PhotobiontDiversity
Genetic diversity of lichen photobionts and related organisms

Another perspective on diversity of symbiotic cyanobacteria: 16S

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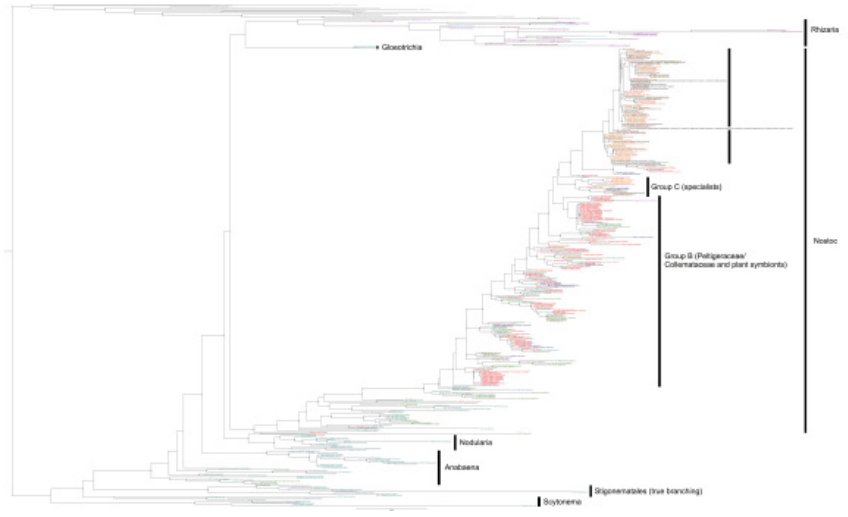
Up to this point, I have been focusing on the *rbcX* locus for all investigations of cyanobacterial photobionts because it is probably the most extensively sampled locus and it is more variable than 16S rDNA. However, it is limited because some groups of symbiotic cyanobacteria do not have *rbcX* sequences in the database. These include symbionts of the water fern *Azolla* which has traditionally been called *Anabaena azolae* and the photobionts of a variety of primarily tropical lichens that have traditionally been classified within the genus *Scytonema*. 16S sequences are available for both of these groups, as are sequences from a variety of other related genera of cyanobacteria. Furthermore, it is useful to compare the patterns revealed from analyses of *rbcX* to those based on an independent locus, often sampled from independent specimens.

Unfortunately, my usual approach of identifying sequences using blast isn't very practical for the 16S because there are (literally) millions of sequences in the database from metagenomic surveys. Since these environmental samples can generally include both free-living colonies and lichen fragments, they aren't of much use for the questions that I'm interested in here. Instead, I made a list of relevant accession numbers culled from the literature. This includes both symbiotic and free-living strains, focused primarily on *Nostoc*, but including a representative sampling of other genera of heterocystous cyanobacteria, as well as some outgroup taxa. This list is far from exhaustive, and I intend to add additional sequences to it as I come across them in the literature. Currently, I'm including sequences from the these studies.

Once the list of accession numbers was assembled (556 in total), the analyses proceeded as described previously. See the details here. The resulting phylogeny looks like this (see high res. pdf version here):



Cyanobacterial 16S phylogeny, coloured by host family (light purple: Stereocaulaceae, dark purple: Basidiolichens, dark brown: Geosiphon, light brown: Lobariaceae, red: Peltigeraceae, dark blue: Collemetaceae, light blue: Coccocarpiaceae, orange: Nephromataceae, pink: Pannariaceae, green: plant hosts, cyan: free-living). Names in black indicate genotypes found in more than one group.Grey indicates outgroups. Circles on internal nodes indicate aLRT ≥0.9.

Notes:

Members of the Stigonematales (heterocystous cyanobacteria with true branching) form a monophyletic group, but they are nested within the Nostocales (non-branching heterocystous cyanobacteria).

Most of the *Nostoc* strains form a large monophyletic lineage, but there are a few strains identified as *Nostoc* that cluster with *Anabaena*.

Anabaena is paraphyletic and includes strains identified as *Aphanizomenon*, *Trichormus*, *Dolichospermum*, and *Cyclindrospermopsis*.

Nodularia and *Scytonema* each forms a discrete monophyletic group, though *Anabaenopsis* and *Cyanospira* strains group within the *Nodularia* clade.

Lichen photobionts that have been described as members of *Scytonema* form an independent lineage, sister to *Nostoc* (along with *Gloeotrichia*). This novel exclusively lichenized lineage has been given the name *Rhizonema*.

Symbionts of the water fern *Azolla* form a monophyletic lineage within one of the *Anabaena* clades, supporting the traditional classification and earlier phylogentic analyses.

All other symbiotic strains cluster within *Nostoc* except for one symbiot of the flowering plant *Gunnera* which forms a distinct lineage along with three free-living *Nostoc* strains within *Anabaena*. There are also two symbiotic strains at the base of the *Nostoc* clade that branch earlier than a strain identified as *Cylindrospermum*, meaning either that an early branching *Nostoc* strain has been misidentified or that these represent an additional symbiotic lineage. Similar early-branching strains are also present in the *rbcX* phylogeny.

Along with photobionts of the Basidiolichens *Dictyonema* and *Acantholichen* and the Peltigeralean lichen *Coccocarpia*, several *Stereocaulon* photobionts group within *Rhizaria*. I reported previously that *rbcX* sequences from *Stereocaulon*, as well as from *Protopannaria* formed a distinct lineage sister to all other *Nostoc* strains. I suspect that these sequences also represent members of *Rhizaria*.

In contrast to the *rbcX*, where photobionts of members of the Lobariaceae, Nephromataceae and Pannariaceae (group A) formed a paraphyletic grade at the base of a clade composed of photobionts of members of the Peltigeraceae and the Collemataceae, as well as free-living strains and plant symbiont (group B), in this tree group B forms a paraphyletic grade basal to a well supported group A clade.

As with the *rbcX*, Collemataceae photobionts are distinct from Peltigeraceae photobionts, though the sampling of Collematacerae photobionts is much less, so the pattern is not as apparent.

There is a *Peltigera malaceae/Nephroma arcticum/Sticta hypochra/Leptogium lichenoides* clade (also including several photobionts of *N. expallidum*, another trimembered *Nephroma* species), though it is deeply nested within *Nostoc*, almost sister to group A (I'll call this group of specialist photobionts group C).

Photobionts of the flowering plant *Gunnera magellanica* form two distinct lineages within *Nostoc*, but in this case, there are 13 sequences from other species of *Gunnera*, none of which group with *G. magellanica* symbionts. Instead they form 7 other groups, three of which include symbionts of cycads or bryophytes. Symbionts of *G. megellanica* still stand out on long branches, but not as dramatically as they do for *rbcX* and symbionts of other *Gunnera* species do not appear to be on long branches.

Overall, these results support previous findings in the literature regarding the distinctness of symbiots of *Azolla* and of "scytonemoid" lichen photobionts. They are also broadly consistent with my results for *rbcX*, except that the rooting is different within the main *Nostoc* lineage. In *rbcX*, the root connects to the "specialist" group C lineage, resulting in a paraphyletic group A. In the 16S, the root connects within group B, causing it to be paraphyletic. In the future, I hope to do a combined analysis of both genes to try to resolve this discrepancy.

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