



Review

The evolution of land plant hemoglobins

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ABSTRACT

This review discusses the evolution of land plant hemoglobins within the broader context of eukaryote hemoglobins and the three families of bacterial globins. Most eukaryote hemoglobins, including metazoan globins and the symbiotic and non-symbiotic plant hemoglobins, are homologous to the bacterial 3/3-fold flavohemoglobins. The remaining plant hemoglobins are homologous to the bacterial 2/2-fold group 2 hemoglobins. We have proposed that all eukaryote globins were acquired via horizontal gene transfer concomitant with the endosymbiotic events responsible for the origin of mitochondria and chloroplasts. Although the 3/3 hemoglobins originated in the ancestor of green algae and plants prior to the emergence of embryophytes at about 450 mya, the 2/2 hemoglobins appear to have originated via horizontal gene transfer from a bacterium ancestral to present day *Chloroflexi*. Unlike the 2/2 hemoglobins, the evolution of the 3/3 hemoglobins was accompanied by duplication, diversification, and functional adaptations. Duplication of the ancestral plant *nshb* gene into the *nshb-1* and *nshb-2* lineages occurred prior to the monocot–dicot divergence at ca. 140 mya. It was followed by the emergence of symbiotic hemoglobins from a non-symbiotic hemoglobin precursor and further specialization, leading to leghemoglobins in N₂-fixing legume nodules concomitant with the origin of nodulation at ca. 60 mya. The transition of non-symbiotic to symbiotic hemoglobins (including to leghemoglobins) was accompanied by the alteration of heme-Fe coordination from hexa- to penta-coordination. Additional genomic information about Charophyte algae, the sister group to land plants, is required for the further clarification of plant globin phylogeny.

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Abbreviations: Hb, hemoglobin; Lb, leghemoglobin; MYA, million of years ago; nsHb, non-symbiotic hemoglobin; nsHb-1, non-symbiotic hemoglobin type 1; nsHb-2, non-symbiotic hemoglobin type 2; sHb, symbiotic hemoglobin; tHb, truncated (2/2) hemoglobin.

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1. Introduction

1.1. What is a globin?—a historical perspective

Globins are proteins with a characteristic α -helical secondary structure comprised of helices A–H, known as the myoglobin-fold, and a heme group ensconced within a hydrophobic cavity formed by a 3/3 sandwich of helices A, B, C, and E over helices F, G, and H. Of the two heme-Fe axial sites, the proximal one is coordinated to a His at position 8 of helix F, while the distal site can coordinate either with a side-chain group of residues located in helix E or bind small molecule ligands, including O₂, CO, and NO. Historically, the familiar vertebrate O₂-binding hemoglobin, a tetramer of α - and β -globins, and myoglobin were among the first proteins whose sequences and structures were determined over 50 years ago [1]. At that time, the hemoglobins in metazoans other than vertebrates were investigated mostly in cases where the hemoglobin presence was visible. These included the larval hemoglobin of the insect *Chironomus* [2] and the intracellular hemoglobin of the annelid *Glycera* [3]. Comparison of several vertebrate and the invertebrate hemoglobin structures led to the recognition of a highly conserved tertiary structure, the myoglobin-fold, underpinned by the conservation of over 30, mostly solvent-inaccessible hydrophobic residues [4], even in cases of <20% identity to vertebrate globins. The 3/3 α -helical myoglobin-fold is not unique: it is shared with phycocyanins and other proteins [5]. The transport of O₂ for aerobic respiration is thought to be the major function of vertebrate globins related to their ability to reversibly bind O₂ [1]. However, evidence has accrued over the last two decades indicating that both bacterial and eukaryote globins have enzymatic and sensing functions in addition to O₂-transport and storage [6].

1.2. Diversity of globins in living organisms

The availability of numerous sequenced genomes over the past 20 years allowed the identification of globins in a wide variety of organisms, ranging from bacteria to vertebrates. The bacterial globin superfamily encompasses three families/lineages that belong to two structural classes: the 3/3- and 2/2-fold globins (Fig. 1) [7,8]. The two globin families/lineages with the 3/3-fold

are the F family comprising the flavohemoglobins and related single domain globins [9], and the S (for sensor) family, encompassing globin coupled sensors and protoglobins [10,11], and related single domain globins [12]. The third family consists of truncated myoglobin-fold globins, with the 3/3-fold reduced to a 2/2-fold due to a shortened or absent helix A and conversion of the F helix into a loop (Fig. 1) [13–17]. The T family exists in three structurally distinct subfamilies, T1–T3 [13–17].

Recent genomic information has also greatly extended the structural and functional diversity of vertebrate globins through the discovery of novel globins like neuroglobin and cytoglobin [18,19], which are hexacoordinated [20,21], and perform yet-to-be-determined functions in nerve and fibroblast-like cells, respectively [22,23]. Furthermore, the identification of additional globins with unknown physiological functions and restricted phyletic distributions, globin X in some protostomes and chordates [24], globin Y in amphibians and monotreme mammals, and globin E the avian eye globin has added complexity to vertebrate globin gene evolution [25–29]. Phylogenetic analyses of these vertebrate globins revealed that erythroid-specific globins have independently evolved O₂-transport functions in different lineages [30]. Most recently, a new metazoan globin lineage was discovered, consisting of large, ca. 1600 residues, chimeric proteins with an N-terminal cysteine protease domain and a central globin domain, named androglobins, because of their specific expression in testis tissue [31].

All metazoan globins, vertebrate and non-vertebrate, symbiotic and non-symbiotic plant globins, and many globins in microbial eukaryotes have the 3/3 α -helical fold and have sequences that are homologous to the F family bacterial globins. T family group 1 and 2 globins occur in microbial eukaryotes (ciliates, stramenopiles, oomycets, opisthokonts, etc.) and in plants [7]. Fungi are unique in having only flavohemoglobins and S family single domain globins [32]. We have proposed that eukaryote globins evolved from the respective bacterial lineage via horizontal gene transfer resulting from one or both of the accepted endosymbiotic events responsible for the origin of mitochondria and chloroplasts, involving an α -proteobacterium and a cyanobacterium, respectively [12]. The present *status* of our knowledge of the three globin families and their subgroups in bacteria and the relationships between them and eukaryote globins is shown in Fig. 2. Within this

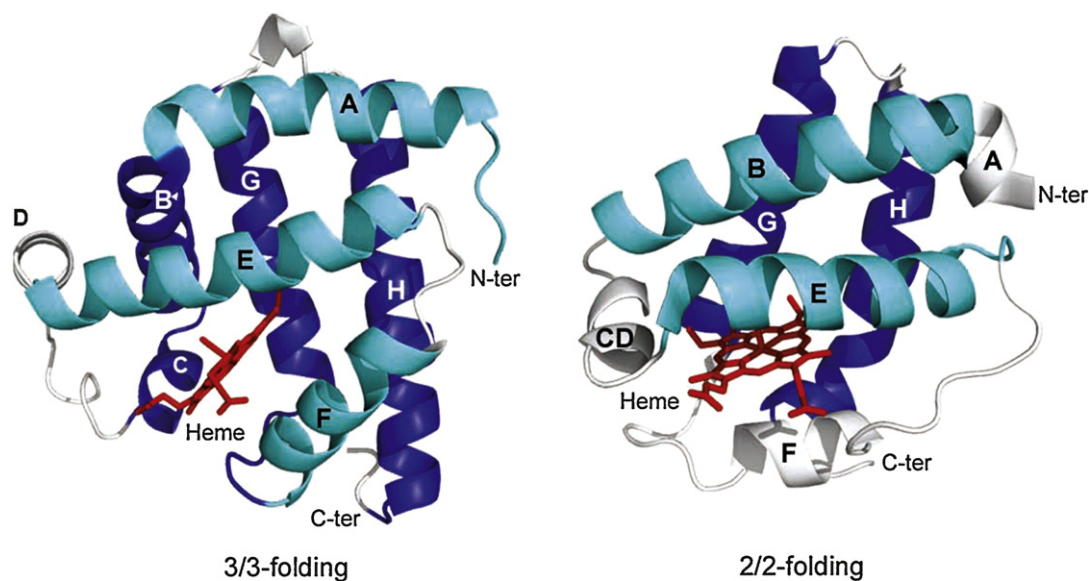


Fig. 1. Structure of 3/3-folding spermwhale myoglobin and 2/2-folding *Chlamydomonas* T1 truncated hemoglobin (Brookhaven Protein Data Bank identification number 1MCY and 1DLY, respectively). Helices are indicated with letters A–H. Note the overlapping of helices A, E, and F to helices B, G, and H in the 3/3-folding, and overlapping of helices B and E to helices G and H in the 2/2-folding.

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