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Review

Evolution and expression of class III peroxidases

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ABSTRACT

Class III peroxidases are members of a large multigenic family, only detected in the plant kingdom and absent from green algae *sensu stricto* (chlorophyte algae or Chlorophyta). Their evolution is thought to be related to the emergence of the land plants. However class III peroxidases are present in a lower copy number in some basal Streptophytes (Chararpyceae), which predate land colonization. Gene structures are variable among organisms and within species with respect to the number of introns, but their positions are highly conserved. Their high copy number, as well as their conservation could be related to plant complexity and adaptation to increasing stresses. No specific function has been assigned to respective isoforms, but in large multigenic families, particular structure–function relations can be expected. Plant peroxidase sequences contain highly conserved residues and motifs, variable domains surrounded by conserved residues and present a low identity level among their promoter regions, further suggesting the existence of sub-functionalization of the different isoforms.

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Introduction

Peroxidases (EC 1.11.1.X) can be defined as enzymes that catalyze the oxidation of various substrates by reducing hydrogen peroxide to water. They can be heme or non-heme containing proteins. Most of the heme peroxidases belong to two large families: animal and non-animal peroxidases. The non-animal peroxidase superfamily contains three different classes of peroxidases, namely class I, II and III peroxidases [1]. These three classes have in common a heme formed by protoporphyrin IX and Fe(III) (ferric form in ground state) and share a very similar three-dimensional structure [1–3]. However, they present a low level of identity in their amino acid sequences and are associated to distinct functions and subcellular localizations [4].

The intracellular class I such as ascorbate peroxidases (APx)¹ and cytochrome c peroxidases (CcP) can be found in most organisms, except animals. Their main function in the cell is the scavenging of excess H₂O₂ [5–7]. APx are specific to chloroplast-containing organisms. In higher plants, chloroplastic and cytosolic isoforms are detected. They have been shown to be necessary to prevent cell damage caused by H₂O₂ mainly in chloroplasts [8,9]. CcP have a

similar function in mitochondria associated organisms [8]. However, CcP are not detected in plants, they seem to manage mitochondria-produced H₂O₂ thanks to other enzymes (glutathione peroxidases, thioredoxines, peroxiredoxin or catalase) or with an alternative respiratory pathway (alternative oxidase, AOX) [10,11]. The class II peroxidases, encoded exclusively by fungi, have a major role in the degradation of lignin-containing soil debris [12,13]. The class III peroxidases are only found in plants and are implicated in various processes detailed further. Classes II and III are glycosylated, contain calcium ions and present the peculiarity of having four or five disulfide bridges, in analogous positions for some [14,1]. Both of them possess a signal peptide for their secretion across the endoplasmic reticulum.

Class III peroxidases are present as large multigenic families in all land plants [15–17] (Fig. 1). They are generally secreted into the cell wall or the apoplastic compartment and the vacuole [18–20]. They play a role in two different catalytic cycles: (i) their regular peroxidative cycle, class III plant peroxidases catalyze the reduction of H₂O₂ by transferring electrons from various donor molecules such as phenolic compounds, lignin precursors, auxin or secondary metabolites [21–23]; (ii) a separate hydroxylic cycle, which leads to the formation of reactive oxygen species (ROS) has been described [22,24]. They could be associated with land colonization by plants, either by allowing formation of rigid plant structures or by adapting the organism to a more oxygenated environment [16,17].

Interestingly, hybrid sequences containing part of the classes I and III peroxidase domains and some disulfide bridges have been found in Chlorophyta – *Chlamydomonas reinhardtii*. In addition,

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¹ Abbreviations used: APx, ascorbate peroxidases; CcP, cytochrome c peroxidases; AOX, alternative oxidase; ROS, reactive oxygen species; SBP, soybean seed coat peroxidase; RPTP, royal palm tree peroxidase; pI, isoelectric point; MnP, manganese peroxidase; SP, signal peptide; CT, C-terminal extension.

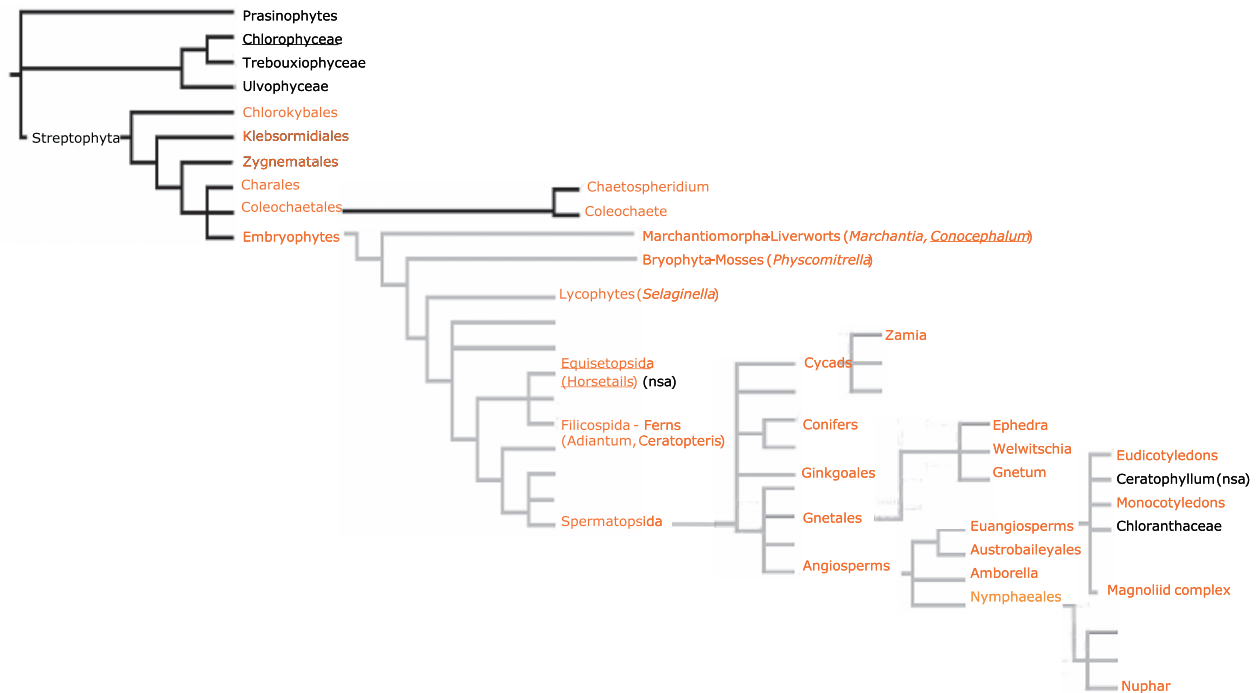


Fig. 1. Schematic taxonomic distribution of class III peroxidases. nsa: no sequence available from repository databases (NCBI, EMBL, UniProtKB...). Orange, organisms containing Class III peroxidases encoding sequences (ESTs, DNA available in the PeroxiBase (<http://peroxibase.toulouse.inra.fr>, [48]) or presenting enzymatic activity. The peroxidase activity in the underlined families was verified using colorimetric peroxidase assay (guaiacol as electron donor). Adapted from Tree of life web project (<http://tolweb.org/tree/>) and [22].

plants containing class III peroxidase genes lack CcP encoding sequences. Moreover, class I peroxidases do not have disulfide bridges, contrary to class III peroxidases that form four disulfide bridges [8,25]. Together, these facts may bring evidences of the transition from class I to class III but more sequences of *Chlorophyta* need to be analyzed to confirm this hypothesis.

Gene structure of class III peroxidases

In *Arabidopsis*, the coding sequences of most peroxidase genes are disrupted by three introns (classical pattern) at perfectly conserved positions (Fig. 2C and B). Introns 1 and 3 are positioned in the middle of the highly conserved domains I and III, respectively, and intron 2 is localized just after the domain II (Fig. 2C). This may suggest a common ancestral gene with the classical pattern of four exons and three introns detected in *Arabidopsis* [15]. However, variations in this basic gene structure were observed, implicating mainly losses of one or more introns. Gain of introns was observed in the case of genes with additional introns disrupting either the first or the last exon.

Similar intron structure analyses have been done using sequences from other organisms available on the PeroxiBase (<http://peroxibase.toulouse.inra.fr>). Monocotyledons and two recently sequenced organisms, *Physcomitrella patens* and *Selaginella moellendorffii*, have been studied. The classical intron/exon structure is still a majority in *Selaginella* genes, but the structure with the introns 1 and 2 (called “c”) is also abundant (unpublished data, Fig. 3C). Interestingly, this pattern also coincides with the distribution of gene structure patterns reported in the moss *Physcomitrella* [26]: classical three intron genes and genes with the two first introns constitute the main proportions. However, larger diversity was observed for monocotyledons species, which contain more genes with the single intron 1 than genes with the classical three introns structure [17] (Table 1 and Fig. 3), and even possess many

intronless genes. Roughly the same distribution of intron/exon structures was observed in *Sorghum bicolor*.

The abundance of genes with a lower number of introns in monocotyledons and in basal viridiplantae is consistent with the hypothesis that intron loss occurred mainly during evolution [27,28], which is in agreement with the idea of the common classical pattern with three introns. Moreover, the inspection of clusters of duplicated genes in rice confirms an intron loss tendency associated with duplication events [24]. When focusing on genes with orthologs in *Arabidopsis*, rice and *Selaginella*, we observe a global reduction in the number of introns through evolution. But a more exhaustive comparative analysis must still be performed. Indeed, the higher number of introns per gene (Table 1) in dicotyledons is puzzling: it raises the reverse hypothesis of an ancestral sequence with few or no introns, and possible gain of introns.

Conserved intron/exon gene structures were observed among clusters of peroxidases in the chromosomes (or scaffolds) of *Selaginella* and *Physcomitrella*, indicating gene tandem duplication, such as in *Oryza sativa* and *Arabidopsis thaliana* [15,17], but also between species members of the same family such as Brassicaceae. The size of the intronic sequences is largely variable between mono- and dicotyledonous species, introns being much larger in monocotyledons [15,17], which is consistent with the comparison of intron length in whole genome [29]. On the contrary, intron length is shorter in *Selaginella* genes, as it may be expected in such a compact genome (~100 Mb, [30]), and as revealed by global analysis (http://wiki.genomics.purdue.edu/index.php/Distribution_of_genes).

Although there are large variations of intron number and length among peroxidase class III paralogs and orthologs, intron positions and phases (with a high majority of phase 0 introns, i.e., introns occurring between two codons, accordingly with the data of [31]) are remarkably conserved. This suggests that intron loss, or more marginally intron gain, probably occurred during the expansion of the gene family in some plant lineages. Then, the hypothesis

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