

Progress in Plastid Research

The Plastids. Their Chemistry, Structure, Growth and Inheritance. JOHN T. O. KIRK and RICHARD A. E. TILNEY-BASSETT. Second edition. Elsevier/North-Holland, New York, 1978. xx, 960 pp., illus. \$150.

Research on the nature and function of green plant plastids is broadly based and encompasses the tools and techniques of both the physical and the biological sciences. Almost any question that can be asked of a biological system can be studied using a plastid system. The dominant and most commonly known plastid, the chloroplast, was first described in the literature by Nehemiah Grew in 1682. It was not until the 1930's, however, that these organelles were successfully isolated and detailed work on their functions became possible. Plastid research through 1967 was exhaustively reviewed by Kirk and Tilney-Bassett in the first edition of *The Plastids*. It was clear that much progress had been made, particularly in our understanding of plastid ultrastructure, the biochemistry of the light and dark reactions of photosynthesis, the basic physiology of chloroplast development in angiosperms, the genetic basis of variegation, and the inheritance properties of plastids. It had been reasonably well established that chloroplasts contained their own DNA, RNA, and ribosomes. However, no substantial information was available to establish what the function of plastid DNA was, how much there was, and whether the amount was adequate to serve a genetic role. Despite this lack of information, chloroplasts were known to show a high degree of autonomy in their ability to synthesize many of their own constituents, even though the syntheses of some major chloroplast components were controlled by nuclear genes. These findings provided the framework for studies aimed at defining the extent of chloroplast autonomy.

There has been an explosion in our knowledge of the genetics, biochemistry, biophysics, and physiology of plastids since the publication of the first edition of this book. The second edition contains nearly twice as many pages as the first,

with some chapters nearly tripling in length and in number of literature citations. The second edition retains many features of the first, at least organizationally and in exhaustiveness of literature reviews. However, it is distinguished by more evaluative and critical discussion and by a far less encyclopedic style.

There are too many topics that have been expanded greatly from the first edition to discuss in detail here; three topics are worthy of consideration, however, because of the overwhelming increase in knowledge about them: the nature of chlorophyll *in vivo*, pattern genes for variegation, and the molecular biology and genetic function of plastids.

The extent of knowledge of the nature of chlorophyll *in vivo* in 1967 was small. It was known that chlorophyll in a living leaf or algal cell showed much longer-wavelength absorption than that extracted into hydrocarbons—663 nanometers *in vitro* in acetone, for example, compared with 678 nanometers *in vivo*. The reasons for the red shift were at best speculative. The aggregation of chlorophyll molecules *in vivo*, their possible association with protein, and changes in their molecular environment were suggested. In the last decade it has been reasonably well established that chlorophyll exists *in vivo* in at least four universal spectroscopic forms and that probably all of the magnesium porphyrin molecules are bound in a highly specific manner to proteins (much like heme in hemoglobin and cytochromes), giving rise in part to the spectral forms observed *in vivo*. Chlorophyll-binding proteins are discussed by Kirk in the context of plastid protein composition, location and organization of chlorophyll, the molecular structure of plastid membranes, plastid genetics, genetic control of plastid biogenesis, and growth and differentiation of plastid membranes. In particular, there is a detailed discussion of the known protein chemistry (subunit structure, amino acid composition, and so on) of the chlorophyll-binding proteins. Their spectral properties and protein characteristics are detailed in relation to their functional organization and biosyn-

thesis. It is emphasized that further detailed studies are needed to provide a complete chemical description of these proteins and of the nature of chlorophyll *in vivo*.

The genetic basis of variegation and inheritance in plants has been much more than a curiosity, as is demonstrated by the thorough, nearly 300-page discussion by Tilney-Bassett. In the discussion the heterogeneous group of known variegated plants is separated into figurative patterns, general chlorosis, and mosaic and striped patterns. These patterns are discussed in terms of environmental influences, morphological and morphogenic responses, and breeding behaviors. It is emphasized that in the true-breeding variegated plants the figurative patterns of variegation are principally a result of physiological modifications influencing the regulation of normal chloroplast development rather than a result of a specific gene mutation. In other cases mutable homozygous recessive nuclear genes, arising from repeated "back-mutations," give rise to a heterozygous genotype. It is proposed that these unstable genes that give rise to variegations are governed by controlling elements that become integrated into the affected gene, thereby influencing its normal activity. Leaf chimeras and the sorting out of normal and mutant plastids are also discussed. The discussion of the latter aspect emphasizes the genetics of plastome (chloroplast) and nonplastome origins of the mutations.

The number of molecular biological investigations of plastids has increased logarithmically in the past decade. The authors have added a chapter on cytoplasmic inheritance and the characterization of the plastid genome in *Chlamydomonas*. The chapter includes a historical discussion of the methods of recovery of cytoplasmic genes and points out the lack of substantial evidence that the "chloroplast" linkage groups that are being intensively mapped are in fact solely in the chloroplast genome. The lack of standardization in mapping techniques and the nonuniformity of the nomenclature used even within the same laboratory have led to a rather confused picture of cytoplasmic inheritance. Tilney-Bassett deliberately emphasizes the weakness in the *Chlamydomonas* system in order to stress the need for the establishment of a more substantial foundation for this important work.

Kirk provides a well-organized chapter on the tremendous advances made in techniques for DNA analysis and in the use of restriction endonucleases for

DNA fragmentation that have enabled researchers to provide a wealth of information on the physical and genetic nature of plastid DNA. Further, he points out that it is reasonably well established that the number of copies of the chloroplast genome ranges between 30 and 60 per plastid in higher plants and up to about 100 per plastid in various algae (assuming that one copy is 90 million daltons in higher plants and 128 million daltons in the green algae). In most cases these estimates have been confirmed by electron microscopy. On the basis of these analyses it is now known that there is enough unique chloroplast DNA to code for about 126 proteins of 40,000 daltons (allowing for the redundant DNA in the inverted repeats). To date about 12 percent of the plastid DNA sequence has been provisionally identified as coding for plastid components, including subunits of ribulose biphosphate carboxylase, coupling factor (CF₁), and genes for ribosomal and transfer RNA's. Recognizing that there is cooperation between nuclear and cytoplasmic genomes to synthesize and maintain chloroplast integrity and function, Kirk thoroughly and accurately discusses the state of knowledge of the control of plastid biogenesis. He states his belief that we have merely broken the surface of the genetic control of plastid formation and function, since it is unlikely that any significant portion of the plastid DNA is genetically non-functional.

One last aspect of plastid research that has been successfully developed since 1967 is the isolation of intact chloroplasts that are capable of protein synthesis in the presence of either adenosine triphosphate or light. The protein synthesis products of these isolated chloroplasts have been shown to be identical to authentic chloroplast proteins, a demonstration that indicates that isolated chloroplasts have fully functional protein synthesis machinery in which messenger RNA is translated accurately. The use of chloroplast protein synthesis in conjunction with interspecific hybridization has provided the bulk of the evidence for the role of chloroplast DNA.

The authors' discussions extend beyond the chloroplast. Detailed and up-to-date discussion of other plastids, such as proplastids, etioplasts, chromoplasts, and amyloplasts, is provided. Specific considerations are made of the composition, structure, and biogenesis of these plastids.

The second edition of *The Plastids* is a monumental work that successfully covers the major and related aspects of

plastids. I recommend it highly. It is written in a clear manner, with evaluative discussion, wise speculation, and useful identification of gaps in our knowledge and understanding. The book will be valuable to researchers and students in the field, and it explains the development of current ideas in enough detail that the nonspecialist will find it quite readable. For a book that covers so much information, there is surprisingly little redundancy and internal contradiction. The text is amazingly error-free, though the uneven printing is somewhat distracting. The greatly expanded subject index is welcome.

Many of the areas of research recognized as important and needing future work pointed out in the first edition have been admirably tackled in the ensuing 12 years. We can hope that the many important remaining questions the authors have identified in the final chapter of the second edition will receive as much attention and resolution in the next decade.

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Lacustrine Deposits

Modern and Ancient Lake Sediments. Proceedings of a symposium, Copenhagen, Aug. 1977. ALBERT MATTER and MAURICE E. TUCKER, Eds. Blackwell, Oxford, England, 1979 (U.S. distributor, Halsted [Wiley], New York). vi, 290 pp., illus. \$32.50. Special Publication No. 2 of the International Association of Sedimentologists.

Few environments are as potentially interesting to the sedimentologist as lakes. Compared to the oceans, which are relatively constant in both salinity and ionic ratios, lakes can range from fresh to salt to soap, often within close proximity of one another. Furthermore, because lakes often are close to both their water and their sediment sources, peak events can have maximum impact upon the depositional environment. Unfortunately, however, lakes tend to be ephemeral features and with few exceptions probably do not exist for more than 10⁵ to 10⁶ years. As a result, few ancient lacustrine deposits have been described. North American geologists, perhaps, are particularly ignorant about lakes. Possibly they can quote chapter and verse about the Green River Formation in Wyoming being the penultimate example of ancient lacustrine deposits.

They may even have read something about modern environments in reservoirs or saline lakes. But a detailed understanding of geological processes active in lakes and examples in both modern and ancient lakes are often lacking.

The volume edited by Matter and Tucker tries to remedy this lack. The 14 papers in the volume are more or less evenly split between those dealing with modern lakes and those dealing with ancient deposits. Lakes discussed range from modern to Proterozoic, from temperate to tropical, and from freshwater to saltwater.

The quality of the papers tends to be uniformly good, but this reviewer gets the impression of having read many of the papers (or permutations of them) before. Fully one-half to three-quarters of the papers seem to have been published in some form or other previously. Thus, one may not get too many surprises, although this does not detract from the stimulating insights that the papers individually and collectively offer.

I was particularly impressed with three papers. Hardie, Smoot, and Eugster present a readable and useful review of saline lakes and their sediments. While this paper derives largely from the authors' wide experience with western lakes of the United States, enough foreign examples are thrown in to keep the review worldwide in scope. In another paper, Smoot proposes that the Wilkins Peak Member of the famous Green River Formation did not accumulate in a perennial salt lake, as had been hypothesized by W. H. Bradley and others, but rather was formed as a playa-lake complex. Finally, the contention that lakes, being ephemeral on a geologic time scale, tend to deposit relatively thin sequences is put to rest effectively by Link and Osborne, who show that more than 9000 meters of Pliocene lacustrine sediments accumulated in the Ridge Basin Group in southern California; perhaps even more surprising is their conclusion that the lake was mostly shallow, sometimes (judging from the abundance of stromatolites and mud cracks) a playa.

The general layout, editing, and scientific quality of the book appear excellent. Clearly, however, this book will not appeal nearly as much to those lake workers who are familiar with the state of the art as it will to geologists who may be interested in lakes but, somehow or other, have not delved into the available literature.

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