A chronology of multicellularity evolution in cyanobacteria

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Abstract: The transition from unicellular to multicellular organisms is one of the most significant events in the history of life. Key to this process is the emergence of Darwinian individuality at the higher level: groups must become single entities capable of reproduction for selection to shape their evolution. Evolutionary transitions in individuality are characterized by cooperation between the lower level entities and by division of labor. Theory suggests that division of labor may drive the transition to multicellularity by eliminating the trade-off between two incompatible processes that cannot be performed simultaneously in one cell. Here we examine the evolution of the most ancient multicellular transition known today, that of cyanobacteria. We developed a novel approach for the precedence polarization of trade-off phenotypic traits that employs gene phylogenies and does not require a species tree. Applying our procedure to cyanobacterial genomes we reconstruct the chronology of ecological and phenotypic trait evolution in cyanobacteria. Our results show that the prime driver of multicellularity in cyanobacteria was the expansion in metabolic capacity offered by nitrogen fixation, which was accompanied by the emergence of the filamentous morphology and a reproductive life cycle. This was followed by a range of niche expansions and interactions with other species, and the progression of multicellularity into higher complexity in the form of differentiated cells and patterned multicellularity.

Introduction

Multicellularity is considered a characteristic trait of eukaryotes, but has evolved independently several times in diverse prokaryote taxa, including actinobacteria, myxobacteria, and cyanobacteria (*1*). Bacterial multicellularity ranges from transient associations, such as colonies, biofilms and cellular aggregations, to permanent multicellular forms (*2*). Instances of multicellular bacterial species present the major traits of eukaryotic multicellularity, including cell-to-cell adhesion, peri- or cytoplasmic continuity, intercellular communication, patterning, programmed cell death (PCD), and division of labor (*3*). Aggregative forms of multicellularity are common among bacterial species, for example, those that form a biofilm under specific external conditions (*4*). *Bacillus subtilis*, for instance, forms biofilms upon nutrient deprivation in which cells differentiate into motile, matrix producing, or spore cells depending on the environmental cues (*3*). Notably, cell differentiation in aggregates is adaptive at the level of the individual cell as it directly confers a fitness benefit to that particular cell. In contrast, under true division of labor, cells are interdependent upon each other and specialize in performing complementary tasks. These tasks (e.g., somatic functions or PCD) are not regarded beneficial on the level of the individual cell, but are considered advantageous for the colony; thus, they are emergent properties on a higher level of organization (*5*).

True division of labor in bacteria is best described in actinobacteria and cyanobacteria (*5*). In cyanobacteria, the most complex of the filamentous species can differentiate up to five different cell types: vegetative (photosynthetic) cells, akinetes (spore-like cells), hormogonia (reproductive, motile filaments), necridia (dead cells resulting from PCD for hormogonia release), and heterocysts (*3*, *6*). Heterocysts differentiate under nitrogen deprivation and are specialized in nitrogen (N_2) fixation by the enzyme nitrogenase (*7*). As this enzyme is sensitive to oxygen (O_2), these cells are characterized by the absence of photosynthesis and by

a thick cell wall, which maintains an anaerobic environment. Heterocysts and vegetative cells in the filament are metabolically interdependent with the heterocysts providing combined nitrogen to the other cells within the filament and receiving fixed carbon compounds in return. Heterocysts cannot reproduce hence they represent a prime example for emergent traits on the level of a multicellular organism.

Cyanobacteria possess the hallmark traits reminiscent of complex eukaryotic multicellularity (except for tissues and organs) making the order of trait emergences essential for understanding the origin of higher-level complexity in organismal evolution. Here we determine the evolutionary trajectory of the emergence of traits in the evolution of multicellularity in cyanobacteria.

Results and Discussion

To reconstruct the order of trait emergence in the evolution of cyanobacterial multicellularity, we evaluated 25 phenotypic traits variably present in 199 cyanobacterial species using a genomic sample of gene trees for 1671 protein coding gene families (Tables S1 - S2).

Previous studies of trait precedence relied on a single fully resolved species tree (*8*), with conclusions ultimately depending on the quality of the hypothesized species tree. To illustrate this point, we constructed a phylogenetic network derived from the common single copy genes in our sample (Fig. 1). Clearly, no single species tree based on that data can be correct in all its topological details, and the conclusions derived from any single species tree are frequently different from those derived from individual gene trees (*9*). Furthermore, superposition of traits on the network (colors in Fig. 1) shows that any inference of trait precedence will critically depend on the topological resolution of highly uncertain parts of the species network.

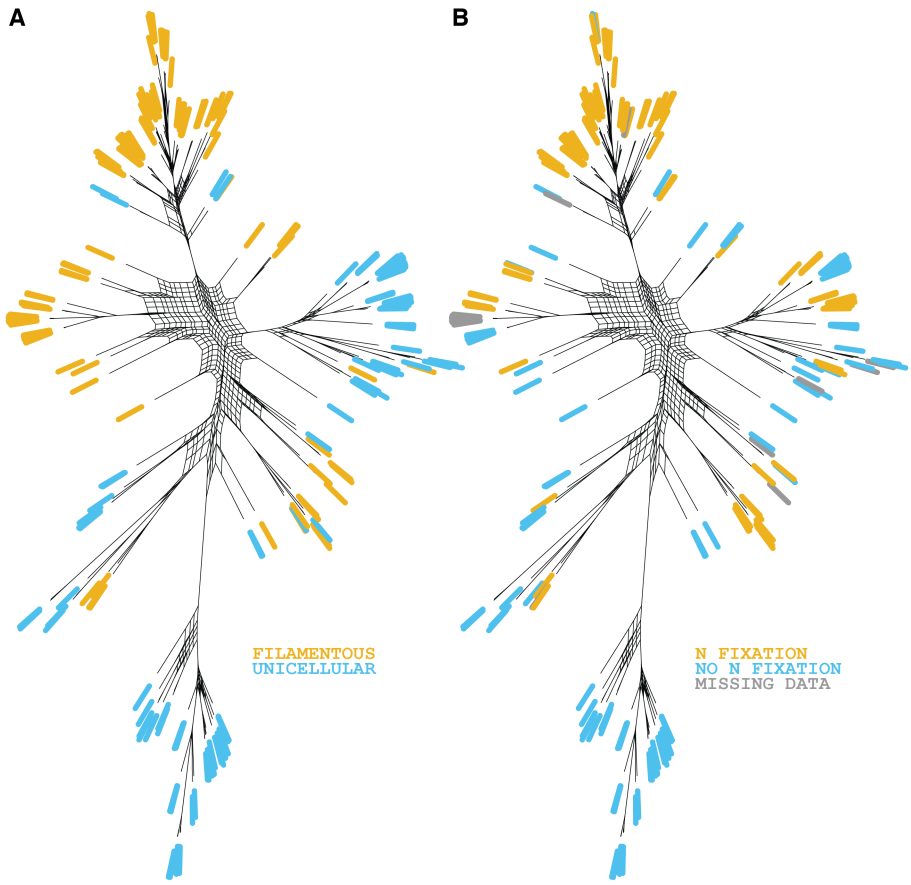

Fig. 1. Species tree uncertainty and presence of traits for (A) FILAMENTOUS **and (B)** N FIXATION. Species tree reconstruction for 199 cyanobacteria genomes, based on 17 common single-copy genes. The phylogenetic network summarizes 100 bootstrap replicates of maximum likelihood inference from 3744 alignment columns.

An alternative to the species tree approach, is to consider individual gene trees and the information they contain about the last common ancestor (LCA) of traits and their precedence, as in the method we developed and applied here. Our approach, hereby termed *trait-pair polarity*, avoids the commitment to a single species tree topology, while at the same time provides statistical power thanks to inference drawn from large samples – rather than a sample of one tree (see comprehensive description in Materials and methods and Fig. 2). Even higher power can be achieved by breaking down the full order of trait emergences into a series of pairwise polarizations since, for a specific pair of traits, the resolution of precedence depends only on the precedence of the LCAs of the two traits. This polarization is

independent of large parts of the full branch topology of the trees, rendering the inference immune to high amounts of phylogenetic noise.

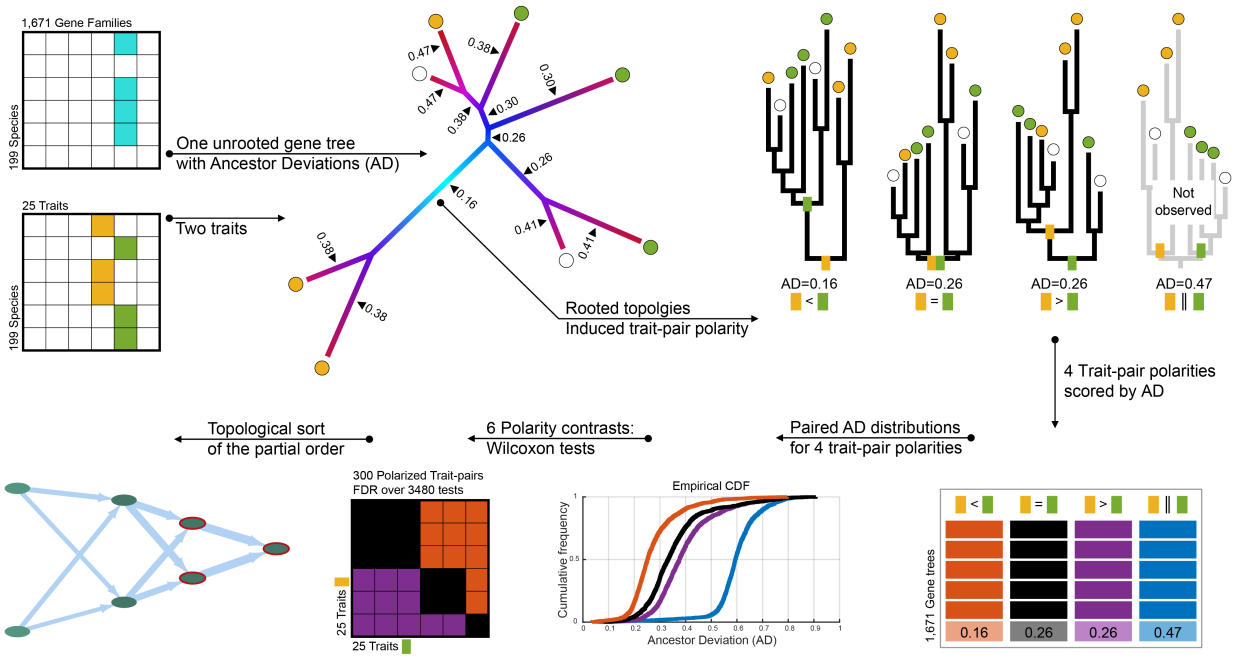

Fig. 2. Phylogenomic reconstruction of trait emergence chronology. Stages in the procedure are depicted clockwise from top-left. A genome-wide sample of single-copy protein coding genes provides measures of ancestor-descendant relations (Ancestor Deviation, AD) (*32*). The AD support is then coupled to traits presence-absence patterns for each gene tree. Considering a specific pair of traits, their emergence polarity is deduced from formal statistical tests that contrast alternative hypothesized ancestor-descendant relations, utilizing paired information from all gene trees. All pairwise comparisons of traits are then combined into an overall trait-pairs polarity matrix, and if partial ordering of the traits (i.e., no polarity cycles) is possible, a feed-forward network can be inferred by topological sorting.

Employing the trait-pair polarity phylogenomic inference procedure to determine pairwise trait precedence in the data, we reconstructed a trait-pair polarity matrix (Fig. 3a). The trait-pair polarity matrix shows the best-supported emergence order among all trait pairs, as determined from Wilcoxon tests with four possible polarities: trait A originates before trait B; B originates before A; A and B emerge simultaneously (i.e., their LCAs coincide); and A and B originate in independent lineages.

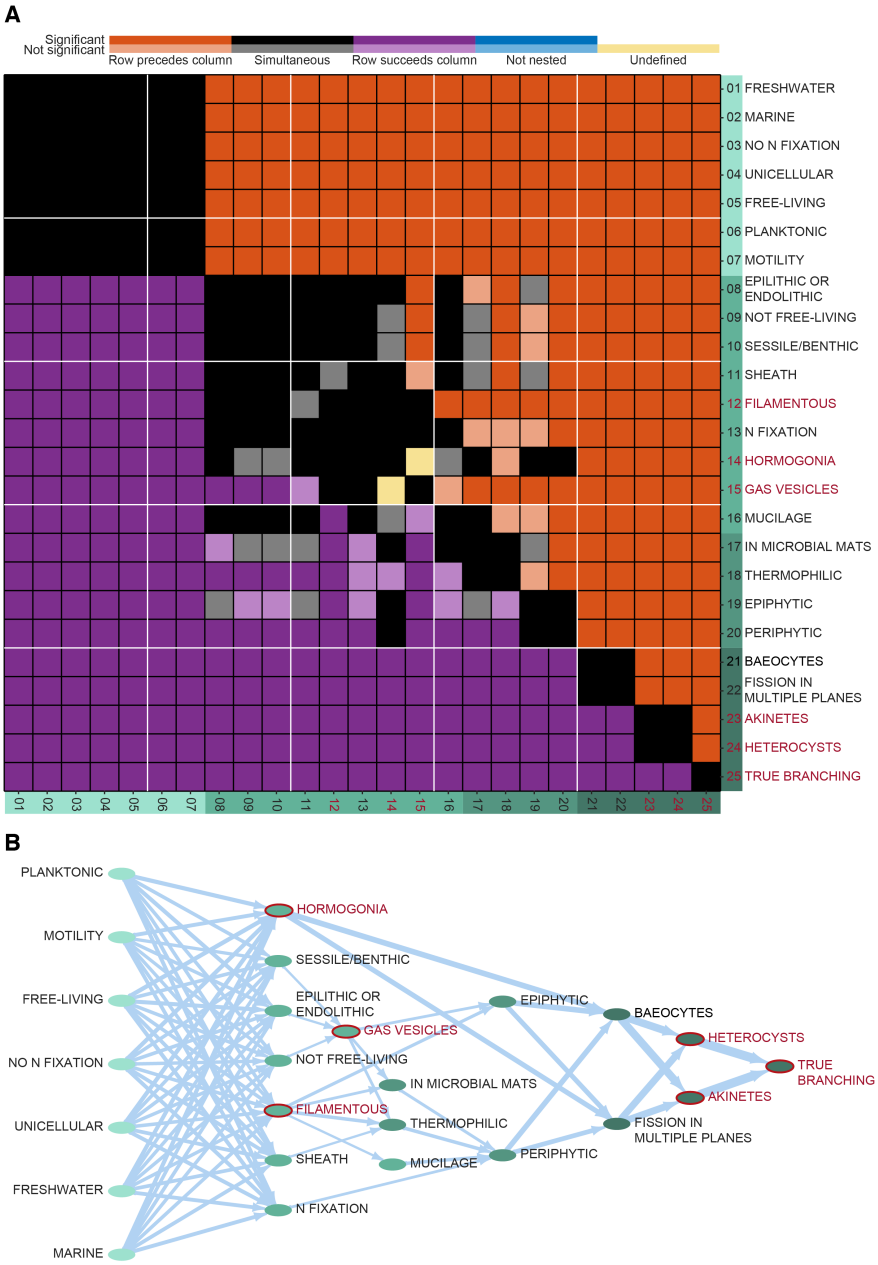

Fig. 3. Trait precedence in the evolution of cyanobacteria. (**A**) Trait-pairs polarity matrix. (**B**) Trait emergence order network. Cells in the matrix are shaded according to the polarity of the row and column traits, and the FDR-corrected significance of the Wilcoxon tests (for trait presence/absence states and test results see Tables S2 and S3). In this dataset there are no cycles of conflicting ordering among the 300 inferred pairwise polarities. Thus, the traits form a *partial order* that is used to determine the trait order in the matrix (**A**) and is visualized as a feed-forward network (**B**). Shades of green mark the four phases of trait emergence. Traits that can be regarded as multicellularity markers in cyanobacteria are labeled in red.

Table 1. Resolution of on-going debates regarding trait precedence in cyanobacterial evolution. P-values are for FDR adjusted Wilcoxon tests (see methods). A naïve voting scheme restricted to common single copy gene trees, as well as a species tree derived from their concatenation, yield the same conclusions (Table S3).

Debate and resolution	Description of debate
Unicellular – Filamentous Trait-pair polarity tests show that the cyanobacterial ancestor was UNICELLULAR and that the FILAMENTOUS morphology arose later (p-value 2.3×10^{-110}).	Whereas early work(*28*) suggested that both morphologies had multiple origins, a subsequent analysis found the ancestor to be unicellular and the filamentous morphology to arise in independent lineages of the cyanobacterial tree(*29*). Another view is that the filamentous morphology evolved early during cyanobacterial evolution and was subsequently lost and regained several times(*30*).
Planktonic - Benthic Our results show that the cyanobacteria ancestor traits include PLANKTONIC, MOTILITY and FREE LIVING (all p-values $<8.2\times10^{-33}$, Table S3).	Whether the cyanobacteria ancestor was planktonic is a matter of debate and opposing views on the topic have been published(*8*, *29*).
N_2 fixation – No N_2 fixation Trait-pair polarity tests show that N FIXATION is a derived trait and that the ancestor of cyanobacteria was lacking the ability to fix N_2 (p-value 2.6×10^{-125}).	Whereas some studies claimed the last cyanobacterial common ancestor to fix N_2(*31*), there are others that concluded that it could not fix N_2 and that cyanobacteria must have acquired this trait several times independently(*29*).
Freshwater – Marine Our results show that there is no evidence for either MARINE or FRESHWATER environments as ancestral or derived habitat (simultaneous polarity, p-value 5.4×10^{-148}).	Some studies suggest that early cyanobacteria lived in freshwater and subsequently diverged into marine environments(*8*, *25*, *29*), whereas others provide evidence in support of a marine origin(*32*). The cyanobacteria ancestor most likely inhabited an aquatic environment and colonized both environments early.
Akinetes – Heterocysts Our results show that AKINETES and HETEROCYSTS emerged simultaneously (p-value 1.8×10^{-124}).	There is a common agreement that these cell types appeared late in cyanobacterial evolution(*31*), but there is a controversy about whether they shared a common ancestor and appeared simultaneously(*33*) or successively(*31*).

Several of the pairwise tests are instrumental in resolving outstanding debates about trait precedence in cyanobacterial evolution (Table 1). Furthermore, the 300 pairwise polarities form a partial order, which can be divided into four temporal phases: (phase i) the

cyanobacteria ancestor (traits 1-7); (phase ii) the transition to multicellular individuality (traits 8-16); (phase iii) the expansion of niche occupation and species interactions (traits 17-20); and (phase iv) the evolution of higher complexity (traits 21-25).

Considering the set of traits in its entirety, the polarity matrix leads to the following scenario for the evolution of multicellularity in cyanobacteria (Fig. 3b). The prime driver of multicellularity in cyanobacteria was the expansion in metabolic capacity offered by N FIXATION (phase ii). This emergence was accompanied by two other cardinal innovations: the emergence of the FILAMENTOUS morphology and the emergence of HORMOGONIA, and thus a reproductive life cycle. Together, these traits form the essential elements of true multicellularity. Secondary traits that played a role in stabilizing the nascent multicellular organism emerged in close succession, and include GAS VESICLES, SHEATH, and MUCILAGE. There followed a cascade of niche expansions and species interactions, and the culmination of complex multicellularity in the form of differentiated cells and patterned multicellularity.

To elaborate on the scenario for cyanobacteria multicellularity evolution, N_2 fixation – the reduction of molecular dinitrogen (N_2) to ammonium (NH_3) – is catalyzed by the enzyme nitrogenase. Whereas present day cyanobacteria, other microorganisms, and most plants are able to take up nitrogen in various combined forms, such as nitrate, ammonium, organic nitrogen, or urea, these combined forms of nitrogen are scarce in most environments (e.g., open oceans or terrestrial habitats (*10*)). Combined nitrogen, which is critical for the biosynthesis of amino and nucleic acids, was likely a limiting resource in the early Earth environment (*11*). Hence, the capability of N FIXATION was key for cyanobacterial radiation into new habitats and subsequent diversification (phases ii and iii).

The realization of the full metabolic potential of N_2 fixation, however, faced the challenge of the incompatibility of nitrogenase with intracellular oxygen (*12*). When the cyanobacterial ancestor first acquired the capacity of N_2 fixation, it must have imposed a

strong selection pressure on the individual cells. The trade-off between photosynthesis and nitrogen fixation led to the evolution of multiple solutions, which are still present in today's cyanobacteria: the circadian rhythm of N_2 fixation in unicellular cyanobacteria (*13*) and the differentiation of the highly specialized heterocyst (*14*).

Theory predicts that within a population of genetically identical unicellular nitrogen fixing cyanobacteria, cell differentiation and phenotypic heterogeneity would have been adaptive if this increased the fitness of the organisms in groups (*15*). In the case of unicellular cyanobacteria this means that cells evolved adhesion and exchanged fixed nitrogen and carbon products within early cell groups such as filaments. Indeed, our results indicate that the FILAMENTOUS morphology emerged simultaneously with N FIXATION (phase ii). Notably, while the species tree shows N FIXATION and FILAMENTOUS to be derived characters, it concludes that the LCA of FILAMENTOUS forms preceded the LCA of N FIXATION. Indeed, it is questionable whether a single species tree can capture these deep phylogenetic relations, as demonstrated in Fig. 1. In contrast, even a naïve voting scheme restricted to common single copy genes is in agreement with our statistical conclusion (Table S3).

In filamentous cyanobacteria, where dividing cells remain linked in a chain, surface-associated growth, SHEATH, and MUCILAGE lead to a localization of cells in close spatial proximity, facilitating metabolite exchange between the individual cells. When compared to the more transient associations in spatially structured communities, such as in extracellular polymeric substance (EPS) imbedded biofilms, the development of filaments opens possibilities for a more direct exchange of molecules with high specificity. Metabolic exchange could have evolved as described for the evolution of metabolic cross-feeding (*16*), as the exchange of carbon and nitrogen against other products is generally common in photosynthetic or nitrogen-fixing organisms (*17*).

The trait HORMOGONIA is inferred to occur simultaneously with the appearance of the FILAMENTOUS morphology. Its co-occurrence with other traits, such as NOT FREE-LIVING BENTHIC/SESSILE, EPILITHIC/ ENDOLYTHIC, SHEATH, and MUCILAGE underline the transition from a planktonic to a benthic lifestyle (phase ii). The differentiation of HORMOGONIA can be induced by environmental stimuli, such as nitrogen deprivation (*18*). After breaking off from the mother filament at the necridia, HORMOGONIA disperse via gliding motility or float thanks to GAS VESICLES, ensuring the reproduction of benthic species (*19*). The differentiation into HORMOGONIA is reversible – they change back to the sessile lifestyle, where they grow into a new vegetative filament (*18*). Here we observe the emergence of a life cycle with two-phases, an important event for the transition to multicellularity (*20*).

Traits that are indicative of higher complexity emerged late in the evolution of cyanobacteria (i.e., phase iv) and conclude the polarity matrix. We observe the occurrence of AKINETES and the irreversibly differentiated HETEROCYSTS. HETEROCYSTS represent not only a morphological adaptation to the obstacle of N_2 fixation under oxic conditions but also an elaborate and highly specialized communication and metabolite exchange system. In *Anabaena* sp., for example, where several hundred cells communicate within a filament, a regular heterocyst formation pattern along the filament must be achieved to guarantee that every cell is adequately supplied with fixed nitrogen compounds (*6*). For this, the inhibitory signaling peptide PatS needs to be distributed along the filament with heterocyst formation occurring only in cells with low PatS concentration (*21*). Whether the exchange of metabolites and regulators happens via the continuous periplasm (*22*) or through septal junctions (*23*) is still not fully resolved.

Another central innovation that occurs in this phase of the polarity matrix is the ability to FISSION IN MULTIPLE PLANES. This trait co-occurred with the ability to produce BAEOCYTES, differentiated cells, which are the reproductive stages in the order Pleurocapsales (*24*).

Notably, baeocyte-forming cyanobacteria, that have been traditionally grouped together with unicellular cyanobacteria (*19*), appear to immediately predate the evolution of akinetes and heterocysts and thus emerge much later than filamentous forms. The ability to fission in multiple planes is known to underlie the TRUE-BRANCHING morphology, where cells in a filament divide in more than one plane, and which is the last trait to emerge in our analysis. Members of the Haphalosiphon/Stigonematales clade having true-branching and multiseriate filament morphology are considered as the latest evolutionary innovations (*19*) and this is further observed in cyanobacterial phylogenies (*25*).

Common features of evolutionary transitions in individuality comprise cooperation between the lower level units (*1*) and the division of labor (*26*). The latter might be of particular advantage, and serve as the driver of the transition to multicellularity when there is a strong trade-off between processes that cannot be performed in a single cell at one time (*15*, *26*). Our current findings support this theory and point to nitrogen fixation, and its incompatibility with photosynthesis, as the trigger for the evolution of multicellularity in cyanobacteria. One open question concerns how the underlying genetics of novel traits, such as the division of labor, arise within a newly emerging multicellular individual. In the case of cyanobacteria multicellularity, as also suggested for animal multicellularity (*27*), we propose that no new genes were required and that higher complexity was achieved by regulatory changes in gene expression patterns. Basic communication and metabolite exchange was pre-existing as single-celled bacteria frequently engage in cell-cell communication and cross-feeding of metabolites via the external environment (*16*). Division of labor between photosynthesis and nitrogen fixation was likely first established by the regulatory mechanism of temporal switching. Once simple forms of division of labor and metabolic exchange existed, the transition into spatial separation in differentiated cells could have evolved mainly by regulatory modifications.

Differentiated cells are one of the hallmarks of complex multicellularity. It is therefore significant that we observe six distinct cell types in cyanobacteria: photosynthetic, hormogonia, necridia, akinetes, baeocytes, and heterocysts. Such a plurality indicates that the underlying regulatory mechanisms are well developed and that their plasticity and adaptability are a matter of course. It is also significant that three of the differentiated cell types, hormogonia, akinetes, and baeocytes, offer novel reproductive potential and the establishment of a multicellular life cycle. Moreover, signs of a nascent developmental plan can be observed in both the distribution of heterocysts along filaments and in the patterning of true branching cyanobacteria. These elements have no fitness value for the individual cell, but are selectable adaptations on the higher level, the filament. The chronology of the evolution of multicellularity in cyanobacteria shows that, once established, multicellular individuality opens new vistas of opportunities.

Materials and Methods

Data

The data underlying this study consists of the genomic sequences and phenotypic traits of 199 cyanobacterial species. These were selected from the available genomes so that the number of represented taxa will be as large as possible and genus-level redundancy will be reduced (Table S2 for the complete list of species).

Phenotypic traits

Phenotypic traits were chosen for their potential relevance to the evolution of multicellularity in cyanobacteria, such as environmental factors that might facilitate multicellularity and markers that are indicative for the transition to multicellularity (Table S1). Information on presence and absence of traits was obtained from the published literature

and from the Pasteur Culture Collection of cyanobacteria, extending the work by Uyeda et al (*8*), and coded as binary trait states. Traits included morphology, nitrogen fixation, freshwater, marine, baeocytes, hormogonia, thermophilic, akinetes, heterocysts, true branching, epi/ endolithic, epiphytic, periphytic, mats, free-living, habitat, sheath, mucilage, gas vesicles, motility, and fission in multiple planes (Table S2).

Protein families and gene trees

The cyanobacteria protein families were constructed from completely sequenced genomes available in RefSeq database (*34*) (ver. May 2016). For the construction of protein families, at the first stage, all protein sequences annotated in the genomes were blasted all-against-all using stand-alone BLAST (*35*) ver. 2.2.26. Protein sequence pairs that were found as reciprocal best BLAST hits (rBBHs) (*36*) with a threshold of E-value $\leq 1x10^{-5}$ were further compared by global alignment using needle (*37*). Sequence pairs having ≥30% identical amino acids were clustered into protein families using the Markov clustering algorithm (MCL) (*38*) ver. 12-135 with the default parameters. By requiring a gene to be present in the genomes of the SynProCya clade and in at least one other major cyanobacterial clade, we identified 1671 gene families that are present on both sides of the cyanobacterial root, i.e., ancient proteins families. Protein sequences of these families were aligned using MAFFT version 7.027b employing the L-INS-i strategy (*39*). Maximum likelihood trees were reconstructed with PhyML version 20120412 (*40*) with parameters -b -4 -v e -m LG -c 4 -s SPR.

Trait ordering

We consider four possible polarizations of a pair of traits ***A*** and ***B***: ***A*** originates before ***B***; ***B*** originates before ***A***; ***A*** and ***B*** emerge simultaneously; and ***A*** and ***B*** are not nested but originate in independent lineages. We infer the pairwise emergence order of the traits by

collecting evidence from a set of phylogenetic trees of independent protein families, and conducting a formal statistical test for the best-supported polarization. Finally, the set of all pairwise polarities is used to derive the order of emergence of all traits (Fig. 2).

Polarization evidence from a single phylogenetic tree

Given an unrooted phylogenetic tree, we first consider all possible rooted versions of the tree. In an *n*-OTU (*Operative Taxonomic Unit*) unrooted tree, the root can be placed on any of the $2n-3$ branches of the tree. For each of the $2n-3$ rooted trees, we label the OTUs by the presence of the two traits ***A*** and ***B***, and infer the most parsimonious *Last Common Ancestor* (LCA) of each trait, assuming a single trait origin and possible trait losses. We then record the polarity induced by the putative root position according to whether the LCAs of ***A*** and ***B*** coincide, are descended one from the other, or are located on independent lineages.

Next we conduct a MAD analysis (*32*), yielding an *Ancestor Deviation* (AD) statistic for every branch of the tree. The AD measure quantifies the amount of lineage rate heterogeneity that is induced by postulating a branch as harboring the root of the tree. We have previously shown that the AD measure provides robust evidence for the inference of the root of the tree. In the current study we do not infer a single root, but use the AD measure to assess the relative strength of alternative rootings of the same tree.

Thus, for each possible root position we obtain a polarity state for ***A*** and ***B*** and a corresponding AD value. For each of the four polarities, we take the minimal AD value as the tree support of that polarity. Note that for certain trees and trait pairs, some polarities may not occur. We differentiate between two such possibilities. First, a certain tree is *Uninformative* regarding a specific trait-pair polarity if the species composition of the tree renders the observation of the polarity impossible in any possible topology. For example, the polarity ***'A precedes B'*** is impossible to observe in trees where the ***A*** OTUs are a subset of the ***B*** OTUs, regardless of the specific topology or root position. In contrast, a certain polarity may be

unobserved in any of the rootings of a specific unrooted tree, while still being a possible observation for a different tree topology. An example of such *Informative absent-observation* is when ***A*** and ***B*** label disjoint sets of OTUs yet the ***'Not nested'*** polarity is not observed in the actual tree topology. In the latter case, the absence of an observation is evidence *against* that specific polarity, and the polarity is assigned the maximal observed AD as its score. When the tree is uninformative regarding a polarity, on the other hand, it is assigned a *'missing'* value, and is excluded from subsequent analyses.

Statistical inference of pairwise polarity

Repeating the preceding procedure for trees derived from all different single-copy proteins families yields a phylogenomic sample of four variables - the AD scores of each of the four polarities for the pair of traits. The four distributions are paired, as each tree brings in a 4-tuple of values, and a significant difference in support values can be tested using the non-parametric Wilcoxon signed-rank test (*41*). In all, we conduct twelve one-sided tests of contrasting polarities, while employing an FDR (*42*) correction for multiple comparisons. A trait-pair is considered polarized if there exists one polarity where all three tests against the other polarities recover significantly lower AD values at the 1% FDR level. In exceptional situations we again encounter polarity contrasts that cannot be tested. For some polarity contrasts the sample size may not meet our threshold (10 paired observations), and the test is conservatively considered valid but not significant with a p-value of 1.0. A second exception occurs when one trait (***A***) is present only in a strict subset of the species that possess the other trait (***B***). In this case it is impossible to observe the polarities ***'not nested'*** and ***'A precedes B'*** in any tree, and we restrict the testing to the single contrast ***'B precedes A'*** versus ***'Simultaneous'***.

The pairwise polarity inference is applied to each pair of traits and summarized in a trait-pair polarity matrix. We again apply the FDR correction, this time over all trait-pairs and

polarity contrasts. In the present study, with 25 traits, we apply FDR over 3,480 tests. To derive an ordering of the traits, we apply 'Topological sort' (*43*) to the significant polarities of type ***'A precedes B'***, or vice versa. In the present study the significant polarities form a partial order, i.e., there are no self-contradicting precedence cycles, and the topological sorting order is used to order the polarities matrix and to reduce it to a feed-forward network (Fig. 2).

Comparison to traditional approaches

We compare our analysis to the traditional type of analysis that considers a single species tree derived from single-copy genes present in all studied taxa. In our dataset there are 17 common single-copy genes with a total alignment length of 3744 columns. We reconstructed a species tree using iqtree version 1.5.5 *(44)* with the '-sp -mset LG' model selection options and a bootstrap analysis with 100 replicates. The trait polarities derived from the species tree, as well as a simple voting scheme of the 17 common genes are reported in Table S3. We visualized the uncertainties in the species tree by a super-network of the 100 bootstrap replicates using splitstree4 *(45)* (Fig. 1 and its annotation in Fig. S1).

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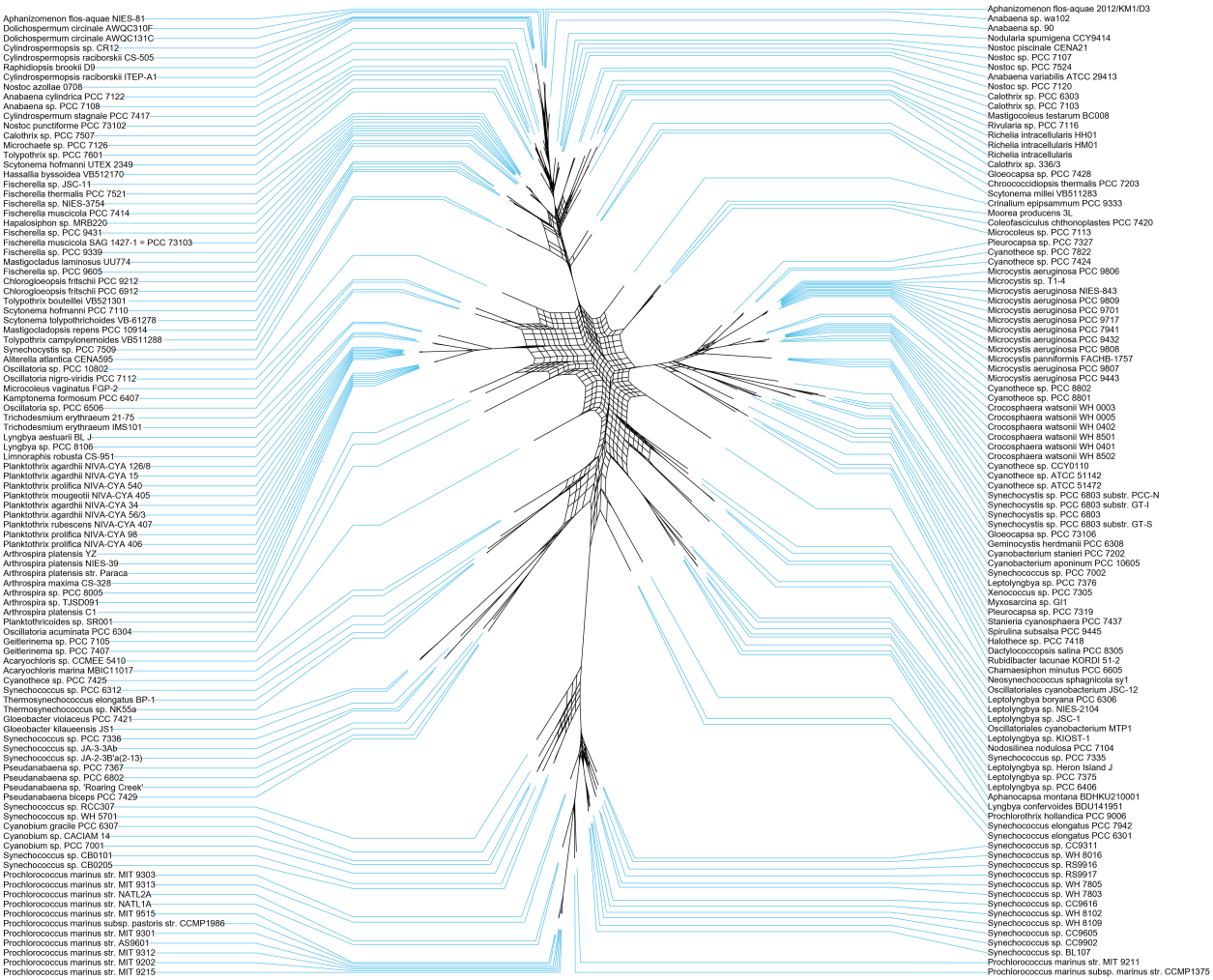

Fig. S1. Genome identifiers for the phylogenomic network of Fig. 1.

Table S1.
Description of cyanobacterial cell types, morphological and physiological traits, their habitat and life style.

Cell types	
Vegetative cells	Photosynthetic cells.
HORMOGONIA*	Motile reproductive cells that result from repeated rounds of fission without intermittent growth phases. They break of the mother filament, ensuring the reproduction and dispersal of benthic species.
Necridia*	Dead cells resulting from PCD for hormogonia release.
HETEROCYSTS*	Thick-walled cells that are specialized in fixing N_2.
AKINETES*	Thick-walled, spore-like cells that provide reproduction, dormancy, and resilience.
BAEOCYTES*	Reproductive cells that result from repeated rounds of fission without intermittent growth phases.
Morphological and physiological traits	
UNICELLULAR	Single-celled morphology. After cell division cells separate.
FILAMENTOUS*	Multi-celled morphology. Cells remain attached after cell division.
NITROGEN FIXATION	Fixation of N_2 into ammonium.
SHEATH	Part of the cell envelope, located outside the cell wall.
MUCILAGE	Part of the envelope, located outside the cell wall, comprised of EPS, without a defined structure.
GAS VESICLES*	Intracellular gas-filled chambers for regulating buoyancy in the water column.
MOTILITY	Movement across surfaces or through a liquid medium.
FISSION IN MULTIPLE PLANES	Cell division in two or three perpendicular planes.
TRUE BRANCHING*	Fission in multiple planes leads to branches that remain attached to the main filament.
Habitat and life style	
FRESHWATER	Aquatic environments with salinity between 0-0.5ppt.
MARINE	Aquatic environments with salinity between 30–50ppt.
THERMOPHILIC	Optimal growth temperature above 45°.
PLANKTONIC	Organism that lives in the plankton (not attached).
SESSILE/ BENTHIC	Attachment to a substrate.
MATS	Growth inside thick, laminated, microbial structures.
FREE-LIVING	Organism that lives autonomously, in contrast to:
NOT FREE-LIVING	Organism that lives in a symbiotic relationship.
EPILITHIC/ ENDOLITHIC	Growth on or inside rocky substrates.
EPIPHYTIC	Growth on plants.
PERIPHYTIC	Attachment to underwater substrates.

* Multicellularity markers: traits that are adaptations on the level of the filament.
Small caps indicate the traits that have been used in the analysis.

Table S2. Phenotypic traits in cyanobacteria.

Presence absence matrix of 25 traits in 199 species. See table S1 for trait definition. Numbered uppercase trait-state names are as reported in Fig. 2. 'Phase' corresponds to green shades and 'Group adaptation' to red labels in Fig. 2.

	Trait	01 FRESHWATER	02 MARINE	03 NO N FIXATION	04 UNICELLULAR	05 FREE-LIVING	06 PLANKTONIC	07 MOTILITY	08 EPILITHIC OR ENDOLITHIC	09 NOT FREE-LIVING	10 SESSILE/ BENTHIC	11 SHEATH	12 FILAMENTOUS	13 N FIXATION	14 HORMOGONIA	15 GAS VESICLES	16 MUCILAGE	17 IN MICROBIAL MATS	18 THERMOPHILIC	19 EPIPHYTIC	20 PERIPHYTIC	21 BAEOCYTES	22 FISSION IN MULTIPLE PLANES	23 AKINETES	24 HETEROCYSTS	25 TRUE BRANCHING
	Phase during cyanobacterial evolution	i	i	i	i	i	i	i	ii	ii	ii	ii	ii	ii	ii	ii	ii	iii	iii	iii	iii	iv	iv	iv	iv	iv
	Group adaptation												*		*	*								*	*	*
Assemby accession	**Species**																									
GCA_000346485.2	Scytonema hofmanni PCC 7110	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	1	0
GCA_000012525.1	Synechococcus elongatus PCC 7942	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000010625.1	Microcystis aeruginosa NIES-843	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
GCA_000020025.1	Nostoc punctiforme PCC 73102	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0	1	1	0
GCA_000011345.1	Thermosynechococcus elongatus BP-1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
GCA_000014265.1	Trichodesmium erythraeum IMS101	0	1	0	0	0	1	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0
GCA_000011385.1	Gloeobacter violaceus PCC 7421	1	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
GCA_000167195.1	Crocosphaera watsonii WH 8501	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000018105.1	Acaryochloris marina MBIC11017	0	1	1	1	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
GCA_000210375.1	Arthrospira platensis NIES-39	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000340565.3	Nodularia spumigena CCY9414	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0
GCA_000155555.1	Coleofasciculus chthonoplastes PCC 7420	0	1	1	0	0	0	1	1	1	1	1	1	0	1	0	1	0	0	1	1	0	0	0	0	0
GCA_000204075.1	Anabaena variabilis ATCC 29413	1	0	0	0	0	0	1	1	1	0	0	1	1	0	1	1	1	0	1	0	0	0	1	1	0
GCA_000173555.1	Arthrospira maxima CS-328	0	1	1	0	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
GCA_000196515.1	Nostoc azollae 0708	1	0	0	0	0	0	1	0	1	1	1	1	1	1	0	1	0	0	0	0	0	0	1	1	0
GCA_000175835.1	Cylindrospermopsis raciborskii CS-505	1	0	0	0	1	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	1	0
GCA_000175855.1	Raphidiopsis brookii D9	1	0	1	0	1	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0
GCA_000214075.2	Microcoleus vaginatus FGP-2	1	0	0	0	0	0	1	1	1	1	1	1	1	1	0	1	0	0	1	1	0	0	0	0	0
GCA_000309945.1	Oscillatoriales cyanobacterium JSC-12	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0
GCA_000464785.1	Planktothrix rubescens NIVA-CYA 407	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000317125.1	Chroococcidiopsis thermalis PCC 7203	1	0	0	1	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	1	1	1	0	0	0
GCA_000317655.1	Cyanobacterium stanieri PCC 7202	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000317695.1	Anabaena cylindrica PCC 7122	1	0	0	0	1	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0
GCA_000309385.1	Nodosilinea nodulosa PCC 7104	1	1	0	0	0	0	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000426925.1	Dolichospermum circinale AWQC310F	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0
GCA_000710505.1	Planktothrix agardhii NIVA-CYA 126/8	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000007925.1	Prochlorococcus marinus subsp. marinus str. CCMP1375	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000332235.1	Geminocystis herdmanii PCC 6308	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0

Assemby accession	Species	01 FRESHWATER	02 MARINE	03 NO N FIXATION	04 UNICELLULAR	05 FREE-LIVING	06 PLANKTONIC	07 MOTILITY	08 EPILITHIC OR ENDOLITHIC	09 NOT FREE-LIVING	10 SESSILE/ BENTHIC	11 SHEATH	12 FILAMENTOUS	13 N FIXATION	14 HORMOGONIA	15 GAS VESICLES	16 MUCILAGE	17 IN MICROBIAL MATS	18 THERMOPHILIC	19 EPIPHYTIC	20 PERIPHYTIC	21 BAEOCYTES	22 FISSION IN MULTIPLE PLANES	23 AKINETES	24 HETEROCYSTS	25 TRUE BRANCHING
	Phase during cyanobacterial evolution	i	i	i	i	i	i	i	ii	ii	ii	ii	ii	ii	ii	ii	ii	iii	iii	iii	iii	iv	iv	iv	iv	iv
	Group adaptation												*		*	*								*	*	*
GCA_000332315.1	Prochlorothrix hollandica PCC 9006	1	0	1	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
GCA_000317285.1	Chlorogloeopsis fritschii PCC 6912	1	0	0	0	1	0	1	0	0	1	1	1	1	1	0	1	0	1	0	0	0	1	1	1	0
GCA_000317225.1	Fischerella thermalis PCC 7521	1	0	0	0	0	0	1	1	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	1	1
GCA_000317245.1	Fischerella muscicola SAG 1427-1 = PCC 73103	1	0	0	0	0	0	1	1	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	1	1
GCA_000350105.1	Richelia intracellularis HH01	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0
GCA_000316515.1	Cyanobium gracile PCC 6307	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000317615.1	Dactylococcopsis salina PCC 8305	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
GCA_000317105.1	Oscillatoria acuminata PCC 6304	1	0	1	0	0	0	0	1	1	1	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0
GCA_000315565.1	Mastigocladopsis repens PCC 10914	1	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1
GCA_000317535.1	Cylindrospermum stagnale PCC 7417	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0
GCA_000317495.1	Crinalium epipsammum PCC 9333	1	0	1	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000332215.1	Pseudanabaena biceps PCC 7429	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0
GCA_000317575.1	Stanieria cyanosphaera PCC 7437	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	1	1	1	0	0	0
GCA_000353285.1	Leptolyngbya boryana PCC 6306	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
GCA_000012505.1	Synechococcus sp. CC9902	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_001456025.1	Mastigocoleus testarum BC008	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1
GCA_000482245.1	Leptolyngbya sp. Heron Island J	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000009705.1	Nostoc sp. PCC 7120	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0	1	1	0
GCA_000009725.1	Synechocystis sp. PCC 6803	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
GCA_000734895.2	Calothrix sp. 336/3	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0
GCA_000332335.1	Oscillatoria sp. PCC 10802	1	0	1	0	0	0	0	1	1	1	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0
GCA_000317065.1	Pseudanabaena sp. PCC 7367	0	1	1	0	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
GCA_000317045.1	Geitlerinema sp. PCC 7407	1	1	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0
GCA_000312705.1	Anabaena sp. 90	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0
GCA_000332295.1	Microchaete sp. PCC 7126	1	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	1	0	0	1	1	0
GCA_000517105.1	Fischerella sp. PCC 9605	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1
GCA_000317515.1	Microcoleus sp. PCC 7113	1	0	0	0	0	0	1	1	1	1	1	1	1	1	0	1	0	0	1	1	0	0	0	0	0
GCA_000317025.1	Pleurocapsa sp. PCC 7327	1	0	0	1	0	0	1	1	1	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0
GCA_000317555.1	Gloeocapsa sp. PCC 7428	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	1	1	0	0	1	0	0	0
GCA_000332055.1	Xenococcus sp. PCC 7305	0	1	0	1	0	0	0	1	1	1	1	0	1	0	0	1	0	0	1	0	1	1	0	0	0
GCA_000169095.1	Lyngbya sp. PCC 8106	0	1	0	0	0	0	1	0	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0
GCA_000238775.2	Acaryochloris sp. CCMEE 5410	0	1	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
GCA_000017845.1	Cyanothece sp. ATCC 51142	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0

Assemby accession	Species	01 FRESHWATER	02 MARINE	03 NO N FIXATION	04 UNICELLULAR	05 FREE-LIVING	06 PLANKTONIC	07 MOTILITY	08 EPILITHIC OR ENDOLITHIC	09 NOT FREE-LIVING	10 SESSILE/ BENTHIC	11 SHEATH	12 FILAMENTOUS	13 N FIXATION	14 HORMOGONIA	15 GAS VESICLES	16 MUCILAGE	17 IN MICROBIAL MATS	18 THERMOPHILIC	19 EPIPHYTIC	20 PERIPHYTIC	21 BAEOCYTES	22 FISSION IN MULTIPLE PLANES	23 AKINETES	24 HETEROCYSTS	25 TRUE BRANCHING
	Phase during cyanobacterial evolution	i	i	i	i	i	i	i	ii	ii	ii	ii	ii	ii	ii	ii	ii	iii	iii	iii	iii	iv	iv	iv	iv	iv
	Group adaptation												*		*	*								*	*	*
GCA_000155635.1	Cyanobium sp. PCC 7001	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000300115.1	Tolypothrix sp. PCC 7601	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0
GCA_000317635.1	Halothece sp. PCC 7418	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
GCA_000973065.1	Arthrospira sp. PCC 8005	0	1	1	0	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
GCA_000316665.1	Rivularia sp. PCC 7116	0	1	0	0	0	0	1	1	1	1	1	1	1	1	0	1	0	0	1	1	0	0	0	1	0
GCA_000297435.1	Microcystis sp. T1-4	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
GCA_000211815.1	Moorea producens 3L	0	1	1	0	0	0	1	1	1	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0
GCA_000317145.1	Chamaesiphon minutus PCC 6605	1	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
GCA_000317675.1	Cyanobacterium aponinum PCC 10605	1	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
GCA_000317475.1	Oscillatoria nigro-viridis PCC 7112	1	0	1	0	0	0	0	1	1	1	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0
GCA_000473895.1	Rubidibacter lacunae KORDI 51-2	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000332155.1	Kamptonema formosum PCC 6407	1	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0
GCA_000314005.1	Spirulina subsalsa PCC 9445	0	0	1	0	0	0	1	0	1	1	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0
GCA_000464765.1	Planktothrix prolifica NIVA-CYA 406	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000478195.2	Lyngbya aestuarii BL J	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000505665.1	Thermosynechococcus sp. NK55a	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
GCA_000582685.1	Scytonema hofmanni UTEX 2349	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0
GCA_000464745.1	Planktothrix mougeotii NIVA-CYA 405	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000484535.1	Gloeobacter kilaueensis JS1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000521175.1	Aphanizomenon flos-aquae NIES-81	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0
GCA_000180455.1	Oscillatoria sp. PCC 6506	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0
GCA_000756305.1	Myxosarcina sp. GI1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
GCA_000760695.2	Tolypothrix bouteillei VB521301	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0
GCA_000775285.1	Neosynechococcus sphagnicola sy1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000817735.1	Scytonema millei VB511283	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0
GCA_000817745.1	Aphanocapsa montana BDHKU210001	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000817785.1	Hassallia byssoidea VB512170	1	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0
GCA_000817775.1	Lyngbya confervoides BDU141951	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000828075.1	Tolypothrix campylonemoides VB511288	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0
GCA_000828085.1	Scytonema tolypothrichoides VB-61278	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0
GCA_000934435.1	Mastigocladus laminosus UU774	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	1	1
GCA_000952155.1	Aliterella atlantica CENA595	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
GCA_000972705.2	Limnoraphis robusta CS-951	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0

Assemby accession	Species	01 FRESHWATER	02 MARINE	03 NO N FIXATION	04 UNICELLULAR	05 FREE-LIVING	06 PLANKTONIC	07 MOTILITY	08 EPILITHIC OR ENDOLITHIC	09 NOT FREE-LIVING	10 SESSILE/ BENTHIC	11 SHEATH	12 FILAMENTOUS	13 N FIXATION	14 HORMOGONIA	15 GAS VESICLES	16 MUCILAGE	17 IN MICROBIAL MATS	18 THERMOPHILIC	19 EPIPHYTIC	20 PERIPHYTIC	21 BAEOCYTES	22 FISSION IN MULTIPLE PLANES	23 AKINETES	24 HETEROCYSTS	25 TRUE BRANCHING
	Trait																									
	Phase during cyanobacterial evolution	i	i	i	i	i	i	i	ii	ii	ii	ii	ii	ii	ii	ii	ii	iii	iii	iii	iii	iv	iv	iv	iv	iv
	Group adaptation												*		*	*								*	*	*
GCA_001264245.1	Microcystis panniformis FACHB-1757	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_001275395.1	Hapalosiphon sp. MRB220	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1
GCA_001276715.1	Planktothricoides sp. SR001	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
GCA_001298445.1	Nostoc piscinale CENA21	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0
GCA_001432185.1	Cylindrospermopsis sp. CR12	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0
GCA_001482745.1	Oscillatoriales cyanobacterium MTP1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
GCA_000789435.1	Aphanizomenon flos-aquae 2012/KM1/D3	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0
GCA_000464805.1	Planktothrix prolifica NIVA-CYA 540	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000974245.1	Arthrospira sp. TJSD091	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000708525.1	Cyanobium sp. CACIAM 14	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000021805.1	Cyanothece sp. PCC 8801	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000332035.1	Gloeocapsa sp. PCC 73106	1	0	1	1	0	0	1	1	1	1	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0
GCA_000332195.1	Pleurocapsa sp. PCC 7319	0	1	1	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
GCA_001548455.1	Fischerella sp. NIES-3754	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	1	1
GCA_000332135.1	Anabaena sp. PCC 7108	1	0	0	0	0	0	1	1	1	0	0	1	1	0	0	1	1	0	1	0	0	0	1	1	0
GCA_000332355.1	Geitlerinema sp. PCC 7105	0	1	1	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0
GCA_000332175.1	Pseudanabaena sp. PCC 6802	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0
GCA_000316575.1	Calothrix sp. PCC 7507	1	0	0	0	0	0	1	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0	1	1	0
GCA_000332075.2	Synechocystis sp. PCC 7509	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
GCA_000316645.1	Nostoc sp. PCC 7524	1	0	0	0	0	0	1	1	1	1	1	1	0	1	0	1	0	0	1	0	0	0	1	0	0
GCA_000332095.2	Leptolyngbya sp. PCC 6406	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0
GCA_000013205.1	Synechococcus sp. JA-3-3Ab	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
GCA_000350125.1	Richelia intracellularis HM01	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0
GCA_000317205.1	Fischerella muscicola PCC 7414	1	0	0	0	0	0	1	1	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	1	1
GCA_000317265.1	Chlorogloeopsis fritschii PCC 9212	1	0	0	0	1	0	1	0	0	1	1	1	1	1	0	1	0	1	0	0	0	1	1	1	0
GCA_000464665.1	Planktothrix agardhii NIVA-CYA 15	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000426905.1	Dolichospermum circinale AWQC131C	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0
GCA_001586755.1	Cylindrospermopsis raciborskii ITEP-A1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0
GCA_001611905.1	Arthrospira platensis YZ	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000235665.2	Crocosphaera watsonii WH 0003	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
GCA_000963755.2	Trichodesmium erythraeum 21-75	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000010065.1	Synechococcus elongatus PCC 6301	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000011465.1	Prochlorococcus marinus subsp. pastoris str. CCMP1986	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Assemby accession	Species	01 FRESHWATER	02 MARINE	03 NO N FIXATION	04 UNICELLULAR	05 FREE-LIVING	06 PLANKTONIC	07 MOTILITY	08 EPILITHIC OR ENDOLITHIC	09 NOT FREE-LIVING	10 SESSILE/ BENTHIC	11 SHEATH	12 FILAMENTOUS	13 N FIXATION	14 HORMOGONIA	15 GAS VESICLES	16 MUCILAGE	17 IN MICROBIAL MATS	18 THERMOPHILIC	19 EPIPHYTIC	20 PERIPHYTIC	21 BAEOCYTES	22 FISSION IN MULTIPLE PLANES	23 AKINETES	24 HETEROCYSTS	25 TRUE BRANCHING
	Trait	01 FRESHWATER	02 MARINE	03 NO N FIXATION	04 UNICELLULAR	05 FREE-LIVING	06 PLANKTONIC	07 MOTILITY	08 EPILITHIC OR ENDOLITHIC	09 NOT FREE-LIVING	10 SESSILE/ BENTHIC	11 SHEATH	12 FILAMENTOUS	13 N FIXATION	14 HORMOGONIA	15 GAS VESICLES	16 MUCILAGE	17 IN MICROBIAL MATS	18 THERMOPHILIC	19 EPIPHYTIC	20 PERIPHYTIC	21 BAEOCYTES	22 FISSION IN MULTIPLE PLANES	23 AKINETES	24 HETEROCYSTS	25 TRUE BRANCHING
	Phase during cyanobacterial evolution	i	i	i	i	i	i	i	ii	ii	ii	ii	ii	ii	ii	ii	ii	iii	iii	iii	iii	iv	iv	iv	iv	iv
	Group adaptation												*		*	*								*	*	*
GCA_000011485.1	Prochlorococcus marinus str. MIT 9313	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000307995.2	Microcystis aeruginosa PCC 9432	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
GCA_001039555.1	Crocosphaera watsonii WH 8502	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000307915.1	Arthrospira platensis C1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000464725.1	Planktothrix agardhii NIVA-CYA 34	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000613065.1	Richelia intracellularis	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0
GCA_000013225.1	Synechococcus sp. JA-2-3B'a(2-13)	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
GCA_000733415.1	Leptolyngbya sp. JSC-1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0
GCA_000316625.1	Nostoc sp. PCC 7107	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0	1	1	0
GCA_000270265.1	Synechocystis sp. PCC 6803 substr. GT-S	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
GCA_000317435.1	Calothrix sp. PCC 6303	1	0	0	0	0	0	1	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	1	0
GCA_001402795.1	Pseudanabaena sp. 'Roaring Creek'	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_001277295.1	Anabaena sp. wa102	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0
GCA_000315585.1	Fischerella sp. PCC 9339	1	0	0	0	0	0	1	1	1	1	0	1	1	1	0	1	0	0	1	0	0	1	1	1	1
GCA_000021825.1	Cyanothece sp. PCC 7424	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
GCA_000464845.1	Planktothrix prolifica NIVA-CYA 98	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000022045.1	Cyanothece sp. PCC 7425	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
GCA_000447295.1	Fischerella sp. PCC 9431	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1
GCA_000331305.1	Calothrix sp. PCC 7103	1	0	0	0	0	0	1	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	1	0
GCA_000284135.1	Synechocystis sp. PCC 6803 substr. GT-I	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
GCA_000763385.1	Leptolyngbya sp. KIOST-1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000014585.1	Synechococcus sp. CC9311	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000464825.1	Planktothrix agardhii NIVA-CYA 56/3	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000175415.3	Arthrospira platensis str. Paraca	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
GCA_001039615.1	Crocosphaera watsonii WH 0401	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000312165.1	Microcystis aeruginosa PCC 9717	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
GCA_000012465.1	Prochlorococcus marinus str. NATL2A	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000012645.1	Prochlorococcus marinus str. MIT 9312	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000312185.1	Microcystis aeruginosa PCC 9443	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
GCA_001039635.1	Crocosphaera watsonii WH 0402	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000019485.1	Synechococcus sp. PCC 7002	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000316605.1	Leptolyngbya sp. PCC 7376	0	1	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0
GCA_000284215.1	Synechocystis sp. PCC 6803 substr. PCC-N	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

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	Phase during cyanobacterial evolution	i	i	i	i	i	i	i	ii	ii	ii	ii	ii	ii	ii	ii	ii	iii	iii	iii	iii	iv	iv	iv	iv	iv
	Group adaptation												*		*	*								*	*	*
GCA_000231365.2	Fischerella sp. JSC-11	1	0	0	0	0	0	1	1	1	1	0	1	1	1	0	1	0	1	1	0	0	1	1	1	1
GCA_000169335.1	Cyanothece sp. CCY0110	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
GCA_000147335.1	Cyanothece sp. PCC 7822	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
GCA_000316115.1	Leptolyngbya sp. PCC 7375	0	1	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0
GCA_001050835.1	Crocosphaera watsonii WH 0005	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000312205.1	Microcystis aeruginosa PCC 7941	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
GCA_000015645.1	Prochlorococcus marinus str. AS9601	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000015665.1	Prochlorococcus marinus str. MIT 9515	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000312225.1	Microcystis aeruginosa PCC 9807	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
GCA_000063505.1	Synechococcus sp. WH 7803	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_001485215.1	Leptolyngbya sp. NIES-2104	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
GCA_000024045.1	Cyanothece sp. PCC 8802	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
GCA_000231425.3	Cyanothece sp. ATCC 51472	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000063525.1	Synechococcus sp. RCC307	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000312245.1	Microcystis aeruginosa PCC 9808	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
GCA_000015965.1	Prochlorococcus marinus str. MIT 9301	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000018065.1	Prochlorococcus marinus str. MIT 9215	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000312265.1	Microcystis aeruginosa PCC 9809	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
GCA_000515235.1	Synechococcus sp. CC9616	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000153045.1	Synechococcus sp. WH 5701	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000312285.1	Microcystis aeruginosa PCC 9701	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
GCA_000018585.1	Prochlorococcus marinus str. MIT 9211	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000312725.1	Microcystis aeruginosa PCC 9806	1	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
GCA_000153065.1	Synechococcus sp. RS9917	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000153285.1	Synechococcus sp. WH 7805	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000015685.1	Prochlorococcus marinus str. NATL1A	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000153825.1	Synechococcus sp. RS9916	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000155595.1	Synechococcus sp. PCC 7335	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000158595.1	Prochlorococcus marinus str. MIT 9202	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000179235.1	Synechococcus sp. CB0101	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000179255.1	Synechococcus sp. CB0205	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000195975.1	Synechococcus sp. WH 8102	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000316685.1	Synechococcus sp. PCC 6312	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Trait	01 FRESHWATER	02 MARINE	03 NO N FIXATION	04 UNICELLULAR	05 FREE-LIVING	06 PLANKTONIC	07 MOTILITY	08 EPILITHIC OR ENDOLITHIC	09 NOT FREE-LIVING	10 SESSILE/ BENTHIC	11 SHEATH	12 FILAMENTOUS	13 N FIXATION	14 HORMOGONIA	15 GAS VESICLES	16 MUCILAGE	17 IN MICROBIAL MATS	18 THERMOPHILIC	19 EPIPHYTIC	20 PERIPHYTIC	21 BAEOCYTES	22 FISSION IN MULTIPLE PLANES	23 AKINETES	24 HETEROCYSTS	25 TRUE BRANCHING
	Phase during cyanobacterial evolution	**i**	**i**	**i**	**i**	**i**	**i**	**i**	**ii**	**ii**	**ii**	**ii**	**ii**	**ii**	**ii**	**ii**	**ii**	**iii**	**iii**	**iii**	**iii**	**iv**	**iv**	**iv**	**iv**	**iv**
	Group adaptation												*****		*****	*****								*****	*****	*****
Assemby accession	**Species**																									
GCA_000332275.1	Synechococcus sp. PCC 7336	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000012625.1	Synechococcus sp. CC9605	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000161795.2	Synechococcus sp. WH 8109	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000015705.1	Prochlorococcus marinus str. MIT 9303	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000153805.1	Synechococcus sp. BL107	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCA_000230675.2	Synechococcus sp. WH 8016	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table S3. Trait-pair polarity tests.

Wilcoxon signed-rank tests p-values and number of trees are for the *least* significant test for the inferred polarity. False discovery rate (FDR) are p-values adjusted over 3480 tests (300 pairs with 12 or 2 tests each, see Methods). Statistics that refer to Table 1 are marked according to the order of debates in the table.

This highlighting: Non significant

This highlighting: species tree discordance

Species tree inferred from 17 common single-copy genes, and the naive voting of the corresponding gene trees.

Trait A	Trait B	Table 1 debate	Trait pair polarity	False discovery rate	Wilcoxon p-value	Number of tests	Number of trees	Polarity in species tree	Polarity in 17 common single-copy gene trees: A preceds B	Simultaneous	B preceds A	Not nested
01 FRESHWATER	02 MARINE	(4)	Simultaneous	5.4E-148	8.3E-149	12	1463	Simultaneous	0	17	0	0
01 FRESHWATER	03 NO N FIXATION		Simultaneous	4.4E-155	3.1E-156	12	1425	Simultaneous	0	17	0	0
01 FRESHWATER	04 UNICELLULAR		Simultaneous	2.6E-156	1.7E-157	12	1456	Simultaneous	0	17	0	0
01 FRESHWATER	05 FREE-LIVING		Simultaneous	5.6E-125	2.3E-125	12	1459	Simultaneous	1	16	0	0
01 FRESHWATER	06 PLANKTONIC		Simultaneous	8.4E-123	3.6E-123	12	1467	Simultaneous	1	16	0	0
01 FRESHWATER	07 MOTILITY		Simultaneous	9.0E-68	6.0E-68	12	1344	Simultaneous	1	16	0	0
01 FRESHWATER	08 EPILITHIC OR ENDOLITHIC		A preceds B	4.7E-84	3.0E-84	12	1314	A preceds B	15	2	0	0
01 FRESHWATER	09 NOT FREE-LIVING		A preceds B	2.5E-88	1.5E-88	12	1329	A preceds B	13	4	0	0
01 FRESHWATER	10 SESSILE/BENTHIC		A preceds B	1.9E-92	1.2E-92	12	1317	A preceds B	13	4	0	0
01 FRESHWATER	11 SHEATH		A preceds B	4.2E-115	2.0E-115	12	1271	A preceds B	15	2	0	0
01 FRESHWATER	12 FILAMENTOUS		A preceds B	4.3E-65	2.9E-65	12	1353	A preceds B	14	3	0	0
01 FRESHWATER	13 N FIXATION		A preceds B	1.1E-78	7.1E-79	12	1370	A preceds B	15	2	0	0
01 FRESHWATER	14 HORMOGONIA		A preceds B	1.0E-100	6.0E-101	12	1337	A preceds B	15	2	0	0
01 FRESHWATER	15 GAS VESICLES		A preceds B	1.4E-120	6.3E-121	12	1233	A preceds B	14	3	0	0
01 FRESHWATER	16 MUCILAGE		A preceds B	5.3E-104	2.9E-104	12	1309	A preceds B	15	2	0	0
01 FRESHWATER	17 IN MICROBIAL MATS		A preceds B	2.3E-139	5.8E-140	12	1080	A preceds B	13	4	0	0
01 FRESHWATER	18 THERMOPHILIC		A preceds B	1.2E-135	3.3E-136	2	1046	A preceds B	13	4	0	0
01 FRESHWATER	19 EPIPHYTIC		A preceds B	5.0E-134	1.6E-134	12	1216	A preceds B	15	2	0	0
01 FRESHWATER	20 PERIPHYTIC		A preceds B	5.9E-147	9.6E-148	12	1067	A preceds B	15	2	0	0
01 FRESHWATER	21 BAEOCYTES		A preceds B	6.4E-153	6.4E-154	12	936	A preceds B	15	2	0	0
01 FRESHWATER	22 FISSION IN MULTIPLE PLANES		A preceds B	2.2E-154	1.6E-155	12	1165	A preceds B	15	2	0	0
01 FRESHWATER	23 AKINETES		A preceds B	1.4E-156	8.2E-158	12	1116	A preceds B	17	0	0	0
01 FRESHWATER	24 HETEROCYSTS		A preceds B	2.1E-153	1.9E-154	12	1156	A preceds B	17	0	0	0
01 FRESHWATER	25 TRUE BRANCHING		A preceds B	1.0E-136	2.8E-137	12	827	A preceds B	17	0	0	0
02 MARINE	03 NO N FIXATION		Simultaneous	1.0E-180	6.7E-183	12	1427	Simultaneous	0	17	0	0
02 MARINE	04 UNICELLULAR		Simultaneous	4.8E-177	4.8E-179	12	1408	Simultaneous	0	17	0	0
02 MARINE	05 FREE-LIVING		Simultaneous	3.0E-134	9.3E-135	12	1417	Simultaneous	1	16	0	0
02 MARINE	06 PLANKTONIC		Simultaneous	4.5E-142	9.8E-143	12	1424	Simultaneous	1	16	0	0
02 MARINE	07 MOTILITY		Simultaneous	9.8E-66	6.6E-66	12	1327	Simultaneous	1	16	0	0
02 MARINE	08 EPILITHIC OR ENDOLITHIC		A preceds B	5.7E-105	3.1E-105	12	1306	A preceds B	15	2	0	0
02 MARINE	09 NOT FREE-LIVING		A preceds B	2.9E-90	1.8E-90	12	1333	A preceds B	13	4	0	0
02 MARINE	10 SESSILE/BENTHIC		A preceds B	4.2E-93	2.5E-93	12	1320	A preceds B	13	4	0	0
02 MARINE	11 SHEATH		A preceds B	3.2E-122	1.4E-122	12	1272	A preceds B	15	2	0	0
02 MARINE	12 FILAMENTOUS		A preceds B	4.4E-83	2.8E-83	12	1361	A preceds B	14	3	0	0
02 MARINE	13 N FIXATION		A preceds B	5.3E-100	3.1E-100	12	1359	A preceds B	15	2	0	0
02 MARINE	14 HORMOGONIA		A preceds B	4.7E-113	2.4E-113	12	1325	A preceds B	15	2	0	0
02 MARINE	15 GAS VESICLES		A preceds B	7.6E-138	2.0E-138	12	1213	A preceds B	14	3	0	0
02 MARINE	16 MUCILAGE		A preceds B	7.0E-117	3.2E-117	12	1293	A preceds B	15	2	0	0
02 MARINE	17 IN MICROBIAL MATS		A preceds B	1.3E-137	3.5E-138	12	1079	A preceds B	13	4	0	0
02 MARINE	18 THERMOPHILIC		A preceds B	1.9E-140	4.3E-141	12	1033	A preceds B	13	4	0	0
02 MARINE	19 EPIPHYTIC		A preceds B	1.3E-142	2.7E-143	12	1200	A preceds B	15	2	0	0
02 MARINE	20 PERIPHYTIC		A preceds B	6.7E-148	1.1E-148	12	1069	A preceds B	15	2	0	0
02 MARINE	21 BAEOCYTES		A preceds B	5.1E-151	5.9E-152	12	967	A preceds B	15	2	0	0
02 MARINE	22 FISSION IN MULTIPLE PLANES		A preceds B	6.7E-157	3.8E-158	12	1142	A preceds B	15	2	0	0
02 MARINE	23 AKINETES		A preceds B	3.6E-160	1.4E-161	12	1084	A preceds B	17	0	0	0
02 MARINE	24 HETEROCYSTS		A preceds B	4.1E-160	1.8E-161	12	1127	A preceds B	17	0	0	0

Trait A	Trait B	Table 1 debate	Trait pair polarity	False discovery rate	Wilcoxon p-value	Number of tests	Number of trees	Polarity in species tree	Polarity in 17 common single-copy gene trees			
									A preceds B	Simultaneous	B preceds A	Not nested
02 MARINE	25 TRUE BRANCHING		A preceds B	3.3E-151	3.7E-152	12	923	A preceds B	17	0	0	0
03 NO N FIXATION	04 UNICELLULAR		Simultaneous	1.2E-182	4.1E-185	12	1237	Simultaneous	0	17	0	0
03 NO N FIXATION	05 FREE-LIVING		Simultaneous	1.2E-134	3.7E-135	12	1462	Simultaneous	1	16	0	0
03 NO N FIXATION	06 PLANKTONIC		Simultaneous	3.3E-140	7.7E-141	12	1473	Simultaneous	1	16	0	0
03 NO N FIXATION	07 MOTILITY		Simultaneous	1.6E-51	1.1E-51	12	1342	Simultaneous	1	16	0	0
03 NO N FIXATION	08 EPILITHIC OR ENDOLITHIC		A preceds B	4.9E-115	2.3E-115	12	1329	A preceds B	15	2	0	0
03 NO N FIXATION	09 NOT FREE-LIVING		A preceds B	1.1E-103	6.0E-104	12	1357	A preceds B	13	4	0	0
03 NO N FIXATION	10 SESSILE/BENTHIC		A preceds B	7.1E-104	4.0E-104	12	1345	A preceds B	13	4	0	0
03 NO N FIXATION	11 SHEATH		A preceds B	4.6E-135	1.3E-135	12	1285	A preceds B	15	2	0	0
03 NO N FIXATION	12 FILAMENTOUS		A preceds B	2.2E-104	1.2E-104	12	1389	A preceds B	14	3	0	0
03 NO N FIXATION	13 N FIXATION	(3)	A preceds B	2.6E-125	1.1E-125	12	1383	A preceds B	15	2	0	0
03 NO N FIXATION	14 HORMOGONIA		A preceds B	1.3E-132	4.4E-133	12	1347	A preceds B	15	2	0	0
03 NO N FIXATION	15 GAS VESICLES		A preceds B	1.2E-144	2.3E-145	12	1235	A preceds B	14	3	0	0
03 NO N FIXATION	16 MUCILAGE		A preceds B	8.8E-127	3.4E-127	12	1323	A preceds B	15	2	0	0
03 NO N FIXATION	17 IN MICROBIAL MATS		A preceds B	3.6E-142	7.7E-143	12	1082	A preceds B	13	4	0	0
03 NO N FIXATION	18 THERMOPHILIC		A preceds B	5.7E-143	1.2E-143	12	1044	A preceds B	13	4	0	0
03 NO N FIXATION	19 EPIPHYTIC		A preceds B	1.6E-150	2.0E-151	12	1219	A preceds B	15	2	0	0
03 NO N FIXATION	20 PERIPHYTIC		A preceds B	7.8E-153	8.1E-154	12	1070	A preceds B	15	2	0	0
03 NO N FIXATION	21 BAEOCYTES		A preceds B	1.6E-153	1.3E-154	12	968	A preceds B	15	2	0	0
03 NO N FIXATION	22 FISSION IN MULTIPLE PLANES		A preceds B	5.0E-165	8.3E-167	12	1163	A preceds B	15	2	0	0
03 NO N FIXATION	23 AKINETES		A preceds B	6.7E-164	1.8E-165	12	1104	A preceds B	17	0	0	0
03 NO N FIXATION	24 HETEROCYSTS		A preceds B	1.4E-164	3.2E-166	12	1149	A preceds B	17	0	0	0
03 NO N FIXATION	25 TRUE BRANCHING		A preceds B	6.1E-153	5.9E-154	12	933	A preceds B	17	0	0	0
04 UNICELLULAR	05 FREE-LIVING		Simultaneous	6.4E-135	1.9E-135	12	1462	Simultaneous	1	16	0	0
04 UNICELLULAR	06 PLANKTONIC		Simultaneous	7.6E-138	1.9E-138	12	1476	Simultaneous	1	16	0	0
04 UNICELLULAR	07 MOTILITY		Simultaneous	1.2E-47	8.9E-48	12	1340	Simultaneous	1	16	0	0
04 UNICELLULAR	08 EPILITHIC OR ENDOLITHIC		A preceds B	1.6E-114	7.6E-115	12	1325	A preceds B	15	2	0	0
04 UNICELLULAR	09 NOT FREE-LIVING		A preceds B	1.8E-108	9.5E-109	12	1353	A preceds B	13	4	0	0
04 UNICELLULAR	10 SESSILE/BENTHIC		A preceds B	1.9E-109	1.0E-109	12	1342	A preceds B	13	4	0	0
04 UNICELLULAR	11 SHEATH		A preceds B	2.2E-135	6.3E-136	12	1287	A preceds B	15	2	0	0
04 UNICELLULAR	12 FILAMENTOUS	(1)	A preceds B	2.3E-110	1.2E-110	12	1390	A preceds B	14	3	0	0
04 UNICELLULAR	13 N FIXATION		A preceds B	2.3E-115	1.1E-115	12	1396	A preceds B	15	2	0	0
04 UNICELLULAR	14 HORMOGONIA		A preceds B	6.9E-136	1.9E-136	12	1347	A preceds B	15	2	0	0
04 UNICELLULAR	15 GAS VESICLES		A preceds B	6.5E-147	1.1E-147	12	1234	A preceds B	14	3	0	0
04 UNICELLULAR	16 MUCILAGE		A preceds B	8.7E-126	3.5E-126	12	1329	A preceds B	15	2	0	0
04 UNICELLULAR	17 IN MICROBIAL MATS		A preceds B	1.6E-143	3.3E-144	12	1083	A preceds B	13	4	0	0
04 UNICELLULAR	18 THERMOPHILIC		A preceds B	1.6E-143	3.2E-144	12	1046	A preceds B	13	4	0	0
04 UNICELLULAR	19 EPIPHYTIC		A preceds B	6.9E-151	8.3E-152	12	1215	A preceds B	15	2	0	0
04 UNICELLULAR	20 PERIPHYTIC		A preceds B	1.8E-153	1.5E-154	12	1070	A preceds B	15	2	0	0
04 UNICELLULAR	21 BAEOCYTES		A preceds B	7.8E-153	8.0E-154	2	968	A preceds B	15	2	0	0
04 UNICELLULAR	22 FISSION IN MULTIPLE PLANES		A preceds B	2.3E-156	1.4E-157	12	959	A preceds B	15	2	0	0
04 UNICELLULAR	23 AKINETES		A preceds B	7.6E-165	1.5E-166	12	1105	A preceds B	17	0	0	0
04 UNICELLULAR	24 HETEROCYSTS		A preceds B	5.0E-165	8.3E-167	12	1151	A preceds B	17	0	0	0
04 UNICELLULAR	25 TRUE BRANCHING		A preceds B	5.2E-153	4.9E-154	12	933	A preceds B	17	0	0	0
05 FREE-LIVING	06 PLANKTONIC		Simultaneous	8.5E-152	9.4E-153	12	940	Simultaneous	0	17	0	0
05 FREE-LIVING	07 MOTILITY	(2)	Simultaneous	5.1E-70	3.4E-70	12	1306	Simultaneous	0	17	0	0
05 FREE-LIVING	08 EPILITHIC OR ENDOLITHIC	(2)	A preceds B	2.3E-116	1.1E-116	12	1272	A preceds B	14	3	0	0
05 FREE-LIVING	09 NOT FREE-LIVING	(2)	A preceds B	4.6E-114	2.3E-114	12	1298	A preceds B	13	3	1	0
05 FREE-LIVING	10 SESSILE/BENTHIC	(2)	A preceds B	4.5E-114	2.2E-114	12	1290	A preceds B	13	3	1	0
05 FREE-LIVING	11 SHEATH		A preceds B	1.8E-133	5.8E-134	12	1245	A preceds B	14	3	0	0
05 FREE-LIVING	12 FILAMENTOUS		A preceds B	2.2E-103	1.3E-103	12	1327	A preceds B	13	4	0	0
05 FREE-LIVING	13 N FIXATION		A preceds B	5.9E-115	2.8E-115	12	1332	A preceds B	14	3	0	0

Trait A	Trait B	Table 1 debate	Trait pair polarity	False discovery rate	Wilcoxon p-value	Number of tests	Number of trees	Polarity in species tree	Polarity in 17 common single-copy gene trees			
									A preceds B	Simultaneous	B preceds A	Not nested
05 FREE-LIVING	14 HORMOGONIA		A preceds B	3.2E-134	9.9E-135	12	1291	A preceds B	14	3	0	0
05 FREE-LIVING	15 GAS VESICLES		A preceds B	1.7E-129	6.0E-130	12	1209	A preceds B	13	4	0	0
05 FREE-LIVING	16 MUCILAGE		A preceds B	1.9E-119	8.5E-120	12	1283	A preceds B	14	3	0	0
05 FREE-LIVING	17 IN MICROBIAL MATS	(2)	A preceds B	1.2E-137	3.2E-138	12	1065	A preceds B	13	3	1	0
05 FREE-LIVING	18 THERMOPHILIC		A preceds B	5.1E-137	1.4E-137	12	1036	A preceds B	13	3	1	0
05 FREE-LIVING	19 EPIPHYTIC	(2)	A preceds B	6.6E-145	1.2E-145	12	1183	A preceds B	14	3	0	0
05 FREE-LIVING	20 PERIPHYTIC	(2)	A preceds B	1.2E-149	1.7E-150	12	1055	A preceds B	14	3	0	0
05 FREE-LIVING	21 BAEOCYTES		A preceds B	1.3E-153	9.9E-155	12	962	A preceds B	14	3	0	0
05 FREE-LIVING	22 FISSION IN MULTIPLE PLANES		A preceds B	4.8E-159	2.2E-160	12	1149	A preceds B	14	3	0	0
05 FREE-LIVING	23 AKINETES		A preceds B	4.1E-157	2.2E-158	12	1089	A preceds B	16	1	0	0
05 FREE-LIVING	24 HETEROCYSTS		A preceds B	2.2E-157	1.1E-158	12	1123	A preceds B	16	1	0	0
05 FREE-LIVING	25 TRUE BRANCHING		A preceds B	2.1E-146	3.7E-147	12	928	A preceds B	16	1	0	0
06 PLANKTONIC	07 MOTILITY		Simultaneous	3.2E-69	2.1E-69	12	1316	Simultaneous	0	17	0	0
06 PLANKTONIC	08 EPILITHIC OR ENDOLITHIC	(2)	A preceds B	1.1E-115	5.2E-116	12	1285	A preceds B	14	3	0	0
06 PLANKTONIC	09 NOT FREE-LIVING	(2)	A preceds B	5.4E-113	2.8E-113	12	1312	A preceds B	13	3	1	0
06 PLANKTONIC	10 SESSILE/BENTHIC	(2)	A preceds B	4.1E-116	1.9E-116	12	1301	A preceds B	13	3	1	0
06 PLANKTONIC	11 SHEATH		A preceds B	6.3E-131	2.2E-131	12	1254	A preceds B	14	3	0	0
06 PLANKTONIC	12 FILAMENTOUS		A preceds B	8.0E-100	4.8E-100	12	1344	A preceds B	13	4	0	0
06 PLANKTONIC	13 N FIXATION		A preceds B	1.2E-115	5.4E-116	12	1350	A preceds B	14	3	0	0
06 PLANKTONIC	14 HORMOGONIA		A preceds B	3.5E-131	1.2E-131	12	1307	A preceds B	14	3	0	0
06 PLANKTONIC	15 GAS VESICLES		A preceds B	8.5E-134	2.7E-134	12	1215	A preceds B	13	4	0	0
06 PLANKTONIC	16 MUCILAGE		A preceds B	5.1E-121	2.2E-121	12	1293	A preceds B	14	3	0	0
06 PLANKTONIC	17 IN MICROBIAL MATS	(2)	A preceds B	8.3E-140	2.0E-140	12	1072	A preceds B	13	3	1	0
06 PLANKTONIC	18 THERMOPHILIC		A preceds B	5.6E-140	1.3E-140	12	1035	A preceds B	13	3	1	0
06 PLANKTONIC	19 EPIPHYTIC	(2)	A preceds B	8.4E-146	1.5E-146	12	1196	A preceds B	14	3	0	0
06 PLANKTONIC	20 PERIPHYTIC	(2)	A preceds B	2.4E-148	3.6E-149	12	1061	A preceds B	14	3	0	0
06 PLANKTONIC	21 BAEOCYTES		A preceds B	2.1E-153	1.8E-154	12	964	A preceds B	14	3	0	0
06 PLANKTONIC	22 FISSION IN MULTIPLE PLANES		A preceds B	8.7E-162	2.6E-163	12	1150	A preceds B	14	3	0	0
06 PLANKTONIC	23 AKINETES		A preceds B	3.6E-160	1.3E-161	12	1092	A preceds B	16	1	0	0
06 PLANKTONIC	24 HETEROCYSTS		A preceds B	1.9E-160	6.5E-162	12	1127	A preceds B	16	1	0	0
06 PLANKTONIC	25 TRUE BRANCHING		A preceds B	1.8E-145	3.2E-146	12	928	A preceds B	16	1	0	0
07 MOTILITY	08 EPILITHIC OR ENDOLITHIC	(2)	A preceds B	1.9E-48	1.3E-48	12	1202	A preceds B	14	3	0	0
07 MOTILITY	09 NOT FREE-LIVING	(2)	A preceds B	8.2E-33	6.1E-33	12	1178	A preceds B	13	3	1	0
07 MOTILITY	10 SESSILE/BENTHIC	(2)	A preceds B	2.3E-33	1.7E-33	12	1201	A preceds B	13	3	1	0
07 MOTILITY	11 SHEATH		A preceds B	1.3E-50	9.6E-51	12	1205	A preceds B	14	3	0	0
07 MOTILITY	12 FILAMENTOUS		A preceds B	7.1E-43	5.2E-43	12	1148	A preceds B	13	4	0	0
07 MOTILITY	13 N FIXATION		A preceds B	5.2E-47	3.8E-47	12	1226	A preceds B	14	3	0	0
07 MOTILITY	14 HORMOGONIA		A preceds B	6.5E-52	4.6E-52	12	1212	A preceds B	14	3	0	0
07 MOTILITY	15 GAS VESICLES		A preceds B	2.7E-76	1.8E-76	12	1179	A preceds B	13	4	0	0
07 MOTILITY	16 MUCILAGE		A preceds B	4.4E-69	2.9E-69	12	1202	A preceds B	14	3	0	0
07 MOTILITY	17 IN MICROBIAL MATS	(2)	A preceds B	2.0E-105	1.1E-105	12	1064	A preceds B	13	3	1	0
07 MOTILITY	18 THERMOPHILIC		A preceds B	1.6E-127	6.1E-128	12	1032	A preceds B	13	3	1	0
07 MOTILITY	19 EPIPHYTIC	(2)	A preceds B	1.1E-78	7.2E-79	12	1163	A preceds B	14	3	0	0
07 MOTILITY	20 PERIPHYTIC	(2)	A preceds B	9.2E-115	4.4E-115	12	1060	A preceds B	14	3	0	0
07 MOTILITY	21 BAEOCYTES		A preceds B	1.1E-141	2.5E-142	12	961	A preceds B	14	3	0	0
07 MOTILITY	22 FISSION IN MULTIPLE PLANES		A preceds B	1.8E-132	6.1E-133	12	1110	A preceds B	14	3	0	0
07 MOTILITY	23 AKINETES		A preceds B	4.8E-143	9.8E-144	12	1078	A preceds B	16	1	0	0
07 MOTILITY	24 HETEROCYSTS		A preceds B	1.3E-134	3.8E-135	12	1104	A preceds B	16	1	0	0
07 MOTILITY	25 TRUE BRANCHING		A preceds B	5.7E-152	6.1E-153	12	929	A preceds B	16	1	0	0
08 EPILITHIC OR ENDOLITHIC	09 NOT FREE-LIVING		Simultaneous	1.3E-60	8.9E-61	12	1180	Simultaneous	0	11	6	0
08 EPILITHIC OR ENDOLITHIC	10 SESSILE/BENTHIC		Simultaneous	2.6E-56	1.8E-56	12	1182	Simultaneous	0	11	6	0
08 EPILITHIC OR ENDOLITHIC	11 SHEATH		Simultaneous	1.4E-113	7.2E-114	12	1203	Simultaneous	0	15	2	0

Trait A	Trait B	Table 1 debate	Trait pair polarity	False discovery rate	Wilcoxon p-value	Number of tests	Number of trees	Polarity in species tree	Polarity in 17 common single-copy gene trees			
									A preceds B	Simultaneous	B preceds A	Not nested
08 EPILITHIC OR ENDOLITHIC	12 FILAMENTOUS		Simultaneous	6.4E-14	5.2E-14	12	1279	B preceds A	6	6	5	0
08 EPILITHIC OR ENDOLITHIC	13 N FIXATION		Simultaneous	1.7E-27	1.3E-27	12	1228	Simultaneous	4	8	5	0
08 EPILITHIC OR ENDOLITHIC	14 HORMOGONIA		Simultaneous	3.8E-11	3.2E-11	12	1190	Simultaneous	6	7	4	0
08 EPILITHIC OR ENDOLITHIC	15 GAS VESICLES		A preceds B	0.0011	0.0010	12	1168	B preceds A	8	6	3	0
08 EPILITHIC OR ENDOLITHIC	16 MUCILAGE		Simultaneous	3.0E-27	2.3E-27	12	1218	A preceds B	3	11	3	0
08 EPILITHIC OR ENDOLITHIC	17 IN MICROBIAL MATS		A preceds B	0.0152	0.0137	12	1056	A preceds B	8	3	6	0
08 EPILITHIC OR ENDOLITHIC	18 THERMOPHILIC		A preceds B	5.2E-07	4.5E-07	12	1027	A preceds B	8	5	4	0
08 EPILITHIC OR ENDOLITHIC	19 EPIPHYTIC		Simultaneous	0.0496	0.0454	12	1148	Simultaneous	5	10	2	0
08 EPILITHIC OR ENDOLITHIC	20 PERIPHYTIC		A preceds B	2.2E-07	1.9E-07	12	1065	Simultaneous	7	10	0	0
08 EPILITHIC OR ENDOLITHIC	21 BAEOCYTES		A preceds B	2.8E-114	1.3E-114	12	963	A preceds B	12	5	0	0
08 EPILITHIC OR ENDOLITHIC	22 FISSION IN MULTIPLE PLANES		A preceds B	2.3E-88	1.4E-88	12	1119	A preceds B	11	6	0	0
08 EPILITHIC OR ENDOLITHIC	23 AKINETES		A preceds B	6.9E-132	2.3E-132	12	1081	A preceds B	15	2	0	0
08 EPILITHIC OR ENDOLITHIC	24 HETEROCYSTS		A preceds B	1.1E-113	5.3E-114	12	1112	A preceds B	15	2	0	0
08 EPILITHIC OR ENDOLITHIC	25 TRUE BRANCHING		A preceds B	4.7E-150	6.1E-151	12	934	A preceds B	16	1	0	0
09 NOT FREE-LIVING	10 SESSILE/BENTHIC		Simultaneous	5.5E-149	8.0E-150	12	1074	Simultaneous	0	17	0	0
09 NOT FREE-LIVING	11 SHEATH		Simultaneous	5.4E-52	3.8E-52	12	1180	Simultaneous	5	12	0	0
09 NOT FREE-LIVING	12 FILAMENTOUS		Simultaneous	1.0E-21	8.0E-22	12	1214	B preceds A	7	7	3	0
09 NOT FREE-LIVING	13 N FIXATION		Simultaneous	3.1E-06	2.8E-06	12	1279	Simultaneous	6	9	2	0
09 NOT FREE-LIVING	14 HORMOGONIA		Simultaneous	0.0205	0.0187	12	1250	Simultaneous	10	6	1	0
09 NOT FREE-LIVING	15 GAS VESICLES		A preceds B	8.3E-08	7.0E-08	12	1186	B preceds A	9	6	2	0
09 NOT FREE-LIVING	16 MUCILAGE		Simultaneous	8.3E-11	6.9E-11	12	1221	A preceds B	9	7	1	0
09 NOT FREE-LIVING	17 IN MICROBIAL MATS		Simultaneous	0.0450	0.0410	2	1066	A preceds B	10	7	0	0
09 NOT FREE-LIVING	18 THERMOPHILIC		A preceds B	4.1E-10	3.4E-10	12	1033	A preceds B	10	6	1	0
09 NOT FREE-LIVING	19 EPIPHYTIC		A preceds B	0.0327	0.0297	2	1163	Simultaneous	10	7	0	0
09 NOT FREE-LIVING	20 PERIPHYTIC		A preceds B	4.4E-24	3.4E-24	2	1068	Simultaneous	11	6	0	0
09 NOT FREE-LIVING	21 BAEOCYTES		A preceds B	5.4E-127	2.0E-127	12	963	A preceds B	15	2	0	0
09 NOT FREE-LIVING	22 FISSION IN MULTIPLE PLANES		A preceds B	3.7E-101	2.1E-101	12	1124	A preceds B	14	3	0	0
09 NOT FREE-LIVING	23 AKINETES		A preceds B	5.6E-141	1.3E-141	12	1090	A preceds B	17	0	0	0
09 NOT FREE-LIVING	24 HETEROCYSTS		A preceds B	3.6E-132	1.2E-132	12	1123	A preceds B	17	0	0	0
09 NOT FREE-LIVING	25 TRUE BRANCHING		A preceds B	4.7E-150	5.9E-151	12	935	A preceds B	17	0	0	0
10 SESSILE/BENTHIC	11 SHEATH		Simultaneous	4.1E-46	2.9E-46	12	1178	Simultaneous	5	12	0	0
10 SESSILE/BENTHIC	12 FILAMENTOUS		Simultaneous	3.0E-17	2.4E-17	12	1291	B preceds A	7	7	3	0
10 SESSILE/BENTHIC	13 N FIXATION		Simultaneous	9.5E-07	8.2E-07	12	1269	Simultaneous	6	9	2	0
10 SESSILE/BENTHIC	14 HORMOGONIA		Simultaneous	0.1352	0.1258	12	1234	Simultaneous	10	6	1	0
10 SESSILE/BENTHIC	15 GAS VESICLES		A preceds B	0.0001	0.0001	12	1183	B preceds A	9	6	2	0
10 SESSILE/BENTHIC	16 MUCILAGE		Simultaneous	3.5E-15	2.9E-15	12	1212	A preceds B	9	7	1	0
10 SESSILE/BENTHIC	17 IN MICROBIAL MATS		Simultaneous	0.0111	0.0100	12	1064	A preceds B	10	7	0	0
10 SESSILE/BENTHIC	18 THERMOPHILIC		A preceds B	3.4E-08	2.9E-08	12	1031	A preceds B	10	6	1	0
10 SESSILE/BENTHIC	19 EPIPHYTIC		A preceds B	0.0801	0.0743	12	1163	Simultaneous	10	7	0	0
10 SESSILE/BENTHIC	20 PERIPHYTIC		A preceds B	9.0E-23	7.1E-23	12	1068	Simultaneous	11	6	0	0
10 SESSILE/BENTHIC	21 BAEOCYTES		A preceds B	8.7E-125	3.6E-125	12	961	A preceds B	15	2	0	0
10 SESSILE/BENTHIC	22 FISSION IN MULTIPLE PLANES		A preceds B	2.1E-91	1.3E-91	12	1119	A preceds B	14	3	0	0
10 SESSILE/BENTHIC	23 AKINETES		A preceds B	2.1E-138	5.2E-139	12	1089	A preceds B	17	0	0	0
10 SESSILE/BENTHIC	24 HETEROCYSTS		A preceds B	1.9E-131	6.8E-132	12	1124	A preceds B	17	0	0	0
10 SESSILE/BENTHIC	25 TRUE BRANCHING		A preceds B	6.8E-150	9.1E-151	12	934	A preceds B	17	0	0	0
11 SHEATH	12 FILAMENTOUS		Simultaneous	0.1894	0.1786	12	1255	B preceds A	6	7	4	0
11 SHEATH	13 N FIXATION		Simultaneous	1.2E-20	9.9E-21	12	1229	Simultaneous	5	8	4	0
11 SHEATH	14 HORMOGONIA		Simultaneous	8.8E-08	7.5E-08	12	1173	Simultaneous	7	7	3	0
11 SHEATH	15 GAS VESICLES		A preceds B	0.0716	0.0661	12	1152	B preceds A	8	6	3	0
11 SHEATH	16 MUCILAGE		Simultaneous	1.9E-40	1.4E-40	12	1167	A preceds B	5	9	3	0
11 SHEATH	17 IN MICROBIAL MATS		Simultaneous	0.3923	0.3793	12	1052	A preceds B	8	4	5	0
11 SHEATH	18 THERMOPHILIC		A preceds B	1.5E-05	1.3E-05	12	1014	A preceds B	8	5	4	0

Trait A	Trait B	Table 1 debate	Trait pair polarity	False discovery rate	Wilcoxon p-value	Number of tests	Number of trees	Polarity in species tree	Polarity in 17 common single-copy gene trees: A preceds B	Simultaneous	B preceds A	Not nested
11 SHEATH	19 EPIPHYTIC		Simultaneous	0.1849	0.1738	12	1136	Simultaneous	7	8	2	0
11 SHEATH	20 PERIPHYTIC		A preceds B	3.2E-07	2.7E-07	12	1062	Simultaneous	8	9	0	0
11 SHEATH	21 BAEOCYTES		A preceds B	7.5E-114	3.8E-114	12	963	A preceds B	13	4	0	0
11 SHEATH	22 FISSION IN MULTIPLE PLANES		A preceds B	1.1E-77	7.1E-78	12	1102	A preceds B	12	5	0	0
11 SHEATH	23 AKINETES		A preceds B	1.1E-139	2.7E-140	12	1062	A preceds B	16	1	0	0
11 SHEATH	24 HETEROCYSTS		A preceds B	8.2E-134	2.6E-134	12	1102	A preceds B	16	1	0	0
11 SHEATH	25 TRUE BRANCHING		A preceds B	3.6E-148	5.5E-149	12	923	A preceds B	16	1	0	0
12 FILAMENTOUS	13 N FIXATION		Simultaneous	1.6E-34	1.2E-34	12	1270	A preceds B	5	10	2	0
12 FILAMENTOUS	14 HORMOGONIA		Simultaneous	1.6E-15	1.3E-15	2	1219	A preceds B	7	10	0	0
12 FILAMENTOUS	15 GAS VESICLES		Simultaneous	2.4E-27	1.8E-27	12	1199	Simultaneous	3	14	0	0
12 FILAMENTOUS	16 MUCILAGE		A preceds B	1.7E-08	1.4E-08	12	1270	A preceds B	8	3	6	0
12 FILAMENTOUS	17 IN MICROBIAL MATS		A preceds B	2.3E-22	1.8E-22	12	1070	A preceds B	9	5	3	0
12 FILAMENTOUS	18 THERMOPHILIC		A preceds B	2.9E-24	2.3E-24	12	962	A preceds B	9	4	4	0
12 FILAMENTOUS	19 EPIPHYTIC		A preceds B	1.8E-05	1.6E-05	12	1212	A preceds B	8	8	1	0
12 FILAMENTOUS	20 PERIPHYTIC		A preceds B	2.1E-26	1.6E-26	12	1068	A preceds B	9	8	0	0
12 FILAMENTOUS	21 BAEOCYTES		A preceds B	4.2E-134	1.3E-134	12	960	A preceds B	14	3	0	0
12 FILAMENTOUS	22 FISSION IN MULTIPLE PLANES		A preceds B	4.2E-119	1.9E-119	12	1137	A preceds B	13	3	1	0
12 FILAMENTOUS	23 AKINETES		A preceds B	3.3E-127	1.3E-127	2	1097	A preceds B	16	1	0	0
12 FILAMENTOUS	24 HETEROCYSTS		A preceds B	2.2E-114	1.1E-114	2	1128	A preceds B	16	1	0	0
12 FILAMENTOUS	25 TRUE BRANCHING		A preceds B	1.5E-149	2.1E-150	2	932	A preceds B	16	1	0	0
13 N FIXATION	14 HORMOGONIA		Simultaneous	7.8E-29	5.9E-29	12	1286	Simultaneous	5	12	0	0
13 N FIXATION	15 GAS VESICLES		Simultaneous	9.4E-17	7.6E-17	12	1198	B preceds A	5	7	5	0
13 N FIXATION	16 MUCILAGE		Simultaneous	1.0E-06	8.8E-07	12	1282	A preceds B	7	6	4	0
13 N FIXATION	17 IN MICROBIAL MATS		A preceds B	0.0176	0.0159	12	1072	A preceds B	8	5	4	0
13 N FIXATION	18 THERMOPHILIC		A preceds B	0.0457	0.0417	12	1036	A preceds B	8	3	6	0
13 N FIXATION	19 EPIPHYTIC		A preceds B	0.3609	0.3465	12	1208	Simultaneous	7	9	1	0
13 N FIXATION	20 PERIPHYTIC		A preceds B	3.1E-06	2.7E-06	12	1069	Simultaneous	7	10	0	0
13 N FIXATION	21 BAEOCYTES		A preceds B	7.7E-105	4.3E-105	12	964	A preceds B	12	5	0	0
13 N FIXATION	22 FISSION IN MULTIPLE PLANES		A preceds B	1.3E-85	7.8E-86	12	1144	A preceds B	12	4	1	0
13 N FIXATION	23 AKINETES		A preceds B	7.7E-126	3.0E-126	12	1097	A preceds B	15	2	0	0
13 N FIXATION	24 HETEROCYSTS		A preceds B	2.0E-113	1.0E-113	2	1123	A preceds B	15	2	0	0
13 N FIXATION	25 TRUE BRANCHING		A preceds B	1.3E-148	1.8E-149	2	931	A preceds B	16	1	0	0
14 HORMOGONIA	15 GAS VESICLES		Undefined	0.1931	0.1828	12	1137	B preceds A	3	7	7	0
14 HORMOGONIA	16 MUCILAGE		Simultaneous	0.1988	0.1889	12	1238	A preceds B	5	6	6	0
14 HORMOGONIA	17 IN MICROBIAL MATS		Simultaneous	0.0004	0.0003	12	1009	A preceds B	4	9	4	0
14 HORMOGONIA	18 THERMOPHILIC		A preceds B	0.3711	0.3575	12	978	A preceds B	7	3	7	0
14 HORMOGONIA	19 EPIPHYTIC		Simultaneous	1.5E-60	1.1E-60	12	1190	Simultaneous	2	13	2	0
14 HORMOGONIA	20 PERIPHYTIC		Simultaneous	4.6E-12	3.8E-12	12	1068	Simultaneous	5	12	0	0
14 HORMOGONIA	21 BAEOCYTES		A preceds B	2.5E-111	1.3E-111	12	958	A preceds B	12	5	0	0
14 HORMOGONIA	22 FISSION IN MULTIPLE PLANES		A preceds B	8.8E-89	5.4E-89	12	1126	A preceds B	12	4	1	0
14 HORMOGONIA	23 AKINETES		A preceds B	3.7E-126	1.5E-126	12	1085	A preceds B	15	2	0	0
14 HORMOGONIA	24 HETEROCYSTS		A preceds B	9.3E-113	4.8E-113	12	1114	A preceds B	15	2	0	0
14 HORMOGONIA	25 TRUE BRANCHING		A preceds B	2.1E-136	5.8E-137	12	825	A preceds B	16	1	0	0
15 GAS VESICLES	16 MUCILAGE		A preceds B	0.1579	0.1474	12	1135	A preceds B	5	5	7	0
15 GAS VESICLES	17 IN MICROBIAL MATS		A preceds B	3.6E-07	3.1E-07	12	1045	A preceds B	7	6	4	0
15 GAS VESICLES	18 THERMOPHILIC		A preceds B	1.2E-07	1.0E-07	12	1008	A preceds B	7	6	4	0
15 GAS VESICLES	19 EPIPHYTIC		A preceds B	1.5E-10	1.3E-10	12	1133	A preceds B	6	8	3	0
15 GAS VESICLES	20 PERIPHYTIC		A preceds B	2.9E-23	2.2E-23	12	1037	A preceds B	7	9	1	0
15 GAS VESICLES	21 BAEOCYTES		A preceds B	8.6E-124	3.6E-124	12	938	A preceds B	14	3	0	0
15 GAS VESICLES	22 FISSION IN MULTIPLE PLANES		A preceds B	9.1E-71	5.9E-71	12	1086	A preceds B	13	3	1	0
15 GAS VESICLES	23 AKINETES		A preceds B	1.3E-128	4.9E-129	12	1044	A preceds B	16	1	0	0
15 GAS VESICLES	24 HETEROCYSTS		A preceds B	7.9E-125	3.2E-125	12	1067	A preceds B	16	1	0	0

Trait A	Trait B	Table 1 debate	Trait pair polarity	False discovery rate	Wilcoxon p-value	Number of tests	Number of trees	Polarity in species tree	Polarity in 17 common single-copy gene trees: A preceds B	Simultaneous	B preceds A	Not nested
15 GAS VESICLES	25 TRUE BRANCHING		A preceds B	4.2E-145	7.7E-146	12	922	A preceds B	16	1	0	0
16 MUCILAGE	17 IN MICROBIAL MATS		Simultaneous	4.3E-12	3.6E-12	12	1061	B preceds A	6	7	4	0
16 MUCILAGE	18 THERMOPHILIC		A preceds B	0.2340	0.2231	12	1023	B preceds A	9	4	4	0
16 MUCILAGE	19 EPIPHYTIC		A preceds B	0.1673	0.1568	12	1167	B preceds A	5	9	3	0
16 MUCILAGE	20 PERIPHYTIC		A preceds B	4.7E-30	3.6E-30	12	1060	B preceds A	9	5	3	0
16 MUCILAGE	21 BAEOCYTES		A preceds B	1.1E-103	6.4E-104	12	960	A preceds B	13	4	0	0
16 MUCILAGE	22 FISSION IN MULTIPLE PLANES		A preceds B	3.6E-53	2.5E-53	12	1131	A preceds B	12	5	0	0
16 MUCILAGE	23 AKINETES		A preceds B	4.6E-136	1.3E-136	12	1076	A preceds B	15	2	0	0
16 MUCILAGE	24 HETEROCYSTS		A preceds B	8.7E-127	3.3E-127	12	1115	A preceds B	15	2	0	0
16 MUCILAGE	25 TRUE BRANCHING		A preceds B	1.5E-149	2.1E-150	12	932	A preceds B	16	1	0	0
17 IN MICROBIAL MATS	18 THERMOPHILIC		Simultaneous	6.0E-18	4.8E-18	12	968	Simultaneous	5	8	4	0
17 IN MICROBIAL MATS	19 EPIPHYTIC		Simultaneous	0.3463	0.3313	12	1011	B preceds A	5	7	5	0
17 IN MICROBIAL MATS	20 PERIPHYTIC		A preceds B	1.2E-24	9.1E-25	12	993	B preceds A	7	7	3	0
17 IN MICROBIAL MATS	21 BAEOCYTES		A preceds B	1.5E-106	8.2E-107	12	916	A preceds B	13	4	0	0
17 IN MICROBIAL MATS	22 FISSION IN MULTIPLE PLANES		A preceds B	1.3E-82	8.2E-83	12	1010	A preceds B	13	3	1	0
17 IN MICROBIAL MATS	23 AKINETES		A preceds B	6.4E-135	1.9E-135	12	976	A preceds B	17	0	0	0
17 IN MICROBIAL MATS	24 HETEROCYSTS		A preceds B	7.0E-129	2.5E-129	12	994	A preceds B	17	0	0	0
17 IN MICROBIAL MATS	25 TRUE BRANCHING		A preceds B	1.7E-143	3.4E-144	12	898	A preceds B	17	0	0	0
18 THERMOPHILIC	19 EPIPHYTIC		A preceds B	0.0684	0.0629	12	1009	B preceds A	6	4	7	0
18 THERMOPHILIC	20 PERIPHYTIC		A preceds B	1.2E-12	9.7E-13	12	969	B preceds A	7	7	3	0
18 THERMOPHILIC	21 BAEOCYTES		A preceds B	2.1E-77	1.3E-77	12	899	A preceds B	14	3	0	0
18 THERMOPHILIC	22 FISSION IN MULTIPLE PLANES		A preceds B	2.4E-56	1.7E-56	12	978	A preceds B	13	3	1	0
18 THERMOPHILIC	23 AKINETES		A preceds B	6.9E-123	2.9E-123	12	938	A preceds B	17	0	0	0
18 THERMOPHILIC	24 HETEROCYSTS		A preceds B	1.3E-113	6.5E-114	12	946	A preceds B	17	0	0	0
18 THERMOPHILIC	25 TRUE BRANCHING		A preceds B	1.9E-131	6.8E-132	12	896	A preceds B	17	0	0	0
19 EPIPHYTIC	20 PERIPHYTIC		Simultaneous	4.2E-38	3.1E-38	12	1051	Simultaneous	6	11	0	0
19 EPIPHYTIC	21 BAEOCYTES		A preceds B	1.1E-98	6.5E-99	12	953	A preceds B	13	4	0	0
19 EPIPHYTIC	22 FISSION IN MULTIPLE PLANES		A preceds B	4.0E-64	2.7E-64	12	1088	A preceds B	12	5	0	0
19 EPIPHYTIC	23 AKINETES		A preceds B	4.9E-128	1.8E-128	12	1047	A preceds B	15	2	0	0
19 EPIPHYTIC	24 HETEROCYSTS		A preceds B	2.2E-118	9.7E-119	12	1063	A preceds B	15	2	0	0
19 EPIPHYTIC	25 TRUE BRANCHING		A preceds B	9.6E-147	1.6E-147	12	928	A preceds B	16	1	0	0
20 PERIPHYTIC	21 BAEOCYTES		A preceds B	1.0E-65	7.0E-66	12	934	A preceds B	11	6	0	0
20 PERIPHYTIC	22 FISSION IN MULTIPLE PLANES		A preceds B	8.1E-42	5.9E-42	12	1016	A preceds B	11	5	1	0
20 PERIPHYTIC	23 AKINETES		A preceds B	1.1E-131	3.8E-132	12	970	A preceds B	15	2	0	0
20 PERIPHYTIC	24 HETEROCYSTS		A preceds B	7.6E-127	2.9E-127	12	984	A preceds B	15	2	0	0
20 PERIPHYTIC	25 TRUE BRANCHING		A preceds B	1.2E-144	2.2E-145	12	899	A preceds B	16	1	0	0
21 BAEOCYTES	22 FISSION IN MULTIPLE PLANES		Simultaneous	3.7E-32	2.7E-32	12	941	Simultaneous	0	16	1	0
21 BAEOCYTES	23 AKINETES		A preceds B	5.1E-111	2.7E-111	12	899	A preceds B	15	2	0	0
21 BAEOCYTES	24 HETEROCYSTS		A preceds B	9.9E-101	5.7E-101	12	913	A preceds B	15	2	0	0
21 BAEOCYTES	25 TRUE BRANCHING		A preceds B	4.8E-130	1.7E-130	12	847	A preceds B	16	1	0	0
22 FISSION IN MULTIPLE PLANES	23 AKINETES		A preceds B	3.5E-112	1.8E-112	12	1017	A preceds B	15	2	0	0
22 FISSION IN MULTIPLE PLANES	24 HETEROCYSTS		A preceds B	3.6E-107	2.0E-107	12	1038	A preceds B	15	2	0	0
22 FISSION IN MULTIPLE PLANES	25 TRUE BRANCHING		A preceds B	7.5E-140	1.8E-140	12	921	A preceds B	16	1	0	0
23 AKINETES	24 HETEROCYSTS	(5)	Simultaneous	1.8E-124	7.6E-125	12	1036	Simultaneous	0	17	0	0
23 AKINETES	25 TRUE BRANCHING		A preceds B	3.1E-98	1.8E-98	12	925	A preceds B	14	3	0	0
24 HETEROCYSTS	25 TRUE BRANCHING		A preceds B	4.4E-114	2.2E-114	2	929	A preceds B	14	3	0	0