Hypothesis

A redox switch hypothesis for the origin of two light reactions in photosynthesis

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Abstract **Photosynthesis provides energy in the Earth's biosphere and oxygen in its atmosphere. For oxygen to be produced, two different light reactions must operate simultaneously and in series. Known anaerobic, photosynthetic bacteria contain one or other of these photosystems, but never both. Here, I propose that the two photosystems diverged, in structure and function, from a common ancestor, within a single, continuous, anaerobic lineage. In such cells, living examples of which are predicted, the two photosystems are isoenzymes encoded by orthologous genes under co-ordinated, redox regulatory control. A redox switch responds to defined environmental conditions and selects which set of genes is expressed. In these cells, the two photosystems are thus synthesised at different times. It is further proposed that the origin of oxygen-evolving photosynthesis was a simple mutation that disabled the redox switch, permitting simultaneous expression of the two sets of genes. The two, newly co-existing photosystems became connected by shared electron carriers, allowing generation of electrochemical potential high enough to oxidise water; an inexhaustible supply of reductant; and the selective advantages and pressures of an aerobic world.**

Keywords: Oxygen; Reaction centre; Photosystem; Redox control; Gene expression; Evolution

1. Introduction: light reactions use reaction centres of two types

Photosynthetic oxygen evolution is coupled to energy-conserving reactions such as ATP synthesis and CO_2 assimilation by means of membrane-intrinsic, vectorial electron and proton transfer. These reactions generate a soluble, chemical reductant [1], and a proton-motive force [2]. Oxygen evolution occurs in illuminated plant and algal chloroplasts and in cyanobacteria, where two types of light reaction cooperate: photosystem I produces soluble reductant, and photosystem II passes electrons on to photosystem I by removing electrons and protons from water, thus liberating oxygen [3]. In contrast, anaerobic, photosynthetic bacteria contain only one of two types of light reaction driving electron transport, and water cannot be oxidised [4].

All primary electron transfers in photosynthesis occur in photochemical reaction centres of one of two types, termed I and II [5] (Fig. 1). Type I reaction centres are found in chloroplast photosystem I, and in green bacteria such as *Chlorobium* species and heliobacteria. Type I centres have iron–sulfur electron acceptors, and contain a large membrane-extrinsic domain to carry electrons out into the soluble phase, to ferredoxin and $NADP^+$ [5–8]. Type II reaction centres are found in water-oxidising chloroplast photosystem II and in the purple photosynthetic proteobacteria. Type II centres have quinone electron acceptors, and, in bacteria, usually participate in a cyclic electron transport pathway [6,9]. Type II centres usually pass electrons to a proton-motive cytochrome b–c_1 complex. The electrons either move back the type II reaction centre, giving the bacterial, cyclic pathway, or move on to the type I reaction centre of chloroplast photosystem I.

Despite differences in detail and overall pathways of electron transfer, it is now clear from functional [10] and structural [11] studies that type I and type II photosynthetic reaction centres are homologous, that is, that they are derived from a common ancestral form. It follows that chloroplast photosystem I and photosystem II, now mutually interdependent, originated by evolutionary divergence, and so their independent actions must have been subject to natural selection. It is commonly assumed that this selection occurred when each type of reaction centre was the only one present in an evolutionary lineage [12,13] (see, however [5]). In this letter, I propose that the two reaction centres indeed diverged as a result of selection acting upon them individually, but that this occurred in a single, continuous, evolutionary line of cells: these cells were able to induce either form of reaction centre, but not both, according to environmental conditions.

2. Problem: how did two, homologous reaction centres diverge and yet become interdependent?

Fig. 1 depicts the evolutionary derivation of separate type I and type II photosynthetic reaction centres from a common ancestor. The proposed prototype reaction centre shares the properties of both type I and type II reaction centres [10,14]: it supplies electrons, as reduced quinone species, into a proton (H^+)-pumping complex shared with a respiratory chain (type II behaviour); and it reduces soluble electron acceptors, via ferredoxin, using electrons supplied from a donor such as H_2S (type I behaviour). These two functions were likely to have been favoured under different environmental conditions, and to have been in competition with each other in a single reaction centre.

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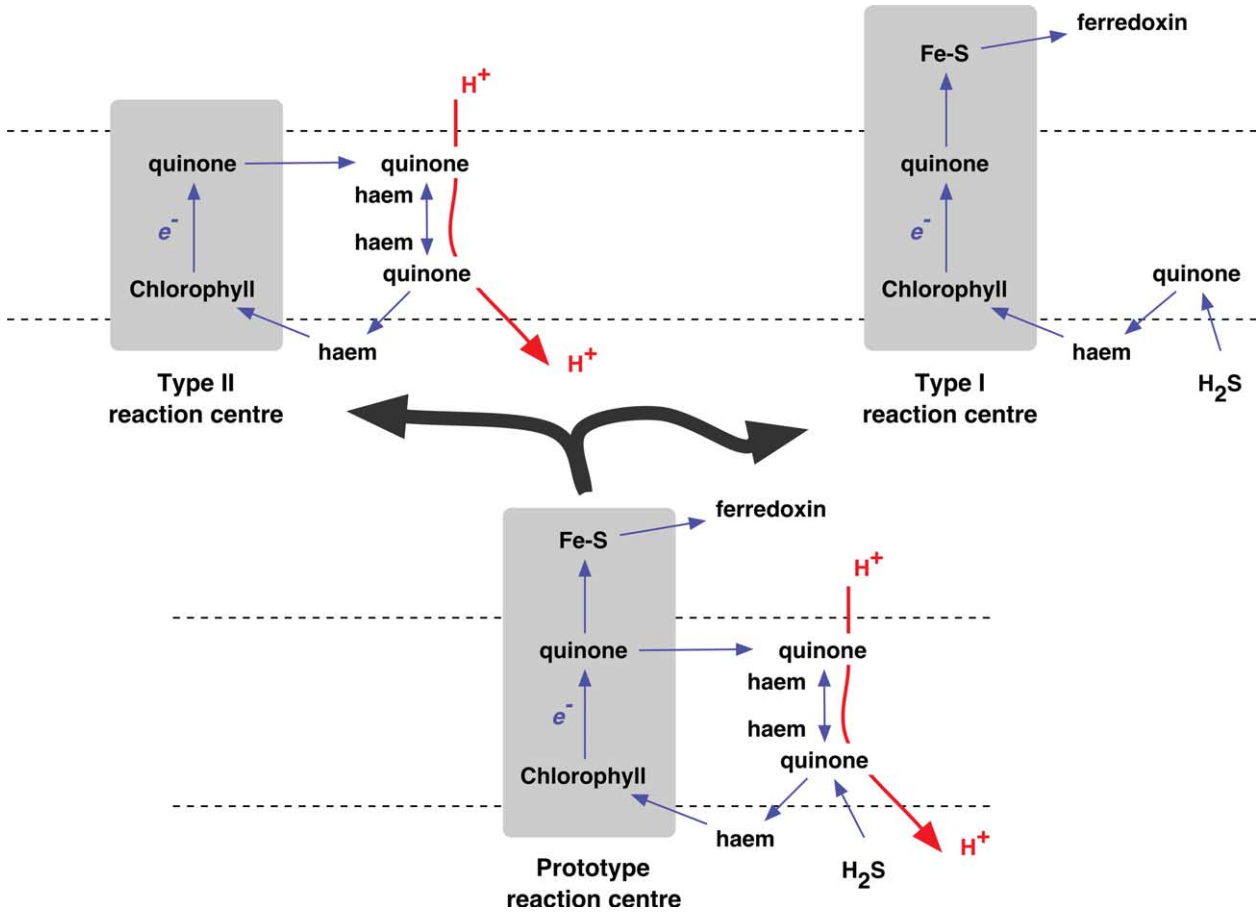

Fig. 1. *Divergence of reaction centre structure and function.* A prototype photosynthetic reaction centre diverges to give separate, type I and type II reaction centres, each with a subset of its functions, and adapted either to linear, H_2S-oxidising electron transport supporting photoautolithotrophic growth (type I) or to cyclic electron transport supporting photoheteroorganotrophic growth (type II).

Photoautotrophy requires net reduction of CO_2, and is typical of photosynthesis using type I centres, becoming possible when an environmental electron donor such as H_2S is readily available. In type I reaction centres, electrons from ferredoxin may also be fed back into a respiratory-type proton-motive Q-cycle [15]. In contrast, the Q-cycle is served directly by type II centres, where it is unaccompanied by linear electron flow from a donor to ferredoxin. Thus, light energy is used predominantly for net oxidation–reduction in organisms with type I centres only, and ATP synthesis is coupled indirectly. In contrast, type II centres serve to pump protons, drive ATP synthesis, and, where they drive autotrophic metabolism, they often do so by use of ATP and the proton-motive force to reduce CO_2 at the expense of organic electron donors such as succinate.

The emergence of two-photosystem, oxygen-evolving photosynthesis from anaerobic, bacterial photosynthesis must have required either an anaerobic, two-photosystem precursor [5], or else wholesale, lateral, and fully functional gene transfer from one single-photosystem anaerobe into another [7,14]. A model is now outlined for evolution of both types of photosynthetic reaction centres from a single, common progenitor; for their maintenance in some anaerobic lineages and loss from others; and for the origin of their cooperative, complementary functions in the linear electron transport required for oxygen evolution in chloroplasts and cyanobacteria.

3. Hypothesis: two reaction centres diverged whilst encoded by genes expressed in different environments and selected by a redox switch

Most species of single-photosystem, anaerobic phototrophs seem to have opted for specialisation to type I (typically photolithotrophic) or type II (typically photoorganotrophic) behaviour [16]. However, photosynthetic bacteria are usually versatile in their ability to use energy, carbon, and electron sources, and adaptation – division of labour according to different environmental conditions – is common [16]. Therefore, evolutionary divergence of type I and type II reaction centres may not have required loss of the complementary reaction centre and its genes, and can plausibly be considered to have occurred within a single lineage of cells. Metabolic flexibility in anaerobic photosynthesis is particularly advantageous in environments with fluctuating supplies of H_2S, such as hot springs and in the vicinity of marine hydrothermal vents [17].

Fig. 2 proposes that redox regulation of gene expression, under anaerobic conditions, determines whether type I or type II

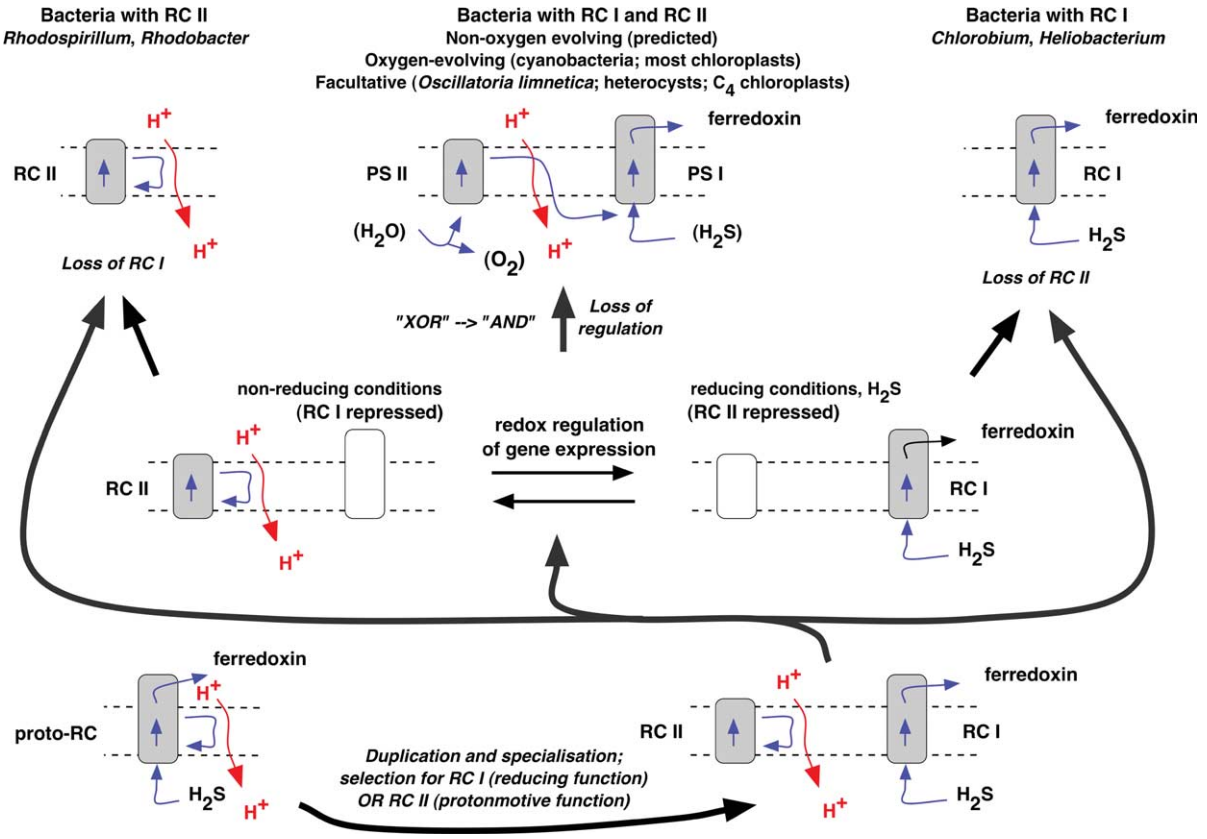

Fig. 2. *Retention of type I and type II centres, selected by a redox switch.* Type I (RC I) and type II (RC II) reaction centres separate, allowing specialisation and eventual loss of the redundant reaction centre in photoautochemotrophic (type I-containing) lineages (e.g., *Chlorobium*, *Heliobacillus* spp.) and in photoheteroorganotrophic (type II-containing) lineages (e.g., *Rhodobacter*, *Rhodospirillum* spp.). However, a versatile, facultatively chemoautotrophic photosynthetic bacterium retains genes for both type I and type II reaction centres. In this hypothetical ancestor of cyanobacteria and chloroplasts, expression of type I centre genes in the presence of H_2S is accompanied by silent type II genes, which are themselves induced under non-reducing conditions, when type I genes become repressed. Subsequent loss of regulatory control allows co-existence of type I and type II reaction centres, with complementary functions. In place of H_2S, the type II centre, as photosystem II (PS II), oxidises water, liberating oxygen, and donating electrons to the type I centre, as photosystem I (PS I). The proposed loss of the redox regulatory switch replaces the logical (Boolean) relation "type I ***XOR*** type II" (each type excluding the other) with "type I ***OR*** type II" (either is, and both are, allowed). This in turn leads to "type I ***AND*** type II" when interdependency of PS I and PS II becomes established.

reaction centre genes are expressed in a single bacterial cell containing them. Quinone-level redox control provides a suitable mechanism, given the established redox regulatory control of gene transcription in both phototrophic [18–20] and chemotrophic [21–24] bacteria. An inducible type II reaction centre is retained as photosystem II in the cyanobacterium *Oscillatoria limnetica*, which exhibits anaerobic type I photosynthesis in the presence of H_2S, but oxygenic, two-light reaction photosynthesis in its absence [25].

4. Water as a poising reductant

Cyclic photosynthetic electron transport requires redox poise: electron carriers must be present in both their oxidised and reduced forms, in order to function both as electron acceptors and as donors [26–29]. In the absence of H_2S, selection would favour opportunistic use of other environmental reductants in order to allow slow, catalytic injection of electrons into a cyclic chain that would otherwise become over-oxidised. I propose that the manganese-containing catalyst of photosynthetic water oxidation [30,31] first served such a poising role for purely anaerobic, type II photosynthesis, and that this occurred in the inducible type II photosynthesis of the bacterium which also contained genes for a reaction centre of type I (Fig. 2). The small amounts of oxygen, produced as a by-product of water oxidation, would be scrubbed from the immediate environment by acting as a respiratory electron sink.

5. Hypothesis: The Z-scheme and oxygen evolution are consequences of failure of the redox switch

Once a mechanism for water oxidation was in place, however sluggish and infrequent, any mutation producing constitutive expression of both type I and type II genes would provide new functions for the two reaction centres. Their coupling to a single quinone pool allowed the reaction centres to function, for the first time, in series, and in cooperation: the acceptors for the type II centre, oxidising water, became the donors for the type I centre, reducing ferredoxin. This coupling provided the first oxygen-evolving bacteria with the advantages of both modes of photosynthesis (ATP synthesis and reduction of soluble electron carriers), and released them from dependency on

transient supplies of H_2S for photoautolithotrophic growth: the novel electron donor, H_2O, was ubiquitous, and present at 55 M. It is proposed here (Fig. 2) that the origin of the "Z-scheme" of two light reactions, connected in series [3], occurred by these means.

The selective advantage of using water as an electron donor might initially have been small, since the reaction would have been slow, and the product, molecular oxygen, was toxic. Subsequent selection, however, increased the redox midpoint potential of the primary (bacterio)chlorophyll electron donor [32,33], while more effectively coupling the manganese-containing water-oxidation complex to re-reduction of the donor, now observed in oxygenic photosynthetic organisms as P_{680} [9,32,33].

6. Conservation of the redox switch and diversity of its applications

This "redox switch" hypothesis for the origin in oxygenic photosynthesis also suggests an ancestral function for redox control of reaction centre gene expression, which is known to balance the stoichiometry of photosystem I and photosystem II, both on cyanobacteria [19,34,35] and chloroplasts [36,37] (Fig. 3). It has been proposed that the requirement for redox control of reaction centre gene expression is the function of the chloroplast genome [37–39]. In eukaryotes, where photosynthetic reaction centres exist at all, they seem always to be encoded by chloroplasts genes, rather than by genes that have moved, with the majority of those from the ancestral, cyanobacterial endosymbiont, to the cell nucleus [40]. Furthermore, balancing the activity of photosystems I and II is essential, both for efficiency and as protection [36], and it is likely that the quinone redox-sensing machinery depicted schematically in Fig. 2 serves also as a component of post-translational mechanisms, such as protein phosphorylation [41,42], which serve to adjust the light-harvesting capacity of the two photosystems (Fig. 3) in the phenomenon of "state transitions" [43,44]. However, the diversity and heterology of the light-harvesting, antenna components of photosystems [45] suggest that a common redox signalling system has been used to provide regulatory input to diverse protein structures and functions. A good candidate for a single, conserved mechanism is a two-component system consisting of a redox sensor histidine kinase acting upon a redox response regulator [46]. Such two-component regulatory systems provide the basis of bacterial "neural networks" of connected logical gates [47,48] and mutation can easily be envisaged to produce the constitutive expression involved in the proposed failure of the redox switch (Fig. 2).

Developmental repression of photosystem II is still widely distributed in specialised cells of oxygen-evolving photosynthetic organisms, as seen in cyanobacterial heterocysts, and the bundle sheath chloroplasts of C_4 plants. In these cases, photosystem I is thought to function in its secondary role of cyclic electron transport, giving ATP synthesis without the

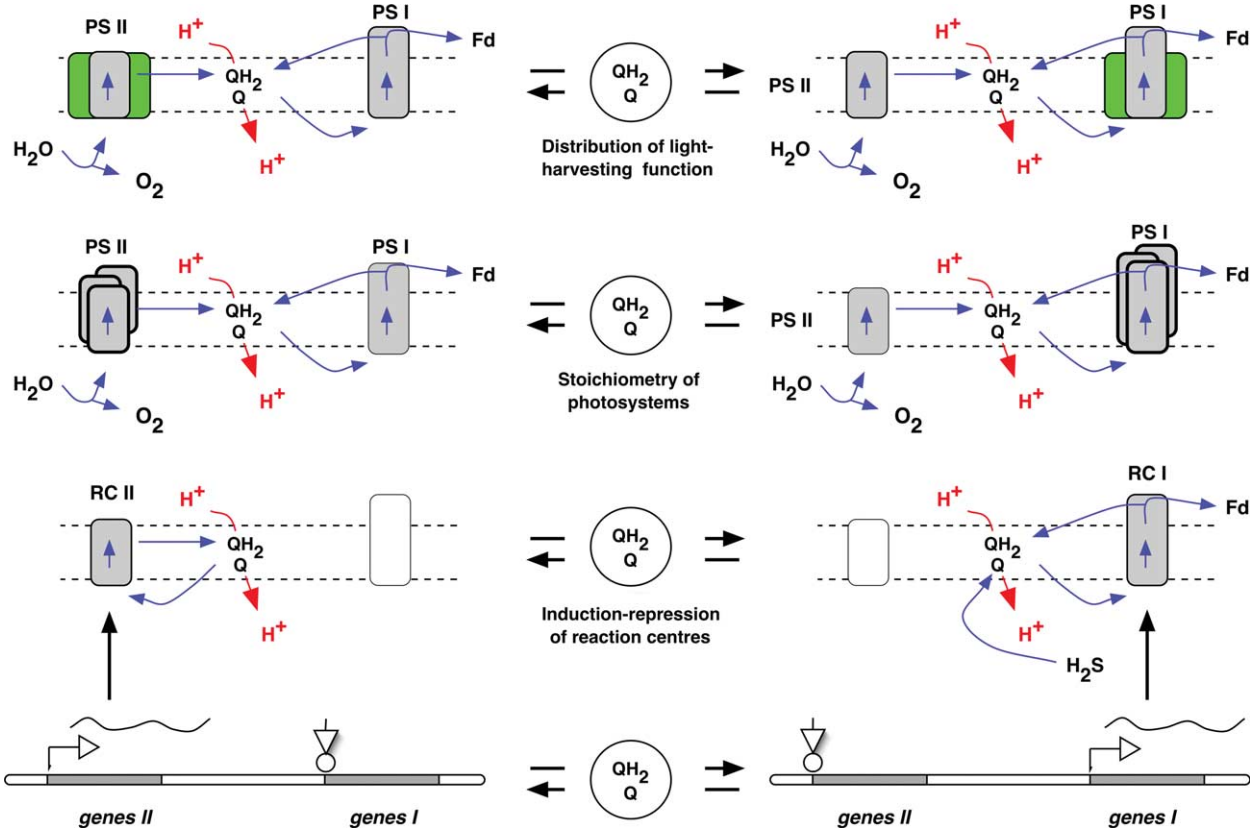

Fig. 3. *The redox switch in adaptations of photosynthesis to environmental change.* Quinone-level redox control of gene expression (lower panel) is retained: in switching transcription between a single reaction centre of either type I or type II (next to lower panel); in transcriptional adjustment of the stoichiometry of type I and type II centres as photosystems I and II of cyanobacteria and chloroplasts (next to upper panel); and in post-translational modification and distribution of light-harvesting (green) function between photosystems I and II (upper panel).

penalty of oxygen production, thus circumventing the inhibitory effect of oxygen on nitrogen fixation in heterocysts and on carbon dioxide fixation in bundle sheath chloroplasts. It is interesting to consider the possibility that selective repression of photosystem I also still occurs in similar situations and for a similar reason. A non-oxygen-evolving photosystem II that reverts to its primordial role as a type II centre for cyclic electron transport and ATP synthesis (Fig. 1) would also satisfy a demand for energy conversion without oxygen production. Both cytochrome b_{559} and the cytochrome c_{550} of cyanobacterial photosystem II [49–51] might function in such a pathway.

7. What the redox switch hypothesis predicts and explains

The first appearance of oxygen-evolving photosynthesis had global, irreversible impact, and can be viewed as the most profound and far-reaching event in the history of life in Earth [52]. The hypothesis put forward here for the origin of this event predicts the existence of a two-light-reaction, phototrophic anaerobe retaining genes for both type I and type II reaction centres, and the capacity to switch between sulfide-oxidising, photolithotrophic, type I photosynthesis, and sulfide-independent, photoorganotrophic, type II photosynthesis. The predicted organism can be autotrophic (fixing carbon dioxide) in both modes of photosynthetic metabolism.

The green, filamentous, anaerobic phototroph *Chloroflexus aurantiacus* grows in environments with variable sulfide content [17]. *Chloroflexus* has genes only for type II reaction centre core proteins (PufLM) and not for type I cores proteins (PscA) (Chloroflexus genome Database at ORNL Computational Biology Group http://maple.lsd.ornl.gov/microbial/caur/). However, *Choroflexus* has a light-harvesting antenna, the chlorosome, more commonly associated with type I-reaction centre-containing bacteria [16]. *Chloroflexus* may therefore be a close relative both of cyanobacteria and of the anaerobic phototroph predicted by the hypothesis proposed here. Facultative type I and type II-plus-type I photosynthesis is seen in the cyanobacterium *O. limnetica*, which has reaction centre core proteins homologous to PscA and PufLM. *O. limnetica* induces photosystem II, and becomes oxygenic, in environments with low sulfide content [53].

The redox switch hypothesis also predicts specific, sulfide-responsive redox regulatory control in the anaerobic, phototrophic bacterium containing genes for both type I and II reaction centres. The predicted organism will share some of the characteristics of *Chloroflexus* and *Oscillatoria*. It is possible to imagine that all such lineages have died out, but this seems unlikely, since suitable habitats still exist. It is therefore to be expected that this bacterium is either undiscovered, or a known species, as yet incompletely described. According to the redox switch hypothesis, this bacterium will be a modern example of the species in which photosynthetic oxygen evolution originated, and from which cyanobacteria, and the chloroplasts of plants, evolved (Fig. 2). It is also predicted that the mechanism of the redox switch will be found to share components in common with the quinone redox regulatory mechanisms involved in control of respiration and photosynthesis in bacteria, as well as in state transitions and control of photosystem stoichiometry in cyanobacterial and chloroplasts (Fig. 3).

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