Prologue

Photosynthesis has provided life-energy for the biosphere during most of earth's history. It provides us with all our food and fuel for our vehicles, and much of our building materials and other commodities. When our society now faces the big energy crisis, this ancient process may come to our rescue, both in the form of biofuel produced by plants and in novel, technologically modified versions. Current Science has begun the publication of a series of articles on the theme of 'Photosynthesis and the Global Issues'. Those who would solve the energy crisis would need information on all aspects of the process of photosynthesis. In this first review article, Lars Olof Björn (Sweden) and Govindjee (USA) discuss the very first theme: the evolution of photosynthesis and the chloroplasts.

The evolution of photosynthesis and chloroplasts[†],[§]

Lars Olof Björn[1],* and Govindjee[2]

[1]Lund University, Department of Cell and Organism Biology, Sölvegatan 35, SE-22362 Lund, Sweden and
Key Laboratory of Ecology and Environmental Science in Guangdong Higher Education, School of Life Science,
South China Normal University, Guangzhou 510631, China
[2]Departments of Plant Biology and Biochemistry and Center of Biophysics and Computational Biology, 265 Morrill Hall,
505 South Goodwin Avenue, Urbana, IL 61801, USA

This review focuses on what has been learned about the evolution of photosynthesis in the past five years, and omits evolution of CO_2 assimilation. Oxygenic photosynthesis (using both photosystems I and II) has evolved from anoxygenic photosynthesis. The latter occurs in different variants, using either a type 1 photosystem resembling photosystem I, or a type 2 photosystem resembling photosystem II. Opinions differ as to how two types of photosystem came to be combined in the same organism, whether by gene transfer between bacteria, by fusion of bacteria, or as a result of gene duplication and evolution within one kind of bacterium. There are also different opinions about when oxygenic photosynthesis arose, in conjunction with the Great Oxygenation Event, 2.3 billion years before the present, or more than a billion years before that.

Cyanobacteria were the first organisms to carry out oxygenic photosynthesis. Some of them gave rise to chloroplasts, while others continued to evolve as independent organisms, and the review outlines both lines of evolution. At the end we consider the evolution of photosynthesis in relation to the evolution of our planet.

Keywords: Bacteria, bacteriochlorophyll, chloroplast, cyanobacteria, horizontal gene transfer, red algae.

THERE are three forms of life: Archaea, Bacteria and Eukarya[1]. The first common ancestor of these three forms is thought to have possessed membrane-bounded cells, a translation machinery for synthesis of proteins, an energy transducing system involving electron transport and high-energy phosphate, but no photosynthesis. Photosynthesis has arisen in the Bacteria, but when we encounter the word 'photosynthesis', we are likely to first think of land plants with green leaves. Plants are eukaryotes, just as we are, composed of cells with a nucleus and organelles separated from other cell constituents by membranes. There are many other kinds of photosynthetic organisms, many of which are lumped together under 'algae'[2]. Some live in water. Many are also living in symbiosis, either with terrestrial organisms such as fungi (forming lichens), or with aquatic organisms such as corals or molluscs. A common trait for the photosynthesis carried out by eukaryotes[3,4] is that it involves oxidation of water and evolution of molecular oxygen, O_2.

In addition to eukaryotic photosynthesizers, there are bacteria carrying out photosynthesis. Among bacteria, only the cyanobacteria are able to oxidize water and evolve oxygen[5]. Another type of photosynthesis is carried out by several other coloured (e.g. green, purple) bacteria; it is anoxygenic and does not evolve oxygen[6,7]. Chen and Zhang[8] have discussed an interesting relationship between the oxygen content of the peptides and the proteins of the oxygenic and anoxygenic organisms; in particular that the D1 and D2 polypeptides of oxygenic photosystem II contain more oxygen than the corresponding polypeptides in anoxygenic bacteria.

Olson and Blankenship[9] have pioneered many thoughts about the evolution of photosynthesis; most importantly that different parts of the photosynthetic apparatus of green plants have different evolutionary histories. Much

has been published since then. In this review we shall focus on some of the current thinking about the evolution of photosynthesis and of chloroplasts. We shall restrict our discussion to organisms containing chlorophyll or chlorophyll-like pigments. However, it is also known that some bacteria (and some archaea) harvest light energy by means of a rhodopsin-like pigment.

Phylogeny of photosynthetic bacteria

Photosynthetic bacteria that lack the ability to evolve oxygen, possess one of the two different types of photosynthetically active pigment protein complexes, called type 1 and type 2 photosystems. Both have various forms of bacterial chlorophyll (called bacteriochlorophyll) in

the 'reaction centers' (RC-1 and RC-2), where light-requiring primary charge separation takes place: electrons are transferred to an acceptor molecule, leaving a hole (or a positive charge) on the bacteriochlorophyll molecules. The principal difference between type 1 and type 2 photosystems lies in the kinds of acceptor molecules or groups of atoms that take up the electron from bacteriochlorophyll. In the case of type 1 reaction centres, these are nonheme iron–sulphur proteins, but in the case of type 2 reaction centres, they are quinone molecules.

We can imagine that both type 1 and type 2 reaction centres were first together in an ancient anoxygenic cyanobacterium, and by a loss of type 1 or type 2 different branches of anoxygenic photosynthetic bacteria evolved (the loss hypothesis); however, addition of the oxygen evolving complex (OEC) lead to the oxygenic
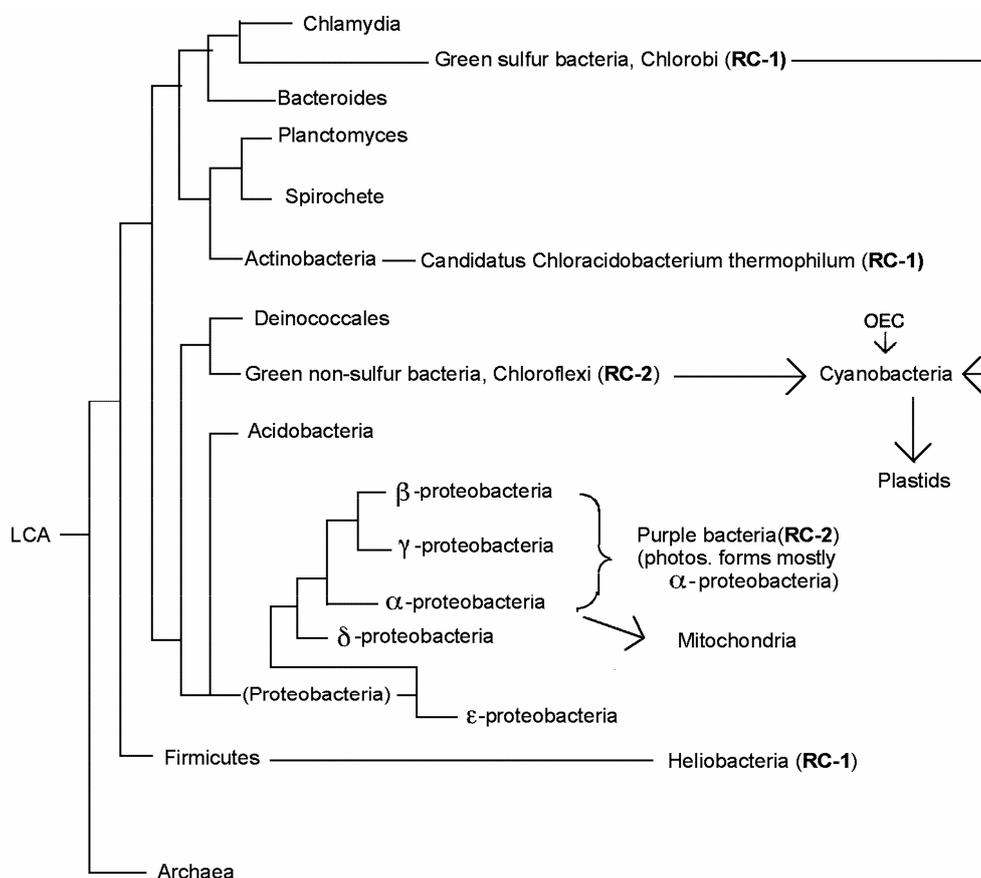

Figure 1. A scheme for a bacterial tree of relationships (LCA, last common ancestor). In those groups where photosynthetic forms occur, the type of photosystem is indicated in bold letters. The α-, β-, and γ-proteobacteria are collectively referred to as purple bacteria. Most of the photosynthetic purple bacteria are α-proteobacteria, but there are also some among the β- and γ-proteobacteria. Mitochondria of eukaryotic organisms are derived from α-proteobacteria. As can be seen from this diagram, the various types of bacteria having RC-1 are not closely related, neither are those having RC-2. The oxygenic cyanobacteria harbour both photosystems I and II, clearly derived from RC-1 and RC-2 respectively, but from where they have acquired these is uncertain. A major difference is that RC-2 has now evolved to be able to split water to oxygen using the oxygen evolving complex (OEC). We have added OEC at the same point as where the two kinds of photosystems join in the evolution of cyanobacteria, but it is unlikely that these events took place simultaneously. One possibility is that cyanobacteria are derived from green sulphur bacteria, and have taken up RC-2 from green sulphur bacteria by horizontal gene transfer. The green non-sulphur bacteria are also called 'filamentous anoxygenic phototrophs', since several members of the group do indeed obtain electrons from sulphur or sulphide compounds. The above diagram is speculative, because of the high frequency of horizontal gene transfer taking place among prokaryotes.

cyanobacteria[10]. An alternate hypothesis is the fusion hypothesis, where type 1 and type 2 reaction centres came together later[10]. There is great uncertainty concerning the path of organismal evolution among Archaea and Bacteria[11,12]. A possible scheme is shown in Figure 1. Because horizontal gene transfer occurs frequently, it is more appropriate to consider the evolution of genes, or groups of genes. That horizontal gene transfer still takes place among genes for proteins involved in photosynthesis is well known. The marine environment is full of viruses harbouring such genes[13–15]; cf[16,17]. Because of this high frequency of horizontal gene transfer, it is more appropriate for us, at least for Archaea and Bacteria, to speak of a 'web of life' rather than a 'tree of life' (Figure 2)[18].

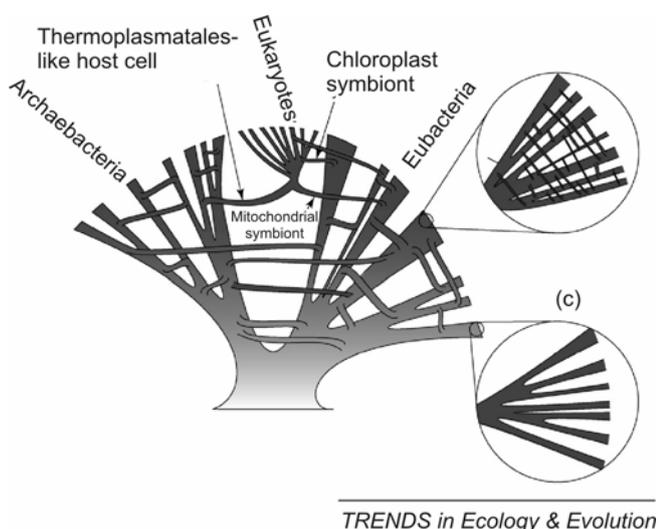The step from anoxygenic to oxygenic photosynthesis required a number of innovations, of which we mention

Figure 2. The 'web of life' according to McInerney *et al.*[18], slightly modified. Lateral gene transfer, here indicated as connections between the 'branches' is common in some groups, and almost absent in others.
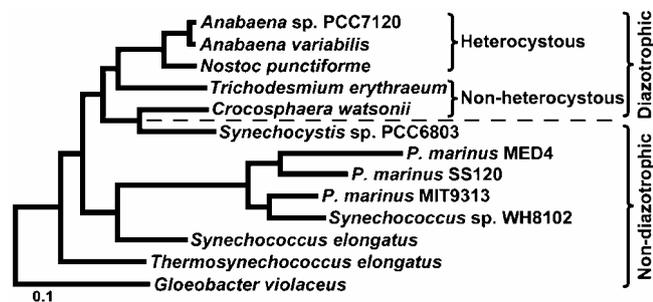

Figure 3. The 'tree of evolution' for cyanobacteria according to Shi and Falkowski[26], slightly simplified. The tree is econstructed based on the concatenation of 323 core proteins. *Gloeobacter* is a primitive organism differing from other cyanobacteria in lacking thylakoids. The scale bar refers to the number of amino acid substitutions per site. Copyright (2008) National Academy of Sciences, USA.

here only the most important. This type of photosynthesis uses two photosystems: photosystem II (PSII; light-induced water plastoquinone oxidoreductase[3]) and photosystem I (PSI)[19]. There must be an OEC attached to the type 2 photosystem to make it a true PS II. The two photosystems must be connected in series to generate sufficient difference in redox potential between the oxidizing and reducing ends of the process, water on one side and CO_2 on the other. In between the series-connected photosystems there is an 'electron buffer' in the form of a plastoquinone pool. The oxidation state of this pool controls the channelling of energy from light-harvesting complexes for short-term adjustment of energy allocation. But it also controls, via gene regulation, the synthesis of new reaction centres according to long-term needs[20]. For this series connection to have any effect, the redox potential spans of the two photosystems must also be adjusted to be sufficiently different. This has been achieved using chlorophyll *a* (in some cases also chlorophyll *d*) instead of bacteriochlorophyll in the reaction centers, and by modifications of the bonding to protein and other effects on pigment environments[21–23]. For a description of chlorophylls and bacteriochlorophylls, see Grimm *et al.*[24].

Finally, a mechanism must be provided to make the two photosystems work 'in step'. This last feature was achieved by a newly discovered redox regulator, sensing the redox potential between the photosystems[19].

The most primitive cyanobacteria, of the genus *Gloeobacter*, lack thylakoids and harbour the photosynthetic apparatus in the cell membrane. They may provide a link to anoxygenic photosynthetic bacteria, and may be close to the last common ancestor of oxygenic organisms[25]. (For a 'tree of evolution' of cyanobacteria, see Figure 3.)

Although horizontal gene transfer among and to cyanobacteria is frequent, it is possible to define a 'core' of genes and to construct from this a more tree-like evolution[26] (Figure 3). According to Nelissen *et al.*[27], the evolutionary path to plastids of eukaryotic organisms diverges (based on 16 S rRNA) from extant cyanobacteria before the branching-off of *Gloeobacter*, while Deusch *et al.*[28], based on other genes, regard an origin within the heterocystous clade as probable. Further, Gross *et al.*[29] show that not all photosynthetic genes in plastids are derived from cyanobacteria closely related to any extant ones, and this brings us to the phylogeny of genes important for photosynthesis.

Phylogeny of genes important for photosynthesis

As already pointed out, phylogenetic relationships among bacteria are blurred by horizontal gene transfer. However, more certain conclusions can be drawn regarding individual genes or groups of genes. An example is provided by the enzymes catalysing some of the final steps in the synthesis of chlorophyll *a* and of bacteriochlorophyll. All photosynthetic prokaryotes (and many eukaryotes) having

chlorin-type chlorophylls (like chlorophyll *a* and bacteri-ochlorophyll *a*) possess a light-independent (**d**ark) **p**rotochlorophyllide-**o**xido**r**eductase (DPOR) by which they can carry out the reduction of the D-ring (Figure 4) in the absence of light. This enzyme is derived from nitro-genase[30–33]. In the synthesis of bacteriochlorophyll *a*, the same enzyme catalyses two different reduction steps[34]. Also, the light-dependent NADPH-protochlorophyllide oxidoreductase, typical of angiosperms, traces its origins back to cyanobacteria[35], as do genes for the synthesis of cellulose[36] and starch[37], and for the photorespiratory gly-colate metabolism[38].

The most important difference between the type 2 photo-system of non-oxygenic photosynthetic bacteria and PSII of cyanobacteria and eukaryotes is the presence of an OEC in the latter; its origin has been reviewed by Ray-mond and Blankenship[39]. The OEC is a metallo-enzyme that has a redox-active core with four manganese atoms and one calcium atom. These authors speculate that a precur-sor of the OEC might first have associated with a manga-nese catalase (having two manganese atoms; however, no calcium atom). The precursor might then have developed its own suitably positioned binding site for two manga-nese atoms and taken these over from the catalase. Asso-ciation with another molecule of catalase would then result in a four-manganese core. Further studies on how the OEC is assembled during development might show whether this scenario is plausible.

Ribulose-*bis*-phosphate carboxylase-oxygenase (RuBis CO), the enzyme binding carbon dioxide in many photo-synthetic organisms, is derived from a similar enzyme in bacteria carrying out carbon dioxide assimilation chemo-synthetically before the origin of the extant forms of pho-tosynthesis[40,41].

When did oxygenic photosynthesis arise: 3.7 Ga versus 2.3 Ga ago?

The timing of the origin of oxygenic photosynthesis is controversial. Buick[42], based on hydrocarbon biomarkers in sandstone, suggests that oxygenic organisms existed 2.45 Ga (2,450,000 years) ago, and that a transient pulse of oxygen took place 2.5 Ga ago. He also considers it as likely that stromatolites and biomarkers as old as 2.7 Ga indicate oxygenic organisms; however, it is possible that 3.2-Ga-old kerogenic shales indicate the presence at that time of oxygenic photoautotrophs, and that oxygenic photo-synthesis could have evolved as early as 3.7 Ga ago. Hoashi *et al.*[43] have come to a similar conclusion from the study of hematite formation. However, Kirschvink and Kopp[44] suggest a different scenario. They depart from the notion that (1) systems to detoxify molecular oxygen or superoxide anion must precede the origin of oxygenic photo-synthesis, (2) there would be no evolutionary pressure for the evolution of such biochemical systems in the absence of oxygen, and (3) there must have been another source of

sufficient molecular oxygen before the origin of oxygenic photosynthesis. Such a source could have been hydrogen peroxide, and it is likely that catalase, the enzyme decom-posing hydrogen peroxide to water and molecular oxygen, is older than the oxygen evolving enzyme in PSII. In fact, this enzyme could have evolved from the manganese-containing form of catalase (see above). A possible source of hydrogen peroxide could be the glaciers. Hydrogen per-oxide is formed by the action of solar ultraviolet radiation on cloud droplets, brought to the earth's surface with snow, and embedded in the glacier ice. When the ice melts the hydrogen peroxide, and oxygen formed from it, become available to the biosphere.

According to Kirschvink and Kopp[44], oxygenic photo-synthesis could have commenced as late as 2.3 Ga ago, triggering global glaciation (by lowering the amount of the greenhouse gases methane and carbon dioxide).

Phylogeny of eukaryotic photosynthesizers

Eukaryotic organisms carry out photosynthesis in organ-elles called chloroplasts, which we now know for certain are derived from cyanobacteria, which more than 1.2 billion years ago entered into intimate symbiosis with a non-photosynthetic host organism (also see Wise and Hoo-ber[45]). Because of this composite nature of eukaryotes, their phylogeny is somewhat complicated. We must dis-tinguish between the phylogeny of the host organisms (Figure 5) and of the chloroplasts (Figure 6), and start with the former.

According to Burki *et al.*[46], the 'host' of most photo-synthetic organisms is a member of the same 'megagroup', which is a sister group to another 'megagroup' containing animals, fungi and Amoebazoa.

A third, less well-supported 'megagroup' contains, among the investigated organisms, a single photosyn-thetic member, the genus *Euglena*. This latter 'megagroup'
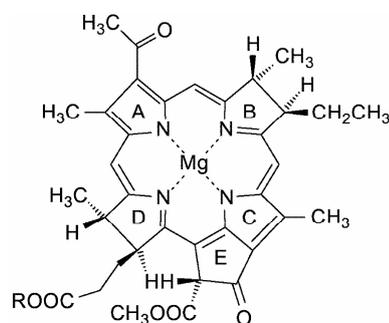

Figure 4. The structure of bacteriochlorophyll *a*. R is a hydrocarbon group. Chlorophyll *a* differs by having two double bonds in the B ring, and a vinyl (–CH=CH$_2$) instead of a formyl (–CO–CH$_3$) side group in ring A.
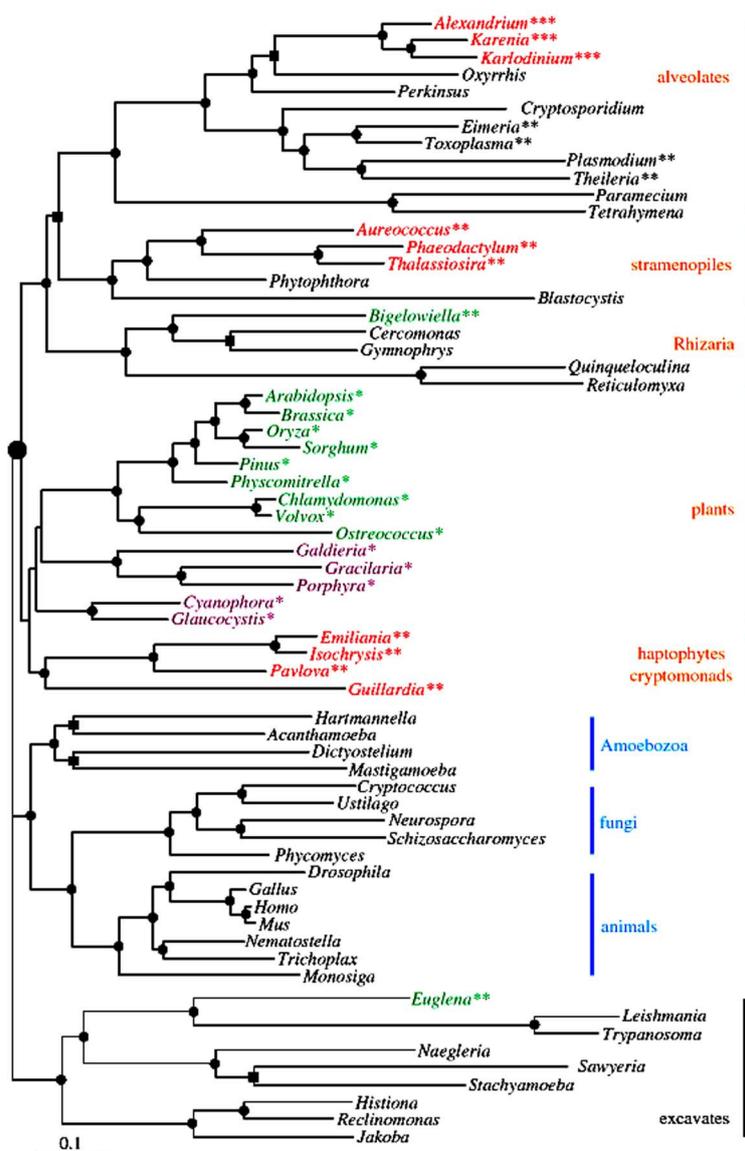
Figure 5. The 'host' phylogenetic tree according to Burki *et al.*[46], slightly simplified. There exists no consensus on what the real relationships are; so this figure represents one opinion. The same DNA sequences can give rise to different trees depending on the statistical method used. The tree is 'unrooted', i.e. does not show the position of the LCA. It shows three main groups, of which the top one is deeply split into two groups. The asterisks show organisms with plastids acquired by primary (*), secondary (**), or tertiary (***) symbiosis. The scale bar represents the estimated number of amino acid substitutions per site.

also contains the genera *Leishmania* and *Trypanosoma*, which are parasitic organisms descended from photosynthetic ancestors.

There are strong indications that the primary endosymbiotic event giving rise to plastids took place very early, before the divergence of the 'green' and 'red' evolutionary lines described below. This does not preclude that many extant organisms harbour symbiotic photosynthesizers, and occasionally they almost appear on the way to become chloroplasts. But there is a big difference bet-

ween an endosymbiotic cyanobacterium and a chloroplast. A chloroplast has lost many genes (mostly transferred to nucleus) that are essential for a free-living organism, and it must have acquired new import mechanisms for proteins as well as export mechanisms for metabolites. The endosymbiont of *Paulinella chromatophora*[47] has been described as a plastid in the making[48].

Whatever we call it, it is different from the plastids of the 'red' and 'green' evolutionary lines[49] described below. One of its characteristics is that it retains the cyanobacte-

rial phycobiliproteins. Another similar case is the endosymbiont of the diatom, *Rhopalodia gibba*[50]. The *Rhopalodia* endosymbiont, contrary to real plastids, has retained the ability to fix molecular nitrogen.

Arguments for assigning the origin of all true plastids to a common endosymbiotic event are reviewed by McFadden and Van Dooren[51], and Nozaki[52]. They include similar import mechanisms into the plastids for nuclear-encoded proteins, and similarity in a chlorophyll-binding protein, which differs from the corresponding one in cyanobacteria.

Phylogeny of plastids

An overview of plastid phylogeny is shown in Figure 6.

Only in three organismal groups, the Chlorophyta (green algae, and plants that have evolved from them), the Rhodophyta (red algae) and Glaucophyta (Glaucocystophyta), the chloroplasts are direct descendents of the cyanobacterium engulfed in the primary endosymbiosis. Among these, the evolutionary path to the Glaucophyta is the first one to branch-off[53]. Stiller and Harrell[54] point out the great uncertainties and show how different methods can result in different patterns of deep eukaryotic phylogeny. Thc Glaucophyta is a small group without great ecological importance, consisting of the genera *Glaucocystis*, *Cyanophora* and *Gloeochaete*.

The Embryophyta (which we usually understand to be plants) have evolved from the Chlorophyta, specifically
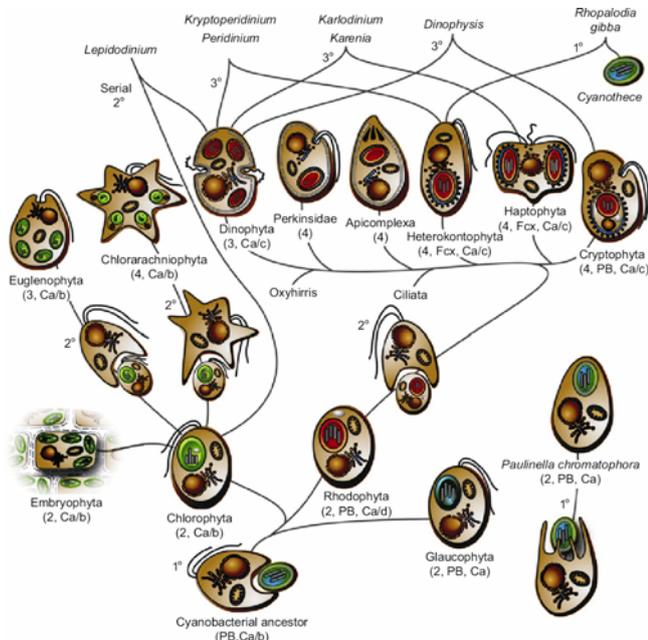

Figure 6. Evolutionary relations of plastids. The main branches diverging from the primary endosymbiotic event are those going to Chlorophyta (the 'green line') and Rhodophyta (the 'red line'), but even before their divergence the Glaucophyta plastids branch-off. For an explanation of other relationships, see text. From Gould *et al.*[59]. Reprinted, with permission, from the *Annual Review of Plant Biology*, vol. 59. © 2008 by Annual Reviews http://www.annualreviews.org/.

from the group within them, the Charophyta. The Chlorophyta have also contributed to Euglenophyta and Chlorarachniophyta, not by straightforward evolution, but by being engulfed into other organisms by a secondary endosymbiotic event.

Similarly, the Rhodophyta have contributed to a range of other algae by secondary endosymbiosis. When there has been a secondary endosymbiosis, the chloroplast is shown to have four membranes surrounding it. An example is a haptophyte, *Emiliania huxleyi*. There are also indications that there has been only one event of endosymbiosis, with later divergence into several evolutionary lines[55].

There are also examples of tertiary endosymbiosis, in which case the plastids obtained by secondary endosymbiosis have been replaced with others. The dinoflagellates (Dinophyta) constitute an organismal group excelling in experimentation with plastids. Normally their chloroplasts are derived from endosymbiotic red algae. In Figure 6, three cases are shown where these chloroplasts have been replaced by respectively, a heterocontophyte, an haptophyte and a cryptophyte. Each one of those latter organisms contains a plastid evolved from an rhodophyte.

We have used the word 'chloroplast' frequently above. However, not all the plastids are chloroplasts. In all higher plants we also have other types of plastids, which lack chlorophyll, at least (in most cases) in the roots. In most higher plants also the colourless, endosymbiotic, red alga plastids retain the ability to develop, under appropriate environmental conditions, into chloroplasts[56], and whole green plants can be regenerated even from roots that have been grown isolated in culture for a long time[57]. In some parasitic seed plants, this ability has been lost, but the plastids are retained. Even if they cannot carry out photosynthesis they have a range of other important functions. There are also a number of non-photosynthetic protists evolved from photosynthetic forms that maintain plastids, which in some cases are so reduced that it took a long time to recognize them, e.g. the malaria parasite[58].

Detailed reviews of the evolution of plastids have been published[59–62]. For the evolution of photosynthetic carbon dioxide assimilation, we refer to Björn and Govindjee[40] and Mueller-Cajar and Badger[63]. Estimated divergence times during evolution[64] are shown in Figure 7.

The continued evolution of free-living cyanobacteria

As shown in Figure 7, plastids arose from cyanobacteria well over one and a half billion years ago; most cyanobacteria remained not only free-living, but also continued to evolve. The most remarkable innovations among the free-living cyanobacteria are mechanisms for the concentration of CO_2. Such mechanisms probably mostly evolved when the availability of CO_2 started to fall and the O_2 concentration started to rise around 400 million years

ago[65]. By this change in ratio between CO_2 and O_2, the ability of CO_2 to compete with O_2, at the surface of rubisco decreased. Carbon dioxide concentrating mechanisms evolved along several paths, and they consist of membrane pumps for both CO_2 and the bicarbonate ions, the key enzyme being carbonic anhydrase. This enzyme catalyses the interconversion between CO_2 and bicarbonate. Many cyanobacteria possess a complex structure, the carboxysome, that is situated in the lumen; it has a protein shell that is permeable to bicarbonate and other ions, but not to carbon dioxide. However, most other cyanobacteria accumulate bicarbonate in the cytosol using pumps in the cell membrane. The cytosol does not contain carbonic anhydrase, so the bicarbonate is maintained as such as it diffuses into the thylakoid lumen. In carboxysome containing cyanobacteria, carbonic anhydrase and rubisco are located inside that shell[66]. When bicarbonate diffuses in, it is converted to CO_2 that cannot escape, and reaches a high concentration at the surface of the rubisco, which therefore can work efficiently despite its low affinity for this substrate.

Since the evolution of carboxysomes started after the origin of plastids, algae and plants do not have this method of concentrating CO_2, but many other concentration mechanisms have evolved on this line[40,67–69]. Some plants have evolved CAM (crassulacean acid metabolism) and C4 metabolism, which allow them to use CO_2 efficiently[40].
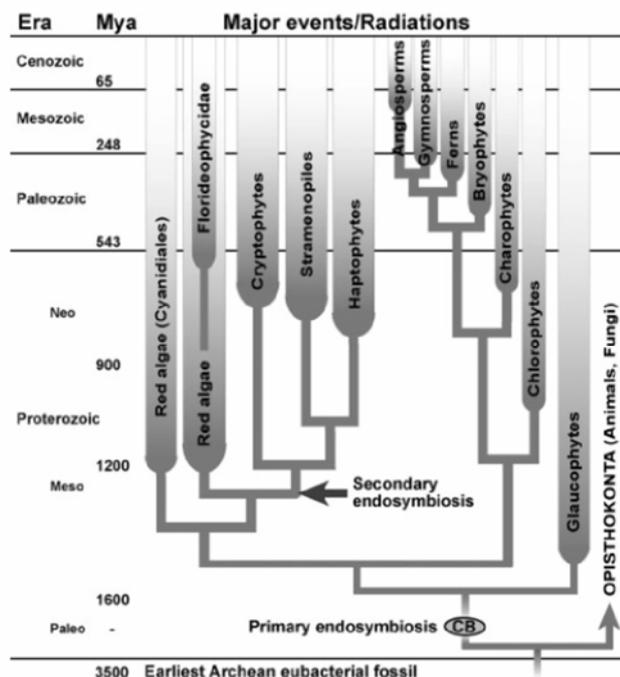

Figure 7. Schematic representation of the evolutionary relationships and divergence times for the red, green, glaucophyte and chromist algae, according to Yoon et al.[64]. The branches on which the cyanobacterial (CB) primary and red algal chromist secondary endosymbioses occurred are shown. Divergence times in the evolution of eukaryotic phototrophs; Mya, million years; CB, Paleo, Paleozoic.

The evolution of photosynthesis in relation to the evolution of the earth

The evolution of photosynthesis has affected the planet as a whole, and not only its atmosphere. For instance, the evolution of a terrestrial biosphere, made possible by photosynthesis, has greatly increased weathering of rocks, and indirectly erosion of the continents.

On the other hand, processes such as plate techtonics have also had an effect on photosynthesis. The increase over the ages in atmospheric oxygen and the decrease in atomspheric carbon dioxide is a result of photosynthesis, but it is a mistake to think that other processes have not been necessary to make this evolution possible. It is not only the gradual increase in the efficiency of photosynthesis by evolution, and the creation of terrestrial flora that has caused the atmospheric change. Continents collide periodically to form supercontinents with a life-time of ca 340 million years[70], which then break up again into smaller continents. When continents collide, mountain ranges result (such as the Himalayas, resulting from a collision between India and the rest of Asia). Mountain formation results in increased erosion, which makes more mineral nutrition available to photosynthetic organisms, and also increased sedimentation and burial of organic carbon, resulting in a net increase in molecular oxygen[71]. Rey and Coltice[72] have calculated that the early earth was 'flat', without mountains. Because of insufficient supporting strength of the mantle, the highest mountains could not have reached a height of 1749 m until 2.7 Ga ago. Thus, even if oxygenic organisms would have existed much earlier, sedimentation would not have been sufficient to bury the organic carbon and prevent its reoxidation. In other words, lack of oxygen in the atmosphere at earlier epochs is no proof that oxygenic photosynthesis did not take place.

Glaciations offer another case of interaction between geological processes and photosynthesis. Increase in photosynthesis removes the greenhouse gas carbon dioxide from the atmosphere, and may favour the initiation of glaciation. The immediate effect of the initiation of a glaciation is decreased photosynthesis, but in the longer perspective glaciation increases erosion and nutrient supply. And these processes interact with the supercontinent cycles just described.

Conclusion

The origin of photosynthesis is almost as ancient as life itself. A turning point for the biosphere was the Great Oxidation Event, around 2.3 billion years ago, caused by the appearance of oxygen evolving photosynthesis at least several hundred million years earlier. Another important step was the evolution of eukaryotic organisms containing chloroplasts, which were derived from endosymbiotically

acquired cyanobacteria. The relation between photosynthesis and the rest of the planet and the biosphere has been two-sided. The evolution of photosynthesis could not have taken the course it did without the special circumstances on our planet, with plate tectonics and gradually growing continents, and the atmosphere and the surface of earth have been drastically affected by photosynthesis. Thus the chance of finding spectroscopic signature of oxygenic photosynthesis on an exoplanet is very small[73].

1. Woese, C. R., Kandler, O. and Wheelis, M. L., Towards a natural system of organisms – Proposal for the domains Archaea, Bacteria and Eucarya. *Proc. Natl. Acad. Sci. USA*, 1990, **87**, 4576–4579.
2. Larkum, A. W. D., Douglas, S. and Raven, J. A. (eds), *Photosynthesis in Algae. Advances in Photosynthesis and Respiration*, Springer, Dordrecht, 2004, vol. 14.
3. Wydrzynski, T. J. and Satoh, K. (eds), *Photosystem II: The Light-induced Water: Plastoquinone Oxidoreductase. Advances in Photosynthesis and Respiration*, Springer, Dordrecht, 2005, vol. 22.
4. Barber, J., Photosynthetic generation of oxygen. *Philos. Trans. R. Soc. London, Ser. B*, 2008, **363**, 2665–2674.
5. Bryant, D. R. (ed.), *The Molecular Biology of Cyanobacteria. Advances in Photosynthesis and Respiration*, Springer, Dordrecht, 1994, vol. 1.
6. Blankenship, R. E., Madigan, M. T. and Bauer, C. E. (eds), *Anoxygenic Photosynthetic Bacteria. Advances in Photosynthesis and Respiration*, Springer, Dordrecht, 1995, vol. 2.
7. Hunter, C. N., Daldal, F., Thurnauer, M. C. and Beatty, J. T. (eds), *The Purple Phototrophic Bacteria. Advances in Photosynthesis and Respiration*, Springer, Dordrecht, 2009, vol. 28.
8. Chen, M. and Zhang, Y. Tracking the molecular evolution of photosynthesis through characterization of atomic contents of the photosynthetic units. *Photosynth. Res.*, 2008, **97**, 255–261.
9. Olson, J. M. and Blankenship, R. E., Thinking about the evolution of photosynthesis. *Photosynth. Res.*, 2004, **80**, 373–386.
10. Allen, J. F. and Martin, W., Out of thin air. *Nature*, 2007, **445**, 610–612.
11. Kunin, V., Goldovsky, L., Darzentas, N. and Ouzounis, C. A., The net of life: reconstructing the microbial phylogenetic network. *Genome Res.*, 2005, **15**, 954–959.
12. Konstantinidis, K. T., Prokaryotic taxonomy and phylogeny in the genomic era: advancements and challenges ahead. *Curr. Opin. Microbiol.*, 2007, **10**, 504–509.
13. Mann, N. H., Cook, A., Millard, A., Bailey, S. and Clokie, M., Bacterial photosynthesis genes in a virus. *Nature*, 2003, **424**, 741.
14. Lindell, D. *et al.*, Genome-wide expression dynamics of a marine virus and host reveal features of co-evolution. *Nature*, 2007, **449**, 83–86.
15. Sharon, I. *et al.*, Viral photosynthetic reaction center genes and transcripts in the marine environment. *ISME J.*, 2007, **1**, 492–501.
16. Nagashima, K. V. P., Hiraishi, A., Shimada, K. and Matsuura, K., Horizontal transfer of genes coding for the photosynthetic reaction centers of purple bacteria. *J. Mol. Evol.*, 1997, **45**, 131–136.
17. Bryant, D. A. and Frigaard, N.-U., Prokaryotic photosynthesis and phototrophy illuminated. *Trends Microbiol.*, 2006, **14**, 488–496.
18. McInerney, J. O., Cotton, J. A. and Pisani, D., The prokaryotic tree of life: past, present. . . and future? *Trends Ecol. Evol.*, 2008, **23**, 276–281.
19. Golbeck, J. H. (ed.), *Photosystem I: The Light-induced Plastocyanin: Ferredoxin Oxidoreductase. Advances in Photosynthesis and Respiration*, Springer, Dordrecht, 2006, vol. 24.
20. Puthiyaveetil, S. *et al.*, The ancestral symbiont sensor kinase CSK links photosynthesis with gene expression in chloroplasts. *Proc. Natl. Acad. Sci. USA*, 2008, **105**, 10061–10066.
21. Ishikita, H., Saenger, W., Biesiadka, J., Loll, B. and Knapp, E.-W., How photosynthetic reaction centers control oxidation power in chlorophyll pairs P680, P700, and P870. *Proc. Natl. Acad. Sci. USA*, 2006, **103**, 9855–9860.
22. Sugiura, M., Boussac, A., Noguchi, T. and Rappaport, F., Influence of histidine-198 of the D1 subunit on the properties of the primary electron donor, P680, of photosystem II in *Thermosynechococcus elongatus*. *Biochim. Biophys. Acta*, 2008, **1777**, 331–342.
23. Björn, L. O., Papageorgiou, G. C., Blankenship, R. E. and Govindjee, A viewpoint: Why chlorophyll *a*? *Photosynth. Res.*, 2009, **99**, 85–98.
24. Grimm, B. *et al.* (eds), *Chlorophylls and Bacteriochlorophylls: Biochemistry, Biophysics, Functions and Applications. Advances in Photosynthesis and Respiration*, Springer, Dordrecht, 2006, vol. 25.
25. Mimuro, M., Tomo, T. and Tsuchiya, T., Two unique cyanobacteria lead to a traceable approach of the first appearance of oxygenic photosynthesis. *Photosynth. Res.*, 2008, **97**, 167–176.
26. Shi, T. and Falkowski, P. G., Genome evolution in cyanobacteria: The stable core and the variable shell. *Proc. Natl. Acad. Sci. USA*, 2008, **105**, 2511–2515.
27. Nelissen, B., Van de Peer, Y., Wilmotte, A. and De Wachter, R., An early origin of plastids within the cyanobacterial divergence is suggested by evolutionary trees based on complete 16S rRNA sequences. *Mol. Biol. Evol.*, 1995, **12**, 1166–1173.
28. Deusch, O. *et al.*, Genes of cyanobacterial origin in plant nuclear genomes point to a heterocyst-forming plastid ancestor. *Mol. Biol. Evol.*, 2008, **25**, 748–761.
29. Gross, J., Meurer, J. and Bhattacharya, D., Evidence of a chimeric genome in the cyanobacterial ancestor of plastids. *BMC Evol. Biol.*, 2008, **8**, 117.
30. Fujita, Y., Takahashi, Y., Chuganji, M. and Matsubara, H., The NIFH-like (FRXC) gene is involved in the biosynthesis of chlorophyll in the filamentous cyanobacterium *Plectonema boryanum*. *Plant Cell Physiol.*, 1992, **33**, 81–92.
31. Fujita, Y. and Bauer, C. E., Reconstitution of light-independent protochlorophyllide reductase from purified Bch1 and BchN-BchB subunits – *in vitro* confirmation of nitrogenase-like features of a bacteriochlorophyll biosynthesis enzyme. *J. Biol. Chem.*, 200, **275**, 23583–23588.
32. Nomata, J., Nitrogenase Fe protein-like Fe-S cluster is conserved in L-protein (BchL) of dark-operative protochlorophyllide reductase from *Rhodobacter capsulatus*. *FEBS Lett.*, 2006, **580**, 6151.
33. Bröcker, M. J. *et al.*, ATP-driven reduction by dark-operative protochlorophyllide oxidoreductase from *Chlorobium tepidum* mechanistically resembles nitrogenase catalysis. *J. Biol. Chem.*, 2008, **275**, 23583–23588.
34. Nomata, J., Mizoguchi, T., Tamiaki, H. and Fujita, Y., A second nitrogenase-like enzyme for bacteriochlorophyll biosynthesis – Reconstitution of chlorophyllide *a* reductase with purified X-protein (BchX) and YZ-protein (BchY-BchZ) from *Rhodobacter capsulatus*. *J. Biol. Chem.*, 2006, **281**, 15021–15028.
35. Yang, J. and Cheng, Q., Origin and evolution of the light-dependent protochlorophyllide oxidoreductase (LPOR) genes. Sequences of LPOR. *Plant Biol.*, 2004, **6**, 537–544.
36. Nobles Jr. R. and Brown Jr. R. M., The pivotal role of cyanobacteria in the evolution of cellulose synthases and cellulose synthase-like proteins. *Cellulose*, 2004, **11**, 437–448.
37. Deschamps, P. *et al.*, Metabolic symbiosis and the birth of the plant kingdom. *Mol. Biol. Evol.*, 2008, **25**, 536–548.
38. Eisenhut, M., Ruth, W., Haimovich, M., Bauwe, H., Kaplan, A. and Hagemann, M., The photorespiratory glycolate metabolism is essential for cyanobacteria and might have been conveyed endosymbiontically to plants. *Proc. Natl. Acad. Sci. USA*, 2008, **105**, 17199–17204.

39. Raymond, J. and Blankenship, R. E., The origin of the oxygen-evolving complex. *Coord. Chem. Rev.*, 2008, **252**, 377–383.

40. Björn, L. O. and Govindjee, The evolution of photosynthesis and its environmental impact. In *Photobiology: The Science of Life and Light* (ed. Björn, L. O.), 2008, pp. 243–274.

41. Tabita, F. R., Hanson, T. E., Satagopan, S., Witte, B. H. and Kreel, N. E., Phylogenetic and evolutionary relationships of RubisCO and the RubisCO-like proteins and the functional lessons provided by diverse molecular forms. *Philos. Trans. R. Soc. London, Ser. B*, 2008, **363**, 2629–2640.

42. Buick, R., When did oxygenic photosynthesis evolve? *Philos. Trans. R. Soc. London, Ser. B*, 2008, **363**, 2731–2743.

43. Hoashi, H. *et al.*, Primary hematite formation in an oxygenated sea 3.46 billion years ago. *Nature Geosci.*, 2009, **2**, 301–306.

44. Kirschvink, K. L. and Kopp, R. E., Palaeoproterozoic ice houses and the evolution of oxygen-mediating enzymes: the case for a late origin of photosystem II. *Philos. Trans. R. Soc. London, Ser. B*, 2008, **363**, 2755–2765.

45. Wise, R. R. and Hoober, J. K. (eds), *The Structure and Function of Plastids. Advances in Photosynthesis and Respiration*, Springer, Dordrecht, 2006, vol. 23.

46. Burki, F., Shalchian-Tabrizi, K. and Pawlowski, J., Phylogenomics reveals a new 'megagroup' including most photosynthetic eukaryotes. *Biol. Lett.*, 2008, **4**, 366–369.

47. Lauterborn, R., Protozoenstudien II. *Paulinella chromatophora* nov. gen., nov. spec., ein beschalter Rhizopode des Süsswassers mit blaugrünen chromatophorenartigen Einschlussen. *Z. Wiss. Zool.*, 1895, **59**, 537–544.

48. Marin, B., Nowack, E. C. M. and Melkonian, M., A plastid in the making: evidence for a second primary endosybiosis. *Protist*, 2005, **156**, 425–432.

49. Yoon, H. S., Reyes-Prieto, A., Melkonian, M. and Bhattacharya, D., Minimal plastid genome evolution in the *Paulinella* endosymbiont. *Curr. Biol.*, 2006, **16**, R670–R672.

50. Kneip, C., Voß, C., Lockhart, P. J. and Maier, U. G., The cyanobacterial endosymbiont of the unicellular algae: *Rhopalodia gibba* shows reductive genome evolution. *BMC Evol. Biol.*, 2008, **8**, 30.

51. McFadden, G. I. and van Dooren, G. G., Evolution: Red algal genome affirms a common origin of all plastids. *Curr. Biol.*, 2004, **14**, R514–R516.

52. Nozaki, H., A new scenario of plastid evolution: plastid primary endosymbiosis before the divergence of the 'Plantae', emended. *J. Plant Res.*, 2005, **118**, 247–255.

53. Reyes-Prieto, A. and Bhattacharya, D., Phylogeny of nuclear-encoded plastid-targeted proteins supports an early divergence of glaucophytes within plantae. *Mol. Biol. Evol.*, 2007, **24**, 2358–2361.

54. Stiller, J. W. and Harrell, L., The largest subunit of RNA polymerase II from the Glaucocystophyta: functional constraint and short-branch exclusion in deep eukaryotic phylogeny. *BMC Evol. Biol.*, 2005, **5**, article #71.

55. Petersen, J., Teich, R., Brinkmann, H. and Cerff, R., A green phosphoribulokinase in complex algae with red plastids: Evidence for a single secondary endosymbiosis leading to haptophytes, cryptophytes, heterokonts, and dinoflagellates. *J. Mol. Evol.*, 2006, **62**, 143–157.

56. Björn, L. O., Chlorophyll formation in excised wheat roots. *Physiol. Plant.*, 1965, **18**, 1130–1142.

57. Bhat, S. R., Chitralekha, P. and Chandel, K. P. S., Regeneration of plants from long-term root culture of lime *Citrus aurantifolia* (Swing). *Plant Cell Tissue Organ Cult.*, 1992, **29**, 19–25.

58. Williams, B. A. P. and Keeling, P. J., Cryptic organelles in parasitic protists and fungi. *Adv. Parasitol.*, 2003, **54**, 9–68.

59. Gould, S. B., Waller, R. F. and McFadden, G. I., Plastid evolution. *Annu. Rev. Plant Biol.*, 2008, **59**, 491–517.

60. Ravi, V., Khurana, J. P., Tyagi, A. K. and Khurana, P., An update on chloroplast genomes. *Plant Syst. Evol.*, 2008, **271**, 101–122.

61. Howe, C. J., Barbrook, A. C., Nisbet, R. E. R., Lockhart, P. J. and Larkum, A. W. D., The origin of plastids. *Philos. Trans. R. Soc. London, Ser. B*, 2008, **363**, 2675–2685.

62. Parker, M. S., Mock, T. and Armbrust, E. V., Genomic insights into marine microalgae. *Annu. Rev. Genet.,* 2008, **42**, 619–645.

63. Mueller-Cajar, O. and Badger, M. R., New roads lead to rubisco in Archaebacteria. *BioEssays*, 2007, **29**, 722–724.

64. Yoon, H. S., Hackett, J. D., Ciniglia, C., Pinto, G. and Bhattacharya, D., A molecular timeline for the origin of photosynthetic eukaryotes. *Mol. Biol. Evol.*, 2004, **21**, 809–818.

65. Badger, M. R. and Price, G. D., CO_2 concentrating mechanisms in cyanobacteria: molecular components, their diversity and evolution. *J. Exp. Bot.*, 2003, **54**, 609–622.

66. Cot, S. S.-W., So, A. K.-C. and Espie, G., A multiprotein bicarbonate dehydration complex essential to carboxysome function in cyanobacteria. *J. Bacteriol.*, 2008, **190**, 936–945.

67. Giordano, M., Beardall, J. and Raven, J. A., CO_2 concentrating mechanisms in algae: mechanisms, environmental modulators, and evolution. *Annu. Rev. Plant Biol.*, 2005, **56**, 99–131.

68. Lapointe, M., McKenzie, T. D. B. and Morse, D., An external δ-carbonic anhydrase in a free-living marine dinoflagellate may circumvent diffusion-limited carbon acquisition. *Plant Physiol.*, 2008, **147**, 1427–1436.

69. Spalding, M. H., Microalgal carbon-dioxide-concentrating mechanisms: *Chlamydomonas* inorganic carbon transporters. *J. Exp. Bot.*, 2008, **59**, 1463–1473.

70. Bobrov, A. M. and Trubitsyn, A. P., Numerical model of the supercontinental cycle stages: Integral transfer of the oceanic crust material and mantle viscous shear stresses. *Stud. Geophys. Geodyn.*, 2008, **52**, 87–100.

71. Campbell, I. H. and Allen, C. M., Formation of supercontinents linked to increases in atmospheric oxygen. *Nature Geosci.*, 2008, **1**, 554–558.

72. Rey, P. F. and Coltice, N., Neoarchean lithospheric strengthening and the coupling of Earth's geochemical reservoirs. *Geology*, 2008, **36**, 635–638.

73. Björn, L. O., Papageorgiou, G. C., Dravins, D. and Govindjee, Detectability of life and photosynthesis on exoplanets. *Curr. Sci.*, 2009, **96**, 1171–1175.