Why is the Land Green and the Ocean Red?

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Summary

Fossil evidence suggests that during the Paleozoic Era, green algae dominated eukaryotic phytoplankton taxa. One branch of this originally aquatic clade colonized terrestrial ecosystems to form what would become a green hegemony on land – with few exceptions, terrestrial plants are green. In contrast to land plants, contemporary oceanic phytoplankton are represented by relatively few species that are phylogenetically deeply branching. Since the Triassic Period, the major taxa of eukaryotic phytoplankton preserved in the fossil record have been dominated by organisms containing plastids derived from the "red", chlorophyll *c* containing algal clade. The ocean became "red" sometime during the Triassic or early Jurassic periods. The evolutionary success of the red line in Mesozoic and younger oceans appears related to changing oceanic conditions. In this chapter, we briefly explore the evolutionary processes and ecological traits that potentially led to the success of the red line in the oceans.

Introduction

All eukaryotic photosynthetic organisms are oxygenic (Falkowski and Raven 1997). The apparatus responsible for the photochemical production of oxygen is contained within distinct organelles, called plastids, that retain a complement of DNA, but are incapable of self-replication without supporting genes that are resident in the host cell's nuclear genome. Based on small subunit ribosomal RNA

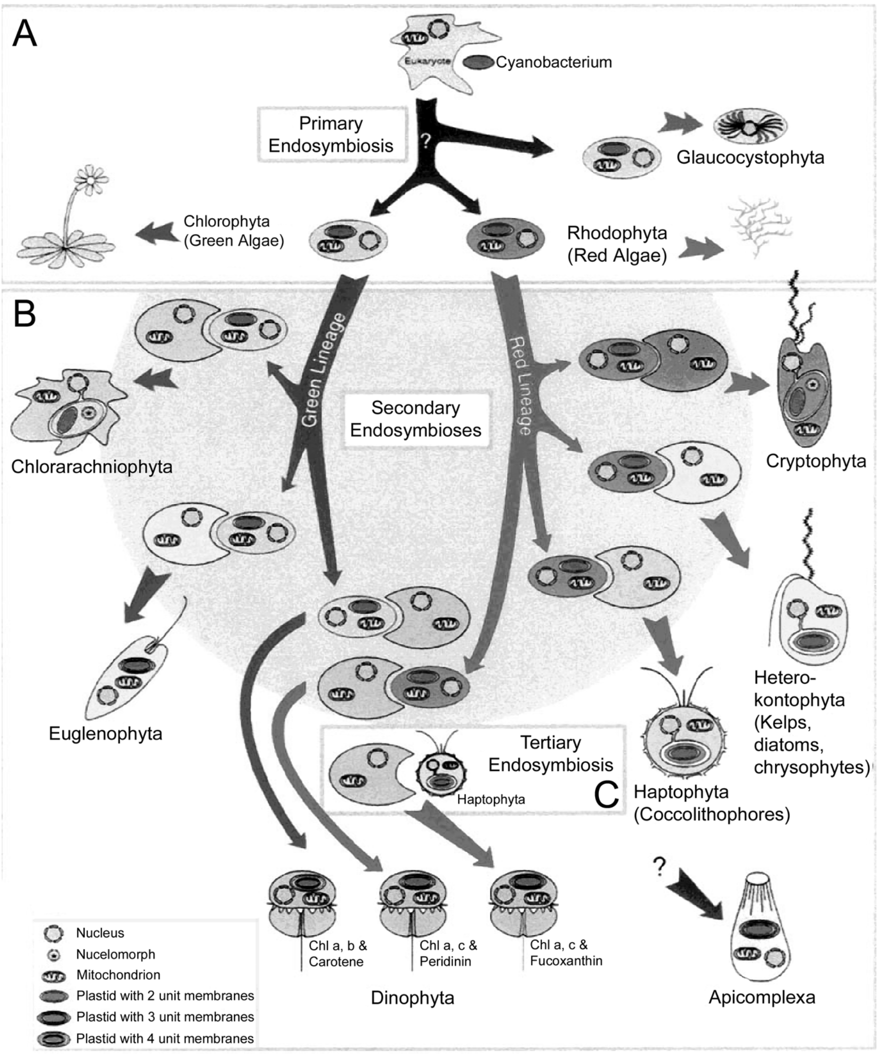


Fig. 1. The evolutionary inheritance of red and green plastids in eukaryotic algae. The ancestral eukaryotic host cell appropriated a cyanobacterium to form a primary photosynthetic symbiont. Three groups split from this primary association: one formed a “green” line, one a “red” line and the third is represented by the Glaucocystophyta. One member of the green line was the progenitor of higher plants. Two members of the extant green line form secondary eukaryotic associations, however neither of these taxa are ecologically significant. Several, independent secondary associations were formed from the primary red symbiont, including the haptophytes, heterokonts, and chrysophytes. The dinoflagellates appropriated plastids from both red and green lineages; however, the dominant group in the contemporary ocean is overwhelmingly red. (Adapted from Delwiche (1999), with permission).

sequences, it would appear that all plastids are derived from a single common ancestor that was closely related to extant cyanobacteria (Bhattacharya and Medlin 1995; Palmer 2003); however, early in the evolution of eukaryotic photoautotrophs major schisms occurred that gave rise to two major clades from which all eukaryotic photoautotrophs descended (Delwiche 1999) (Fig. 1). While all eukaryotic photoautotrophs contain chlorophyll *a* as a primary photosynthetic pigment, one group utilizes chlorophyll *c* and the other appropriated chlorophyll *b* as primary accessory pigments. No extant chloroplast contains all three pigments.

The chlorophyll *c* containing plastid lineage is widely distributed among at least six major groups (i.e., phyla or divisions) of aquatic photoautotrophs, but with the exception of some soil-dwelling diatoms and xanthophytes, is not present in any extant terrestrial photoautotroph. In contrast, the chlorophyll *b* containing plastid lineage is in three groups of eukaryotic aquatic photoautotrophs and in all terrestrial plants. Because additional accessory pigments (carotenoids) found in the chlorophyll *c* containing group have yellow, red, and orange reflectance spectra (i.e., they absorb blue and green light), the ensemble of organisms in this group are referred to, in the vernacular, as the “red lineage”, most of which are members of the sub-Kingdom Chromista (Table 1). The chlorophyll *b* containing group contains a much more limited set of carotenoids in the chloroplast, and members of this group generally have a green color. Thus, in effect, the ensemble of organisms responsible for primary production on land is green, while the ecologically dominant groups of eukaryotic photoautotrophs in the contemporary oceans are red. In this chapter, we explore the fossil evidence of the radiations of eukaryotic phytoplankton and consider some hypotheses that may account for the origin and ecological success of the red line in the oceans, while the green line maintained genetic hegemony on land.

Phytoplankton evolution in the geologic record

Long-term, macroevolutionary trends

Although the fossil record is clearly incomplete, analysis of microfossils from the Proterozoic through the end-Permian suggests that early oceans were not always dominated by the red lineage. For most of our planet’s Proterozoic history, cyanobacteria were probably the primary producers in the oceans, with eukaryotic algae rising to taxonomic and ecological prominence only near the end of the eon (Knoll 1992; Anbar and Knoll 2002). Well preserved fossils of vaucherian algae show that the secondary endosymbiosis that initiated “red lineage” diversification had already taken place by the Neoproterozoic (German 1990; Butterfield 2000). However, fossils in Neoproterozoic and especially Paleozoic shales indicate that phytoplankton with morphological features similar to members of extant green lineages were abundant and diverse in waters overlying contemporary continental shelves (e.g., Tappan 1980). For example, the prasinophyte, *Tasmanites* spp. (Fig.

Table 1. The higher taxa of oxygenic photoautotrophs, with estimates of the approximate number of total known species, and their distributions between marine and freshwater habitats*

Taxonomic Group	Known Species	Marine	Freshwater
Empire: Bacteria (= Prokaryota)			
Kingdom: Eubacteria			
Subdivision: Cyanobacteria (sensu strictu) (= Cyanophytes, blue-green algae)	1,500	150	1,350
Subdivision: Chloroxybacteria (= Procholrophyceae)	3	2	1
Empire: Eukaryota			
Kingdom: Protozoa			
Division: Euglenophyta	1,050	30	1,020
Class: Euglenophyceae			
Division: Dinophyta (Dinoflagellates)			
Class: Donophyceae	2,000	1,800	200
Kingdom: Plantae			
Subkingdom: Biliphyta			
Division: Glaucocystophyta			
Class: Glaucocystophyceae	13	_	_
Division: Rhodophyta			
Class: Rhodophyceae	6,000	5,880	120
Subkingdom: Viridiplantae			
Division: Chlorophyta			
Class: Chlorophyceae	2,500	100	2,400
Prasinophyceae	120	100	20
Ulvophyceae	1,100	1,000	100
Charophyceae	12,500	100	12,400
Division: Bryophyta (mosses, liverworts)	22,000	_	1,000
Division: Lycopsida	1,228	_	70
Division: Filicopsida (ferns)	8,400	_	94
Division: Magnoliophyta (flowering plants)	(240,000)		
Subdivision: Monocotyledoneae	52,000	55	455
Subdivision: Dicotyledoneae	188,000	_	391
Kingdom: Chromista			
Subkingdom: Chlorechnia			
Division: Chlorarachniophyta			
Class: Chlorarachniophyceae	3–4	3–4	0
Subkingdom: Euchromista			
Division: Crytophyta			
Class: Cryptophyceae	200	100	100
Division: Haptophyta			
Class: Prymnesiophyceae	500	100	400
Division: Heterokonta			
Class: Bacillariophyceae (diatoms)	10,000	5,000	5,000
Chrysophyceae	1,000	800	200
Eustigmatophyceae	12	6	6
Fucophyceae (brown algae)	1,500	1,497	3
Raphidophyceae	27	10	17
Synurophyceae	250	_	250
Tribophyceae (Xanthophyceae)	600	50	500
Kingdom: Fungi			
Division: Ascomycotina (lichens)	13,000	15	20

*The difference between the number of marine and freshwater species, and that of known species, is accounted for by terrestrial organisms. Dashes indicate that no species are known (by us) for their particular group in this environment.

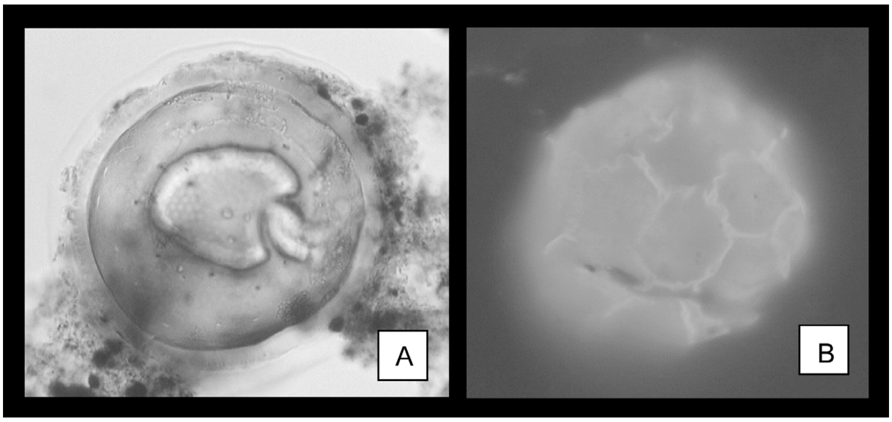


Fig. 2. The association of prasinophytes with anoxic conditions is also evident in the Early Jurassic (Toarcian) Posidonia Shales of NW Europe that may contain up to 105 prasinophyte cysts/g rock (Feist-Burkhardt 1992; Prauss et al. 1989; Prauss et al. 1991). However, the Toarcian appears to have been the last time these so-called “disaster species” (Tappan 1980) dominated organic-rich sediments on a global scale. Marine prasinophytes declined in importance during the Jurassic and Cretaceous and do not seem to have been major constituents of later Mesozoic ocean anoxic events (OAEs). Extant relatives of *Tasmanites* (e.g., *Halosphaera viridis*, *Pachysphaera* spp.) occasionally bloom in Norwegian and North Sea coastal waters, in the sub-arctic Pacific, as well as in the Mediterranean during winter and early spring blooms, however they seldom dominate eukaryotic phytoplankton assemblages (Van de Schootenbrugge et al. in press).

2) and other prasinophyte phycomata (e.g., *Cymatiosphaera*, *Dictyotidium*) are relatively common in Paleozoic black shales. Tyson (1995) suggested the abundance of these cells was “more than a preservational effect”.

In the Middle Triassic, two new groups of single-celled photosynthetic algae emerged in the fossil record (Fig. 3). One, the dinoflagellates, is recorded by carbonaceous microfossils with distinctive walls of polymerized glycans, relict cysts that were preserved in shallow marine continental margin regions. While dinoflagellates may be present among Neoproterozoic and Paleozoic microfossils (e.g., Moldowan and Talyzina 1998), identification remains uncertain. Further, although molecular biomarkers of dinoflagellates, such as the sterane and dinosterane, are present in Neoproterozoic sedimentary rocks, these markers only become prominent constituents of marine bitumens in the Triassic, when microfossils more securely document their radiation (Moldowan et al. 1996). The second group to radiate was the coccolithophores, a clade within the haptophytes that is armored with miniature plates (holococcoliths) of calcite (see Young et al. this volume). Later in the Mesozoic Era, the silica-encased diatoms emerged. Although Rothpletz (1896) reported diatom frustules in Jurassic sediments, the observations have proven difficult to replicate by later workers. Unquestionably,

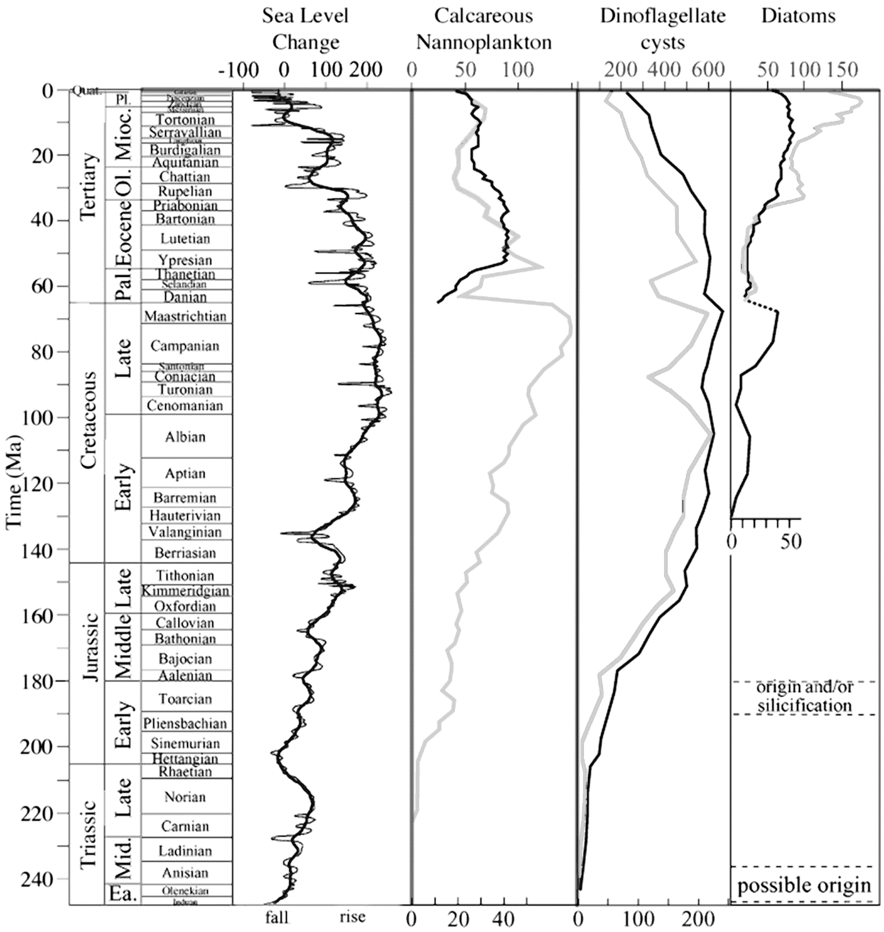


Fig. 3. Eukaryotic phytoplankton diversity curves compared with sea-level change. Phytoplankton species diversities (gray) are from published studies (calcareous nannofossils, Bown et al. this volume; dinoflagellates, Stover et al. 1996; diatoms, Spencer-Cervato 1999). Phytoplankton genus diversities (black) were compiled from publicly available databases (calcareous nannofossils and diatoms, Spencer-Cervato 1999; dinoflagellates, Mac Rae unpublished data). Sea-level curve is from Haq et al. (1987). All records are adjusted to a uniform time-scale (Berggren et al. 1995 for the Cenozoic and Gradstein et al. 1995 for the Mesozoic). (After Katz et al. in review)

however, diatoms had begun to radiate in the oceans by the Early Cretaceous (Harwood and Nikolaev 1995) and were present in non-marine environments by 70 million years ago (Chacon-Baca et al. 2002).

All three groups, the dinoflagellates, the coccolithophores, and the diatoms and their relatives, contain red plastids. These groups came to largely, but not totally displace green eukaryotic algae from Mesozoic time to the present.

Mesozoic-Cenozoic Phytoplankton Evolution

In spite of continued controversy over the details of evolutionary origins, the fossil record suggests that diversity within the red phytoplankton lineage was low in the early Triassic and increased rapidly in the Early Jurassic (e.g., Tappan and Loeblich 1988; Harwood and Nikolaev 1995; Stover et al. 1996; Bown et al. this volume). The long-term radiations in the Jurassic coincide with the opening of the Atlantic Ocean, accompanied by a sustained increase in sea level that flooded continental shelves. Indeed, observed Mesozoic increases in diversity of eukaryotic phytoplankton parallel the rise in sea level that began in the Early Jurassic (Haq et al. 1987; Hallam 2001) (Fig. 3).

In part, this correspondence surely reflects preservation and sampling – sediment abundance and availability commonly correlate with apparent diversity. Nonetheless, insofar as the Mesozoic diversity increase is apparent both within and among assemblages, biological explanations must contribute to observed patterns of fossil diversity. We suggest that the correspondence between sea stand and the radiation of the red lineages in the Jurassic may be related to life-cycle strategies. All three red eukaryotic taxa, the dinoflagellates, coccolithophores, and diatoms, produce resting stages; that is, following a bloom, a small fraction of the population of cells becomes arrested in a specific portion of a life cycle, increases the production of cell armor, and sinks to the sediments until such time as it is favorable to bloom (usually the following year). The timing of the bloom is generally keyed to changes in day length and water temperature. The resting stage is often associated with gamete formation and gene exchange in the planktic portion of the life cycle. This life cycle strategy for photoautotrophic organisms requires relatively shallow ocean regions, but moreover, promotes genetic isolation by reducing the planktic life cycle to well defined periods. Gene transfer, through sexual recombination and/or lateral vectors (such as viral infection), is highly attenuated in benthic stages. The genetic isolation may, over relatively short periods of time, have increased the tempo of evolution (i.e., rate of speciation) and phenotypic selection; processes that are observable in contemporary phytoplankton assemblages (Medlin et al. 1997).

Phytoplankton diversity was transiently uncoupled from long-term sea-level trends at the Cretaceous-Tertiary boundary, when mass extinctions, caused by a bolide impact, removed much of the diversity that had developed over the preceding hundred million years, especially among coccolithophores and dinoflagellates. Although dinoflagellate and, to some extent, coccolithophorid diversities recovered by the earliest Eocene, they began a long-term decline in the mid-Eocene; a trend that continues to the present time. Among fossilizable taxa, modern dinoflagellate species diversity is similar to levels found in the early Middle Jurassic, whereas modern coccolithophorid species diversity has dropped to levels last seen in the Late Jurassic. The decline of species richness in both groups corresponds with a long-term regression in sea level, primarily associated with the resurgence of permanent polar ice at the beginning of the Oligocene. In contrast to the dinoflagellates and coccolithophores, however, the tempo of evolution of diatoms has been extraordinary from the Eocene/Oligocene boundary to the present.

Rise of the red lineages and competition among them

It is certainly possible that the radiations of diatoms, coccolithophores, and dinoflagellates reflect taxon-specific adaptations without a common explanatory basis. For example, it could be argued that diatoms expanded because of ecological advantages such as the retardation of predation or viral attack conferred by the evolution of the organosilicate frustules (Smetacek 1999; Hamm et al. 2003). Alternatively, we might seek explanations in the common features of their metabolism or in secular, long-term changes in marine environments. There are several issues embedded in the macroevolutionary pattern of eukaryotic phytoplankton, however, that are not readily explained by or correlated with such physical drivers. We can cluster these issues into three fundamental questions:

1. Why did the green lineage rapidly decline in ecological importance during the early Mesozoic? Like the “red” groups, prasinophyte green algae have resting stages that, in principle, could have fueled diversification as sea level rose in the Mesozoic. However, this did not happen. Moreover, major sea-level rise accompanied the Cambro-Ordovician radiation of eukaryotic phytoplankton, but did not foster a radiation of red lineage taxa. Thus, to explain why the red lineage rose to prominence in the Mesozoic, we must ask how the Mesozoic oceans differed from that of the Early Paleozoic.
2. What circumstances facilitated the radiation of the dinoflagellates and coccolithophores, but not the diatoms, in the Mesozoic, and why have the two former groups receded, while the last has risen to prominence in the Cenozoic?
3. Why have terrestrial photoautotrophs not followed similar trajectories following the end-Permian extinction? Or, simply put, why has the land remained green while the ocean became red?

We consider these issues in turn.

Selective pressures in Mesozoic oceans

Light

One potential selection mechanism for red and green plastids is spectral irradiance. Compared to land plants, the majority of the phytoplankton biomass in the oceans is light-limited for growth and photosynthesis. On land, competition for light within a canopy is based on total irradiance, not primarily on the spectral distribution of irradiance. On average, 85 to 90% of the total incident photosynthetically available radiation on a leaf is absorbed; to first order, leaves are optically black. Hence, the small fraction of light that penetrates the first leaf level in a terrestrial plant is virtually ensured of being absorbed by any secondary leaves. Canopies dominate the irradiance distributions in terrestrial ecosystems. In contrast, in the oceans, absorption of light by seawater itself is critical to the spectral distribution of irradiance. The spectral irradiance is further modified by dissolved organic matter, sediments, and the spectral properties of the phytoplankton themselves. Hence, it is not surprising that phytoplankton have evolved an extensive array of accessory pigments, including carotenoids and chlorophylls, that permit light absorption throughout a wide range of the visible spectrum (Jeffrey et al. 1997).

A calculation of the spectrally weighted absorption for some of the major light harvesting pigments demonstrates that, while the overall absorption capability of chlorophyll *a* decreases with depth, the absorption capabilities for chlorophyll *b*, chlorophyll *c*, and the photosynthetically active carotenoids remain high and even increase with depth (Fig. 4). Given that chlorophyll b is as effective as chlorophyll c at absorbing light, it would appear highly unlikely that spectral irradiance was a selective force that led to the relative success of the red algal lineages compared to the green lineages in the modern oceans. In fact, the persistence of the eukaryotic green picoplankton (Glover 1985) and the bacterial *Prochlorococcus* (Chisholm et al. 1988) in both the deep portion of euphotic zone, as well as in the near surface ocean, clearly indicates that spectral irradiance per se is not a strong selective agent. Simply put, having chlorophyll *c* or chlorophyll *b* does not significantly alter the light-harvesting potential of the plastid. Answers for selective mechanisms almost certainly lie elsewhere.

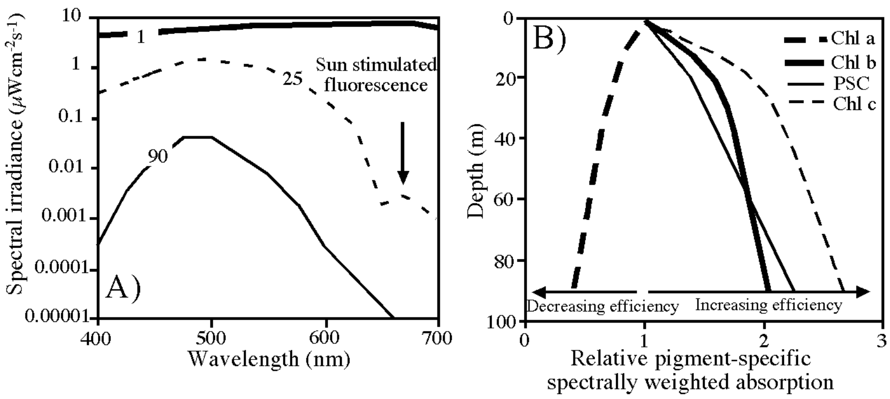


Fig. 4. (**A**) Representative spectral irradiance for clear ocean waters measured at the surface, 25 and 90 m depths. Note the strong attenuation of blue and red wavelengths of the spectrum. (**B**) Calculated absorption efficiency of major photosynthetic pigments as a function of depth. (PSC is photosynthetic carotenoids).

Trace elements and ocean redox chemistry

The end-Permian extinction appears to be marked by hypoxic, if not anoxic oceanic conditions (Isozaki 1997). Such conditions alter the distributions of many trace elements (Whitfield 2001), thereby potentially exerting selective pressure on specific taxa of phytoplankton. Indeed, elemental analysis of 16 species of marine phytoplankton from six taxonomic groups reveals clear, taxon-specific patterns of variation in chemical composition (Fig. 5), that largely cluster, with overlaps, among red, green and cyanobacterial lineages (Quigg et al. 2003). The primary differences between taxa appear to correlate with the differential distributions of trace elements. For example, algae with green plastids have 3–4 fold higher quotas for iron and copper (i.e., Fe:P and Cu:P ratios) than red eukaryotes, while the latter have higher quotas for Cd, Co and Mn. Based on pairwise t-tests and ANOVA, the differences are statistically different. Clearly these differences in trace element composition must reflect phenotypic expression that is ultimately related to a fundamental genomic schism between the green and red lineages.

The genes responsible for the distribution of these trace elements are not localized in the plastid, yet the cells segregate along clade-specific lines according to

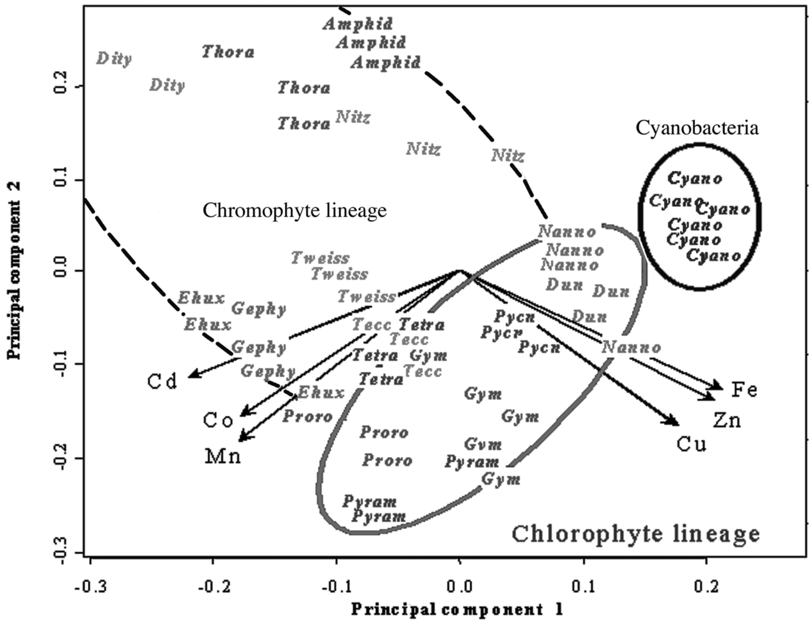


Fig. 5. A principal component analysis of the elemental composition of 16 species of algae including cyanobacteria, and eukaryotic red and eukaryotic greens. The results suggest that trace elemental composition can separate these major groups. (Adapted from Quigg et al, 2003.)

plastid type. This apparent paradox can be reconciled by recognizing that upon acquisition of either a primary or secondary plastid, the host cell appropriates and retains numerous plastid-encoded genes in the nucleus. The gene transfers appear to occur early in the evolutionary history of the symbiotic association (Delwiche 1999; Grzebyk et al. 2003) Hence, the phenotypic manifestation of trace element composition reflects selection pressures that occurred early in the evolution of the major phytoplankton taxa, and predicts a highly conserved set of primary and secondary gene products that are specific to a plastid inherited superfamily.

The elemental composition of dinoflagellates provides one test of this “plastid imprint” hypothesis. Dinoflagellates are promiscuous; they appropriate plastids from several primary and possibly secondary symbionts (Fig. 1). Assuming that the genetic backgrounds of the primordial host cells were similar, the plastid imprint hypothesis would predict that the trace element composition of dinoflagellates with plastids inherited from the red lineage would cluster more closely with other members of the red superfamily, while dinoflagellates with green plastids would cluster with the green superfamily. Indeed, based on trace element profiles, the three chlorophyll *c* containing dinoflagellates we examined, *Thoracosphaera heimii, Prorocentrum minimum* and *Amphidinium carterae*, are affiliated with the red lineage, and the chlorophyll *b* containing dinoflagellate, *Gymnodinium chlorophorum*, is associated with the green lineage. However, the host cells’ genetic backgrounds of these four species do not discriminate among the plastid types based on C:N:P stoichiometry (Quigg et al. 2003). These results strongly imply that plastid inheritance, but not contemporary plastid genomes, is a key factor dictating the trace element quotas in marine phytoplankton.

These results lead to the hypothesis that the phenotypic memory of trace element composition of eukaryotic phytoplankton is related to redox chemistry of the ocean. These biologically important trace elements are redox sensitive. Thus, their abundances in seawater through time will reflect the oxidation state of the oceans but may or may not be altered with diagenesis. For the first half of recorded Earth history, pO_2 appears to have been low in both surface and deep water masses (e.g., Holland 1984). Under these circumstances, Fe and Mn would have been abundant (relative to the requirements of photoautotrophs), whereas Cu and Mo would have been scarce (Williams 1981; Lipps 1993; Falkowski and Raven 1997; Raven 1997; Whitfield 2001; Anbar and Knoll 2002). Surface waters became oxic early in the Proterozoic Eon, yet the persistence of banded iron formations for more than six hundred million years after the initial rise of oxygen indicates that oxygen tensions must have remained low in many subsurface water masses (Canfield 1998). Indeed, black shales deposited beneath an anoxic water column are relatively common in Proterozoic marine successions (Shen et al. 2002; Shen et al. 2003), and widespread black shales persist through much of the Paleozoic Era (Arthur and Sageman 1994).

Deep-water anoxia may have been particularly pronounced near the end of the Permian Period (Isozaki 1997), and whatever events caused end-Permian mass extinction also introduced a remarkable, expanded oxygen minimum zone that persisted through the Early Triassic (Twitchett 1999; Wignall and Twitchett 2002). Widespread anoxic events occurred in the Mesozoic oceans, but were sufficiently infrequent such that each draws widespread notice from geologists (e.g., (Arthur and Sageman 1994). In the Cenozoic record, global oceanic anoxic events (OAE) are essentially absent.

From the foregoing comments, one can conclude that temporal changes in the availability of trace metals broadly coincide with the biological transition to red lineage dominance of phytoplankton. Thus, long-term changes in the ventilation of the world's oceans may have been significant in turning the seas red during the Mesozoic. The causes of changes in redox chemistry remain obscure; however, OAEs are recorded in the Triassic, at the Triassic-Jurassic boundary and several times later in the Mesozoic. While ocean anoxia leads to increased availability of Fe, Co, P and simultaneously to decreased Cu, Zn, and Cd, the return to oxic conditions would have witnessed a reversal in the availability of redox sensitive elements (Williams 1981; Raven 1997; Whitfield 2001). However, once established, members of the red lineage retained their ecological advantage as eukaryotic photoautotrophs. Hence, the initial selection pressure in oceanic ecosystems (i.e., redox state) may have permitted ecosystem displacement of the green lineage by the red lineage, but, in and of itself, this phenomenon cannot explain the continued success of the red lineage for the past 250 Ma.

We note that such redox based selection pressure almost certainly was not a factor in terrestrial plant evolution; throughout all of the Phanerozoic, atmospheric concentrations of oxygen have been well above any threshold to alter trace element chemistry in soils or precipitation. The dramatic changes in ocean redox chemistry were not mirrored in terrestrial ecosystems after the rise of the eukaryotic algae. Thus, there was no selection against green photoautotrophs and their high metal quotas. In conjunction with biochemical traits that enabled greens to thrive in the harsh conditions inherent to the land surface (Knoll et al. 1986), this ensured that while the oceans turned red, the continents bloomed green. The absence of this strong selective force allowed the green photoautotrophs, which had already established a foothold on land, to diversify through their morphology to better cope with the major stresses encountered on land.

Plastid portability

The continued success of the red lineage throughout the Mesozoic to present time requires one or more processes or properties that maintains evolutionary competitive advantage under a wide range of climatological, physical, and chemical conditions. One potential property that differentiates between the evolutionary trends and ecological success of the red and green lineage is contained in the plastid genome. Following an endosymbiotic event, most of the genes in the photosynthetic partner were lost or transferred to the host cell nucleus (McFadden 1999). Could there be a differential segregation of genes between red and green plastids that accounts for the success of the former in a widely diverse set of host cells?

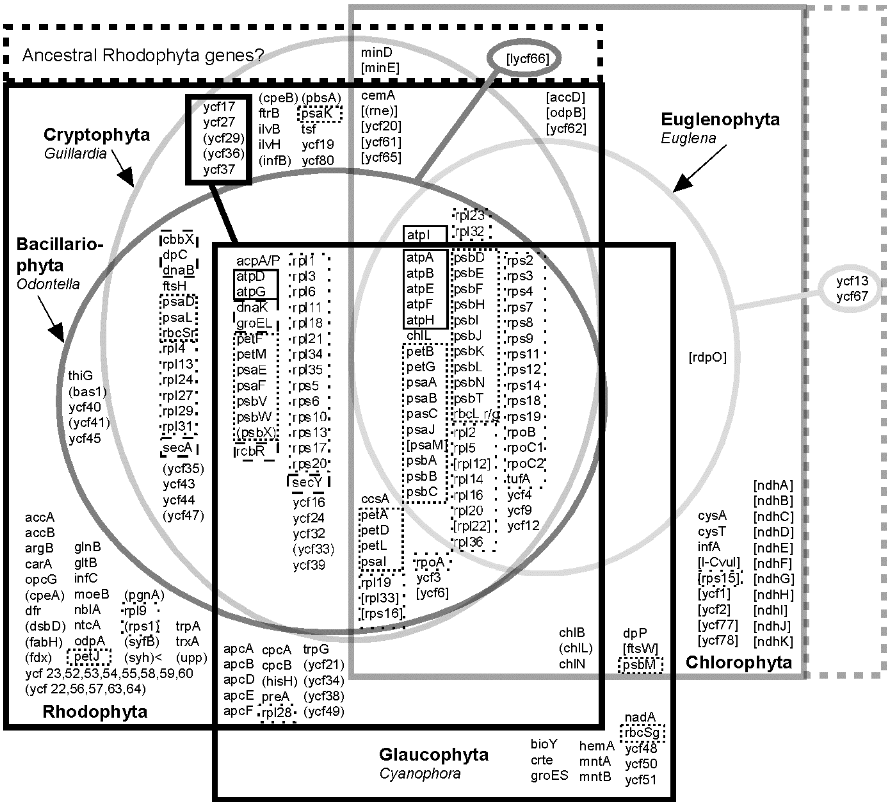


Fig. 6. Distribution of the 190 first identified and 66 hypothetical (ycf) protein-coding genes in nine photosynthetic algal plastid genomes. Primary endosymbiotic genomes (Glaucophyta, Rhodophyta, Chlorophyta) are represented with square boxes, and the secondary endosymbiotic genomes (Euglenophyta, Cryptophyta, Bacillariophyta) with circles. Genes involved in the three main plastid functions represented in the core set are highlighted: ATP synthase genes (—), photosynthetic processes (·····), and housekeeping genes (· ·). In red plastids, the complementary gene set contains specific genes (- - -) involved in protein regulatory pathways (transcriptional and post-transcriptional regulation). After Grzebyk et al. 2003 (original color figure on http://www.coccoco.ethz.ch).

Analysis of the distribution of plastid genes in extant chloroplasts reveals a set of ca. 50 core protein-coding genes retained in all taxa (Fig. 6). These genes are broadly clustered into three major functional domains: (a) genes encoding for the proton coupled ATP synthase (*atp* genes); (b) genes encoding for photosynthetic processes, including reaction center proteins (*psa*, *psb* genes), most of the electron transport components that connect the two photosystems (*pet* genes), and the large subunit of ribulose 1,5-bisphosphate carboxylase/oxygenase (*rbcL* genes); and (c) housekeeping genes that include the plastid ribosomal proteins (*rpl*, *rps* genes), RNA polymerase (*rpo* genes), and elongation factor (*tufA* gene). Only one biosynthetic gene that is involved in chlorophyll synthesis (*chlI*) is retained in all photosynthetic algae; this gene was transferred to the nucleus in higher plants.

Gene retention and losses in chloroplast genomes reflect evolutionary patterns

The gene loss from plastids (a process which is effectively irreversible) can provide evolutionary information about the endosymbiotic associations. There are 200 or fewer protein-coding genes in primary plastids. Whereas the number of primary endosymbiotic events is still unresolved (McFadden 2001), assuming that the number of genes in the original photosynthetic prokaryote was similar to that found in the extant cyanobacterium *Synechocystis* PCC6803 (3168 protein-coding genes (Kaneko et al. 1996)), >93% of the ancestral endosymbiont genome were lost or transferred to the host nucleus in the primary plastid lineages (Grzebyk et al. 2003). From a hypothetical ancestral plastid genome containing the whole gene set of extant plastids, the three primary plastid genomes result from specific gene losses and from parallel gene losses in two plastid lineages. Green plastids exhibit the most numerous gene losses, either specific losses or losses common to the glaucocystophyte plastid. Subsequently, patterns of gene losses occurred differently at genus level radiations within primary lineages and at radiations accompanying secondary symbiotic events. Between 1% and 10% of the remaining plastid genes were lost at genus level radiations within rhodophytes and chlorophytes. A large number of the remaining primary plastid genes were lost at radiations linked to the secondary symbiotic events. For example, 15% to 20% of the plastid genes were lost with the divergence of cryptophytes and bacillariophytes from the rhodophytes, and about 30% of genes were lost at the divergence of euglenoid plastids from chlorophytes. This analysis indicates that endosymbiotic events resulted in relatively rapid, massive gene losses in plastids, whereas the radiations within phyla were accompanied by slower and more gradual genomic erosion.

One can hypothesize that the retention of complementary core set genes in the primary plastid genomes of rhodophytes was critically important for the endosymbiotic radiation of the red lineage. In this scenario, gene retention improved the evolutionary potential of red plastids to be transferred to a collection of new, phylogenetically diverse, heterotrophic host cells. In contrast, the transfer of some of these complementary core set genes to the host nuclear genome decreased the portability of primary green plastids. Once these genes were lost in a primary plastid, a potential secondary host would had to have either retrieved them from the primary host nucleus, or obtained analogous non-plastid genes from elsewhere by lateral gene transfer.

The number of secondary endosymbioses involving green symbionts is similar to the number of “red” endosymbioses – at least three groups of protists imported plastids from green algal symbionts, whereas “red” symbioses occurred two to four times, depending on one’s phylogenetic framework (Cavalier-Smith and Beaton 1999; Delwiche 1999). One might propose that green symbioses occurred early in eukaryotic history, before plastid gene loss was completed. For the euglenophytes and chlorarachniophytes, the plastid phylogeny inferred from 16S rDNA suggests their plastids are derived early within the green plastid lineage (Bhattacharya and Medlin 1998), a conclusion supported by both the retention of the *rpl22* gene in the euglenophyte plastid genome and by fossils of photosynthetic euglenids (identified by features of lorica ultrastructure) in Ordovician rocks (Leander et al. 2001). Subsequent gene transfers from secondary green plastids paralleled those from primary green plastids (e.g., the transfer of the *rbcS* gene to the nucleus of euglenophytes). Key tests of the plastid portability hypothesis will come from genomic analyses of "green" dinoflagellates, which would not appear to be early branches on the dinoflagellate tree.

The portable plastid hypothesis also predicts that secondary endosymbioses of the "red" lineage occurred relatively late in biological history, after the importation of green plastids became genetically difficult. Fossils, however, indicate that photosynthetic heterokonts existed during the Proterozoic Eon – fossils of *Palaeovaucheria* in >1000 Ma old shales of Siberia share numerous features with extant species of the xanthophyte genus *Vaucheria* (German 1990; Woods et al. 1998), and recently discovered populations in ca. 800 million year old rocks from Spitsbergen preserve nearly the complete vaucherian life cycle (Butterfield 2000). While plastid portability may have influenced the establishment of novel photosynthetic lineages within the eukaryotes, functional biology must provide explanations for the rise of the red lineage of phytoplankton to taxonomic and ecological prominence.

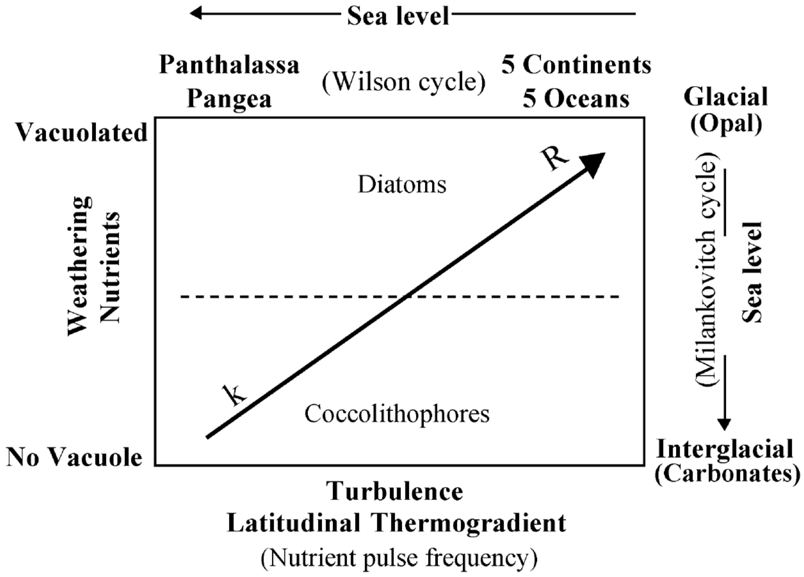
Competition among the red taxa

We now consider the possible causes for the radiation of both dinoflagellates and coccolithophores, but not diatoms in the Mesozoic, and the reversal in the fortunes of the former two taxa with respect to the latter in the Cenozoic. Our models are based on the macroecological features of the three taxa derived largely from physiological studies of extant species.

One striking feature that emerges is the nutritional characteristics and differences among the three clades. Many photosynthetic dinoflagellates can assimilate dissolved and particulate organic matter, thereby supplementing their photoautotrophic metabolism. While mixotrophy is hardly unique to dinoflagellates, the extent to which they exploit this nutritional lifestyle is remarkable. Mixotrophy is advantageous under two conditions: (a) in oligotrophic environments, where (by definition) inorganic nutrients are scarce and both dissolved organic nitrogen and phosphorus are relatively plentiful, and (b) in coastal regions, which are enriched in terrestrial and/or estuarine derived particulate and dissolved organic matter. We suggest that overall rise in sea level facilitated the expansion of these two conditions through the Jurassic and Cretaceous. At the same time, the vast extent of the Panthalassic Ocean, coupled with a general sluggish thermohaline circulation, would have contributed to an unusually widespread distribution of subtropical and tropical oligotrophic marine ecosystems.

Contemporary coccolithophores are generally mesotrophic/oligotrophic taxa, and are widely distributed throughout the subtropical seas. Two contemporary species, *Emiliania huxleyi* and *Coccolithus pelagicus*, form blooms, usually at mid to high latitudes. The blooms, which are detectable from satellite imagery (see Balch et al. this volume), are keyed to a shoaling of the mixed layer, an increase in incident solar radiation, and decreasing concentrations of nitrate and phosphate. Whereas coccolithophores are obligate photoautotrophs, available physiological data indicate that they have a relatively high affinity (low half-saturation constant) for both macronutrients. In the North Atlantic, coccolithophore blooms always succeed blooms of diatoms.

Arguably, diatoms are the most ecologically successful eukaryotic algae in the contemporary ocean. They currently are responsible for ca. 40% of the net primary production and upwards of ca. 50% of the organic carbon exported to



Modified Margalef's Mandala

Fig. 7. An extension of Margalef's Mandala (Margalef 1997), showing that increased turbulence and subsequent increased available nutrients lead to a shift from K to r species. Turbulence and nutrient concentration in the ocean reflect the latitudinal thermogradient that is function of radiative forcing, continent dislocation and sea level.

the ocean interior (Smetacek 1999). Diatoms began their rise to prominence in the late Eocene when dinoflagellate and calcareous nannoplankton diversities began to decrease and diatom diversities began to increase at the level of genera (Fig. 7). These diversity changes correspond to a time when sea level began a long-term fall through the Cenozoic, decreasing the extent of flooded continental shelf area. This indicates that tectonics and the Wilson cycle may have played a role in diatom evolution in the Cenozoic. However, diatom evolution at the species level occurred in two pulses: 1) a dramatic radiation at the Eocene/Oligocene boundary; and 2) sustained increase in diversity through the middle and late Miocene to present time. These results suggest that tectonics and extent of continental shelf flooded were not the primary driver of diatom evolution; rather, diversity changes in diatoms appear to be linked to major changes in both Cenozoic climate and the terrestrial biosphere. What are the possible links?

Diatoms are unique among extant photoautotrophic taxa in that they have an absolute requirement for orthosilicic acid, which they polymerize on a protein matrix to form strong shells called frustules. Silica is introduced into the oceans primarily by continental weathering, but the present day surface ocean is strongly undersaturated with respect to silica as a direct consequence of diatom growth. Diatoms are basically neritic, and blooms are largely confined to continental margins, and shallow seas, and such open ocean regions as the North Atlantic and Southern Ocean where silica can be supplied through upwelling. Hence, one possible clue to the rise of diatoms in the Cenozoic may lie in an increased flux of silicic acid from the continents.

A second feature that distinguishes diatoms from dinoflagellates and coccolithophores is the evolution of a true nutrient storage vacuole. The vacuole occupies approximately 35% of the volume of the cell, and can retain high concentrations of nitrate and phosphate. Importantly, ammonium cannot be (or is not) stored in a vacuole. The vacuole allows diatoms to access and hoard inorganic nutrients, thereby potentially depriving competing groups of these essential resources. Consequently, diatoms thrive best under eutrophic conditions and in turbulent regions where nutrients are supplied in frequent high pulses. The competition between diatoms and coccolithophores can be modeled easily using a resource acquisition model based on Droop’s formulation for nutrient uptake (Droop 1974). In such a model, diatoms dominate under highly turbulent conditions, when their nutrient storage capacity is maximally advantageous, while coccolithophores dominate under relatively quiescent conditions (Tozzi et al. in press). These results fit the classical r and K paradigm, where r strategists (e.g., diatoms) dominate in high mixing environments and K strategists (e.g., coccolithophores) dominate oligotrophic conditions. Although it is theoretically possible that competitive exclusion could occur under extreme conditions, it does not do so in the real ocean. The coexistence of two taxa competing for a single resource is a consequence of the dynamically unstable nature of aquatic ecosystems (Li 2002).

Recognizing these fundamental differences in physiology, Ramon Margalef proposed that competition among these three major taxa could be related to turbulence in the upper ocean (Fig. 7). The so-called Margalef “mandala,” can be extended over geological time to infer selection processes that have led to the early rise of dinoflagellates and coccolithophores followed by the rise of diatoms in the Cenozoic. Can we extend Margalef’s “mandala” to a geological (and hence, evolutionary) context?

On relatively recent time-scales, such as Pleistocene, the sedimentary record reveals a periodicity of opal/calcite deposition corresponding to glacial/interglacial periods. We propose that such alterations in mineral deposition are related to upper ocean turbulence; i.e., the sedimentary record is a "fax" machine of mixing (Falkowski 2002). Glacial periods appear to be characterized by higher wind speeds and a stronger thermal contrast between the equator and high latitudes. In accordance with our simple nutrient uptake model, these two factors would favor diatoms over coccolithophores. During interglacials, more intense stratification, weaker winds, and a weaker thermal contrast between the equator and poles would tend to reduce upper ocean mixing and favor coccolithophores. While other factors (e.g., silica availability) undoubtedly would also influence the relative success of diatoms and coccolithophores on these time-scales, we suggest that the climatically forced cycle, played out on time scales of 20–100 ky (over the past 3 my), can be understood as a long-term competition that never reaches an exclusion equilibrium condition.

Can the turbulence argument be extended to even longer time-scales to account for the switch in the dominance from coccolithophores to diatoms in the Cenozoic? Even though the fossil record of diatoms in the Mesozoic is obscured by problems of preservation, several diatom species have been reported from the late Jurassic (Harwood and Nikolaev 1995), and the group could have existed much earlier (Moldowan and Jacobson 2000). However, the diatoms found in Cretaceous marine deposits almost uniformly belong to extinct stem taxa, indicating that both modern taxa and the modern importance of diatoms in export production were not established before the late Mesozoic. We suggest that the ongoing ecological and evolutionary displacement of coccolithophores by diatoms in the Cenozoic is, to first order, driven by tectonics. The Mesozoic interval was relatively warm and was characterized by a two cell Hadley circulation, with obliquity greater than 37.6°, resulting in a relatively well-mixed atmosphere. The atmospheric meridional heat transport decreased the latitudinal thermogradients; global winds and ocean circulation were both sluggish (Huber et al. 1995). This relatively quiescent period of Earth's history was ideal for coccolithophorids. However, climate conditions began to deteriorate in the mid-Eocene. Tectonic gateways opened through the Drake Passage and between Australia and Antarctica by the Eocene/Oligocene boundary (33.7 Ma) (Kennett 1977; Barrett 1996). The resulting surface and intermediate water circulation around Antarctica most likely contributed to the thermal isolation of the continent at this time. In addition, modeling studies show that declining atmospheric CO_2 levels played a major role in ice volume increase at the same time (DeConto and Pollard 2003). With the establishment of a large, permanent Antarctic ice sheet by the Eocene/Oligocene boundary, Hadley circulation changed dramatically. The net result was more intense thermohaline circulation, greater wind mixing and decreased stability (Chandler et al. 1992; Barron et al. 1995). Hence, decreased stability of the upper ocean may have contributed to the rise of the diatoms in the Cenozoic.

The isotopic record from carbonates suggests that orogenic uplift in the Cenozoic, coupled with a decline in volcanism, have further led to a long-term depletion of CO_2 and a corresponding decrease in temperature of the ocean's interior (Crowley and North 1991; Kump and Arthur 1999). These geochemically driven climate changes may have increased oceanic stratification, which has, in turn, led to an increased importance for wind-driven upwelling and mesoscale eddy turbulence in providing nutrients to the upper ocean. The ecological dominance of diatoms under sporadic mixing conditions indicates that their long-term success in the Cenozoic reflects an increase in event scale turbulent energy dissipation in the upper ocean. But was tectonics the only driver?

The coevolution of mammals, grasses, and diatoms

Through the silicate weathering cycle, orogeny may have been a catalyst in the long-term radiation of diatoms in the Cenozoic. Huh and Edmond (1999) have argued that on million year timescales, continental elevation determines weathering fluxes to the oceans. Insofar as both uplift and regression have characterized nearly all continents throughout the Cenozoic, increasing nutrients in general, and increasing fluxes of silica in particular, might have facilitated diatom expansion. $^{87}Sr/^{86}Sr$ values began a long-term increase (suggestive of an increase in continental weathering) near the Eocene/Oligocene boundary, at about the same time as the first major radiation in diatoms (Fig. 3). However, orogeny alone cannot explain the relatively sharp increase in diatoms at the Eocene/Oligocene boundary and in the middle through late Miocene. We must look for other contributing processes.

True grasses arose shortly after, or perhaps coincident with, the Paleocene/Eocene Thermal Maximum (PETM) (Kellogg 2000). The first definite occurrence of C_3 grass pollen has been dated as ~55 Ma (Jacobs et al. 1999). Grasses remained sparse until the Eocene/Oligocene boundary (33.7 Ma) (Retallack 2001), corresponding to a global climatic drying associated with the establishment of major glaciation in the Antarctic. The rapid co-evolution of grazing ungulates accompanied the expansion of grasses at this time, displacing browsers (Janis et al. 2002). Grasses contain up to 15% dry weight of silica, which forms micromineral deposits in the cell walls, called phytoliths. Indeed, the selection of hypsodont (high crown) dentition in ungulates from the brachydont (leaf eating) early-appearing browsing mammals coincides with the widespread distribution of phytoliths and grit in grassland forage. It is tempting to suggest that the rise of grazing ungulates and the radiation of grasses in effect was a biologically catalyzed silicate weathering process. The deep root structure of Eocene grasses certainly facilitated silicate mobilization into rivers and ground waters. The increase in phytolith diversity and abundance since the late Eocene (Retallack 2001) indicates that the mobilization of silica from soils by grasses increased as the grasses evolved and expanded. The subsequent transfer of this silica to the oceans (via fluvial and aeolian transport) must have increased the bioavailability of silica to diatoms, which also began to diversify at the genus level in the late Eocene (Fig.

3). We propose that this mechanism can account for the close correlation between evolutionary pulses of grasses and diatoms.

Short grasslands became widespread by ~17 Ma (Retallack 1997; Retallack 2001), and initially were dominated by C_3 grasses (Retallack 1997; Retallack 2001) even though C_4 grasses evolved ~15 Ma or earlier (Latorre et al. 1997). The second pulse of diatom diversification at the species level in the Neogene coincides with the expansion of grasslands coupled with a shift from C_3 to C_4 grasses in the late Miocene.

The feedback between the co-evolution of mammals and grasses and the supply of silicates to the ocean potentially explains the punctuated radiation of diatoms, and the continued dominance of diatoms in the Cenozoic. There is another potential feedback at play however, that “locked in” diatom preeminence. Indeed, one could argue that the increase in diatom dominance, and the associated increase in the efficiency of carbon burial, played a key role in decreasing atmospheric CO_2 over the past 55 My. If so, diatoms have inadvertently helped to make the ocean more turbulent, thereby potentially decreasing competition from dinoflagellates and coccolithophores. Perhaps ironically, humans, through the combustion of fossil fuels, are fleetingly interrupting this long-term process. That biological selection may influence climate is clearly controversial, however, the evident trends in succession between taxa on long time-scales, and cycles in dominance on shorter geological time-scales beg for explanation.

Conclusions

Evolution, like any other complex system with emergent properties, cannot be explained by a set of ordinary differential equations. Rather, the links among processes, which are non-linear and fluctuating, form patterns are recorded in the geological record and presumably reflect preserved patterns in ecological structure. Just as a family’s history cannot be completely understood from a photo album, we cannot look at snapshots of the geologic record and totally understand why the ocean is dominated by red eukaryotic phytoplankton while the land has been conquered by green plastids. In our analysis however, we have suggested some processes that address the three basic issues we raised.

We proposed that a major factor that contributed to the decline of the green lineage in ecological importance following the end-Permian extinction was a long-term change in the chemistry of the ocean, specifically a long-term decline in the formation of anoxic/hypoxic waters that began in the mid-Triassic. Our results from trace metal preferences reveal that, while redox states cannot fully account for the selection of the red lineage, trace element distributions keyed to suboxic conditions were probably conducive to the relative fitness of red plastid eukaryotes in the ocean. To our knowledge, this type of selection pressure did not occur in terrestrial ecosystems throughout the Phanerozoic. Once selected, red plastids appear to be much more portable than green plastids by virtue of a complementary set of genes retained in the former organelle.

Finally, we examined some of the potential process(es) that contributed to the radiation of the dinoflagellates and coccolithophores, but not the diatoms, in the Mesozoic, and why the two former groups have receded, while the last has risen to prominence in the Cenozoic. Our analysis suggests that two overarching processes played key roles in the selection of specific red taxa on these time-scales. The first is oceanic turbulence, dictated on all time-scales by the equator to pole and continent to ocean thermal gradients. This hypothesis is testable in the modern ocean on ecological times scales. We suggested that, compared with the late Cenozoic, the Mesozoic oceans were relatively quiescent, whereas over the past 34 Ma there has been an increase in upper ocean turbulent mixing. We couched these notions within the context of Margalef's "mandala" on geological time-scales. However, we further suggest that the long-term rise in fortunes of diatoms over the past ~34 my has been, in part, due to the co-evolution of grasses, which accelerated the silicate weathering cycle, and led to an increased carbon burial, especially on continental margins. This hypothesis led to the corollary that the long-term drawdown of CO_2 and the corresponding decrease in Earth's temperature since the Oligocene has, in part, been a consequence of the rise of diatoms. This hypothesis is supported by the carbon isotope data from carbonates over the last 210 myr (Katz et al. in review). We hope that this brief essay will stimulate further exploration of the macroevolution of marine phytoplankton in the context of Earth's geological history.

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