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Review

The Alba protein family: Structure and function

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ABSTRACT

Alba family proteins are small, basic, dimeric nucleic acid-binding proteins, which are widely distributed in archaea and a number of eukaryotes. This family of proteins bears the distinct features of regulation through acetylation/deacetylation, hence named as acetylation lowers binding affinity (Alba). Alba family proteins bind DNA cooperatively with no apparent sequence specificity. Besides DNA, Alba proteins also interact with diverse RNA species and associate with ribonucleo-protein complexes. Initially, Alba proteins were recognized as chromosomal proteins and supposed to be involved in the maintenance of chromatin architecture and transcription repression. However, recent studies have shown increasing evidence of functional plasticity among Alba family of proteins that widely range from genome packaging and organization, transcriptional and translational regulation, RNA metabolism, and development and differentiation processes. In recent years, Alba family proteins have attracted growing interest due to their widespread occurrence in large number of organisms. Presence in multiple copies, functional crosstalk, differential binding affinity, and posttranslational modifications are some of the key factors that might regulate the biological functions of Alba family proteins. In this review article, we present an overview of the Alba family proteins, their salient features and emphasize their functional role in different organisms reported so far.

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1. Introduction

The regulation of gene expression is an indispensable process in all the domains of life, which widely differs among prokaryotes and eukaryotes. This secret lies in chromatin, where most evolutionarily conserved histones actively participate with DNA to switch on and off certain genes [1–2]. Histones are present in the nuclei of eukaryotic cells and in certain archaea (Euryarchaea) but are not reported in case of bacteria. In contrast to eukaryotic histones, the components of archaeal chromatin display greater heterogeneity, where interplay of two or more unrelated proteins has been observed (instead of single universal chromatin protein) to preserve the structural and functional integrity of the genome [2–4]. In archaea, chromatin proteins belong to either eukaryotic histones (Euryarchaea) or bacterial-like nucleoid-associated small DNA-binding proteins (Crenarchaea), i.e., Alba (Sac10b homologue), Sul7d, Cren7, and CC1. Among them, Alba is one of the most extensively studied nucleoid-associated archaeal proteins, which displayed an important physiological role in archaeal genetics [3–6]. Recent studies have revealed the presence of Alba family proteins in a wide range of organisms and suggest their involvement in variety of cellular functions, including transcriptional and translational regulation, chromatin dynamics, development, and differentiation [5,7–16].

The global attention toward Alba family proteins was received very shortly after the identification of sequence-independent DNA-binding proteins from archaeal hyper-thermophiles [17–19]. These nucleoid proteins were represented by small, highly abundant, basic DNA-binding proteins, which were isolated from extreme thermophilic archaea of the genus *Sulfolobus*. Initially, these proteins were separately grouped according to their respective molecular weights (such as 7, 8, and 10 kDa), and each class was further sub-grouped according to their electrophoretic properties. Out of them, those of the 7 kDa and the 10 kDa family's proteins received special attention and their detailed biochemical and structural characterization were performed [17–19]. These proteins were termed as histone-like proteins, although these proteins had no sequence similarity with archaeal histones or histone-like proteins, discovered in other archaea. Alba family proteins originally belonged to one of these protein families and designated as Sso10b from *Sulfolobus solfataricus*, Ssh10b from *Sulfolobus shibatae*, and Sac10b from *Sulfolobus acidocaldarious* based on their origin [18]. These proteins are highly abundant, basic chromatin proteins that are present in almost all the archaeal genomes sequenced. The term Alba (acetylation lowers binding affinity) for this family of proteins was coined by the S.D. Bell group, who for the first time demonstrated that Alba exists in two different forms, which differ by the presence of an acetyl group at N-terminal Lysine (K16) [17]. It has been proposed that Alba undergoes posttranslational modification (i.e., reversible acetylation) at the N-terminal lysine residues, which results in reduction in the DNA-binding affinity of Alba. Nonacetylated Alba has greater affinity toward DNA, whereas acetylation reduces its affinity [17,20].

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Furthermore, binding of Alba with DNA represses the transcription under *in vitro* conditions, whereas acetylation reduces or inhibits this transcriptional repressor activity. As Alba is acetylated by PAT (protein acetyl transferase) and deacetylated by Sir2 (a NAD^+-dependent histone deacetylase, HDAC), it becomes apparent that Alba can serve as transcriptional regulator similar to histones [17,20–23]. The hallmark of histone regulation was not seen to be involved in chromatin remodeling in archaea since archaeal histones lack the N-terminal and C-terminal tails that are loci of regulatory posttranslational modifications [3–4,6]. In this view, functional resemblance of Alba in terms of acetylation and deacetylation (resulting in transcriptionally active versus inactive chromatin) with that of eukaryotic histones is challenging.

In archaea, Alba is represented as a major architectural DNA-binding protein, which organizes and regulates the genome of both euryarchaea (contain histone) as well as crenarchaea (having no histone) [3,5–6,18]. However, recent studies have revealed the association of Alba with diverse RNA species, ribonucleo-protein complexes, and RNA-binding proteins [8,13,15–16,24–28]. Together, these studies imply the association of Alba with both types of nucleic acids and unravel the complex molecular connections of Alba family proteins to undertake the diverse biological functions. Alba family proteins are present among diverse range of organisms; however, their characterization is limited to archaea and protozoan parasites and biological relevance of these proteins in other species is not yet clear. In this regard, detailed analysis of the precise functions and regulation of Alba family proteins represents a fruitful area for future study.

Here in this review, we present a conceptual overview of comprehensive literature survey of Alba family proteins characterized so far with a view to generate new insights into structure, function, and regulation of Alba family proteins. This review will focus on the genomic organization, evolutionary history, domain architecture, structural, and biochemical properties and functional diversity among the Alba family proteins. We also discuss the molecular mechanism of nucleic acid binding, functional association (genetic and physical interaction), and post-translational modifications of Alba family proteins. Along the way, we describe how these factors together interplay and influence the biological functions of Alba family proteins.

2. Genomic organization and evolutionary history

Members of Alba family were initially discovered from hyperthermophilic archaeon, where they appear to be highly conserved and restricted. However, subsequent studies have documented the presence of Alba family proteins nearly in all the domains of the life [18,24]. Majority of Alba family proteins are typically small and comprise a single domain of >90 amino acids (Alba domain). Alba proteins in some eukaryotes are comparatively bigger in size and consist of multiple domains. Candidate protein domain database and bioinformatics analysis of growing number of sequences from fully annotated genomes revealed the presence of large number of Alba sequences from different species (844 sequences from 348 species), although the size and number of genes/isoforms vary from species to species (http://pfam.xfam.org/family/PF01918) [29]. In archaea, Alba is highly specific and shows sequence conservation in most of sequenced genome, including thermophiles and hypothermophiles [18,24]. In majority of archaea, lineage-specific duplication of Alba (such as *Sulfolobus*, *Aeropyrum*, *Archaeoglobus*, etc.) has been observed. The two paralogues of Alba are thus named as Alba1 and Alba2 [such as Sso10 (SsoAlba1) and Sso10b2 (SsoAlba2) in *S. solfataricus*] to differentiate them from each other (Table 1). Contrary to archaea, in eukaryotes (i.e., plants, fungus, protozoan, and metazoan) multiple copies (paralogues) of Alba proteins have been observed which share very limited sequence identities with each other (Table 2). The reason for this heterogeneity seems to be purely evolutionary and advocates the lineage-specific evolution of Alba proteins in these species. Whatever the roles of multiple copies of Alba, it is generally suggested that increase in the number by gene duplications generated functional redundancy to meet with increasing cellular variety and complexity.

Phylogenetic studies suggest that Alba family basically originated as RNA-binding proteins and is closest with subunits of ribonucleo-protein complexes (RNase P/MRP) and ciliate macronuclear development protein 2 (Mdp2) [24]. RNaseP/MRP subunits are involved in the processing of precursor RNA (rRNA and tRNA) and mitochondrial DNA replication, while Mdp2 is involved in macronuclear development [24]. Detailed phylogenetic analysis of known Alba sequences categorized the Alba family proteins in one archaeal specific and two eukaryotic specific families (Fig. 1). The archaeal specific family predominantly contains archaeal Alba proteins (Fig. 1 and Table 1). The common examples are Alba proteins from *Sulfolobus shibatae*, *Sulfolobus solfataricus*, *Aeropyrum pernix*, *Archaeoglobus fulgidus*, *Thermoplasma acidophilum*, *Pyrococcus furiosus*, *Methanobacterium thermautotrophicum*, *Methanococcus maripaludis*, *and Methanococcus janaschii* etc. [17–18,25,28,30–31,36–38]. The eukaryotic group contains multiple copies of Alba which are distributed in two specific families (Fig. 1 and Table 2). The first

Table 1
Structure, nucleic acid binding, and biological functions attributed to known Alba family proteins from archaea.

Organism	Name	Uniprot ID	Nucleic acid binding	Biological function	Structure (PDB ID)	References
Sulfolobus solfataricus	SsoAlba1 (Sso10b1)	D0KTT2	DNA/RNA	Gene expression and chromatin organization	1H0X (Homodimer), 1H0Y (Homodimer), 2BKY (Heterodimer)	[14,20,38,43]
	SsoAlba2 (sso10b2)	D0KTT4	DNA	Gene expression and chromatin packaging	2A2Y (Homodimer), 1UDV (Homodimer), 2BKY (Heterodimer)	[25,30,38]
Sulfolobus shibitae	SshAlba (Ssh10b)	P60848	DNA/RNA (mRNA, rRNA & ribosomes)	RNA metabolism (stabilization and translational regulation)	1Y9X (Homodimer), 3WBM (Alba–RNA)	[13,27,67]
Aeropyrum pernix.	ApAlba1	Q9YAW1	DNA	Gene expression and chromatin organization	ND	[9]
	ApAlba2	Q9YAX2	DNA	Gene expression and chromatin organization	2H9U (Homodimer), 3U6Y (Alba–DNA)	[31,44]
Pyrococcus horikoshii	PhoAlba	O74101	RNA (RNase P RNA and pre-tRNA)	Catalytic activity (RNase P)	2Z7C (Homodimer)	[28]
Methanobacterium thermoautotrophicum	MthAlba	O27527	None	None	3TOE (Homodimer)	[32,70]
Methanococcus jannaschii	MjaAlba	Q57665	DNA	Gene expression and chromatin organization	1NH9(Homodimer)	[36]
Methanococcus maripaludis	MmaAlba	A4G0V8	DNA	Gene expression	ND	[69]
Archaeoglobus fulgidus	AfAlba2	O28323	DNA	Gene expression and chromatin organization	1NFJ (Homodimer), 1NFH (Homodimer)	[23]

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