Evolution: the great photosynthesis heist

Christopher J. Howe[1] and R. Ellen R. Nisbet[2]

Summary

Many eukaryotes acquired chloroplasts by endosymbiotic acquisition of photosynthetic bacteria or already-domesticated chloroplasts from other eukaryotes. However, the ciliate *Mesodinium rubrum* acquires the nucleus of a photosynthetic eukaryote as well as its chloroplast, resulting in dramatic metabolic remodelling of the ciliate.

Main text

Sadly, the easiest way to get hold of the latest 'must-have' accessory is often to copy it or to steal it from someone else. Getting hold of your own 'must-have' may dramatically affect your life. The same is true in biochemistry. One of the most valuable evolutionary accessories is the machinery for oxygenic photosynthesis – the ability to use sunlight to oxidise water and reduce carbon dioxide, with oxygen as a waste product. Many eukaryotes have acquired photosynthetic capacity, by different routes, usually involving theft from other organisms. A study by Johnson *et al.*[1] shows that the acquisition of photosynthesis by stealing components from an alga results in major metabolic remodelling in the ciliate protist responsible.

Bacteria evolved the desirable attribute of photosynthesis around 3 billion years ago[2], resulting in the cyanobacteria. At least 1.6 billion years ago, eukaryotes evolved[3]. Shortly afterwards, one eukaryotic lineage acquired photosynthesis by endosymbiotic acquisition of a cyanobacterium. Many of the cyanobacterial genes were transferred to the host eukaryote's nucleus. This resulted in the organelle known as a 'primary' chloroplast (or plastid), as found today in the Archaeplastida (a lineage containing red and green algae, as well as green plants)[4, 5]. Around 100 million years ago, a separate eukaryotic lineage (in the Rhizaria) recognised the desirability of a photosynthetic organelle and copied the example of the Archaeplastida, separately acquiring its own cyanobacterium. The resulting organism*,* *Paulinella chromatophora*, represents the only other demonstrated example to date of stable acquisition of a cyanobacterium and conversion into a primary chloroplast, including transfer of genes to the nucleus[6, 7].

Many other eukaryotic lineages also acquired chloroplasts stably, but by stealing them, rather than copying the idea as *Paulinella* did. These lineages engulfed red or green eukaryotic photosynthetic algae - chloroplast, nucleus, mitochondrion and all. This was followed by a decluttering in which the spare nucleus and mitochondrion were dispensed with, leaving just the newly-acquired chloroplast. Genes in the spare nucleus that were needed for chloroplast function were shifted to the nucleus of the host. (In some lineages a small remnant of the spare nucleus was left behind, now called the nucleomorph.) This 'secondary endosymbiosis' process led to lineages with stable chloroplasts, including a wide range of eukaryotic algae such as diatoms, kelps, dinoflagellates and haptophytes (whose calcium carbonate armour-plating resulted in chalk deposits such as the White Cliffs of Dover).

This is just part of the story. Many other eukaryotic lineages also steal chloroplasts, but do not look after them so carefully. They hold onto them for a short period of time, but the relationship is not stable, and after a while the stolen chloroplasts (referred to as ‘kleptoplastids’) are lost. One of the most remarkable examples of this is the sea slug *Elysia* (Figure 1). This animal acquires chloroplasts from the algae it eats, and sequesters them in its gut. The chloroplasts survive for some time and fix carbon dioxide. They are eventually lost and replaced, although how they survive as long as they do remains mysterious[8].

Johnson *et al.*[1] describe work on another remarkable photosynthesis heist, by the ciliate *Mesodinium rubrum*. This single-celled marine eukaryote can proliferate very rapidly, causing red ‘blooms’ in water bodies[9]. Its dramatic growth depends on photosynthesis in chloroplasts that it steals by ingesting a photosynthetic alga, *Geminigera cryophila. M. rubrum* steals not only the *G. cryophila* chloroplast, but also the *G. cryophila* nucleus (and nucleomorph, as *G. cryophila* resulted from secondary endosymbiosis and its cells have a nucleomorph as well as a chloroplast). *M. rubrum* is not unique - related ciliates do a similar thing, preying on a range of algal species[10, 11]. In *M. rubrum*, the *G. cryophila* nucleus is moved to the centre of the *M. rubrum* cell, where it becomes enlarged and forms part of a ciliate-cryptophyte nuclear complex[12]. *M. rubrum* does not just passively retain the algal nucleus; it enslaves it. The algal nucleus remains transcriptionally active, and previous work has shown that there are dramatic shifts in the transcript profile compared to the free-living alga. Transcript levels of algal nuclear genes for a wide range of metabolic processes are greatly increased following acquisition[13]. Johnson *et al*. have extended these studies, providing proteomic and metabolomic, as well as transcriptomic data[1]. Their results show the enslaved nucleus contributes to multiple pathways in the host, including lipid metabolism and amino acid biosynthesis, presumably reflecting the biochemical contribution of chloroplasts to these pathways.

As the authors point out, this becomes a 'precarious' relationship, as *M. rubrum* seems to have become dependent on the stolen nucleus and chloroplasts for several functions. Control of the stolen nucleus and chloroplast is not perfect, and light-dependent responses normally shown by the free-living alga (such as changes in chlorophyll content in response to changes in light intensity) become weaker or slower. Eventually, the nucleus needs to be replaced, although *M. rubrum* prepares for this – it constantly consumes prey, at about the rate of one cell/day, and stores multiple spare *G. cryophila* nuclei around the extremity of its cell. Upon the demise of the first enslaved nucleus, a spare algal nucleus moves to the centre of the cell, and the process continues[12].

It will be fascinating to learn more about how gene expression is regulated in the enslaved algal nucleus, and is co-ordinated with gene expression in the rest of the cell. As Johnson et al. point out, the *M. rubrum* cell contains at least seven types of genome. There are two ciliate nuclear genomes (a transcriptionally active macronucleus, and a micronucleus passed on in sexual reproduction), the ciliate mitochondrial genome and four stolen genomes – the algal nucleus, nucleomorph, chloroplast and mitochondrial genomes. This must surely make it one of the most complex cell systems in existence. It is not known if any genes have transferred from algal prey to ciliate host. Unpicking which gene belongs to which genome will not be straightforward, but if there is evidence of gene transfer it could indicate the beginnings of a more stable organelle relationship.

Mesodinium is not the only example of a host acquiring more than just a chloroplast. The non-photosynthetic flagellate *Hatena* ingests a green alga of the genus *Nephroselmis*. The alga loses some of its cell ultrastructure, but retains its chloroplast, nucleus and mitochondrion. However, the alga fails to divide and is retained by only one host cell when the latter divides, after which the non-photosynthetic host cell has to acquire a new algal cell[14]. Another example comes from ‘dinotoms’. These are dinoflagellates that have acquired whole photosynthetic diatoms as intracellular symbionts. In some cases, the division of the diatom is controlled by the host and the diatom is retained permanently[15, 16]. A third example involves the ciliate *Paramecium bursaris*, which houses intracellular symbiotic green algae of the genus *Chlorella*. Here, an elegant RNAi-based system has recently been implicated in ensuring the stability of the relationship[17].

So we have a remarkable range of examples of eukaryotes acquiring anything up to a whole photosynthetic cell, alongside major metabolic remodelling. Finding out how *M. rubrum* and other protists steal chloroplasts (and perhaps nuclei) with varying degrees of stability, and respond to them, may help us understand the much older origins of primary or secondary chloroplasts. The typical textbook view is that primary or secondary chloroplasts arose from individual endosymbiotic events, each at a particular time and place. This may be an oversimplification, and an alternative, the so-called ‘shopping bag model’, is that each independent origin of chloroplasts developed through a series of failed, transient endosymbioses[18]. Eventually, successful permanent endosymbioses were established, supported by genes and biochemical pathways developed in the earlier, failed endosymbioses. As a result, chloroplasts and the cellular machinery for their maintenance are perhaps mosaics built from those earlier, failed endosymbiotic attempts[19]. As the remarkable world of protists is explored further, more examples of their extraordinary photosynthetic heists will surely come to light, and help us understand how relationships between chloroplasts and their hosts move from transient to permanent, and how chloroplasts originated.

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[1] Department of Biochemistry, University of Cambridge, UK
ch26@cam.ac.uk

[2] School of Biosciences, University of Nottingham, UK
Ellen.Nisbet@nottingham.ac.uk

Figure 1. Stolen chloroplasts in the sea slug *Elysia viridis*. The image shows the whole sea slug and (inset) chloroplasts in its branching digestive system. Image courtesy of Samuel Humphrey, University of Cambridge.