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Plastid Division: The Origin of Replication

The fact that chlorophyll-containing chloroplasts are remarkably abundant organelles in plants is obvious to anyone contemplating the verdant green expanses of most global ecosystems. For those who have viewed leaf mesophyll cells by peering down a microscope, it is also apparent that these specialized cells can contain large numbers of chloroplasts—up to 200 in some cells—and that chloroplasts can cover up to 70% of the mesophyll cell surface. Presumably, as leaves developed to become the major photosynthetic structure in plants, the accumulation of chloroplasts in mesophyll cells was evolutionarily favored because increases in chloroplast number would correlate with increases in photosynthetic capacity.

Just as all the cells in a plant are derived from meristematic cells, all the plastids within the various cells of that plant are derived from proplastids that reside in the meristem cells. These proplastids must divide to ensure that, following cell division, both daughter cells contain proplastids. Similarly, post-meristematic cellular differentiation and maturation events are paralleled by events that define the development and differentiation of proplastids. For example, during the differentiation and development of mesophyll cells, chloroplasts differentiate from proplastids and they divide several times to give rise to the large populations of chloroplasts that are present within individual mesophyll cells.

Both proplastid and chloroplast division seems to take place primarily by a process of binary fission, and the morphological changes that occur during this process have been well characterized (Pyke, 1997). Nevertheless, the only plastid division–specific structure that has been observed in several plant species by electron microscopy is an electron-dense torus around the constriction site, the molecular construction of which is unknown.

In 1995, Osteryoung and Vierling provided a breakthrough in the potential for understanding the molecular mechanisms of plastid division with their discovery of an Arabidopsis homolog of the key protein in bacterial cell division, FtsZ (Osteryoung and Vierling, 1995). The FtsZ protein, which closely resembles tubulin, forms a ring structure inside the prokaryotic cell and is able to polymerize to form filaments (Erickson, 1997). The fact that the first plant FtsZ protein discovered by Osteryoung and Vierling contained a plastid targeting sequence and was correctly processed by intact chloroplasts suggested that plastid division might have some mechanistic basis in the prokaryotic cell division system.

On pages 1991–2004 of this issue, Osteryoung et al. extend these findings, revealing that plastid division in higher plant cells involves a greater level of complexity than does bacterial cell division. Two observations regarding the potential role of FtsZ proteins in plastid division contribute important new details to this story. First, Osteryoung et al. show that at least three *FtsZ* genes exist in the Arabidopsis genome and that comparisons with *FtsZ* sequences from other species allow the plant genes to be placed into two distinct groups. One group, *FtsZ1*, encodes FtsZ proteins that contain a plastid targeting presequence, implying that the functional FtsZ1 proteins are located inside the chloroplast. A second group, *FtsZ2*, encodes FtsZ proteins that are not targeted to chloroplasts and are presumably localized in the cytosol. Because the electron-dense plastid dividing ring is visualized as a two-ring torus that is composed of an internal and an external ring, the simplest hypothesis to develop from these observations is that FtsZ1 proteins participate in forming the internal structure, whereas FtsZ2 proteins may be involved in constructing the external ring.

Osteryoung et al. go on to show that antisense suppression of either *FtsZ* gene in Arabidopsis markedly perturbs the plastid division process. The authors place the *FtsZ* antisense plants into two classes on the basis of their distinct cellular phenotypes. Mesophyll cells in the most severely affected plants possess only one plastid, whereas cells in a second group of plants possess 10 to 30 plastids each (in comparison to a wild-type number of up to ~200). These distinct phenotypes, which are illustrated on the cover of this issue, are similar to those provoked by mutations in specific Arabidopsis *ARC* (for accumulation and replication of chloroplasts) genes (Pyke, 1997), and they suggest events occurring during proplastid and chloroplast division may be differentially affected by perturbations in *FtsZ* expression levels.

Osteryoung et al.'s investigations of the *FtsZ* antisense plants also show that the products of both *FtsZ* genes are required for the normal plastid division process to occur and that the two genes are unable to functionally complement one another. These observations fit nicely with the hypothesis that the Arabidopsis FtsZ proteins are differentially localized—one inside the chloroplast and the other outside—and they strongly suggest that both rings in the torus play a functional role in the division process.

Arabidopsis is not the only plant in which *FtsZ* genes have been identified and investigated. The moss *Physcomitrella patens* expresses a gene called *PpFtsZ* which, on the basis of its

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sequence (Strepp et al., 1998), falls in the cytosolic-localized group of FtsZ proteins. *P. patens* mutants with defects in the *PpFtsZ* gene also exhibit fewer and much larger chloroplasts than those of the wild type (Strepp et al., 1998). Because the cells of Arabidopsis and the moss exhibit subtle differences in chloroplast number and density, it will be interesting to determine how *FtsZ* expression patterns differ with respect to their impact on plastid division control in these two model systems.

Interestingly, there is no evidence that the FtsZ proteins function during mitochondrial division, and Osteryoung et al. suggest that an original FtsZ-based system in mitochondria may have been supplanted by other mechanisms. Dividing mitochondria do exhibit a torus at the point of constriction, and some characteristics of this mitochondrial dividing ring in mitochondria are similar to those of the plastid dividing ring (Kuroiwa et al., 1998). Nevertheless, our understanding of the mitochondrial division process in plant cells is poor, and we will need to invest a similar amount of effort to that afforded to plastids before we can determine whether any molecular components of the two processes are related.

From an evolutionary point of view, the data presented by Osteryoung et al. would imply that the original endosymbiotic precursor of modern chloroplasts carried a single *FtsZ* gene, as is the case in most bacteria studied to date. During evolution, this *FtsZ* precursor gene was presumably transferred from the endosymbiont to the nucleus (like many other plastid genes) and duplicated, with one copy obtaining a chloroplast transit sequence.

This evolutionary hypothesis reflects the most fundamental difference between bacterial and chloroplast division—bacteria divide as free-living entities, whereas chloroplasts divide as a contained population within a eukaryotic cell. Presumably, the apparent requirement for a cytosolic FtsZ component arose from the need of the "host" cell to control the division of the bacterial endosymbiont, a process that would no longer be truly autonomous. One can only speculate, however, how the functions of the host and endosymbiont (i.e., cytoplasmic and plastidic) versions of FtsZ came to be coordinated through the double membrane of the plastid envelope.

As ever, the work of Osteryoung et al. raises many new questions, including the consideration of how far the analogy between plastid division and bacterial cell division can be taken. Will other known players in bacterial cell division prove to have homologs associated with plastid division in higher plants? The discovery of genes from the bacterial *Min* locus on the chloroplast genome of the alga *Chlorella* (Wakasugi et al., 1997) makes this look likely, at least in part (Osteryoung and Pyke, 1998).

However, there are many fundamental differences between plastid and bacterial cell division. Plastids lack a wall, and division has always been perceived to proceed by a pinching and/or squeezing process that finally results in membrane fusion and daughter organelle separation. Considering FtsZ in isolation is undoubtedly a far too simplistic view of plastid division, and many other proteins, including those defined by the Arabidopsis *arc* mutations (Pyke, 1997), must play important roles. So, although the bacterial cell division process continues to provide a very useful analogy for plastid division, to get the full story we may have to look harder for plant-specific factors that are involved in this process. That said, it is clear from this and other recent molecular and genetic studies of plastid division that plastids have come of age.

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