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Daniel Grzebyk, *et al.*
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Response to Comment on “The Evolution of Modern Eukaryotic Phytoplankton”

Falkowski *et al.* (1) examined when, why, and how a diverse group of eukaryotic phytoplankton, which overwhelmingly contain red plastids, rose to ecological prominence in Mesozoic time and continue to dominate the contemporary oceans. Our analysis included the fossil record of thecate dinoflagellates, coccolithophores, and diatoms; biochemical composition of extant taxa and their phylogenetic relationships; geochemical reconstructions of ocean paleochemistry; eustatic changes in sea level; and ecosystem interactions. One facet in our analysis was the portable plastid hypothesis (2), which was included to accommodate the observation that several distinct clades of eukaryotic algae (e.g., heterokonts, haptophytes, cryptophytes, and dinoflagellates) contain secondary plastids derived from a common ancestral red alga.

A comparative analysis of plastid genomes led Grzebyk *et al.* (2) to conclude that not only are more genes retained in red plastids than in green plastids but also many of the retained genes play critical roles in photosynthetic electron transport and carbon fixation. For example, genes that encode key components of both photosystems, ferredoxin, the ATP synthase and, perhaps most important, the small subunit of ribulose 1,5-bisphosphate carboxylase/oxygenase are present in extant red, but not green, plastids. Although originally based on a small number of plastid genomes, the hypothesis subsequently has been supported by analyses of other chromophytes (3, 4). Based on phylogenetic analyses of nuclear and mitochondrial genomes, the hypothesis assumes that the cells serving as hosts to secondary red plastids do not share a recent common ancestor and, hence, that the plastids in each clade were obtained from independent endosymbiotic events (5, 6). As such, the portable plastid hypothesis implicitly conflicts with the “chromalveolate hypothesis” (7), which proposes that all algae believed to possess secondary red plastids acquired them by a single common endosymbiosis.

There is some evidence that secondary red plastids are derived from different taxa within the red algae (8, 9). However, most analyses that consider the phylogeny of plastid-encoded genes, as well as plastid-targeted genes encoded in the nucleus, indicate that

all secondary red plastids are derived from a common ancestral algal clade (10–12). In contrast, however, phylogenetic analyses of nuclear-encoded genes that are not plastid targeted (e.g., 18S rRNA and cytosolic GAPDH) do not support the proposition that cryptophytes, haptophytes, heterokonts, and alveolates (including dinoflagellates) recently diverged from a common ancestor (5, 13–16). Similarly, mitochondrial genome analyses and ultrastructural features do not comport with a recent common ancestor of chromophyte host cells (17, 18). Paradoxically, there is evidence that the ancestor of heterokonts and alveolates was not photosynthetic. Thus, while the chromalveolate hypothesis is consistent with current phylogenetic data that support a common origin of all secondary red plastids, it is not strongly supported by phylogenetic analyses of the host cells.

A major problem with the chromalveolate hypothesis is that it requires multiple plastid losses in the evolution of alveolates and heterokonts. If the basal groups of alveolates and heterokonts contained a plastid, how and why did nonphotosynthetic alveolates, such as Ciliates, Colpodellids, and Perkinsids (19), and several basal groups of dinoflagellates, lose their plastids? Plastid losses must also be invoked to account for basal heterotrophic heterokonts (20). Plastid losses are not explained by the chromalveolate hypothesis but are not required by the portable plastid hypothesis. Hence, while the chromalveolate hypothesis aims at making a single red plastid acquisition the most parsimonious event in the evolution of secondary symbionts, it is hardly the most parsimonious hypothesis.

Plastid portability is not limited to secondary endosymbiosis of red plastids, but also holds for tertiary endosymbioses and kleptoplastidy. Tertiary red plastids were acquired on at least three occasions in dinoflagellates: from cryptophytes, diatoms, or haptophytes. There are no known tertiary green plastids. Kleptoplastidy (the capability for heterotrophic organisms to temporarily retain functional photosynthetic plastids from algal prey) occurs in dinoflagellates, ciliates, foraminifera, and mollusks. The vast majority of the retained plastids are obtained from chromophytes (21, 22).

Although the vast majority of plastid-targeted genes present in the primary algal cell nucleus were clearly transferred to the secondary host as part of the endosymbiotic process, secondary plastid associations are relatively rare. Assuming that all secondary red plastids originated from a single endosymbiotic event (as the chromalveolate hypothesis proposes) would give even more support to this claim. Although Keeling *et al.* (23) claim that red plastids are no more portable than green plastids, secondary green plastid-containing algae are rare in the contemporary oceans. If green plastids were as portable as red plastids, why is the eukaryotic phytoplankton community in the contemporary ocean dominated by such a diverse group of secondary symbionts that contain red plastids?

Although we believe that current genomic data support the portable plastid hypothesis, the explosion of genomic information expected in the next several years will provide the opportunity to test this hypothesis and the competing chromalveolate alternative.

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