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RESEARCH ARTICLE

Diversification of the Histone Fold Motif in Plants: Evolution of New Functional Roles

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ABSTRACT

The Histone fold motif (HFM) is one of the most conserved structural motifs in biology, mainly found in the core histone sub-units of all eukaryotes. The HFM represents a helix-strand-helix motif having three alpha helices connected by two loops/beta strands. This helix-strand-helix motif has the unique property of binding strongly with proteins as well as with DNA. Apart from core histones, the HFM has been reported in a variety of other proteins in all forms of life. In this work, the various classes of proteins that contain the HFM, as well as the diverse roles played by these proteins in the plant kingdom are reviewed. As will be clear from this review, formation of the core histones through multi-merisation is not the only role played by this conserved fold, although the characteristic ability of the HFM to dimerise with suitable partner proteins has been used by nature to perform several non-core-histone functions. Most of the information about plant HFM containing proteins, such as identification and classification, has been done based on homology with yeast and animal counterparts. However, the ability of plants genomes to duplicate extensively has led to the existence of large gene families of the HFM containing proteins, unlike other eukaryotes. Plant HFM containing proteins can broadly be classified under the following major categories; TBP-associated factors (TAF), Nuclear Factor Y (NF-Y), Dr1/DrAp1 proteins and the chromatin accessibility complex (CHRAC). These proteins families are known to be involved in transcriptional regulation, co-activation and chromosome maintenance. Partner recognition through dimer formation remains a major conserved feature of these groups when compared with core histone sub-units.

Keywords: Histone, histone fold motif, Evolution, gene family, sub functionalisation, neo functionalisation, histone proteins

1. INTRODUCTION

Histone proteins are highly conserved throughout the eukaryotes and they have very similar structural topology, as shown in Fig. 1. The four major core histone sub-units are H2A, H2B, H3, and H4 respectively, and these core histones contain highly similar structural folds, predominantly helical in nature. Apart from the helices, all core histones have a long N-terminal tail and unique extra fold, which is also mostly helical. The helices are connected by loops and the overall fold family is called the Histone fold motif (HFM), constituted of three alpha helices of which the middle helix is longest, and is flanked by two shorter helices (Fig. 1).

The HFMs are major structural constituents of the core histones and involved in the dimerisation followed by multi-merisation and binding to the DNA to form a complete nucleosome structure.

The presence of histone fold in all four classes of histones suggests that evolution has favored considerable variation in the primary structure but only to the extent that allows secondary structure to remain preserved. The existence of highly conserved HFM across eukaryotes provides strong evidence for a common ancestor. The presence of histone like proteins in archaebacteria, which were found to be very similar to the eukaryotic core histones strongly support such a common ancestor. The HFM in eukaryotes are found in compact association with DNA and HFM of interacting partner histones, in a way that allows only very few neutral amino acids i.e. amino acid that are not involved in interaction with other histone or DNA. This involvement results in a very slow evolutionary change due to the multiple and simultaneous selection pressures[1].

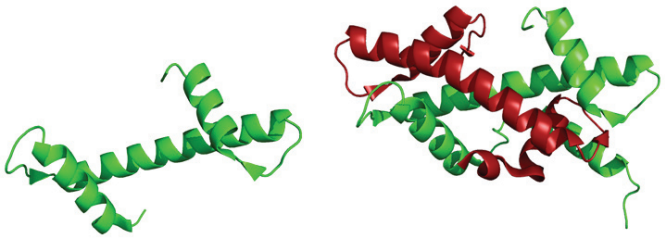

Figure 1. Histone fold motif (HFM) and HFM dimer.

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2. HFM IN ARCHAEAL PROTEINS

The most closely related proteins to histones are

archaeal DNA binding proteins HMf, HMt, and HMv. In *Methanothermus fervidus* the HMf (histone M. fervidus) binds to the DNA through heteromeric complex of two different (HMf1 and HMf2) polypeptides and forms a nucleosome like structure that increases the resistance of bound DNA to the thermal denaturation[2]. The consensus sequences derived from eukaryotic histones H2A, H2B, H3, and H4, show over 30% conserved amino acid residues with HMf-2. Thus the HMf proteins show a similar structural and functional integrity to the histones of eukaryotes.

3. HFM IN EUKARYOTES

A large number of eukaryotic transcription factors contain the HFM. In the mid-nineties E.N. Moudrianakis and his group characterised the histone fold and searched for HFM containing proteins by using amino acid sequence homology. Most of the identified proteins were reported to be involved in transcriptional regulation and DNA compaction[1,3]. These include the TATA binding protein associated factors (TAFs); components of a large multi-polypeptide complex TFIID. Plant TAFs have been discussed in more detail in later sections. In addition to TFIID, TAFs are found in many other protein complexes involved in transcriptional regulation, such as the yeast SAGA (SPT-ADA-GCN5-acetyltransferase) complex, mammalian TFTC (TBP-free TAFII-containing complex), PCAF (p300/CREB-binding protein (CBP)- associated factor) and STAGA (SPT3-TAFII31-GCN5-L acetyltransferase) complexes contain a subset of TAFs. TAFs are particularly well studied in *Drosophila*, human, and yeast. In-vitro studies in human and *Drosophila* showed that TAFs act as co-activators by interacting with transcriptional activators and play important roles in transcriptional initiation and regulation[4]. Yeast contains 14 TAFs and most of them contain the HFM. Their molecular organisation reveals them to be arranged in five interacting histone like pairs[5] and their dimerisation is guided by the HFM in a similar way as with core-histone dimerisation[6]. In *Drosophila,* TAFII40 and TAFII60 are found to contain HFM and pair with each other, and their binding promotes subsequent recognition and sequestration of other TAFs to the complex.

Another identified transcription factor with HFM is Nuclear Factor Y (NF-Y) or CBF. It is a CCAAT-binding heterotrimeric protein complex known to activate a large number of eukaryotic promoters. NF-Y has three subunits, namely the NF-YA, NF-YB and NF-YC, respectively, all of which are necessary for DNA binding. Of these three sub-units, the NF-YB and NF-YC form a heterodimer very similar to the histone H2A-H2B complex. Subsequently, NF-YA sub-unit binds to the NF-YB/NF-YC heterodimer and has very little similarity to any other histone[7]. Yeast contains a complex very similar to the NF-Y, termed as the HAP (hem-associated protein) complex for binding to the CCAAT-box. This complex also has three components HAP2-HAP3-HAP5, of which HAP5 shows similarity to H2B of eukaryotic histone sub-units[3].

4. HFM IN THE PLANT KINGDOM

Most studies of HFM containing proteins have been performed on animals and yeast. Computational studies and homology based protein family databases like the InterPro have revealed the presence of HFM among all eukaryotes and archaea. According to InterPro, 1308 proteins (excluding core histone sub-units) were predicted to contain the HFM. These 1084 were identified in 61 plant species a large majority of these proteins (78%) are still uncharacterised, opening up avenues for future research as shown in Fig. 2 and Table 1.

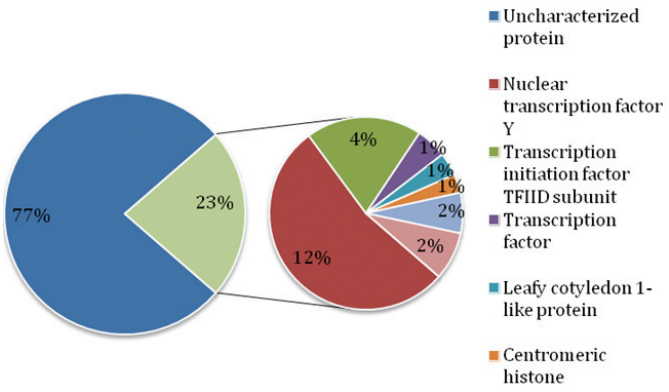

Figure 2. Pie Chart depicting proportions of HFM-containing proteins in the plant kingdom, based on InterPro data.

As shown in Fig. 2, among the characterised HFM proteins in plants, most belong to the NF-Y transcription factors (12%) and TAFs (4%). The remaining HFM proteins are found in variety of DNA binding proteins and transcription factors. HFM containing NF-Ys are found in 14 plant species and are most abundant HFM proteins, as shown in Table 1. TAFs are also found to have HFM in 75 proteins of 14 plants. Apart from these two classes of HFM containing proteins. The InterPro data reveals that a repressor protein family (Dr1/DrAp1) and LEAFY COTYLEDON1(LEC1) family also contains HFM in 26 protein members in 7 plants species and and 15 protein members in 13 plants respectively. Centromere specific proteins are also found to have HFM, DNA Polymerase epsilon protein is the less prevalent HFM containing protein family (Table1).

5. TAFS IN PLANTS: EVIDENCE FOR FUNCTIONAL DIVERGENCE

The first TAF protein was identified in *Drosophila* and human cells; these proteins were identified in a biochemically stable complex with TBP[8]. Subsequently, many TAFs from *Saccharomyces cerevisiae, Schizosaccharomyces pombe, Caenorhabditis elegans, Drosophila melanogaster*, *Homo sapiens, Arabidopsis* and other plants have been identified. The amino acid sequence of TAF proteins, are highly conserved among human, yeast and *Drosophila*, about 14 TAFs were identified in *Arabidopsis* by the help of these conserved sequences. *Arabidopsis* TAFs share high level of similarity (50%-70%) to animal and yeast TAFs, and interestingly, this homology is limited only in the histone fold region. Phylogenetic analyses show that most

Table 1. List of HFM containing proteins among plant species

Name of protein	Total no. of proteins	Name of plant species
Uncharacterised protein	1308	In total 34 plants.
Nuclear factor Y / CBF	206	*Aegilops tauschii, Allium sativum, Arabidopsis thaliana, Cucumis sativus, Hordeum vulgare, Medicago truncatula, Oryza sativa subsp. Japonica, Phaseolus vulgaris, Populus euphratica, Shorea beccariana, Triticum aestivum, Triticum monococcum, Triticum urartu, Zea mays.*
Transcription initiation factor TFIID subunit / TAF	75	*Aegilops tauschii, Arabidopsis lyrata subsp. Lyrata, Arabidopsis thaliana, Capsicum annuum, Oryza sativa subsp. Japonica, Populus trichocarpa, Ricinus communis, Trifolium repens, Triticum urartu, Zea mays, Medicago truncatula.*
Leafy cotyledon1-like protein	15	*Arachis hypogaea, Bixa orellana, Brassica napus, Brassica oleracea, Brassica oleracea var. botrytis, Dimocarpus longan, Helianthus annuus, Jatropha curcas, Kalanchoe daigremontiana, Phaseolus coccineus, Pistacia chinensis, Theobroma cacao, Zea mays.*
DNA binding proteins and transcription factor	20	*Brassica campestris, Glycine latifolia, Lycoris longituba, Populus trichocarpa, Ricinus communis, Zea mays.*
Repressor family (Dr1/DrAp1)	26	*Aegilops tauschii, Medicago truncatula, Triticum urartu Populus trichocarpa, Ricinus communis, Triticum aestivum, Zea mays*
DNA polymerase epsilon subunit	4	*Medicago truncatula, Ricinus communis, Zea mays*
Centromere protein	12	*Medicago truncatula, Olimarabidopsis pumila*
Heading date 5	2	*Oryza sativa subsp. indica*
Floral meristem protein	1	*Festuca arundinacea*
MATE efflux family protein	1	*Brassica rapa subsp. pekinensis*
NAD(P)H-quinone oxidoreductase subunit I	1	*Medicago truncatula*
Putative CONSTANS interacting protein 2b	1	*Capsicum chinense*
Putative F-box/LRR-repeat protein 23	1	*Triticum urartu*
Putative serine/threonine-protein kinase receptor	1	*Aegilops tauschii*
Testis-specific Y-encoded protein	1	*Medicago truncatula*
Ubiquitin-protein ligase, putative, expressed	1	*Triticum aestivum*

of the *Arabidopsis* TAFs (TAF2, TAF4, TAF5, TAF6, TAF7, TAF9, TAF10, TAF11, & TAF13) have similarities to yeast TAFs. Only AtTAF12 and AtBTAF1 are more related to the TAFs of multicellular organisms[9]. After *Arabidopsis*, many other plants have been reported to contain TAF proteins, although structural details have not been fully elucidated. Most of the TAFs contain HFM, as in case of their human and drosophila counterparts.

TAFs are also found to be integral components of histone acetyltransferase (HAT) protein complexes[10]. These HAT protein complexes often also include TAF-like proteins, and are thus homologs of the TAFs, which retain the same structural features, like the HFM. TAFs and their homologs play an important role in maintaining the overall structure of TFIID and HAT complexes[11]. Initial studies suggested that TAFs might act as general co-activators that mediate the transcriptional activation of different activator[12] but later it was shown that TAF have tissue and developmental stage specific expression and may be required for only a subset of genes[13]. This observation implies a very important aspect of HFM evolution in the plant kingdom, namely, that members of the same family may have diverged to perform stage specific or tissue specific functions, in addition to performing back up roles for each other. These may be in turn imply a case of sub-functionalisation within the HFM family in the plant kingdom.

Analysis of TAF10 from (Clustered yellowtops) *Flaveria trinervia (*FtTAF10) showed high degree of similarity to fly counterparts dmTAF10, dmTAF10b that have histone fold motif composed of 3 alpha-helices and 2 loops[5]. Database search using the amino acid sequence of FtTAF10 revealed a cDNA encoding homolog in *Arabidopsis*, and ESTs in soybean, tomato, rice, maize, and wheat, suggesting that TAF10 homologs are present ubiquitously in the plant kingdom.

Sub-functionalisation within the plant HFM family was further elucidated when expression analyses of FtTAF10 (which is nuclear localised) revealed weak expression in all type of cells but abundant expression in the vascular tissue of stem and roots. It was also shown that TAF10

is a plant selective and involved in the expression of a subset of vascular abundant genes. Its appropriate gene expression is necessary for normal plant development[14]. Soon after TAF10, TAF6 was characterised in *Arabidopsis* and two TAF6 homologs (AtTAF6 and AtTAF6b) were identified. These two have significant sequence homology to the known TAF6 protein from yeast, *Drosophila* and humans. The genes encoding these two proteins are quite divergent (35% identical and 53% similar) hinting that they might have evolved new functions after duplication. This interpretation was also supported by mutant analysis when AtTAF6 mutant did not survive in wild type AtTAF6b background. It was later shown that AtTAF6 mutation affects gametophyte development especially in pollen tube development resulting in reduced pollen tube growth[15].

In *Arabidopsis*, TAF1 is encoded by two genes HAF1 and HAF2. HAF2 mutant shows impaired co-activator functions during integration of light signals to the developmental pathways and acetylation of histone H3, suggesting that that HAF1 and HAF2 genes are also not fully redundant[16].

Recently in *Arabidopsis* it was shown that TAF13, a nuclear localised protein during all stages of embryo development, is later directed to plasma membrane especially in the epidermal cells suggesting an active post-translational regulatory mechanism. Interestingly this TAF13 does not have any nuclear localised signal and the probable partner protein that guides its transport to nucleus. A similar scenario has been reported in human TAF10, which also lacks NLS signal[17]. TAF13 is essential for the embryo development and more precisely it is essential after the globular stage of the embryo[18]. TAF13 was found to interact with Polycomb repressive complex2 (PRC2) and it was also inferred that TAF13 plays a role in FIS-PRC2 mediated repression; FIS-PRC2 is a multi-protein complex mainly active during female gametophyte and seed development.

6. NUCLEAR FACTOR Y (NF-Y) IN PLANTS: NOMENCLATURE & EVOLUTION

Over the last decade, NF-Y, also known as Hem-associated protein (HAP) and CCAAT box binding factor (CBF), has emerged as an important regulator of various developmental and stress induced responses in plants. The DNA NF-Y complex can either act as a transcriptional activator or as a repressor, and its activity can be modulated by interaction with other transcription factors (TFs) or regulatory proteins such as TFIID, SP1 or P53[19,20]. Phylogenetic analysis of three NF-Y protein families in four sequenced plant genomes; including both monocot (*Oryza sativa*), and dicots (*Arabidopsis thaliana* and two legumes, namely *Medicago truncatula* and *Glycine max*) showed the interacting part of the NF-Y complex to lie at the HFM[20]. Sequence alignments also show clear conservation among the NF-YB and NF-YC sub-unit counterparts from various organisms, as depicted in Figs. 3 and 4.

In recent years the majority of publications in mammals and various plant species have preferentially used the nomenclature NF-Y for this family of proteins,

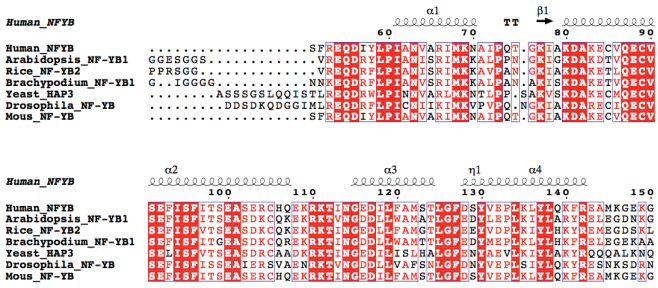

Figure 3. Conserved hydrophobic amino acids in NF-YB protein sequence.

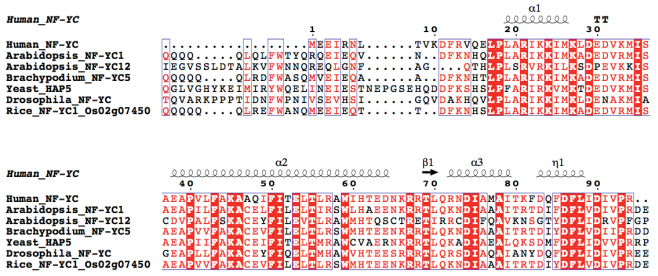

Figure 4. Conserved hydrophobic amino acids in NF-YC protein sequence.

and accordingly, identification and characterisation of this family in *Arabidopsis* followed the NF-Y terminology and recommended the same for further use. Two very recent publications in rice supported the same nomenclature for HAPs and CBFs and classified the rice HAPs by using the term NF-Y[20,7]. Petroni[7], *et al.* discussed the confusion created by varied HAP nomenclature and pointed three principal difficulties as follows:

(i) Plants are devoid of homologs of HAP4, which is required for transcriptional activation in fungi and they form a trimer as seen in mammalian counterparts.

(ii) Many genetic experiments and two thorough biochemical studies were performed in *Arabidopsis*, adhering to the NF-Y terminology[21,22].

(iii) The phylogenetically unrelated HAPLESS mutants of *Arabidopsis* are also known as *hap,* which precludes changing the *Arabidopsis* nomenclature. Based on these points, re-classification of the erstwhile HAP genes to NF-Y was proposed as per *Arabidopsis*[7].

As mentioned earlier, the NF-Y family contains HFM and exhibits unique DNA-binding characteristics at specific sequence site CCAAT as a heteromeric complex. This heteromeric complex is composed of single subunit from three proteins; NF-YA, NF-YB and NF-YC. Each of these subunits belongs to different large protein families. Among plants each of these sub-units are encoded by ~10 genes in both monocot and dicot lineages, presumably a consequence of multiple rounds of whole genome duplications (WGD). In contrast, animals have limited numbers of genes (only one or two genes) encoding each subunit, indicating expansion of the family in plant kingdom[20]. Such an expansion has an important repercussion on the binding preferences of each of the gene families, namely, their ability to bind to alternate members of the respective cognate family. The

NF-YA subunit can only bind to a pre-formed complex of NF-YB/NF-YC heterodimer[7], this HFM mediated dimerisation of NF-YB and NF-YC is because of the presence of HFM at the site of interaction, enabling formation of a tight complex analogous to the histone H2A-H2B dimer[23].

Therefore, an NF-YA subunit can theoretically bind any one of the multiple NF-YB members at a given time. Accodingly, the NF-Y heteromeric complex can potentially be formed by many possible combinations of sub units depending on the number of genes encoding each of the sub-unit proteins. Expansion of NF-Y gene family has made it possible for plants to form large number of possible heteromers of the complex. For example *Arabidopsis* has a total of 36 NF-Y genes (encoding 10 NF-YA, 13 NF-YB, and 13 NF-YC subunits) that theoretically could result in the formation of ~1500 alternative tri-meric combinations. However, plants have evolved some specificity in the formation of heteromeric complexes, allowing them to diversify in function at spatio-temporal scales.

NF-YB subunits are characterised by a central domain that has structural and amino acid similarity with the histone fold motif (HFM) of the core histone H2B. Similar to the NF-YB proteins, NF-YC is also characterised by a histone fold motif (HMF) domain but they are more closely related to the core histone H2A[24]. The histone fold of both NF-YB and NF-YC are conserved among yeast, animals and plants. Even the important hydrophobic amino acids in the alpha helix of the two HFMs are well conserved[7].

7. DOWN REGULATOR PROTEINS 1 (DR1) AND DR1 ASSOCIATED PROTEIN 1 (DRAP1)

The proteins Dr1 and DrAp1 form a complex and act as negative regulators of RNA Pol-II mediated transcription initiation. Dr1/DrAp1 was first identified in humans as TBP dependent basal transcription inhibitor[25]. Dr1 and DrAp1 homologs have significant size difference in dicot and monocot lineages, such that rice Dr1 is twice as large as compared to soybean and Arabidopsis counterpart. HFM is found at N terminal of the proteins and it is the most conserved region among plant and non-plant homologs. HFM of Dr1 and DrAp1 are very similar to the HFM of core histone sub-units H2B and H2A respectively. HFM region of these proteins are necessary for the formation of Dr1/DrAp1 complex and its repressor activity[26].

This negative regulator protein family is most closely (sequence identity 30-35%) related to the previously discussed NF-Y proteins family those were also found similar to the H2A and H2B class of histone family. So they are commonly misunderstood with NF-Y protein family. However, these two related HFM containing protein families are not functionally similar[7].

8. CHROMATIN ACCESSIBILITY COMPLEX (CHRAC)

CHRAC are part of energy dependent nucleosome remodeling machinery, it is well-studied human and drosophila but are poorly known in plants. In drosophila, two subunits of CHRAC, namely CHRAC-14 and CHRAC-16 were found to have histone fold motifs that helps them interact in a similar histone fold handshake fashion of H2A and H2B. HFM of this family protein are also closely related to NF-Y protein family[27].

9. CONCLUSION

The HFM is a structurally conserved motif found near the C-terminus in every core histone sequence in a histone octamer responsible for the binding of histones into heterodimers and thence to nucleosomes. The major role of this fold in core histones is the formation of an octameric structure, which binds to the DNA molecules to form a nucleosome. On average, the HFM is composed of about 70 amino acids and consists of three alpha helices connected by two short, unstructured loops. The core histones have the ability to assemble into head-to-tail intermediates via extensive hydrophobic interactions between each HFM domain in a "handshake motif". Apart from the core histones, the HFM is found in variety of diverse protein families where it helps in the formation of protein complexes, which interact with DNA. From a structural and functional viewpoint, the HFM in non-core-histone protein families appears to have retained its basic characteristic i.e. dimerisation followed by multi-merisation (protein-protein interaction) as well as interaction with DNA. Most of these proteins are well studied in mammals, yeast and drosophila but are poorly characterised in plant systems, despite the ability of plant HFM containing proteins to exist in the form of large gene families, showing evidence for neo-functionalisation as well as sub-functionalisation among member sub-units, following duplication, providing an opportunity for future research endeavors.

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Conflict of Interest : None

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