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Personal perspective

Prochlorophyta – a matter of class distinctions

Ralph A. Lewin
Scripps Institution of Oceanography, University of California (San Diego), La Jolla, CA 92093-0202, USA (e-mail: rlewin@ucsd.edu)

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Abstract

Prochloron (a marine symbiont) and *Prochlorothrix* (from freshwater plankton) contain chlorophylls *a* and *b*; *Prochlorococcus* (common in marine picoplankton) contains divinyl-chlorophylls *a* and *b*. Like cyanophytes they are all clearly photosynthetic prokaryotes, but since they contain no blue or red bilin pigment they were assigned to a new algal sub-class, the Prochlorophyta. However, since their possible phylogenetic relationships to ancestral green-plant chloroplasts have not received support from molecular biology, it now seems expedient to consider them as aberrant cyanophytes.

Introduction

Chloroplasts are autonomous organelles; they reproduce by binary fission and are not generated in plant cells ab initio. Since in this respect they resemble prokaryotic microbes, Schimper (1883) and Mereschkovsky (1910) suggested that they might have arisen (by 'symbiogenesis') from autotrophic photosynthetic microbes which invaded or were ingested by eukaryotic cells, hitherto apochlorotic, and which ultimately settled there to be incorporated as permanent symbionts. Until recent decades there were no means to test this idea, and almost nobody took it seriously. A major counter-argument arose from the fact that the photosynthetic pigments of green plant chloroplasts are chlorophylls *a* and *b*, whereas those of all oxygenic photosynthetic prokaryotes (cyanophytes or cyanobacteria) are typically the green pigment chlorophyll *a* and associated red or blue protein pigments (phycobilins) which act as accessories in photosynthesis.

Green cells closely associated as symbionts of animals, and therefore generally called zoochlorellae, occur in many kinds of marine animals, including didemnid ascidians. (Ascidians are marine invertebrates. The solitary ones include animals called sea-squirts; the colonial ones include didemnids.) Smith (1935), who reviewed the sparse literature on this subject, was the first to distinguish clearly between greenish ascidian haematocytes and unicellular algae occurring within cavities of the testes of certain didemnid species. He described spherical cells, 6–10 micrometres in diameter, living apparently symbiotically in four species of didemnid ascidians from Ceylon (now Sri Lanka) and the Great Barrier Reef of Australia. Eldredge (1967) recorded similar algae in cloacal chambers of the zooids of several species from the Indo-Pacific and Central Pacific regions.

Discovery of Prochloron

Certain green symbiotic algae found associated with didemnid ascidians on the Australian Great Barrier Reef, and at that time considered to be blue-green algae, were reported to contain chlorophylls *a* and *b* but little or no phycobilin, a pigmentation complement quite atypical of cyanophytes (Newcomb and Pugh

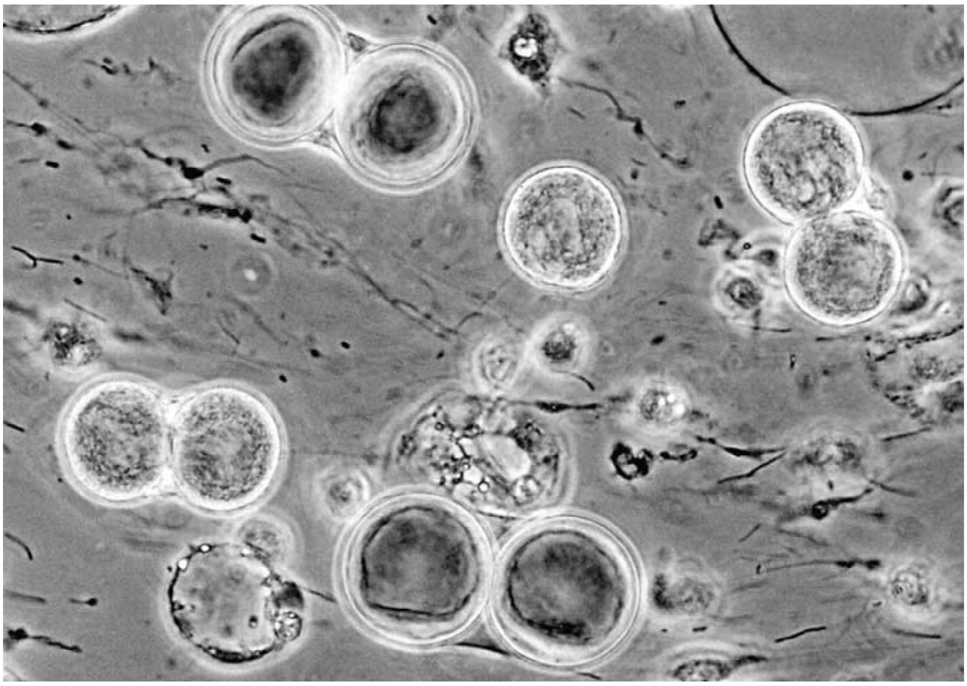

Figure 1. Prochloron cells, some within cells of *Lissoclinum punctatum* (sulphuric acid liberated from damaged host cell vesicles has killed many of the algal cells, turning them from green to orange (for a color version of this figure, see section in the front of the issue). Palau, Western Caroline Islands. Photomicrograph courtesy of T. Maruyama.

1975). At about the same time a similar photosynthetic prokaryote was found, as a unicellular symbiont of didemnid ascidians, along subtropical and tropical marine shores and in coral reef areas on the Mexican coasts. It was given the new generic name *Prochloron* (Lewin 1975) and, since it could not be legitimately considered to belong to the blue-green algae (now commonly called cyanobacteria), it was assigned to a new algal sub-class, the Prochlorophyta (Lewin 1976, 1977). See Figure 1 for a photograph of Prochloron. At the time, it seemed possible that *Prochloron* could be a descendent of the ancestral pre-plastid prokaryote postulated by the theory of symbiogenesis, or at least could constitute a model for such an ancestor. However, *Prochloron* cells generally occur outside the cells of their hosts; they are not intracellular like chloroplasts. [Exceptionally, intracellular *Prochloron* has been found more recently in a saline lake in Palau (the Republic of Belau, Western Caroline Islands) by Hirose et al. (1996)]. Furthermore, although its thylakoids are paired or stacked like those in green chloroplasts, in other cytological and biochemical features it resembles the cyanophytes. Indeed, there are pink cyanophytes, likewise associated with didemnid ascidians living in similar habitats, that are morphologically very similar to *Prochloron* (Lewin 1975), and molecular-biological data indicate that they may well be ancestral to it (A. Shinada, N. Yano, S. Kanai, R.A. Lewin and T. Maruyama, in preparation).

Most of the earlier references can be found in compilations edited by Lewin and Cheng (1989) (Figure 2) and Lewin (1993), and others in more recent publications by Lockhart et al. (1992), LaRoche et al. (1996) and Tomitani et al. (1999). Unfortunately, no strain of *Prochloron* has yet been successfully grown in culture; a claim to have done so (Patterson and Withers 1982) could not be confirmed.

Discovery of *Prochlorothrix* and *Prochlorococcus*

In 1986, Burger-Wiersman discovered a second prochlorophyte as free-floating phytoplanktonic filaments in a freshwater lake in the Netherlands. It too has chlorophylls *a* and *b* and lacks bilin pigments, so it was called *Prochlorothrix* (Burger-Wiersma et al. 1986). More recently Skulberg and coworkers (Pinevich et al. 1999) found it in a lake in Norway and cultured it. Also, a tiny unicellular prokaryote with somewhat similar pigments (divinyl-chlorophylls *a* and *b*) was discovered by Chisholm et al. (1988), and it was called *Prochlorococcus*. This alga, which resembles in many respects a marine picoplanktonic cyanophyte, *Synechococcus* sp., is evidently a major component

Figure 2. Ralph Lewin (author) with his wife Lanna Cheng.

of the marine phytoplankton in lower euphotic zones (Palenik and Swift 1996). Like *Prochlorothrix* , it can be grown in axenic culture, so it is now subject to intensive laboratory research (see, e.g., Garczarek et al. 2001).

Remarks on evolution

It is interesting to note that whereas the genes for chlorophyll *b* synthesis in prochlorophytes are similar to those in chlorophytes, indicating either a shared evolutionary ancestry (Tomitani et al. 1999) or a conceivable lateral gene transfer, the chlorophyll *a*/*b* light-harvesting proteins apparently evolved independently in these two algal classes (LaRoche et al. 1996). Since most nucleotide sequences from molecular-biological studies have indicated that these so-called prochlorophytes are fairly closely related phylogenetically to the blue-greens (for example, see Golden et al. 1993), it is now generally regarded as expedient to subsume the Prochlorophyta into the Cyanophyta or Cyanobacteria.

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