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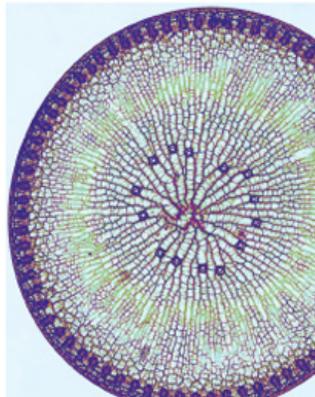
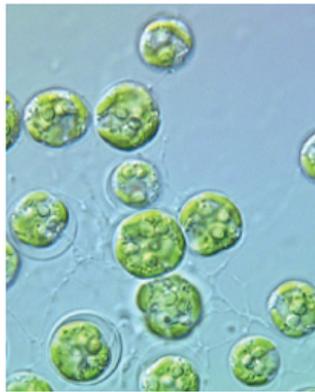
How photosynthetic organisms get taken up, passed around, and discarded throughout the eukaryotic domain

By David Smith | January 1, 2013

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Top row (l to r): *Elysia chlorotica*; spotted salamander adult; *Lotharella globosa*. Bottom row (l to r): diatom (*Campylodiscus* sp.); *Paulinella chromatophora*; diatom (*Thalassiosira pseudonana*). For credits, see end of article.

Our world is swarming with symbioses. Sea anemones and clownfish, land plants and mycorrhizal fungi, rays and remora cleaner fish, corals and algae. All around us, radically different species team up in unconventional ways, forming long-lasting relationships that benefit both parties. Some species take these partnerships to the extreme, with one organism actually moving into the cells or tissues of another. Known as endosymbiosis, this type of interaction led to the creation of key organelles, including the mitochondrion, and has formed the basis of life as we know it.

Among the more profitable endosymbioses is one that allows the host to derive energy from sunlight. The light-harvesting machines of plants and algae, for example, are the products of an ancient merger between a photosynthetic bacterium and a microbial eukaryote. Like mitochondria, present-day plastids—including both pigmented light-harvesting as well as unpigmented nonphotosynthetic chloroplasts—are fully and inescapably integrated into the host cell. Their journey from bacterium to internal solar-powered generator is responsible for much of the success and diversity of life on earth; no other cellular invention has had a greater impact on eukaryotic evolution. In fact, as scientists continue to uncover new and bizarre plastid-bearing lineages, it is becoming clear that many eukaryotic groups lacking plastids actually descend from photosynthetic ancestors. Some species are even in the process of generating novel plastid organelles.

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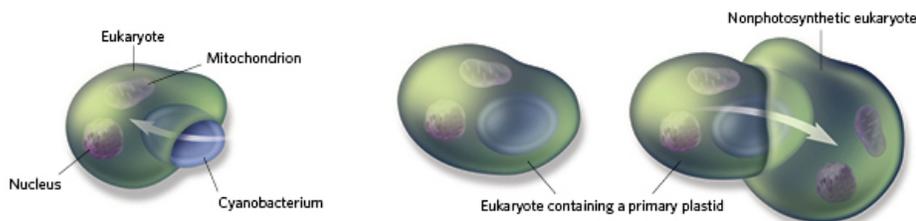
Catch me if you can

The genesis of plastids follows a straightforward and generally agreed-upon plot: about 1.5 billion years ago, a heterotrophic eukaryote, which gained energy by consuming and digesting organic compounds, swallowed and retained a free-living photosynthetic cyanobacterium. Most biologists believe that this event, called a “primary” endosymbiosis, is the source of all known plastids. Genomic analyses of diverse members of land plants, green and red algae, and glaucophytes (tiny inconspicuous freshwater algae), which together form the eukaryotic supergroup Archaeplastida or Plantae, have demonstrated that the plastids within all archaeplastid lineages trace directly back to the original primary endosymbiotic event.¹ The arrival and propagation of plastids within other eukaryotic supergroups, however, has followed a much more circuitous path, with plastids getting passed around and traded like playing cards.

Once established in the Archaeplastida, plastids spread laterally to remote lineages through “secondary” endosymbioses, in which a nonphotosynthetic eukaryote engulfs and retains a eukaryote containing a primary plastid. (See illustration below.) Secondary plastids have popped up in the strangest places. For example, all known members of the eukaryotic supergroup Excavata are nonphotosynthetic with the exception of one lucky lineage of the euglenids, a phylum of ocean- and lake-dwelling unicells that like to snack on microbes, including green algae. This lineage, known as the euglenophytes, bagged a green algal plastid at some point in its evolutionary history, allowing its members to perform photosynthesis in addition to gathering food from their environment.² A similar event occurred within tropical unicells called chlorarachniophytes. In this case, not only did the organisms acquire a photosynthetic plastid from a green alga, they also retained an extra eukaryotic nucleus, now called the nucleomorph. The nucleomorph still contains a functional genome, but it’s been whittled down from millions to a few hundred thousand nucleotides and may one day vanish completely.

Opportunistic eukaryotes have also hijacked plastids from red algae. The number of times this has happened is debated, but it has undoubtedly had an immense impact on the planet’s biodiversity. It is estimated that more than half of all described microbial eukaryotes, including many algal members of phytoplankton, harbor red-algal-derived plastids. Red algal plastids are also found in dangerous human pathogens, such as the causative agents of malaria (*Plasmodium*) and toxoplasmosis (*Toxoplasma*). And like the green variety, red algae can also pass on their nuclei. Cryptophyte algae, unicellular organisms found in marine and freshwater environments, possess the plastid and nucleomorph of a secondary red algal endosymbiont. In a remarkable example of convergent evolution, the nucleomorph genomes of cryptophytes are strikingly similar in architecture to the green algae-derived nucleomorphs of chlorarachniophytes.²

The journey from bacterium to internal solar-powered generator is responsible for much of the success and diversity of life on earth; no other cellular invention has had a greater impact on eukaryotic evolution.



PRIMARY ENDOSYMBIOSIS: About 1.5 billion years ago, a free-living photosynthetic cyanobacterium was engulfed by a heterotrophic eukaryote, which generated the plastids of all archaeplastid organisms—including land plants, green and red algae, and glaucophytes—studied to date.

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SECONDARY ENDOSYMBIOSIS: “Secondary” endosymbioses occur when a nonphotosynthetic eukaryote swallows and retains a eukaryote, such as a green or red alga, which already contains a primary plastid. The secondary host will also sometimes retain the nucleus of the alga it engulfed.

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“Tertiary” endosymbiosis, which occurs when a eukaryote takes up an alga containing a secondary plastid, complicates matters even further. A diversity of algal species, such as diatoms and cryptophytes, have donated their secondary plastids (with varying degrees of integration) to certain dinoflagellates. In

many, or possibly all, of these cases, the dinoflagellate already had a secondary plastid to begin with, but discarded it for the new one. For instance, the spiral-swimming dinoflagellate *Karenia*, famous for causing massive “red tides” off the coast of Florida, swapped its original plastid for one from a haptophyte alga.

One difficulty in tracking this dynamic exchange of plastids is that many species harboring plastids have lost their photosynthetic abilities, though they tend to retain the plastid that once mediated those processes.¹ Green plants have ditched photosynthesis no less than 15 times, one example being the parasitic weed broomrape, a decimator of food crops worldwide. Numerous species with secondary plastids have also abandoned photosynthesis. Such an event is believed to have happened very early in the evolutionary history of apicomplexan protists, spawning an entire parasitic group of photosynthetic duds, which includes the malarial parasite *Plasmodium*. Recently, researchers discovered at the bottom of Sydney Harbor, Australia, the closest known photosynthetic relative of apicomplexan parasites.³ Called *Chromera*, this newly found alga is helping scientists piece together how apicomplexans first acquired their plastid and subsequently lost the ability to carry out photosynthesis.⁴

The fact that some species retain a plastid even after losing photosynthetic ability—the cellular equivalent of lugging around a broken light bulb—hints at additional roles for these acquired organelles. Indeed, research on nonphotosynthetic plants and algae has shown that their plastids still perform crucial steps in a number of cellular pathways, including fatty acid and heme biosynthesis. For example, despite feeding heterotrophically, *Plasmodium* cannot survive in the blood without its red-algal-derived plastid. Recently, scientists discovered that plastid-less *Plasmodium* can be rescued with isopentenyl pyrophosphate, a building block for important cellular lipids called isoprenoids. The finding suggests that during blood-stage growth the malaria plastid has a single, but essential, function: isoprenoid precursor synthesis, a pathway now being investigated as a potential target of new malaria drugs.⁵

Finally, although it is difficult to prove, certain lineages have probably completely lost photosynthetic stowaways acquired earlier in their evolution. Some of the best evidence for plastid extinction comes from the diarrhea-causing pathogen *Cryptosporidium*—cause of the infamous Milwaukee gastroenteritis outbreak of 1993, in which almost half a million people were infected and at least 69 died. *Cryptosporidium*'s ultrastructure and genome sequence reveal no signs of a plastid, but its phylogenetic position deep within the apicomplexan protists leaves little doubt that it descends from a plastid-bearing ancestor.¹ The plastid-less heterokont *Phytophthora*, a nasty plant pathogen and cause of the Great Irish Potato Famine, also appears to have once contained a plastid, harboring genes apparently of red algal and cyanobacterial origin in its nuclear DNA. As more and more nuclear genomes are sequenced, it may turn out that some of the world's shadiest protists once basked in the sunlight.

PHOTOSYNTHETIC WEIRDOS

Some of the strangest creatures have managed to find themselves a photosynthetic companion, and they've done so in very creative ways. Here are a couple of the more bizarre examples of endosymbiosis, the study of which may lead to insights into the evolution of photosymbiosis.

Thieving Slugs

Elysia chlorotica is an inch-long, algae-sucking sea slug that hangs out in salt marshes along the east coast of North America, where it dines on the filamentous photosynthetic alga *Vaucheria litorea*. Using a horny, ribbonlike structure, *Elysia* punctures a hole in the *Vaucheria* cells, slurps up the alga's plastids, sequesters them within its own digestive cells just beneath the epidermis, and feeds on the sugars they produce—a strategy fittingly dubbed kleptoplasty. *Elysia* can survive for months on the photosynthetic products of the stolen *Vaucheria* plastids. What is even more impressive, the plastids remain functional within *Elysia* for almost a year, after which the crafty slug feeds on some more *Vaucheria* to replenish the stock.

If *Elysia* retains only the plastids of its algal prey, and does not maintain the algal nucleus, which contains most of the plastid-related genes, how do the *Vaucheria* plastids remain functional within the *Elysia* cells? The answer, researchers are learning, is that many *Vaucheria* genes are already integrated into *Elysia* DNA. Transcriptome sequencing suggests that more than 50 algal genes have



COURTESY OF ROGER HANGARTER

been horizontally transferred to the *Elysia* genome, allowing the slug to operate the *Vaucheria* plastids and enjoy a solar-powered existence.¹

Symbiotic Salamanders

The spotted salamander *Ambystoma maculatum* is another algal connoisseur, but it prefers green algae, particularly *Oophila amblystomatis*, a unicellular freshwater flagellate closely related to the model organism *Chlamydomonas*. The symbiotic association between the salamander and green algae was described more than 120 years ago, but it wasn't until last year that this relationship was proven to be an endosymbiotic one, making *A. maculatum* the first well-documented case of a vertebrate harboring a phototrophic organism in its cells.

Using fluorescence and transmission electron microscopy as well as DNA sequencing, a team of Canadian and US researchers, led by Ryan Kerney of Dalhousie University in Halifax, Canada, showed that the embryonic tissues of the spotted salamander contain *Oophila* inside their cells.² And although the alga appears to be degraded in adult salamanders, the researchers were able to amplify algal ribosomal RNA from adult reproductive tracts, suggesting that *Oophila* may be transmitted vertically from one *Ambystoma* generation to the next. Moreover, recent data suggest that there may be transfer of the alga's photosynthetic products to its salamander host.³ The exact benefits of the relationship are unknown, but it is thought that the algae aid salamander embryo growth and hatchling survival, and that in return, *Ambystoma* supports the population growth of the algae.

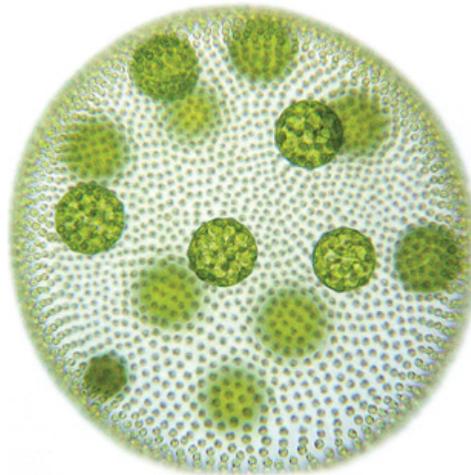
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Moving in

The freewheeling history of plastid acquisition throughout the tree of life can make endosymbiosis seem easy, but hooking up with a photosynthetic partner, assimilating it into the workings of the host cell, and harnessing it for energy production is a long and complex process. A crucial step in keeping and controlling an endosymbiont is commandeering its DNA and controlling its proteins.

After the primary endosymbiotic event, genes belonging to the internalized cyanobacterium began integrating into the host's nuclear genome, or even disappearing completely.⁶ With each gene that migrated, the endosymbiont lost some autonomy and the host gained some control. As a result of this process, contemporary plastid genomes are puny, carrying only around 50–200 genes, whereas the host nucleus contains an enormous endosymbiotic "footprint" comprising between 5–20 percent of its genes. Remarkably, while most of the proteins encoded by these genes service the plastid, some have evolved nonplastid functions.⁶

For species that acquired a plastid secondarily by engulfing and retaining a photosynthetic eukaryote, there were additional waves of gene migration—this time from the nuclear genome of the algal endosymbiont carrying the plastid to the new host nuclear genome. Thus, taxa with secondary plastids, such as *Plasmodium* and the phytoplankton *Thalassiosira*, contain genes that began their journey in a cyanobacterium, migrated to the nuclear genome of an archaeplastid, and then moved again to the nuclear DNA of the secondary host. Organisms that have replaced their secondary plastid with a tertiary or different secondary one have even more complex genomes, in some cases harboring a mosaic of both red- and green-algal-derived genes. And then there are those algal lineages, the chlorarachniophytes and cryptophytes, that still retain the relic algal endosymbiont nuclear genome in a separate organelle (the nucleomorph), which is highly reduced in size, with many of those genes once carried by the primary host's nucleus having migrated to the genome of the secondary host. Analyses of the complete host nuclear genomes of the chlorarachniophyte *Bigelowiella natans* and the cryptophyte *Guillardia theta*, which were recently sequenced by a group of scientists led by Bruce Curtis and John Archibald at Dalhousie University, Canada,⁷ should reveal just how many genes have migrated from the nucleomorph to the new host genome.

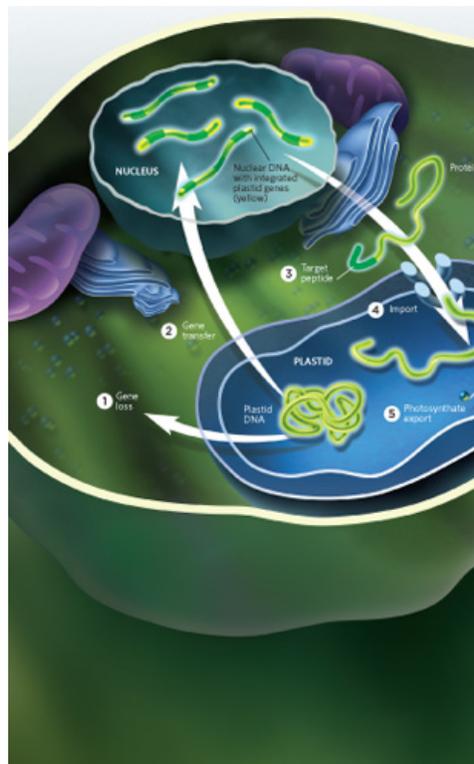


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While the migration of endosymbiont genes to the host nucleus gives the host greater control over the plastid's functions, it also creates a problem: the genes' products must return to the plastid in order to do their job. For species with primary plastids, this has involved the installation of an intricate protein targeting and shuttling system. Decades of research have shown that nuclear-encoded plastid proteins have a unique tag, called a transit peptide, at the front end (N terminus) of their sequences that helps the cell direct them to the plastid, passing them through special import channels called translocons within the plastid membranes. Once inside, the tag is cleaved, and the protein can get to work. (See illustration below.)

Species with secondary and tertiary plastids have built upon this system, but a few tweaks were needed. One of the consequences of being passed from eukaryote to eukaryote is the accumulation of membranes. Primary plastids have two membranes, both of which are cyanobacterial in origin, but secondary and tertiary plastids have three or four membranes. Shipping a protein into a triple-wrapped plastid is tricky. In all of the species for which it has been studied, such transport involves tacking on an additional tag, called a signal peptide, in front of the transit peptide. The signal peptide gets the nuclear-encoded plastid protein through the plastid's outermost membrane, at which point it is clipped off to expose the transit peptide, thereby allowing the protein to pass through the remaining plastid membranes.

Targeting proteins to the plastid is a key step in plastid integration, but exporting materials from the plastid is equally crucial. New findings from the genome of *Cyanophora paradoxa*, a unicellular glaucophyte alga, indicate that plastid-containing eukaryotes had help from an unexpected third party in learning how to transport the riches of photosynthesis from the plastid to the cytosol. When a team of international researchers, headed by Dana Price and Debashish Bhattacharya of Rutgers University, scanned the organism's nuclear genome, they discovered sequences that were related to transporter genes in the bacterial parasites *Chlamydia* and *Legionella*, best known as the causes of chlamydia and Legionnaires'



THE PLASTID GENE SHUFFLE

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disease, respectively.⁸ Turning to the nuclear genomes of red and green algae, the researchers uncovered some of these same genes. These results suggest that early in plastid evolution, genes from *Chlamydia*-like bacteria were horizontally transferred to eukaryotes and ultimately employed to help export photosynthetic products from the plastid to the cytosol. Clearly, the key to understanding plastid integration is in the genes.

A window back in time

Imagine what it would be like to go back in time a billion and a half years and watch the seminal events of the primary plastid integration unfold. Scientists are doing exactly this by studying the single-celled freshwater amoeba *Paulinella chromatophora*. Unlike a typical amoeba, *P. chromatophora* can perform photosynthesis, but it doesn't have a plastid. It has a chromatophore, a pigment-containing, light-reflecting organelle. Like plastids, chromatophores descend from an endosymbiotic photosynthetic cyanobacterium. However, the endosymbiotic event that gave rise to the chromatophore occurred around 60 million years ago. Most species within the *Paulinella* genus do not have a chromatophore and survive by munching on microbes, which they catch using impressive phagocytic tentacles called filopods. But *P. chromatophora* is an exception: since capturing and incarcerating a cyanobacterium, this species has lost its feeding apparatus and gets by on photosynthesis alone. Just as in organisms carrying plastids, host cell division and chromatophore replication are synchronized, meaning that each daughter cell receives a chromatophore.

Paulinella has been at the center of a long-standing debate as to whether the chromatophore is an endosymbiont or a full-fledged photosynthetic organelle, analogous to a plastid. Over the past 5 years, biologists have been sequencing genes within *Paulinella*'s chromatophore and nuclear genomes, and discovered that many of the genes that were originally present in the endosymbiont genome have disappeared, including some that were essential for maintaining a free-living existence. This means that the chromatophore is now permanently wedded to its host, but this alone is not enough to attain full-fledged organelle status. As proof that the assimilation has proceeded even further, at least 30 of the chromatophore's genes have integrated into the host genome.

This past year, Eva Nowack and Arthur Grossman of the Carnegie Institution for Science discovered that three of these migrated genes do in fact code for chromatophore proteins.⁹ More importantly, these proteins are synthesized using the host's cellular machinery and then shipped to the chromatophore, where they appear to be fully functional. This give-and-take relationship between the host and endosymbiont is believed by many to be the definitive step to becoming a genuine organelle, making *P. chromatophora* the only known example—outside the origin and spread of plastids—for which the shift from endosymbiont to photosynthetic organelle has occurred.

Scientists are also studying the genome of the nonphotosynthetic *Paulinella ovalis*, which has neither a plastid nor a chromatophore. There they have identified at least two cyanobacterial-like genes, which were most likely transferred laterally to *P. ovalis* from its cyanobacterial prey.¹⁰ If true, this raises the question: Could horizontal gene transfer from cyanobacteria prior to endosymbiosis play a role in plastid integration? Perhaps *P. chromatophora* was pre-equipped to accept its chromatophore, aiding in its integration and retention.

The answers to this and other questions are likely to be revealed through continued work on the *Paulinella* genus. For example, given *P. chromatophora*'s relatively new relationship with its photosynthetic organelle, it is unlikely that the protein-import apparatus of its chromatophore will prove as sophisticated as that of the plastid, which has had many hundreds of millions more years of fine-tuning. But comparing the architecture of these two systems, researchers should glean insights into the early stages of the formation of organelles. Other endosymbionts, including those yet to be discovered, will also inform the discussion. A quick scan of the tree of life reveals a plethora of taxa, from corals to fungi, that are partnered with photosynthetic species, and as biologists explore new lineages, they are sure to uncover even more examples of organisms engaging in this intimate interspecies relationship.

David Smith is a Killam Postdoctoral Scholar in the Botany Department at the University of British Columbia, Vancouver, Canada.



PAULINELLA CHROMATOPHORA
COURTESY OF EVA NOWACK

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Life:

self-replicating mass format of evolving naturally selected RNA nucleotide(s), which is life's primal organism.

Natural selection:

ubiquitous phenomenon of material that augments its energy constraint.

Mass-Energy:

inert-moving graviton(s), the fundamental particle of the universe, inert extremely briefly at the pre-big-bang singularity .

Intelligence:

learning from experience.

Intelligent Life

Life is an evolving system continuously undergoing natural selection i.e. continuously selecting, intelligently, opportunities to augment its energy constraint in order to survive i.e. in order to avoid its own mass format being re-converted to energy.

Dov Henis

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RetiredInBoyntonBeach

Posts: 5

January 27, 2013

Loved this article! Thank you so much! My only regret is that euglenophytes were mentioned only in passing. A few additional words about my very favorite organism in the whole world, Euglena, would have absolutely made my day. I used to keep pet Euglena gracilis on an agar slant in my refrigerator (really!), back when I was a beginning graduate student a gazillion years ago (well, 44 years ago).

So much has been learned over those years. Sigh. I hereby acknowledge, Norton (may you rest in peace), that you were right (about the genome project) and I was myopically wrong.

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RetiredInBoyntonBeach

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January 27, 2013

Oh -- and kudos to Skip Pierce! Keep on trucking! (we were acquainted with each other when you were a rotator in BIO).

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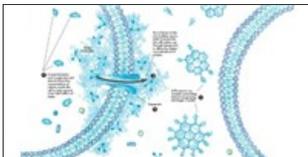
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