

PROTIST *Reviews*

More Membranes, more Proteins: Complex Protein Import Mechanisms into Secondary Plastids

Swati Agrawal^a, and Boris Striepen^{a,b,1}

^aDepartment of Cellular Biology, University of Georgia, 500 D.W. Brooks Drive, Athens, GA 30602, USA

^bCenter for Tropical and Emerging Global Diseases, University of Georgia, 500 D.W. Brooks Drive, Athens, GA 30602, USA

Plastids are found across the tree of life in a tremendous diversity of life forms. Surprisingly they are not limited to photosynthetic organisms but also found in numerous predators and parasites. An important reason for the pervasiveness of plastids has been their ability to move laterally and to jump from one branch of the tree of life to the next through secondary endosymbiosis. Eukaryotic algae have entered endosymbiotic relationships with other eukaryotes on multiple independent occasions. The descendants of these endosymbiotic events now carry complex plastids, organelles that are bound by three or even four membranes. As in all endosymbiotic organelles most of the symbiont's genes have been transferred to the host and their protein products have to be imported into the organelle. As four membranes might suggest, this is a complex process. The emerging mechanisms display a series of translocons that mirror the divergent ancestry of the membranes they cross. This review is written from the viewpoint of a parasite biologist and seeks to provide a brief overview of plastid evolution in particular for readers not already familiar with plant and algal biology and then focuses on recent molecular discoveries using genetically tractable Apicomplexa and diatoms.

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¹Corresponding author; fax +1 706-542-3582
e-mail striepen@cb.uga.edu (B. Striepen).

1. Introduction

The massive expansion of cyanobacteria and oxygenizing photosynthesis, began to transform the atmosphere of our planet about 2.4 billion years ago. This new atmosphere gave birth to an explosion of complex life forms that took advantage of molecular oxygen and the large amount of energy that can be gained through oxidative phosphorylation. Cyanobacteria also gave rise to the chloroplasts of plants and algae further increasing their numbers and ecological impact (Cavalier-Smith 1982; Gray 1993). There is now broad support for an endosymbiosis model of plastid genesis (Gould et al. 2008). According to this model a cyanobacterium was taken up by an early eukaryote and subsequently domesticated into a dependent organelle (Fig. 1A). It appears that a single endosymbiotic event was responsible for the origin of the three major extant lineages of photosynthetic eukaryotes namely the red and green algae (including their progeny, the green plants) and the glaucophytes. Members of these groups possess plastids surrounded by two membranes and we will refer to these as primary plastids (Adl et al. 2005).

2. Endosymbiosis and the Complex Ancestry of Complex Plastids

Primary plastids were massively successful but do not yet represent the end of the journey cyanobacteria have taken through the eukaryotic tree of life. In addition plastids were acquired laterally by secondary endosymbiosis to give rise to “secondary” or “complex” plastids spreading them further into previously non-photosynthetic eukaryotes (Cavalier-Smith 1982). Although the plastid is now the most conspicuous remnant of these events, it is important to bear in mind that as depicted in Figure 1A, an entire eukaryotic alga was the initial endosymbiont in these events. This eukaryotic cell within a second eukaryotic cell was then gradually reduced to the feature most useful to the host, the plastid. This origin is still reflected in the additional membranes found in secondary plastids, and, as we will discuss in more detail below, also in the origin and mechanisms of some of the protein import machinery. Secondary acquisition of plastids appears to have occurred in at least three independent incidents and gave rise to major branches of the eukaryotic tree. The plastids of euglenids and chlorarachniophytes arose by enslavement of two

different green algae with chlorophyll *a* and *b*. Chlorarachniophytes are a group of unicellular green protists with some purely photosynthetic members (*Lotharella globosa*), and other species that are both photosynthetic and phagotrophic (*Chlorarachnion*). Euglenids are nutritionally even more diverse, ranging from photosynthetic species like *Euglena* spp, to phagotrophic petalomonads and peranemids (specialized on bacterial or eukaryotic prey respectively), to saprotrophs, which show no trace of plastids or have lost photosynthesis but retain a colorless plastid with a reduced genome. Initial studies postulated a common origin for chlorarachniophytes and euglenids, but this hypothesis was later refuted (Rogers et al. 2007). Phylogenetic analysis of plastid proteins from the chlorarachniophyte *Bigeloviella natans* supported an independent origin of plastids in these two groups (Rogers et al. 2007). In contrast, the plastids found in cryptomonads, haptophytes, stramenopiles, dinoflagellates and Apicomplexa are of red algal origin. The discovery of apicoplasts, plastids in the non-photosynthetic Apicomplexa, has fostered the idea of a common origin, for an at first sight rather incoherent group of organisms. The chromalveolate hypothesis proposes that a single endosymbiotic event followed by subsequent diversification was responsible for acquisition of the present day complex plastids in all these taxa (Cavalier-Smith 1999). The resulting super-phyllum Chromalveolata (joining chromists and alveolates) represents as much as half of the thus far described protists and also includes many multicellular groups (see Fig. 1B). In addition to the plastid-containing taxa mentioned above the Chromalveolata also include groups such as the oomycetes or ciliates that may have possessed plastids in the past but have subsequently lost them (Cavalier-Smith and Chao 2006). Overall this represents a highly diverse group that has adapted to a tremendous breadth of ecological niches including autotrophy, predation and parasitism. Additional evidence in support of this hypothesis came from phylogenetic studies on glyceraldehyde 3-phosphate dehydrogenase (Fast et al. 2001; Harper and Keeling 2003; Harper et al. 2005). The common ancestor of different chromalveolate groups, cryptomonads, dinoflagellates and Apicomplexa seem to have replaced their plastid GAPDH gene with a cytosolic form that underwent duplication and acquired plastid targeting signal. It is unlikely that four different groups of organisms independently followed this complex path of locus evolution and it appears more parsimonious to conclude that diversification of chromalveolates was preceded by a single common endosymbi-

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