

BOOK REVIEWS

Prokaryote Photosynthesizers

The Molecular Biology of Cyanobacteria. DONALD A. BRYANT, Ed. Kluwer, Norwell, MA, 1994. xiv, 881 pp., illus. \$355 or £233 or Dfl. 555; paper, \$190 or £126 or Dfl. 300. *Advances in Photosynthesis*, vol. 1.

The cyanobacteria are a vast and diverse group of prokaryotes, distinguished by their ability to carry out the same oxygen-evolving reactions as the photochemical apparatus of green plants. It is likely that cyanobacteria were the first organisms, more than 3.5 billion years ago, to put oxygen into the atmosphere of the Earth. Contemporary forms provide the beginning of the food chain in the oceans, nourish the roots of cycads in the tropics, serve as green manure for rice grown in Asian paddies, and could conceivably make deserts arable in the future. Cyanobacteria are not always benign, though. They can form choking blooms on lakes when phosphate levels are sufficient, and some species can produce toxins that mammals find unpleasant. The good and bad sides of these creatures are due to their unique properties: they are the only living organisms that can reduce both CO₂ to carbohydrate and N₂ to ammonia under aerobic conditions, utilizing sunlight to fuel both processes.

Green plant and algal chloroplasts contain two classes of photochemical reaction centers, PSI and PSII, embedded in the photosynthetic membranes called thylakoids. Each reaction center consists of several proteins and a small number of chlorophyll molecules, positioned in such a way that absorption of light energy by one special chlorophyll leads to a series of electron transfers that results in a separation of charge across the thylakoid membrane. This charge separation can do useful work, such as ATP synthesis. Light energy for PSI and PSII is harvested by beds of protein-bound chlorophyll molecules that surround the reaction centers. Energy migration through these beds is rapid and efficient. Cyanobacteria also use chlorophyll to harvest light for PSI, but their accessory pigments for PSII are different and unique. They use elaborate assemblies of proteins bearing covalently attached linear tetrapyrroles, the proteins arranged in disks piled up in cylinders. The most prevalent of these phycobiliproteins, phycocyanin, is responsible for the brilliant

blue-green color of most cyanobacteria and for their obsolete name, blue-green algae. It should be noted, however, that some cyanobacteria, in spite of their name, lack phycocyanin. Many marine strains contain predominantly the red pigment phycoerythrin; such a strain (*Trichodesmium*) is responsible for the name of the Red Sea.

What's in a name? Algae are (or were, before molecular taxonomy) studied and classified according to the Botanical Code, which bases assignments on the features of dried herbarium specimens. The recognition that blue-green algae are prokaryotes, that is, bacteria, led Roger Stanier to urge that they be classified according to the criteria established for bacteria: the growth and nutritional properties of pure cultures and, later, DNA base composition and, still later, sequences. He prevailed, as he had to, and this is reflected in the titles of the major attempts to summarize what is known of these organisms that have been published over the last 25 years. *The Biology of the Blue-Green Algae* appeared in 1973, appropriately timed to summarize a great deal of physiology and biochemical characterization of cell components, and more or less on the eve of the introduction of molecular biology to the subject. The same editors, N. G. Carr and B. A. Whitton, assembled *The Biology of the Cyanobacteria* in 1982. The latter volume displays the lag in assimilation of new information common in such works: there is no mention of the cloning and sequencing of the genes encoding nitrogenase components from cyanobacteria, published in 1980. Only the chapter by Ford Doolittle on molecular evolution properly anticipates the range of contributions that molecular techniques would make to the study of cyanobacteria.

Now we have a massive collection entitled *The Molecular Biology of the Cyanobacteria*, appropriately timed because molecular methods have totally changed the way we should consider cyanobacteria. In the past, we justified their study on the basis of their role in pollution or the food chain or as fertilizer. Now, it is clear that cyanobacteria have made, and will make in the future, major contributions to the understanding of fundamental aspects of evolution, photosynthesis, and cellular differentiation, to cite a few examples. Almost every one of the 28 chapters concludes with a glimpse of the future that promises not just an exten-

sion of the results summarized but a qualitative increase in level of understanding. A sampling of the highlights: site-specific mutations introduced into the proteins of photochemical reaction centers, light regulation of gene expression, physical maps of chromosomes, and developmentally regulated gene rearrangements during differentiation of heterocysts, cells specialized for nitrogen fixation.

The authors come from a total of 12 nations. The editor has managed to obtain a reasonably uniform level of presentation, eliminate most redundancies, and get the authors to refer to each other wherever appropriate. The book has an additionally useful feature: a separate gene and gene product index, in addition to the conventional subject and organism indexes. Ten color plates depicting the x-ray-determined structures of components of the photosynthetic apparatus and several key enzymes precede the chapters.

Topics covered include molecular evolution, oceanic picoplankton, prochlorophytes, cyanelles, chloroplast evolution, membranes, phycobilisomes, photosystems I and II, the cytochrome complex that connects them, ATPase, the soluble electron carriers, respiration, carbon dioxide and nitrogen fixation and metabolism, tetrapyrroles, carotenoids, genetic systems, transcription, responses to light, metal ion, heat shock, and nutrients, and cellular differentiation. In almost every case, the summaries of current knowledge are apt and thorough. The coverage is inclusive with the possible exception of symbiotic associations, where the extensive contributions of Meeks, Bergman, Nierzwicki-Bauer, and their collaborators are missed. *Trichodesmium* is also virtually ignored, but that is probably reasonable given that molecular biology has not had much impact on the studies of that ocean-going genus and another recent book (*Marine Pelagic Cyanobacteria*, E. J. Carpenter *et al.*, Eds.; Kluwer, 1992) has been devoted entirely to its physiology.

How long will this big book be useful? Given the accelerating pace of DNA sequencing, probably fewer years than its predecessors. Within five years, there should be available the complete DNA sequence of one of the smaller genomes, either *Synechocystis* 6803 or *Synechocystis* 7002, both widely used for studies of the photosynthetic apparatus. General schemes for the gene-by-gene analysis of transcription and protein function are available for these strains.

The way is obvious. The only requirements are willing hands and funding.

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