

Rethinking plastid evolution

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How easy is it to acquire an organelle? How easy is it to lose one? These questions underpin the current debate about the evolution of the plastid—that is, chloroplast—the organelle of photosynthesis in eukaryotic cells.

The origin of the plastid has been traced to an endosymbiosis between a eukaryotic host cell and a cyanobacterial symbiont, the latter gradually ceding genetic control to the former through endosymbiotic gene transfer (EGT). The resulting organelle now relies for its biogenesis and function on the expression of a small set of genes retained in the shrunken plastid genome, as well as a much larger set of transferred nuclear genes encoding proteins synthesized in the cytosol and imported into the organelle.

This scenario accounts for the so-called primary plastids in green algae and their land plant relatives, in red algae and in glaucophytes, which together comprise *Plantae* (or *Archaeplastida*)—one of five or six recognized eukaryotic supergroups (Adl *et al.*, 2005). In other algal types, plastids are ‘second-hand’—they have been acquired not by taking up a cyanobacterium, but by taking up a primary-plastid-containing eukaryote (sometimes a green alga, sometimes a red alga) to produce secondary plastids. In most of these cases, all that remains of the eukaryotic symbiont is its plastid; the genes coding for plastid proteins have moved from the endosymbiont to the host nucleus. A eukaryotic host—which may or may not itself have a plastid—might also take up a secondary-plastid symbiont (generating tertiary plastids), or a secondary-plastid host might take up a primary-plastid symbiont. You get the picture: plastid evolution is complicated!

Several excellent recent reviews present expanded accounts of plastid evolution (Reyes-Prieto *et al.*, 2007; Gould *et al.*, 2008; Archibald, 2009; Keeling, 2009). Here, I focus on one particular aspect of plastid

evolutionary theory, the ‘chromalveolate hypothesis’, proposed in 1999 by Tom Cavalier-Smith (1999).

The chromalveolate hypothesis seeks to explain the origin of chlorophyll *c*-containing plastids in several eukaryotic groups, notably cryptophytes, alveolates (ciliates, dinoflagellates and apicomplexans), stramenopiles (heterokonts) and haptophytes—together dubbed the ‘chromalveolates’. The plastid-containing members of this assemblage are mainly eukaryotic algae with secondary plastids that were acquired through endosymbiosis with a red alga. The question is: how many times did such an endosymbiosis occur within the chromalveolate grouping?

A basic tenet of the chromalveolate hypothesis is that the evolutionary conversion of an endosymbiont to an organelle should be an exceedingly rare event, and a hard task for a biological system to accomplish, because the organism has to ‘learn’ how to target a large number of nucleus-encoded proteins—the genes of many of which were acquired by EGT—back into the organelle. Our current understanding of this targeting process is detailed in the reviews cited earlier. Suffice it to say that the evolutionary requirements appear numerous and complex—sufficiently so that the chromalveolate hypothesis posits that secondary endosymbiosis involving a red alga happened only once, in a common ancestor of the various groups comprising the chromalveolates.

Considerable molecular and phylogenetic data have been marshalled over the past decade in support of the chromalveolate hypothesis; however, no single data set specifically unites all chromalveolates, even though there is compelling evidence for various subgroup relationships (Keeling, 2009). Moreover, within the proposed chromalveolate assemblage, plastid-containing lineages are interspersed with plastid-lacking ones—for example, ciliates

in the alveolates, and oomycetes such as *Phytophthora* in the stramenopiles. The chromalveolate hypothesis rationalizes such interspersions by assuming that the plastid was lost at some point during the evolution of the aplastidic lineages. The discovery in such aplastidic lineages of genes of putatively red algal origin, and in some cases suggestive evidence of a non-photosynthetic plastid remnant, would seem to be consistent with this thesis, although these instances are still few and far between.

In this context, two recent papers are notable in that the authors seek to falsify, through rigorous testing, several explicit predictions of the chromalveolate hypothesis—and in both cases they succeed in doing so. Because molecular phylogenies have failed to either robustly support or robustly disprove the chromalveolate hypothesis, Baurain *et al.* (2010) devised a phylogenomic falsification of the chromalveolate hypothesis that does not depend on full resolution of the eukaryotic tree. They argued that if the chlorophyll *c*-containing chromalveolate lineages all derive from a single red algal ancestor, then similar amounts of sequence from the three compartments should allow them to recover chromalveolate monophyly in all cases. The statistical support levels in their analysis refuted this prediction, leading them to “reject the chromalveolate hypothesis as falsified in favour of more complex evolutionary scenarios involving multiple higher order eukaryote–eukaryote endosymbioses”.

In another study, Stiller *et al.* (2009) applied statistical tests to several *a priori* assumptions relating to the finding of genes of supposed algal origin in the aplastidic chromalveolate taxon *Phytophthora*. These authors determined that the signal from these genes “is inconsistent with the chromalveolate hypothesis, and better explained by alternative models of sequence and genome evolution”.

So, is the chromalveolate hypothesis dead? These new studies are certainly the most serious challenge yet. Additional data, including genome sequences of poorly characterized chromalveolate lineages, will no doubt augment comparative phylogenomic studies aimed at evaluating the chromalveolate hypothesis—which these days is looking decidedly shaky.

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So, too, the bright colouration of salt pans is a familiar sight, and these osmotic extremes not only host rich microbial faunas but life that can flourish in the most bitter of brines. What of the extremes of pH—bleach versus battery acid? Once again, alkaliphiles and acidophiles disport themselves in ponds and streams that would have the Health and Safety officers in a state of panic. Pressure, either crushingly high or extremely attenuated? Life, of course, exists in the deepest oceanic trenches, but how much deeper might be viable? The weakest link seems to be the pressure sensitivity of the phospholipid membranes, suggesting that even on planets with titanic oceans life won't survive much deeper than in the Mariana Trench. The same argument applies to the deep crust: at about 5 km the crushingly high pressures also coincide with the thermal limits imposed by the geothermal gradient. Shall we look to the skies? Clouds carry bacteria, but even at quite modest heights it seems to be accidental freight rather than a nebulous ecosystem.

Terrestrial life has conquered nearly all of the 'habitation box' and its evolution begs so many questions. Are some forms, such as the hyperthermophiles, survivors from the Earth's apocalyptic beginnings? Maybe, but most have clearly been reinvented several times. Getting to the limits of life isn't that difficult, but how do extremophiles not only survive but flourish in these environments? Often the adaptations seem minor, which merely means they are more subtle than we might realize. What of the future? So far as the Earth is concerned it must cope with ever increasing solar luminosity: the last men will long predecease the last microbe. Possibly long before, we will engage in the first great galactic diaspora; but wherever our biologists journey they may find that life 'out there' got no further than the blue jewel that is Earth.

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Aliens at home?

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When in 1609 Galileo first saw the moons of Jupiter, he must have been spellbound. I was certainly so enrapt when I saw Europa and her three companions strung like a line of jewels. Galileo may have appreciated the irony that my guide was a Jesuit priest, and the somewhat antiquated telescope we used was but a few yards from the Papal summer residence in Castel Gandolfo. Galileo prized open the door and before long, scientific imagination was fired by the prospect of innumerable inhabited worlds. As the centuries progressed, imagination raced ahead of facts, with the Moon optimistically colonized by Selenites, and Mars transformed by immense canals to supply the parched regions of a planet plunging into desertification. From this dying planet H.G. Wells propelled his aliens to terrorize southern England with immense tripods housing sinister octopoids.

Now we might be closer to knowing if Wells was in any sense on the right track. The spectacular success in detecting extrasolar planets has produced a roster in excess of 450, and this technology potentially allows us to detect Earth-like planets. Even if many of the known planets are too large to be habitable and lie, for the most part, beyond the inferred 'habitable zones', before long we will get some clues as to how densely our galaxy is inhabited. The consensus points in two directions. First, life is a universal. Second, our biosphere will be of almost no use when it comes to comparisons. Let me draw your attention

to a remarkably unappreciated fact: if you want to understand aliens, stay at home.

Am I serious? After all it is already clear that extrasolar planetary systems are vastly different to our Solar System. Immense planets orbit their suns every few days, their surfaces far more torrid than that of Venus. Other planets most likely possess giant oceans, hundreds of kilometres deep. The diversity of moons and planets in our Solar System is a reminder of what may await us light years from Earth. Even among our neighbours, a case can be made for possible life in the clouds of Venus and Jupiter, the oceans of Europa and hydrocarbon lakes of Titan, and—with perennial optimism—in the permafrost of Mars. We might assume, therefore, that the range of environments available to life, its 'habitation box', is gigantic, and that Earth's biosphere just nestles in one tiny corner. Oddly enough the evidence is exactly the opposite. Life on Earth has reached the limits of what is possible—anywhere.

Temperature? The current limit on Earth is 122°C. Plunging in the opposite direction the evidence is just as remarkable. At temperatures well below freezing, life carries on cheerfully. Even far beyond the eutectic, in which free water cannot form, organisms remain in a state of suspended animation with rates of damage and repair almost precisely matched. What of extreme desiccation? Evidently life has reached the limits of water activity. Entertainingly some of the hardest forms are fungi that inhabit the weird alien world of Blue Stilton cheese.