



The Origin of Plastids

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Plastids are core components of photosynthesis in plants and algae. Scientists are currently debating the events leading to the appearance of plastids in eukaryotic cells.

Organelles, called plastids, are the main sites of photosynthesis in eukaryotic cells. Chloroplasts, as well as any other pigment containing cytoplasmic organelles that enables the harvesting and conversion of light and carbon dioxide into food and energy, are plastids. Found mainly in eukaryotic cells, plastids can be grouped into two distinctive types depending on their membrane structure: primary plastids and secondary plastids. Primary plastids are found in most algae and plants, and secondary, more-complex plastids are typically found in plankton, such as diatoms and dinoflagellates. Exploring the origin of plastids is an exciting field of research because it enhances our understanding of the basis of photosynthesis in green plants, our primary food source on planet Earth.

Primary Plastids and Endosymbiosis

Where did plastids originate? Their origin is explained by endosymbiosis, the act of a unicellular heterotrophic protist engulfing a free-living photosynthetic cyanobacterium and retaining it, instead of digesting it in the food vacuole (Margulis 1970; McFadden 2001; Kutschera & Niklas 2005). The captured cell (the endosymbiont) was then reduced to a functional organelle bound by two membranes, and was transmitted vertically to subsequent generations. This unlikely set of events established the ancestral lineages of the eukaryote supergroup "Plantae" (Cavalier-Smith 1998; Rodriguez-Expeleta et al. 2005; Weber, Linka, & Bhattacharya 2006), which includes many photosynthetic algae and land plants.

The idea of endosymbiosis was first proposed by Konstantin Mereschkowski, a prominent Russian biologist, in 1905. He coined the term "symbiogenesis" when he observed the symbiotic relationship between fungi and algae (Mereschkowski 1905). The term "endosymbiosis" has a Greek origin (*endo*, meaning "within"; *syn*, meaning "with"; and *biosis*, meaning "living"), and it refers to the phenomenon of an organism living within another organism. In 1923, American biologist Ivan Wallin expanded on this theory when he explained the origin of mitochondria in eukaryotes (Wallin 1923). However, not until the 1960s did Lynn Margulis, as a young faculty member at Boston University, substantiate the endosymbiotic hypothesis. Based on cytological, biochemical, and paleontological evidence, she proposed that endosymbiosis was the means by which mitochondria and plastids originated in eukaryotes (Sagan 1967; Margulis 1970). In those days, the research community viewed her unconventional idea with much skepticism, but her work was eventually published in 1967 (Sagan 1967) after being rejected by fifteen scientific journals! Today, endosymbiosis is a widely accepted hypothesis to explain the origin of intracellular organelles.

Besides these original and bold ideas, what else have we learned? Since 1990 we have seen rapid advancement in techniques in molecular biology and bioinformatics. Using molecular phylogenetic approaches, numerous comparative studies have demonstrated the cyanobacterial origin of genes encoded in the Plantae plastid and provide evidence for gene transfer from the endosymbiont genome to the "host" nucleus (Bhattacharya & Medlin 1995; Delwiche 1999; Moreira, Le Guyader, & Phillippe 2000; McFadden 2001; Palmer 2003; Bhattacharya, Yoon, & Hackett 2004; Rodriguez-Ezpeleta et al. 2005; Meyer-Prieto, Weber, & Bhattacharya 2007). These studies complement several independent lines of evidence based on protein transport and the biochemistry of plastids (McFadden 2001; Matsuzaki 2004; Weber, Linka, & Bhattacharya 2006; Reyes-Prieto & Bhattacharya 2007). The establishment of primary plastids in eukaryotes is estimated to have occurred 1.5 billion years ago (Hedges 2004; Yoon et al. 2004; Blair, Shah, & Hedges 2005), but dating such an ancient event based on molecular data remains controversial due to the limited support provided by the fossil records (Douzer et al. 2004).

Whereas endosymbiosis involving a cyanobacterium explains the establishment of primary plastids in *Plantae*, the story is more convoluted in other photosynthetic eukaryotes, which harbor secondary plastids with more complex structures. The plastids found in *Paulinella chromatophora* (a filose amoeba) are an exception to the rule. These organisms are derived from a far more recent cyanobacterial primary endosymbiosis that occurred about 60 million years ago (Bhattacharya, Helmchen, & Melkonian 1995; Marin, Nowack, & Melkonian 2005; Yoon et al. 2006). This plastid traces its origin to a cyanobacterial donor of the *Prochlorococcus-Synechococcus* type (Yoon et al. 2006). The closely related *Paulinella ovalis*, although lacking a plastid, is an active predator of cyanobacteria that are commonly localized within food vacuoles (Johnson, Hargraves, & Sieburth 2005). Therefore, the cyanobacterium-derived plastid in the photosynthetic *P. chromatophora* provides an independent example of the phagotrophic origin of a primary plastid.

Secondary Plastids and the Current Scientific Debate

In comparison to *Plantae* and *P. chromatophora*, the origin of plastids in other photosynthetic eukaryotes is more complicated. These organisms possess secondary plastids, which have one or two additional membranes surrounding the existing two membranes of primary plastids. However, an endosymbiosis event involving a cyanobacterium cannot explain the origin of three- and four-membrane-bound plastids. Instead, these extra membranes likely formed due to secondary endosymbiosis, when an existing *Plantae* cell containing a primary plastid was engulfed and reduced to a plastid. There is, however, disagreement among scientists about the number of secondary endosymbioses in eukaryotes. In general, there are opposing viewpoints regarding their establishment, namely, the chromalveolate hypothesis (Cavalier-Smith 1999, 2003; Keeling 2009) and the independent acquisition hypothesis (also known as serial eukaryote-eukaryote endosymbiosis, or the serial EEE) (Archibald 2009; Boudry, Stiller, & Mackiewicz 2009; Baurain et al. 2010) (Figure 1).

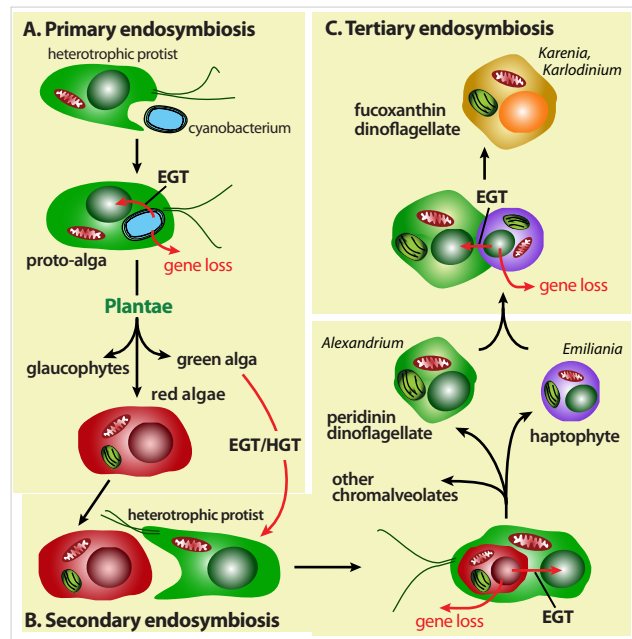


Figure 1: The concept of endosymbiosis
The chromalveolate hypothesis can explain some endosymbiotic events in dinoflagellates.
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What is the chromalveolate hypothesis? This controversial idea proposes that a free-living red algal cell was captured and retained by a nonphotosynthetic heterotrophic protist soon after the evolutionary split of red and green algae (i.e., secondary endosymbiosis), giving rise to the pigmented ancestor of the supergroup "Chromalveolata" (Cavalier-Smith 1999). The red algal endosymbiont was retained in a variety of chromalveolate lineages such as cryptophytes, haptophytes, stramenopiles, and dinoflagellates. This hypothesis is based on numerous phylogenetic studies that support the red algal origin of the plastid in most chromalveolates and of most plastid-localized proteins that are encoded in the nucleus of these taxa (Fast et al. 2001; Harper & Keeling 2003; Bhattacharya, Yoon, & Hackett 2004; Li et al. 2006; Nosenko et al. 2006). Although independent horizontal gene transfer events could explain this observation, the more reasonable explanation is that a secondary endosymbiosis event in red alga involved multiple gene transfers.

What other changes have occurred in organisms containing secondary plastids? With the exception of the cryptophytes, which retain a remnant of the red algal cell (Greenwood 1974), other chromalveolates do not have the nucleus of the red algal endosymbiont, which means that the genes necessary to ensure a fully functional plastid have been transferred to the host nucleus (Douglas & Penny 2001; Douglas et al. 2001). In addition, for a subgroup of dinoflagellates that contain the peridinin pigment, including species that cause "red tide" in the ocean (e.g., *Alexandrium*), the plastid genomes are highly reduced in size due to substantial gene transfer from the endosymbiont to the host nucleus (Hackett 2004).

To further complicate matters, besides tracing their origin not only to red algae as expected, plastid-targeted proteins in many dinoflagellates traced also include proteins derived from other unicellular eukaryotes such as excavates and other chromalveolates (Ishida & Green 2002; Hackett 2004; Yoon et al. 2005; Nosenko 2006), suggesting additional (tertiary) endosymbioses in their evolutionary histories. The recent discovery of a substantial number of red and green algal-derived genes in diatoms (Moustafa et al. 2009) supports the idea of an additional secondary endosymbiotic event with green algae during the early evolution of chromalveolates.

If the chromalveolate hypothesis is true, then why are *not* all chromalveolates (e.g., ciliates and apicomplexans) photosynthetic? Under the assumption of the chromalveolate hypothesis, the lack of plastids in ciliates is explained by subsequent loss of the captured algal cell or by genes of the endosymbiont that were acquired during serial endosymbiosis (Reyes-Prieto, Moustafa, & Bhattacharya 2008). Interestingly, the parasitic Apicomplexans (e.g., *Toxoplasma*), although nonphotosynthetic, possess unique organelles called the apicoplast (also known as the nonphotosynthetic "plastids") that share similar features with secondary plastids (Maréchal & Cesbron-Delauw 2001; Ralph et al. 2004). The apicoplasts may have shared common origins with secondary plastids of the closely related dinoflagellates, but subsequently lost their photosynthetic capability, likely due to the transition to obligate parasitism (Funes et al. 2002; Waller & McFadden 2005).

Alternative Explanations for the Origin of Secondary Plastids

Is there an alternative explanation for the origin of secondary plastids? Indeed, the independent acquisition hypothesis suggests that the origin of secondary plastids in different groups of chromalveolates (e.g., haptophytes, cryptophytes, and stramenopiles) results from independent, serial endosymbioses involving unicellular eukaryotes, not necessarily red algae (Archibald 2009; Bodyl, Stiller, & Mackiewicz 2009; Baurain et al. 2010). Experimental evidence for this hypothesis is not as strong as that for the chromalveolate hypothesis, however. In fact, many recent analyses are tailored to disprove the chromalveolate hypothesis using selective data sampling (Baurain et al. 2010).

What is the advantage of the independent acquisition hypothesis? We know that over evolutionary time plastid-lacking chromalveolates are likely to lose the plastid and nuclear-encoded plastid targeted proteins derived from the red algal endosymbiont. In evolutionary biology, we assume that the least complex (most parsimonious) explanation for an observation is more plausible. The independent acquisition hypothesis avoids a convoluted explanation of organelle and gene losses to explain the sporadic plastid distribution observed today in nonphotosynthetic chromalveolates. In the extreme case, some scientists who support this hypothesis claim that the fundamental grouping of the chromalveolates is itself inaccurate. Given the paucity of empirical data, we need to understand this complex chain of plastid acquisition events much better.

What about the origin of plastids in other eukaryotes? There are other photosynthetic eukaryotes that are not members of Plantae or Chromalveolata, such as the photosynthetic excavates (e.g., *Euglena*) and the chlorarachniophyte amoebae (Rhizaria), but the plastid origins of these organisms are less well-studied. Nonetheless a number of phylogenetic analyses show that these organisms have acquired their plastids in more recent instances of secondary endosymbiosis, during which a green algae was independently captured by their common ancestors (Rogers et al. 2007).

Summary

There is no simple way to explain the gain and loss of plastids in all eukaryotes. The origin of primary plastids via endosymbiosis involving a cyanobacterium is well-established, but the origin of secondary plastids is still controversial. However, the chromalveolate hypothesis (and the secondary endosymbiosis involving a red algae) is the best-supported hypothesis to date based on numerous empirical studies. In addition, subsequent tertiary endosymbioses involving other free-living eukaryotes explain plastid origins in other eukaryote lineages. Additional studies and biochemical validation (where possible) are needed to better test existing hypotheses about the evolutionary origins of plastids in eukaryotes.

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