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R. Bock
(Ed.)

19

Cell and Molecular Biology of Plastids

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Cell and Molecular Biology of Plastids

With 51 Figures, 11 in Color; and 23 Tables

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The cover illustration depicts pseudohyphal filaments of the ascomycete *Saccharomyces cerevisiae* that enable this organism to forage for nutrients. Pseudohyphal filaments were induced here in a wild-type haploid MATa Σ1278b strain by an unknown readily diffusible factor provided by growth in confrontation with an isogenic petite yeast strain in a sealed petri dish for two weeks and photographed at 100X magnification (provided by Xuewen Pan and Joseph Heitman).

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Preface

Ralph Bock

Standard textbooks of genetics and molecular biology pay scant attention to plastids, although the chloroplast is arguably the best-studied genetic compartment in eukaryotic cells. The past two decades have witnessed an enormous progress in our understanding of plastid biogenesis, genome structure and function, gene expression and its regulation as well as plastid-nuclear interaction and communication pathways. In addition, research on plastids has benefited enormously from the development and continuous refinement of transgenic technologies. The possibility to directly alter the genetic information of the plastid has facilitated the study of virtually all aspects of plastid biology *in vivo* and, moreover, has paved the way to diverse applications of transgenic plastids in biotechnology.

It was with this in mind that we approached the writing of the present volume of *Topics in Current Genetics* entitled *Cell and Molecular Biology of Plastids*. The book begins with a chapter on plastid biogenesis, differentiation and division written by Kevin Pyke. The following chapter (contributed by Ralph Bock) covers plastid genome structure and function as well as the inheritance of plastids and their genetic material. Anil Day and Panagiotis Madesis portray the processes and mechanisms involved in both maintenance and structural dynamics of plastid genomes: recombination, DNA replication, and repair. The following four chapters cover the various steps of gene expression in plastids, their molecular components, and how they are regulated: transcription (by Karsten Liere and Thomas Börner), RNA stability and degradation (by David Stern and colleagues), the diverse RNA processing mechanisms operating in plastids, including intron splicing and RNA editing (by Christian Schmitz-Linneweber and Alice Barkan), and protein biosynthesis (by Hadas Peled-Zehavi and Avihai Danon). Three chapters are dedicated to key posttranslational processes in plastid biogenesis and function: protein processing and the assembly of multiprotein complexes (by Eva-Mari Aro and colleagues), protein stability and degradation (by Zach Adam), and protein import and sorting (by Birgit Agne and Felix Kessler). Many of these processes are described using chloroplasts and the photosynthetic apparatus as model system, not least because research on non-green plastid types is still far less advanced.

The chapter written by Bianca Naumann and Michael Hippler provides on overview of plastid proteomics research. It covers both methodological and functional aspects and demonstrates how a highly complex proteome can be dissected by splitting it up into analyzable subproteomes. The multifarious communication pathways between plastids and the nucleo-cytosolic compartment of the plant cell are dealt with in the contribution by Thomas Pfannschmidt and colleagues. Our current knowledge about anterograde (nucleus-to-plastid) and retrograde (plastid-to-nucleus) signalling processes is summarized illustrating the great complexity of the regulatory mechanisms that have evolved to coordinate the activities of the prokaryotic-type genome in the plastid and the eukaryotic-type genome in the nu-

cleus of the plant cell. Last but not least, the chapter by Hans-Ulrich Koop and colleagues describes the state of the art in engineering plastid genomes of algae and higher plants and highlights selected applications of plastid transformation technology in basic research and plant biotechnology.

Cell and Molecular Biology of Plastids is written primarily for those working directly in the fields of plastid biology, organelle genetics and gene expression, photosynthesis research and biotechnology. The authors of the individual chapters have tried to discuss concepts and emphasize general principles that are accepted and proven. Inevitably, there is some overlap between the contributions, which, however, has been limited to the extent needed to ensure that the individual chapters can be read in isolation. Authors and editor hope that this volume will serve as a stepping-stone for graduate students becoming interested in organelle biology and new researchers entering the field.

In closing, I express my sincere thanks to the authors of each chapter – their thoroughness and commitment made this volume possible. I am also very grateful to the many colleagues who willingly acted as reviewers and to Springer Publishers and the editorial office of *Topics in Current Genetics* for their help in editing and formatting this book.

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Plastid biogenesis and differentiation

Kevin Pyke

Abstract

Plastids are crucial to plant functionality and develop from proplastids in meristem cells to generate different plastid forms in different types of plant cells. In addition to the photosynthesis of leaf mesophyll cell chloroplasts, plastids contribute to storage and pigmentation capacities in many different specialised cells as well as contributing essential metabolic pathways within the cell in general. Plastids also have the capacity to interconvert between types according to environmental and molecular signals. Progress in understanding the cell biology and morphological control of different plastid types is considered in the light of modern imaging techniques, which have revealed new aspects of plastid morphology. As well as considering molecular aspects of how plastids control their division, this article discusses also how cell-specific differentiation might be controlled and whether master control genes for plastid biogenesis might be in charge.

1 Introduction

Plastids form a distinct group of organelles in higher and lower plants and are one of the defining characteristics by which plants are different to animals. For many years, most plastid based research focused on the chloroplast and trying to understand the mechanism of photosynthesis and the biochemical interactions of the chloroplast with the cell. With the advent of molecular biology and more recently, a variety of novel imaging techniques, a better understanding of how the chloroplast and other plastid types function within the cell in a truly biological manner is starting to emerge. Even so, the chloroplast remains dominant in providing the bulk of our knowledge about plastid biology. In this article, I consider the structure and morphology of the chloroplast and a range of other plastid types as well as how plastids differentiate and undergo interconversions. Finally, I discuss two fields in plastid biology, which have progressed significantly in recent years, namely plastid division and the biology of stromules.

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2 Proplastids

All plastids within a plant are ultimately derived from those progenitor plastids, which are found in meristem cells called proplastids. These in turn have been derived from the few proplastids, which were present in the zygote and derived potentially from both the maternal egg cell and the paternal pollen grain. However, most Angiosperms have mechanisms to exclude or degrade proplastids in the pollen line and hence the plastids present in the majority of plants are inherited maternally (Mogensen 1996; Corriveau and Coleman 1998; Zhang et al. 2003). In those species in which biparental inheritance occurs, plastids within the zygote constitute a mixed population derived from both parent egg and pollen. However, many factors appear to bias the relative proportion of maternally and paternally-derived plastids and plastid populations in resulting plants can be highly variable with respect to the origins of plastids within them (Mogensen 1996).

Considering the fundamental importance of proplastids to plastid biology, the knowledge of proplastid cell biology and their fine ultrastructure is limited, mostly because of the difficulties with analysing small organelles with no pigment in small regions of dense tissue. Knowledge of the physical appearance of proplastids has been derived largely from electron micrographs (Chaley and Possingham 1981; Akita and Sagisaka 1995; Robertson et al. 1995; Gunning 2004), which show proplastids as small organelles containing limited internal structure that are dispersed throughout the cytoplasm. Most proplastids contain rudimentary pieces of thylakoid membrane, but are unpigmented although those in shoot apical meristems appear to contain more thylakoid in a more organized state than those in the root apical meristem (Gunning 2004). In addition, ingrowths from the inner plastid envelope membrane into the proplastid stroma can also be seen occasionally, as well as ribosomes. Starch grains may be present, especially in proplastids of seeds where starch was laid down in the proplastid during seed development (Gunning 2004). In wheat plumules and potato stolons, starch content of proplastids is variable with some containing significant starch grains and others with no starch. This difference in starch content appears to result from differences in the capacity for starch synthesis since immunogold labelling of the enzyme starch synthase reveals two types of proplastids: those with and those without the enzyme (Akita and Sagisaka 1995).

Estimating proplastid numbers is difficult and to date no studies have definitively counted proplastid populations in meristem cells. However, various studies of shoot meristem cells estimate that they contain 10-20 proplastids per cell (Cran and Possingham 1972; Lyndon and Robertson 1976; Pyke and Leech 1992). Using modern fluorescent protein technology, imaging of proplastids in meristems and during cytokinesis should be feasible, although proplastid dynamics during meristematic cell divisions have yet to be studied in detail. Proplastids with fluorescent marker proteins on board, such as GFP, can be imaged in root meristems (Kohler and Hanson 2000) and those in shoot apical meristems can be observed also (Trynka and Pyke, unpublished), although experiments to determine population