Prochlorophytes

Origins of chloroplasts

from A.E. Walsby

OUR Victorian forebears did such a good job of describing the major groups of plants, animals and microbes that it is now a particular delight to find even a new species, let alone a representative of a new family or higher order. A decade ago, R.A. Lewin's discovery of the Prochlorophyta[1,2], a new division of photosynthetic microbes, was therefore quite momentous, particularly when it was realized that this might be the missing link in the evolution of chloroplasts. The study of prochlorophytes since then has been hampered because only symbiotic forms have been found, none of which can be grown in culture[2]. But on page 262 of this issue[3], T. Burger-Wiersma and her colleagues report the discovery of the first free-living prochlorophyte from the Loosdrecht lakes of the Netherlands.

The *Prochloron* found by Lewin is an oxygen-evolving photosynthetic prokaryote that possesses both chlorophyll *a* and *b*, the photosynthetic pigments of green plants[4]. The serial endosymbiosis theory[5] claims that eukaryotes — all those organisms whose cells have a true nucleus and membrane-bound organelles — arose by the symbiotic merger of prokaryotic organisms, and that in eukaryotic plants the chloroplast developed from a cyanobacterium (blue-green alga). This particular aspect of the theory had one drawback: although cyanobacteria also perform a similar type of photosynthesis based on chlorophyll *a*, they lack chlorophyll *b*, the pigment that is involved in the second oxygenic photosystem of plants (photosystem II). They have instead a photosystem based on pigmented phycobiliproteins which, although functionally homologous, must have evolved by a different route. It is probable that cyanobacteria were the precursors of chloroplasts in red algae, which have almost identical phycobiliproteins, but what of chloroplasts in all the other plant groups? Did they develop from primitive red algae, evolving chlorophyll *b* to replace the phycobiliprotein pigments of photosystem II, or were they products of a separate endosymbiosis involving prochlorophytes[6] that had already adopted such a replacement? One might even ask which came the first, the cyanobacteria or the prochlorophytes?

In an attempt to answer such questions Lewin's *Prochloron* has been investigated from every conceivable angle. The first *Prochloron* was found on the surface of didemnid ascidians (sea squirts, sedentary hemichordates that produce sponge-like incrustations on rocks) in the intertidal region of Baja, California. Other prochlorophytes that differed in size and other minor respects were soon discovered in tropical waters but they, too, were always present in association with these same animals. The failure to grow prochlorophytes in culture even produced some anxiety that they might not be complete organisms but chloroplasts, escaped from some unidentified algae and enslaved by their sea-squirt host. In the absence of cultures there was no option but to analyse the few prochlorophyte cells that could be obtained from the sea-squirts.

Structural and biochemical analyses of precious milligrams of material show *Prochloron* to be closely related to cyanobacteria[7]. The organism possesses a peptidoglycan wall, diagnostic of eubacteria, and polyhedral carboxysomes (stores of the CO_2-fixing enzyme) peculiar to autotrophic prokaryotes. The carotenoids and lipids are similar to those in cyanobacteria, as are other features of the cytoplasm. The most telling comparison is that of their ribosomal RNA sequences, which indicate that *Prochloron* is phylogenetically closer to cyanobacteria than to the chloroplasts of green plants[8]. One important finding[9] was that the symbiotic *Prochloron* had a DNA genome size of relative molecular mass 3.6×10^9, similar to that of many cyanobacteria and 30 times greater than the residual genome of chloroplasts, which is insufficient to support an independent existence by these organelles.

In one respect the prochlorophytes did resemble green chloroplasts more closely than cyanobacteria: their thylakoids (photosynthetic membranes) were paired or stacked. However, this may be a quasi-mechanical consequence of the presence of chlorophyll *b* and the absence of phycobilisome structures, which in cyanobacteria prevent the close juxtaposition of neighbouring thylakoids. It may not, therefore, be of any phylogenetic significance.

With the newly discovered free-living prochlorophytes, which morphologically resemble filamentous cyanobacteria, it will be possible to make even more fundamental comparisons. For example, although Burger-Wiersma *et al.* find no trace of phycobiliproteins in the cells, it would still be interesting to see if there are DNA base sequences homologous with the structural genes for these proteins that have been isolated from several cyanobacteria during the past year. Even more exciting is the prospect of using recombinant DNA technology to transfer the genes required for a chlorophyll *b* photosystem II into phycobilisome-disabled mutants of cyanobacteria (and vice versa). These experiments would define the amount of information required to evolve such a photosystem and in this way shed light on the origins and affinities of these photosynthetic prokaryotes.

In just one respect the discovery of the free-living prochlorophyte has done a disservice to biologists: previously, *Prochloron* could be obtained only by visiting a sun-drenched beach in Baja or a tropical island. A surprising number of biologists not noted for their field work found such visits worthwhile. Now they can investigate the biochemistry of a prochlorophyte in the comfort of the laboratory. □

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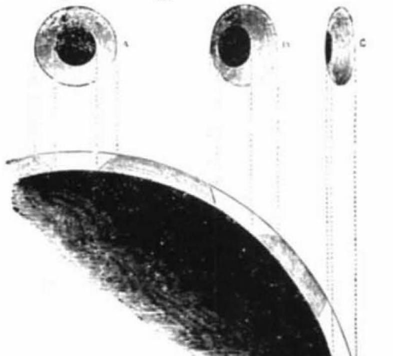
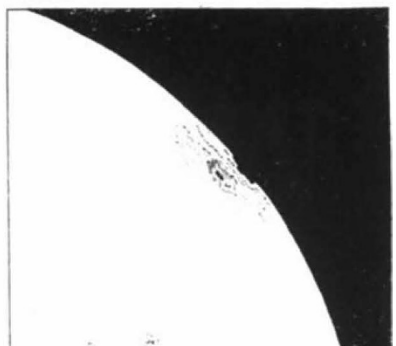
A.E. Walsby is in the Department of Botany, University of Bristol, Bristol BS8 1UG, UK.

100 years ago

from Nature **33**, 469, 18 March 1886



Appearances presented by spots. A is the centre of the disk; B between centre and limb; C, near the limb.



Copy of part of a photograph taken at Dehra Dun in 1884, showing a sunspot passing over the Sun's edge

IN the large photographs now secured at Meudon and in India, showing the sunspots, I am glad to say almost every day now, on a scale of 8 inches to the sun's diameter, we get wonderful records of what a spot really is, and how it changes.