

Introduction. Photosynthetic and atmospheric evolution

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Phil. Trans. R. Soc. B 2008 **363**, 2625-2628

doi: 10.1098/rstb.2008.0058

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Introduction. Photosynthetic and atmospheric evolution

1. INTRODUCTION

The evolution of photosynthesis remade the Archaean Earth. Before photosynthesis, the air and oceans were anoxic. Now the air is a biological construction, a fifth of which is free molecular oxygen, and the ocean can sustain animal life even in the depths. The evolution, first of anoxygenic and then of oxygenic photosynthesis, sharply increased the productivity of the biosphere. Oxygenic photosynthesis sustains free oxygen in the atmosphere. In the oceans, the beneficiaries of the first photosynthetic prokaryotes today range from cyanobacterial and algal plankton to large kelp. Wearing plants as landsuits, from tiny mosses to giant redwoods, cyanobacteria as chloroplasts have occupied the land. The oxygen emitted has allowed the evolution of animal life, to browse the plants and, in turn, to respire the CO₂ that sustains photosynthesis.

The management of the carbon cycle, by photosynthesis coupled with respiration, had profound consequences for the greenhouse setting of the surface temperature. Photosynthetic productivity controls the budgets of atmospheric carbon dioxide and, eventually, methane too. This sets global temperatures, weather patterns and may have even been a cause of the great glacial events, where much of the Earth's surface froze over.

The year 2007 marked the 70th anniversary of the demonstration in Cambridge by Hill that chloroplasts catalysed the photolysis of water into oxygen and reducing power, and that this reducing power was used to fix carbon dioxide (Hill 1937). The year 2007 was also the 60th anniversary of the discovery by Wildman of fraction I protein (Wildman & Bonner 1947) and the 47th anniversary of the proposal by Hill & Bendall (1960) that oxygenic photosynthesis depends on two discrete photosystems arranged in series. Fraction I protein was later identified as carboxydismutase or ribulose diphosphate carboxylase and, after its ability to oxygenate its substrate was recognized (Bowes *et al.* 1971), it eventually became known as ribulose biphosphate carboxylase/oxygenase or Rubisco (originally a joke attributed to David Eisenberg; see Benson 2002; Wildman 2002). The ubiquitous Rubisco is perhaps the most abundant enzyme on Earth today.

To celebrate these anniversaries, the Royal Society held a discussion meeting on 12 and 13 November 2007. The purpose was to provoke cross-disciplinary discussion about the importance of the evolution of photosynthesis in Earth's history. Biologists, geologists and atmospheric chemists were invited. There was much controversy and

speakers were chosen to air, rather than gloss, the disputes. Geologists disagree about the oxidation history of the air and in the dating of the evolution of photosynthesis. Many (e.g. Buick 2008; Nisbet & Nisbet 2008) consider that oxygenic photosynthesis began in the Late Archaean *ca* 2.9–2.7 Ga ago (1 Ga is 10⁹ years). However, some (e.g. Kirschvink & Kopp 2008) feel that oxygenesis came later, while others date the rise of oxygen as very early, perhaps 3.8 Ga ago or even earlier. Biologists similarly puzzle over the evolutionary history of the Rubisco proteins. As yet, there has been little exploration of the complex linkages between carbon capture, methanogenesis, photosynthesis, respiration and the atmospheric greenhouse.

The papers presented in this volume have been written by the 14 speakers at the meeting, and the authors have been asked to include the major discussion points that were raised following their talks in their manuscripts. The papers are arranged in the same order as the talks.

2. BIOCHEMICAL PROCESSES IN PHOTOSYNTHESIS

The key enzyme in photosynthesis is Rubisco, ribulose biphosphate carboxylase/oxygenase. There are four forms of this enzyme: form I found in all plants, most algae, cyanobacteria and some proteobacteria; form II found in other proteobacteria and dinoflagellate algae; form III in archaea; and form IV in some proteobacteria and archaea. Form IV Rubisco does not catalyse the classical photosynthesis reaction and is thus termed 'Rubisco-like protein'. It may be involved in methionine salvage pathways. Tabita *et al.* (2008) discuss the evolution of the various Rubisco proteins, concluding that the first Rubisco may well have evolved in a methanogen-like ancestor, acquiring new functions as it spread through lateral gene transfer.

For the Rubisco enzyme to fix carbon, it must have access to carbon dioxide. When oxygenic photosynthesis first evolved, presumably in small prokaryotes, simple diffusion into the cell provided a sufficient supply of carbon dioxide. However, in a more productive biosphere with less carbon dioxide in the air, and as organisms became larger, simple diffusion was not able to supply sufficient carbon dioxide to the Rubisco proteins. Raven *et al.* (2008) discuss the inorganic carbon-concentrating mechanisms (CCMs) that catalyse the accumulation of CO₂ around Rubisco in all cyanobacteria, most algae and aquatic plants and in vascular plants with C₄ photosynthesis or Crassulacean acid metabolism. The earliest CCMs may have evolved in oxygenic cyanobacteria in stromatolites before the atmosphere became oxygenated.

One contribution of 15 to a Discussion Meeting Issue 'Photosynthetic and atmospheric evolution'.

In what setting did early photosynthesis evolve? Sleep & Bird (2008) show that pre-photosynthetic niches were very meagre in productivity, far less than with modern photosynthesis. Serpentinization, arc volcanism and ridge-axis volcanism reliably provided H₂, while early methanogens and acetogens reacted CO₂ with H₂ to obtain energy and make organic matter. A bacterium in such a setting may have been pre-adapted for anoxygenic photosynthesis, perhaps starting with H₂ in lieu of an oxygen 'acceptor'. After cyanobacterial oxygenic photosynthesis evolved, it appears to have been several million years before an oxygen-rich atmosphere developed. Eventually, anoxygenic and oxygenic photosynthesis oxidized much of the Earth's crust and supplied sulphate to the ocean.

Once Rubisco has captured the carbon dioxide, an electron donor is obtained by splitting water, releasing oxygen into the atmosphere. Light-driven oxidation of water occurs at a catalytic centre contained within a multi-subunit enzyme known as photosystem II located in the photosynthetic membranes of plants, algae and cyanobacteria. Its oxygen-evolving centre (OEC) consists of four manganese ions and a calcium ion surrounded by a highly conserved protein environment. Barber (2008) shows how X-ray crystallography of photosystem II from the cyanobacterium *Thermosynechococcus elongatus* has revealed the structure to a resolution sufficient to determine the positions of almost all the amino acid residues and to show that the most probable structure of the OEC itself is a Mn₃CaO₄ cubane with the fourth Mn outside the cubane cluster. This, together with a wide range of information from biophysical and biochemical techniques, has made it possible to come very close to revealing the precise chemical mechanism of the crucial water-splitting reaction of oxygenic photosynthesis. The close evolutionary relationship between the protein structure, and most of the cofactors, of photosystem II and all other photosystems of both oxygenic and anoxygenic organisms is apparent. But where did this unique 4Mn/1Ca complex come from? Its evolutionary origins, both inorganic and biological, remain an unsolved puzzle. Some of the associated proteins, such as PsbO, are also unique and seem to be restricted to the oxygenic photosystem. These proteins have clearly evolved for a sole purpose and have a unique beta-barrelled structure.

3. ORIGINS AND EVOLUTION OF OXYGEN-FIXING ORGANISMS

The biogeochemical cycles of H, C, N, O and S are discussed by Falkowski & Godfrey (2008). The metabolic processes responsible for maintaining these cycles evolved in Archaean prokaryotes. The evolution of oxygenic photosynthesis in cyanobacteria did not immediately lead to large-scale accumulation of the gas in the atmosphere but, rather, was coupled to the carbon cycle through the burial efficiency of organic matter in the lithosphere. This also fundamentally altered the nitrogen cycle, allowing ammonium to be oxidized to nitrate and subsequently denitrified. As Paul Falkowski elegantly put it in the meeting, 'eukaryotes are organized

E. coli'. Once sufficient oxygen accumulated in the Earth's atmosphere to allow nitrification to out-compete denitrification, a new, stable electron 'market' emerged. This ultimately spread via lateral gene transfer to eukaryotic host cells, allowing the evolution of complex life forms. Eukaryotic cells are far more complex than prokaryotic cells and contain several times as many genes. However, what the first eukaryote looked like is currently under debate.

Perhaps the key defining feature at the start of the eukaryotes was the acquisition of a mitochondrion. Mitochondria are enslaved α -proteobacteria and use respiration to break down complex carbohydrates for an energy source in non-photosynthetic cells. Mitochondria require oxygen to operate, so it could not have occurred before the rise of oxygen driven by photosynthesis. This means that eukaryotes could not have occurred until photosynthetic life was well established and had left an indelible mark on the Earth's atmosphere. Today, all eukaryotes contain mitochondria, though some of these were only recently identified as they occur in anaerobic micro-organisms, and lack defining mitochondrial genes. These hydrogenosomes release hydrogen as a by-product. Mentel & Martin (2008) propose that the ancestral mitochondrion was a facultatively anaerobic microbe that was multi-talented, in that it had all the defining genes for hydrogenosomes, such as pyruvate-ferredoxin oxidoreductase and hydrogenase, as well as the conventional mitochondria-related genes. Developments in biology and geology underscore the evolutionary significance of oxygen-independent ATP-generating pathways in mitochondria, including those of various metazoan groups, as a watermark of the environments within which eukaryotes arose and diversified into their major lineages.

Presumably one ancestral eukaryote lineage engulfed and enslaved a cyanobacterium. This cyanobacterium gave rise to the chloroplast, in an event known as primary endosymbiosis. The cyanobacterium lost the ability for independent life and became the site of photosynthesis in all eukaryotic cells. Later, other non-photosynthetic eukaryotes engulfed this now-photosynthetic cell, spreading photosynthesis skills through many of the eukaryotic lineages. Howe *et al.* (2008) present arguments suggesting that the common view of a single acquisition event is perhaps simplistic. This is due to the lack of information in protein sequences and the many millions of years since the events. The argument follows that it is not possible to exclude the possibility of multiple primary endosymbiosis events with many photosynthetic bacteria donating genes to the eukaryote, such as in the shopping bag model of chloroplast evolution.

Behrenfeld *et al.* (2008) focus on phytoplankton populations of the contemporary ocean. These use varied energetic pathways to optimize problems of resource supply and demand. A reductant formed through photosynthesis has three primary fates: carbon fixation; direct utilization; and ATP generation. The global implications of optimization are illustrated in the 10-year global satellite chlorophyll record, which can be deconvolved into contributions from biomass and physiology, providing a perspective

on the dynamic nature of surface phytoplankton populations and their link to climate.

4. THE GEOCHEMISTRY OF PHOTOSYNTHESIS

Buick (2008) points out that the atmosphere has apparently been continuously oxygenated since the 'Great Oxidation Event' *ca* 2.4 Ga ago, but when photosynthetic oxygen production began is debatable. The geological and geochemical evidence from older sedimentary rocks indicates that oxygenic photosynthesis evolved much earlier. As early as *ca* 2.7 Ga ago, stromatolites and biomarkers from evaporative lake sediments suggest that oxygen-producing cyanobacteria had already evolved. The 2.7 Ga old Tumbiana Formation, laid down in lakes on a basalt flood plain, includes stromatolites with phototropic filaments. This is some of the oldest firm evidence for oxygenic photosynthesis. The evidence indicates that oxidative photosynthesis was occurring in Australia nearly 3 Ga ago. Even at *ca* 3.2 Ga ago, kerogenous shales imply the presence of photoautotrophic marine plankton, and U–Pb data from metasediments of *ca* 3.8 Ga ago suggest that this metabolism could have arisen by the start of the geological record. The hypothesis that oxygenic photosynthesis evolved well before the atmosphere became permanently oxygenated seems well supported.

Nisbet & Nisbet (2008) point out that since 3.5 Ga ago or earlier, the atmosphere has become a biological construction, regulating the planetary climate. Anoxygenic photosynthesis by organisms using Rubiscos IV and II may date back to 3.5 Ga ago or earlier. Oxygenic photosynthesis (Rubisco I) may have begun *ca* 2.9 Ga ago. Rubisco I's specificity, which today may be almost perfectly tuned by evolution, controls the balance of carbon gases and O₂ in the ocean and hence, by equilibration, in the air. In turn, this forces the global greenhouse warming, which maintains liquid oceans and sustains microbial ecology, while nitrifying and denitrifying bacteria, supplemented by anammox planctomycetes, manage the atmospheric nitrogen reservoir and hence air pressure.

Kirschvink & Kopp (2008) suggest that the accumulation in the ice of photochemically produced H₂O₂ could produce O₂ in an environment shielded from the lethal levels of ultraviolet radiation. This could provide a source of oxygen pre-dating the biological oxygen production and capable of driving the evolution of oxygen tolerance. In considering the origin of oxygenic photosynthesis, this work gave an alternative to the views of Nisbet & Nisbet (2008) and Buick (2008), pointing out that 2-methylhopanes, once thought to be unique biomarkers for cyanobacteria, are also produced anaerobically in significant quantities by anoxygenic phototrophs. With this reinterpretation of the biomarker evidence, Kirschvink & Kopp (2008) infer a late origin of photosynthesis, suggesting that oxygenic photosynthesis could have evolved close in geological time to the Makganyene glaciation and there may be a causal link between the two. If so, the evolution of oxygenic photosynthesis could be much later than generally thought.

5. RECENT AND FUTURE PHOTOSYNTHESIS

In the past few hundred million years, the land masses have hosted the plant kingdom. Plants are now ubiquitous on land. However, with the growth of individual plants, acquiring enough carbon dioxide became a problem. A comparison between the photosynthetic physiological ecology and carbon isotope discrimination characteristics for modern-day bryophytes and algae was considered by Griffiths (Meyer *et al.* 2008). This was done by assessing bryophyte distribution and diversification compared with that of more complex land plant groups and by measuring instantaneous carbon isotope discrimination, CO₂ assimilation and electron transport rates. One way that algae evolved to cope with the problem of falling CO₂ was by the evolution of a pyrenoid, an extension of the chloroplast that is made up of over 95% Rubisco protein. Hornworts also contain a pyrenoid, allowing speculation on the origin and function of pyrenoids in land plants.

The workings of the modern climate system are considered by Woodward *et al.* (2008). The El Niño–Southern Oscillation (ENSO) globally exerts an extensive influence on crops and natural vegetation. The resultant changes in gross primary productivity often lead to significant changes in ecosystem structure and dynamics. The cool phase of the Pacific Decadal Oscillation (PDO) acts additively with cool ENSO phases to exacerbate drought in the earlier period for the southwest USA. By contrast, in India, the cool phase of the PDO appears to reduce the negative impacts of warm ENSO events on crop production.

Photosynthesis sustains a large planetary biomass on Earth. Specifically, oxygenic photosynthesis has created an oxygen-rich atmosphere and allowed the evolution of large metabolically demanding creatures. Given that photosynthesis appeared on our planet, the possibility is that it could happen elsewhere (Rothschild 2008). Life is based on carbon, and carbon is found throughout the Universe. Rothschild observed, 'life is lazy'. Clearly, it is possible to get inorganic carbon into cells in a usable format. Present knowledge about planetary systems and extraterrestrial chemistry suggest that if organic carbon-based life occurs elsewhere, photosynthesis—although perhaps not oxygenic photosynthesis—would also have evolved. Photosynthetic protists eat bacteria and stop photosynthesizing if bacteria are available. Thus, life on faraway planets might just look very much like life here at home.

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