Phycobilisome Architecture: the Work of Alexander N. Glazer

Chromophore Content of Blue-Green Algal Phycobiliproteins
(Glazer, A. N., and Fang, S. (1973) J. Biol. Chem. 248, 659–662)

Molecular Architecture of a Light-harvesting Antenna. In Vitro Assembly of the Rod Substructures of Synechococcus 6301 Phycobilisomes
(Lundell, D. J., Williams, R. C., and Glazer, A. N. (1981) J. Biol. Chem. 256, 3580–3592)

Alexander N. Glazer was born in Lodz, Poland in 1935. He moved to Australia with his family shortly after the war ended and earned his bachelor's and master's degrees from the University of Sydney in 1957 and 1958, respectively. His master's thesis involved physicochemical studies of proteins. While at the University of Sydney, Glazer attended a lecture given by Emil L. Smith on structure-function relationships in the proteolytic enzyme papain. (Smith was featured in two previous Journal of Biological Chemistry (JBC) Classics (1, 2).) Inspired by the lecture, Glazer decided to go to the University of Utah to do his graduate studies with Smith. He earned his Ph.D. in 1960 with a thesis titled “The Sulfur Distribution of Papain and Related Studies.”

After graduating, Glazer moved to Israel to do a postdoctoral fellowship with Ephraim Katchalski in the Department of Biophysics at the Weizmann Institute of Science. There he examined structural and enzymatic properties of polypeptide proteins. He continued his postdoctoral work in the MRC Laboratory of Molecular Biology in Cambridge under the guidance of Fred Sanger, exploring the potential of labeling proteins with radioactive iodine isotopes and utilizing the behavior of labeled fragments in chro-
matographic and electrophoretic separations to deduce the amino acid sequence surrounding a labeled residue. In 1964, he returned to the United States to join the faculty of the Department of Biological Chemistry at the University of California Los Angeles School of Medicine. There he continued to collaborate with Smith who had become chairman of the Department of Biological Chemistry at UCLA.

In 1970, Glazer took a sabbatical year with Roger Stanier at the University of California, Berkeley and in collaboration with Stanier and Germaine Cohen-Bazire established the subunit structure of the light-harvesting proteins, phycobiliproteins, of cyanobacteria (formerly blue-green algae) and the cryptomonads. Upon his return to UCLA, Glazer continued this research, focusing on the molecular architecture and the energy transfer pathways of phycobilisomes, the large multisubunit light-harvesting complexes found in cyanobacteria and red algae.

Phycobilisomes consist of two types of proteins: phycobiliproteins that carry covalently attached tetrapyrrole chromophores (bilins) and linker polypeptides that play structural roles. All cyanobacteria contain two phycobiliproteins, allophycocyanin and phycocyanin, and many contain a third, phycoerythrin or phycoerythrocyanin. The monomeric units of each type of phycobiliprotein are composed of two polypeptide chains, each carrying covalently bound chromophore, phycocyanobilin in the case of phycocyanin and allophycocyanin, and phycoerythrobilin in the case of phycoerythrin.

In the first JBC Classic reprinted here, Glazer and Suen Fang described a method for the quantitative separation of the $\alpha$- and $\beta$-subunits of phycocyanin and reported the phycocyanobilin chromophore content of the $\alpha$- and $\beta$-subunits of phycocyanin and allophycocyanin from *Synechococcus* sp., a unicellular cyanobacterium. By spectroscopic analysis, they showed that the $\alpha$-subunit of phycocyanin carries a single chromophore, the $\beta$-subunit carries two chromophores, and the subunits of allophycocyanin carry a single chromophore per polypeptide chain. Experiments with cyanobacteria belonging to other taxonomic groups established the generality of the findings.

In the second Classic, Glazer and postdoctoral fellow, Daniel Lundell, in collaboration with famed electron microscopist Robley Williams, looked at the overall architecture of the phycobilisome. Previous electron microscopy studies had indicated that phycobilisomes have two morphologically differing substructures when they are seen in “face view.” One type consisted of a core of two contiguous disk-like objects from which radiated a hemispherical array of up to six rods composed of a few stacked discs. The other type had a core composed of three contiguous elements arrayed in an equilateral triangle, with the arrangement of the rods similar to the first type.

Focusing on *Synechococcus* sp. 6301, Glazer and his colleagues elucidated the mode of assembly of the rod substructures. They purified four uncoulored polypeptides from the phycobilisomes of this unicellular cyanobacterium and showed that three of these, 33-, 30-, and 27-kDa polypeptides, were involved in the assembly of phycocyanin into $(\alpha\beta)_6$ discs and linked them into rods. Phycocyanin and the 27-kDa polypeptide did form an $(\alpha\beta)_6$-27-kDa complex that did not itself stack into rods, but its addition to a rod terminated further growth.
By the mid-1980s, Glazer and his co-workers had delineated all the broad features of phycobilisome structure and proposed a model (Fig. 1). More information on Glazer’s research on phycobilisomes can be found in his JBC Minireview (3) and in a more recent article (4). In subsequent work, Glazer focused on phycobilisomes from open ocean unicellular cyanobacteria specialized for the absorbance of green light. His research has also led to the use of phycobiliproteins as fluorescence tags for cell surface markers.

Glazer is currently a professor of the graduate school in the Department of Molecular and Cell Biology at the University of California, Berkeley as well as director of the University of California Natural Reserve System (NRS). In recognition of his contributions to science, Glazer has received many honors and awards including the British Association for the Advancement of Science’s Endeavour Prize (1955), two Guggenheim fellowships (1970–1971 and 1982–1983), the Botanical Society of America’s Darbaker Prize (1980), and the National Academy of Sciences Award for Excellence in Scientific Reviewing (1991). He is also a member of the National Academy of Sciences and the American Academy of Arts and Sciences, and he served on the JBC editorial board for a total of 10 years.

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3. Glazer, A. N. (1989) Light guides. Directional energy transfer in a photosynthetic antenna. J. Biol. Chem. 264, 1–4
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