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TECHNICAL COMMENT

Comment on “The Evolution of Modern Eukaryotic Phytoplankton”

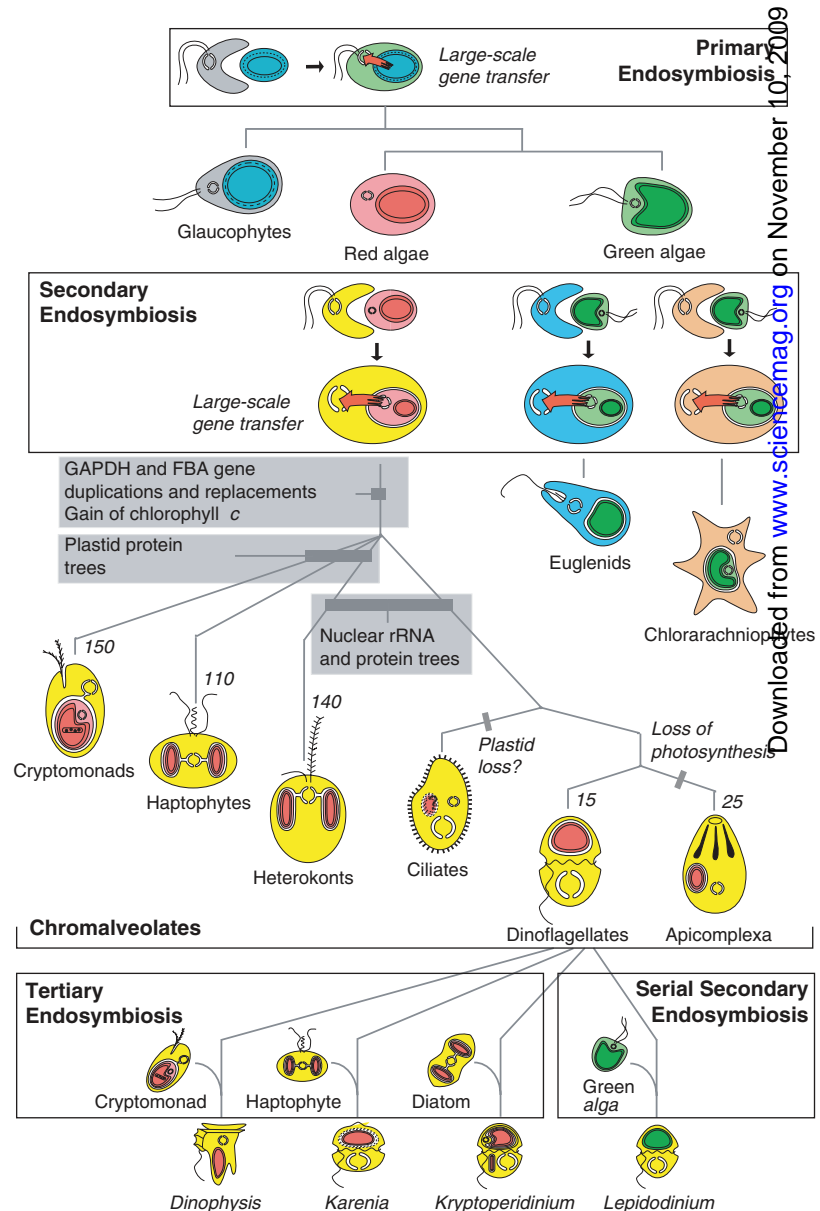
Falkowski *et al.* (1) reviewed the evidence that three disparate groups of algae—dinoflagellates, diatoms, and coccolithophores, each with plastids derived from red algae by secondary endosymbiosis—have come to dominate the oceans’ flora over the past 250 million years and speculated about the forces responsible for this domination. Central to this speculation is the “portable plastid hypothesis” (1, 2), which posits that

the likelihood with which plastids will be transferred between eukaryotes by secondary endosymbiosis is directly related to the number of genes in their genomes. The more genes, the argument contends, the more portable the plastid. This hypothesis rests on three claims: (i) red algal plastids retain more genes than do green algal plastids; (ii) gene transfer from the (primary) endosymbiont nucleus to the (secondary) host nucleus is rare; and (iii) red

algae have been acquired by secondary endosymbiosis more often than have green algae. Although the limited number of red algal plastids examined to date do have more genes (3), claims (ii) and (iii) are not consistent with the available data, thus rendering the hypothesis effectively unsupported.

Although red algal plastids may contain more genes than those of green algae, this difference pales against the nuclear contribution to plastid function. All plastid genomes encode only a small fraction of the proteins needed for plastid function—at most ~10 to 20%, and only ~1% in the case of dinoflagellates. The vast majority of plastid proteins are encoded by nuclear genes; most of these genes are derived from the plastid but have been transferred to the nuclear

Fig. 1. Algal evolution and the origin and spread of plastids by endosymbiosis. At the top is the single origin of plastids by primary endosymbiosis between a cyanobacterium and a eukaryotic host. This endosymbiont was reduced and integrated, and part of this process involved the transfer of hundreds of genes from the cyanobacterium/plastid to the eukaryotic host nucleus (red arrow). Glaucophytes, red algae, and green algae all descended from this fully integrated partnership. Next, plastids spread to other eukaryotic groups by secondary endosymbiosis (middle). Green algae were most likely involved in two independent events, giving rise to euglenids (turquoise) and chlorarachniophytes (orange). A single endosymbiosis involving a red alga probably gave rise to the chromalveolates (yellow); this group is supported by several molecular characters and gene trees (plotted on the figure). Plastids have apparently been lost in ciliates and *Cryptosporidium* (and perhaps other lineages), and photosynthesis has been lost in apicomplexa and many other individual lineages. Numbers indicate the approximate number of protein genes in the plastid genomes of the various lineages with secondary red plastids. Finally, dinoflagellates have substituted their ancestral plastid several times, most notably by tertiary endosymbioses involving other chromalveolates (a cryptomonad, a haptophyte, and a diatom) and by serial secondary endosymbiosis involving a green alga (24).



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genome over time, and their protein products are now targeted back to the plastid (4, 5). Indeed, most algae with secondary plastids have entirely lost their endosymbiont nucleus and, even where retained, this nucleus is largely vestigial and encodes only a few plastid-targeted proteins (6). Therefore, in all known cases of secondary endosymbiosis, the host nucleus must have acquired hundreds of genes encoding plastid-targeted proteins from the endosymbiont nucleus (Fig. 1). Falkowski *et al.* (1) state that such gene transfer “seldom occurs,” but all studies based on single genes, genome surveys, or complete genomes show this to be clearly wrong (7–11). In the face of such massive nucleus-to-nucleus gene transfer, it is very unlikely that the presence, in green algae, of a small proportion of additional nuclear genes encoding plastid-targeted proteins would substantially hinder the portability of their plastids.

What about the claim that red algae have been involved in secondary endosymbiosis twice as often as have green algae? Current evidence suggests that the opposite is true. The “chromalveolate hypothesis” (12)—which posits that all algae believed to possess secondary red plastids [dinoflagellates, heterokonts (including diatoms), haptophytes (including coccolithophores), cryptomonads, and apicomplexa] acquired them by a single common endosymbiosis—is now supported by considerable data. First, there are a number of morphological and biochemical characters that unite some or all chromalveolates, including plastid membrane topology, storage carbohydrates, flagellar structure, and accessory pigments. Most important, all photosynthetic chromalveolates contain chlorophyll *c*, which is absent from red algae and best interpreted as a shared derived character (12). Second, two plastid-targeted proteins—glyceraldehyde-3-phosphate dehydrogenase (GAPDH) and fructose-1,6-bisphosphate aldolase (FBA)—have unusual evolutionary histories that are unique to chromalveolates, which also indicates a common origin of their plastids (13–15). Third, phylogenies of concatenated plastid genes support a clade comprising cryptomonads, heterokonts, and haptophytes, which suggests that their plastids are derived from a single secondary endosymbiotic event (16, 17). Fourth, phylogenies of individual and concatenated cytosolic proteins and rRNAs indicate a sister-group relationship of alveolates (dinoflagellates, apicomplexans, and ciliates) and heterokonts but do not yet resolve the position of haptophytes and cryptomonads (18–21). Taken together, there is increasingly strong evidence for a single, common origin for these

organisms and their plastids, but no strong evidence for any alternative.

We agree with Falkowski *et al.* (1) that there have probably been three independent secondary endosymbioses of green algae. Therefore, red algae have most likely been involved in fewer, not more, secondary endosymbiotic events than have green algae (Fig. 1). Does this mean that green plastids are somehow more portable? The answer is almost certainly no, because the total number of secondary endosymbioses is so low and the differences between these small numbers (four versus two, or one versus three) are insubstantial.

The foundations of the portable plastid hypothesis do not hold up to scrutiny. This is broadly important because the emerging view that “red” secondary plastids probably originated only once has obvious implications for how we interpret not only the process of endosymbiosis but also the fossil record, the evolutionary history of marine algae and their plastids, and their role in shaping today’s oceans.

Patrick J. Keeling

Department of Botany
University of British Columbia
Vancouver, British Columbia V6T 1Z4, Canada
E-mail: pkeeling@interchange.ubc.ca

John M. Archibald

Department of Biochemistry and
Molecular Biology
Dalhousie University
Halifax, Nova Scotia, B3H 1X5, Canada
E-mail: jmarchib@dal.ca

Naomi M. Fast

Department of Botany
University of British Columbia
Vancouver, British Columbia,
V6T 1Z4, Canada
E-mail: nfast@interchange.ubc.ca

Jeffrey D. Palmer

Department of Biology
Indiana University
Bloomington, IN 47405, USA
E-mail: jpalmer@bio.indiana.edu

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2. D. Grzebyk, O. Schofield, C. Vetriani, P. G. Falkowski, *J. Phycol.* **39**, 259 (2003).
3. The claim that red algal plastids contain more protein genes (~200) than do green algal plastids (at most ~100) is consistent with existing data, but only three red algal plastid genomes have been sequenced. The ancestor of red algae must have had at least this many genes, but this does not necessarily mean that the genome of the ancestor (or ancestors) of secondary red algal plastids retained all of these genes. If, as Falkowski *et al.* (1, 2) postulate, there have been multiple red plastid secondary endosymbioses, one must identify the

donor red lineage for each endosymbiosis and show that it contained ~200 plastid protein genes to infer that red plastids are in general twice as portable, with respect to plastid gene content, as are green plastids. Indeed, this is a premature claim, given that the few sequenced plastid genomes from cryptomonads, heterokonts, haptophytes, and dinoflagellates contain only about 150, 140, 110 (22, 23), and 15 protein genes, respectively. Therefore, under the hypothesis of multiple red secondary endosymbioses, it is entirely possible that the red algal progenitors of some or even all of these plastids had many fewer than 200 plastid protein genes.

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24. This depiction of plastid evolution differs from Figure 4 in (1) in several ways. This scheme takes into account evidence for a single origin of chromalveolate plastids and includes plastid-bearing groups not considered in (1). The most important of these groups is the apicomplexa, but we also show that tertiary endosymbiosis has occurred between dinoflagellates and diatoms (*Kryptoperidinium*) as well as cryptomonads and haptophytes. Falkowski *et al.* show the green alga-containing dinoflagellates arising from an ancestral “alveolate” in a secondary endosymbiotic event at the same level as that which gave rise to peridinin-containing dinoflagellate plastids. However, there are only two closely related genera of dinoflagellates with green algal plastids, and it is widely accepted that they originated relatively recently from a peridinin-containing dinoflagellate host, not from an ancestral alveolate. Falkowski *et al.* show all plastids to be morphologically identical and, most important, show all secondary and tertiary plastids as having two membranes. In reality, secondary plastids have four membranes, except those of euglenids and peridinin-containing dinoflagellates, which are bound by three membranes. Membrane structure of tertiary plastids varies. Falkowski *et al.* also omitted the relict nuclei (nucleomorphs) found in the secondary endosymbionts of chlorarachniophytes and cryptomonads (as well as the relict diatom nucleus in the tertiary plastid of *Kryptoperidinium*).

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