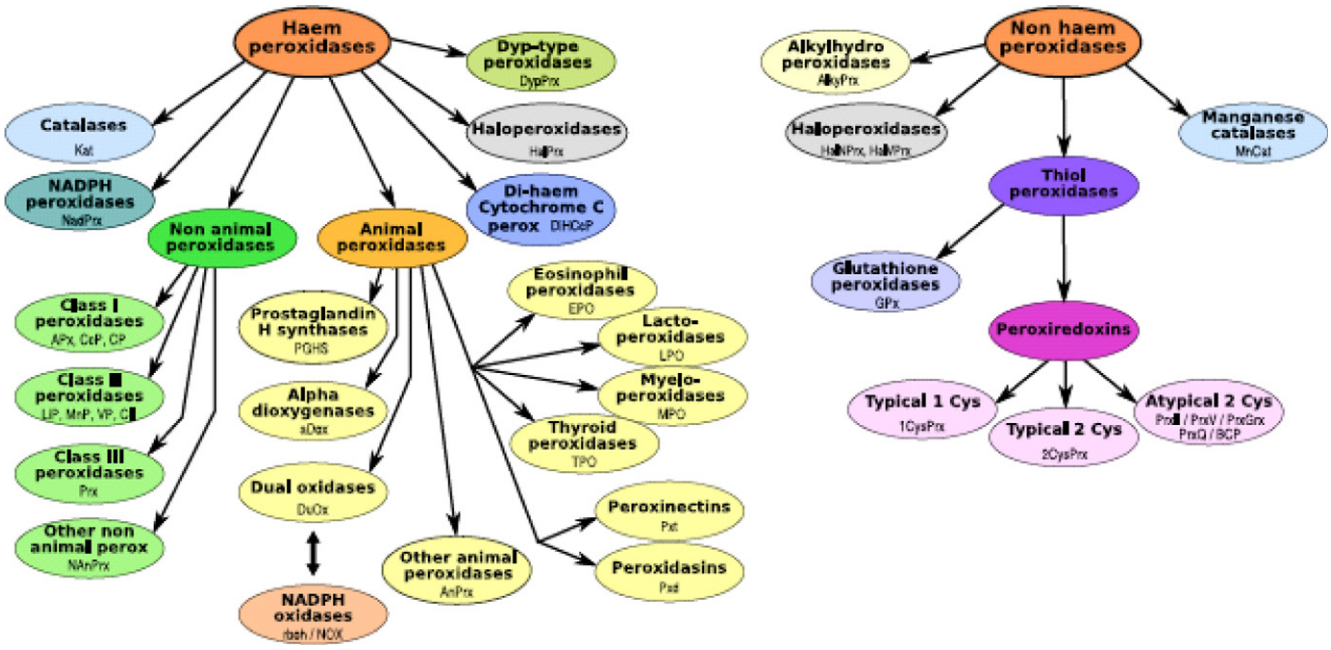

Fig. 1. Schematic representation of the phylogenic relation between the different protein families found in PeroxiBase.

peroxidase-encoding sequences (with or without haem) (Fig. 1 and Table 2) and to make them publicly available, so that the research community has a unique tool for discovery, comparison, and exchange of peroxidase sequences.

2. Acquisition of new entries and peroxidase nomenclature

The construction of the class III PeroxiBase was initially performed by data mining using the plant/fungal/bacterial haem peroxidase motif PEROXIDASE_4 (Prosite PS50873). A systematic mining was accomplished against publicly available EST libraries to identify novel peroxidase sequences. The extension to the classes I and II and finally to the whole family of haem and non-haem peroxidases led us to modify our sequence acquisition procedure. We first incorporated the sequences of the aimed peroxidase classes that were present in the UniProt Knowledgebase/Swiss-Prot (formerly known as Swiss-Prot and TrEMBL) and Pfam, a large collection of protein families (Finn et al., 2006). Additional peroxidases were identified through BLAST searches (against ESTs, translated EST clusters and/or genomic sequences, depending on their availability), followed by manual sequence edition (as described previously (Bakalovic et al., 2006)).

The Pfam database was particularly useful for the AhpD-like superfamily, whose sequence conservation is very low: entries were found through their common "carboxymuconolactone decarboxylase (CMD) motif" (Pfam accession PF02627). Regarding this superfamily, two types of proteins were entered: firstly, those bearing a typical motif essential for alkylhydroperoxidase activity: $E[x]_{11}CxxC[x]_3H$ (Nunn et al., 2002); secondly, those which lacked at least one of the two critical cysteines belonging to this motif and necessary for peroxidase activity. The second category is referred to, in PeroxiBase, as having "no peroxidase activity". Although they cannot be considered as peroxidases, we chose to include these proteins in the database, as they remain valuable for phylogenetic analyses of the AhpD-like superfamily.

Among all the protein classes present in the database, we observed numerous discrepancies regarding the nomenclature. In an attempt to make the names of each class of peroxidases consistent, we introduced a simple nomenclature in which they are constructed after species and class acronyms (Tables 1 and 2). The various names found in the literature and the screened databases have been conserved as synonyms in PeroxiBase, so they can still be identified under their original appellation (Fig. 2). When orthologous peroxidase sequences are found between strains or cultivars, the name of the strain is indicated directly next to the name of the peroxidase. If the orthologs are identical, they are simply entered under the same accession (the strains and the corresponding accessions are indicated in the "Remarks" field). On the other hand, identical peroxidase sequences from different species are entered as separate accessions. Sequences resulting from alternative splicing have been identified by adding -a, -b after the name. A similar approach has been observed with recently duplicated peroxidases: the suffixes -1, -2 have been added after the name.

In the adopted classification, classes of peroxidases were separated into two groups, depending on the presence or the absence of the haem moiety, rather than depending of their origin. For the same reason, haloperoxidases were

Table 2
Representation of the different superfamilies, families and groups of proteins included in PeroxiBase with their distributions within the major kingdoms

	Prokaryotes	Plants	Fungi	Animals	Other eukaryotes	Total sequences
Haem peroxidase						
Animal peroxidase/peroxidase-cyclooxygenase superfamily						
Eosinophil peroxidase (EPO)				✓		6
Lactoperoxidase (LPO)				✓		10
Myeloperoxidase (MPO)				✓		12
Peroxidasin (Pxd)				✓		29
Peroxinectin (Pxt)	✓			✓	✓	61
Thyroid peroxidase (TPO)				✓		9
Alpha-dioxygenase (aDox)		✓				7
Other animal peroxidase (AnPOX)				✓		2
Dual oxidase (DuOx)				✓		15
Prostaglandin H synthase/cyclooxygenase (PGHS)	✓		✓	✓		59
Linoleate diol synthase, PGHS-like (LDS)			✓			2
Catalase (Kat)	✓	✓	✓	✓	✓	22
Di-haem cytochrome *c* peroxidase (DiHC*c*P)	✓					5
Dyp-type peroxidase (DypPrx)	✓					6
Haloperoxidase (HalPrx)			✓		✓	49
Non animal peroxidase						
Class I peroxidase						
Ascorbate peroxidase (APx)		✓		**		352
Catalase peroxidase (CP)	✓	**	**		**	299
Cytochrome *c* peroxidase (C*c*P)			✓		✓	94
Hybrid ascorbate-cytochrome *c* peroxidase (APx-C*c*P)					✓	4
Class II peroxidase						
Lignin peroxidase (LiP)			✓			26
Manganese peroxidase (MnP)			✓			69
Versatile peroxidase (VP)			✓			14
Other class II peroxidase (CII)			✓			10
Class III peroxidase		✓				2625
Other non animal peroxidase (NAnPrx)		✓		✓		5
Non haem peroxidase						
Alkylhydroperoxidase D-like superfamily						
Alkylhydroperoxidase D (AhpD)	✓					68
Carboxymuconolactone decarboxylase, peroxidase activity (CMD)	✓					42
Carboxymuconolactone decarboxylase, no perox. activity (CMDn)	✓		✓			23
Hydrolase-CMD fusion, peroxidase activity (HCMD)						0
Hydrolase-CMD fusion, no peroxidase activity (HCMDn)	✓		✓			22
Double CMD, peroxidase activity (DCMD)	✓					3
Double CMD, no peroxidase activity (DCMDn)	✓					21
Other alkylhydroperoxidase, peroxidase activity (AlkyPrx)	✓					0
Other alkylhydroperoxidase, no peroxidase activity (AlkyPrxn)	✓					10
Haloperoxidase						
No haem, no metal haloperoxidase (HalNPrx)	✓					6
No haem, Vanadium haloperoxidase (HalVPrx)	✓				✓	5
Manganese Catalase (MnCat)	✓					5
NADH peroxidase (NadPrx)	✓					2
Thiol peroxidase						
Glutathione peroxidase (GPx)	✓	✓	✓	✓	✓	196
Peroxiredoxin						
1-Cysteine peroxiredoxin (1CysPrx)	✓	✓	✓	✓	✓	95
Typical 2-cysteine peroxiredoxin (2CysPrx/AhpC)	✓	✓	✓	✓	✓	191
Atypical 2-cysteine peroxiredoxin (PrxII, PrxV, PrxGrx)	✓	✓	✓	✓	✓	105
Atypical 2-cysteine peroxiredoxin (PrxQ, BCP)	✓	✓	✓		✓	95

Prokaryotes comprise archaebacteria, bacteria and cyanobacteria. "Other eukaryotes" includes various protistean organisms.
** Stands for marginal sequence detection due to horizontal gene transfer (Passardi et al., 2007b).

split into two categories (Table 2). Regarding the peroxiredoxin class, we have preserved a particular nomenclature based on taxonomic affiliation, 1-Cys Prx, typical 2-Cys Prx and atypical 2-Cys Prx (Rouhier and Jacquot, 2005; Wood et al., 2003). Atypical 2-Cys peroxiredoxin are generally called type II and Q in plants, whereas peroxiredoxin

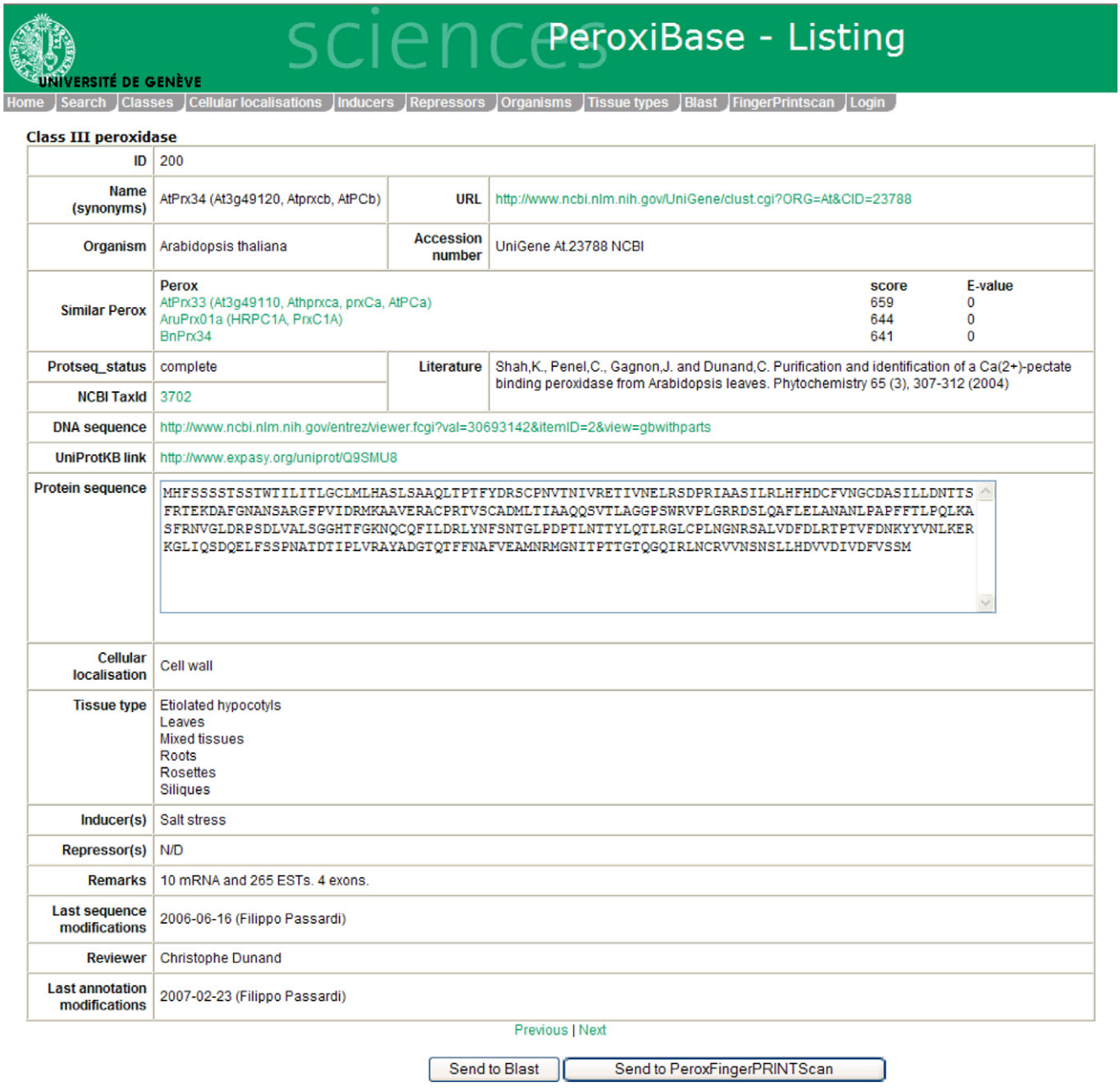

Fig. 2. Typical PeroxiBase data sheet. ID: unique sequence identifier; Name: sequence name and synonyms (into brackets); URL/Accession number: hyperlink to the original webpage containing the protein sequence (or one of the EST or GSS sequences of the entry); Similar perox: automated field reporting the three closest hits to this entry; Protseq_status: complete or partial; NCBI TaxID: NCBI TaxID number and hyperlink to the organism NCBI taxonomy page; Literature: reference(s) of the original sequencing authors; DNA sequence: hyperlink to a "DNA" (EST, mRNA, GSS) sequence (if a protein sequence link was entered in the URL field), or to an alternative DNA sequence (e.g. genomic DNA); UniProtKB link: cross-reference to the UniProt Knowledgebase; Protein sequence: protein sequence in FASTA format; Cellular localisation, Tissue type, Inducer(s), Repressor(s): fixed terms listing of various expression features (multiple choice is available, except for cellular localisation); Remarks: free text field for additional comments; Last sequence modifications: date of first entry, or of last sequence modification, with name of the contributor; Reviewer: name of the curator that operated a double-check on the last sequence modification; Last annotation modifications: date of the last modification of any other field than "Protein sequence", with name of the contributor (no double-check is performed).

type V and BCP (bacterioferritin comigratory protein) are found in animals and prokaryotes, respectively (Table 2). Nevertheless, it is worth mentioning that some atypical 2-Cys peroxiredoxins can contain a fused glutaredoxin domain in C-terminal position (Rouhier and Jacquot, 2003). These hybrid sequences are present both in cyanobacteria and in some bacteria.

Besides the extensive search for annotated sequences and their manual verification, we will now concentrate on improving the representativity of the different classes for each organism present in the database, as it has already been done for class III peroxidases (Passardi et al., 2004; Tognolli et al., 2002). We will also concentrate on improving the representativity of the different classes present in the database.

3. Web interface

The web interface has been improved. In addition to the pages already available (Search, Organisms, Tissue types, Inducers/repressors, Cellular localisations, BLAST and FingerPrintscan), PeroxiBase now includes a page "Classes", which allows visualizing the number of peroxidase sequences in each class present in the database. Various other improvements have been done, such as the classification of the organisms in taxonomic groups, a Search page that now allows multiple criteria and an option for sorting BLAST hits by percentage of identity, which we find more convenient for short matches. The Tissue types, Inducers/repressors, Cellular localisations fields do not any longer accept free text entries: a list of terms is available and can only be modified by the database curators, so that redundancies and synonymous terms can be excluded. Also, in order to increase data reliability, each new entry is double-checked by one of the database curators, even when entered by another curator.

Finally, PeroxiBase entries are now cross-referenced in UniProtKB (SwissProt/TREMBL), which means users can navigate back and forth between the two databases easily.

4. Current status and future developments

The initial objective of the PeroxiBase team was to develop a large database devoted to the class III peroxidases (Bakalovic et al., 2006). With over 2600 class III sequences coming from more than 200 different organisms, this goal has been reached. Very rapidly, it appeared as a necessity to include the other members of the so called "non-animal superfamily" (Passardi et al., 2007a) to have a global overview of their phylogenetic evolution. The classes I and II were thus entered in the database. The most recent step forward was to enlarge the entries by including all the proteins capable of reducing hydrogen peroxide or larger molecules with a hydroperoxo group. PeroxiBase currently contains over 4700 complete or partial peroxidase-encoding sequences distributed among 44 different protein classes (Table 2). The number of protein families should not undergo major changes in the future. Only minor modifications should occur regarding the sub-classification within some classes due to the constant improvements of the entries and to the biochemical characterization of the enzymes.

Continuous data mining will be performed on non-annotated available sequences (EST and genomic sequences), which has not yet been done in other databases. At this point, a semi-automatic update will be set up to collect the peroxidase encoding sequences newly submitted to general databases (NCBI, UniProt KB). Information concerning the expression profile will also be updated.

Numerous additions are already planned. Regarding the BLAST tool, two options will be made available: (i) a limit by query (organism, class and short nearly matches) and (ii) an option for drawing a distance tree from the resulting hits. Users will also be able to download sequences in FASTA format. In the Organisms section, the number of peroxidase sequences of each class for a given organism will be soon available. Data currently stored in "Remarks" will be placed into relevant fields. Among these are organism strain names and database cross-references, for instance. Finally, tissues present in the Tissue types page will be classified according to tissue ontology.

PeroxiBase is a unique repository exclusively dedicated to a superfamily composed of multigenic families from both Eukaryotes and Prokaryotes. Even with the large extension of the database, it is still mainly composed of sequences originated from Viridiplantae. It includes fragments of peroxidase sequences, which are regularly verified for possible annotation updates and sequence completion. Partial genomes are also searched for, particularly in bacteria, and many entries are already issued from non-annotated sequences. Old entries of complete sequences are frequently verified and updated if any changes have occurred.

Haem and non-haem peroxidases are found in all kingdoms: they may hence become key markers for the evolution of living organisms. The PeroxiBase database represents a powerful tool for an efficient analysis and a better understanding of the evolution of protein superfamilies, catalytic domains and peroxidase activity in all the kingdoms of Life.

5. Useful web links as tools

BioEdit: http://www.mbio.ncsu.edu/BioEdit/bioedit.html
ClustalW: http://www.ebi.ac.uk/clustalw/
Expasy translate: http://www.expasy.org/tools/dna.html
FingerPRINTScan: http://www.bioinf.man.ac.uk/fingerPRINTScan/
InterPro Scan: http://www.ebi.ac.uk/InterProScan/
ORENZA (database of Orphan ENZyme Activities): http://www.orenza.u-psud.fr
SoftBerry- FGENESH: http://www.softberry.com/berry.phtml?topic=fgenesh&group=programs&subgroup=gfind

6. Useful web links as source of data

DOE Joint Genome Institute: http://www.jgi.doe.gov/
Gene Indice: http://compbio.dfci.harvard.edu/tgi/
NCBI: http://www.ncbi.nlm.nih.gov/
PlantGDB: http://www.plantgdb.org/
Plant Genome Network: http://pgn.cornell.edu/
Pfam: http://www.sanger.ac.uk/Software/Pfam/
UniProt Knowledgebase (Swiss-Prot and TrEMBL): http://www.expasy.ch/sprot

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