Evolution and Distribution of Cyanobacteria

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Abstract

Cyanobacteria are the ancient group of photosynthetic prokaryotes having pronounced variations in their physiological capacities, cellular differentiation strategies, and choice of habitats. They are the inventors of oxygenic photosynthesis on this planet and hence have played a crucial role in the evolution of biodiversity on Earth by gradually changing the atmospheric chemistry to be suitable for the evolution of eukaryotes. This conversion of atmosphere from anaerobic to an aerobic one was started by cyanobacteria through oxygenic photosynthesis, which finally supplied oxygen to the atmosphere for ~1.5 billion years leading to greater diversification of life on the Earth. Cyanobacteria inhabit a wide range of terrestrial and aquatic environments varying from the hot springs to polar region and other extreme environments. Their long-standing evolutionary history might be the reason for their success in acclimatization and sustenance in such diverse habitats. A high tolerance level of free sulfide and low oxygen, tolerance to lethal ultraviolet radiations, and the capacity to use H_2S in place of H_2O as a photoreductant are some of the various features of cyanobacteria that have aided in supporting their long history on this planet. Still, the picture

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regarding evolution and diversification of this ecologically and biotechnologically important group of photoautotrophs is not very clear. In this chapter, we present an overview of structural and genomic evolution of cyanobacteria and their distribution in diverse habitats on Earth.

1.1   Introduction

Cyanobacteria (blue-green algae) constitute a large and diverse group of photosynthetic bacteria, which range from single cells to large filamentous thallus and have tremendous potentials for applications in biotechnology, mariculture, agriculture, food and fuel, and biomedicals (Rastogi and Sinha 2009; Rajneesh et al. 2017; Singh 2017; Pathak et al. 2018). Being at the base of global carbon and nitrogen biogeochemical cycles, cyanobacteria have played crucial roles in the evolutionary past and in modern ecosystems (Kopp et al. 2005; Larsson et al. 2011). Global oxygenation of the atmosphere resulted in a radical transformation of the Earth, which occurred ~2.45–2.23 billion years ago, and this transformation was termed as the "Great Oxidation Event" (GOE), which changed the chemistry of atmosphere from a reduced state to an oxidized state, and this event was probably associated with the development of cyanobacteria-producing oxygen (Canfield 2005; Holland 2006; Shestakov and Karbysheva 2017; Sánchez-Baracaldo and Cardona 2020). Cyanobacteria might have emerged ∼3 billion years ago and transformed the anoxygenic conditions of Earth to the oxygenic conditions through photosynthesis (Schirrmeister et al. 2011a). First oxygenic photosynthesis performing cyanobacteria could have arisen in the Archean time period in the local environments (Anbar et al. 2007; Lyons and Reinhard 2011), and this rise of oxygen on Earth facilitated the growth and development of complex multicellular life with aerobic respiration and profoundly altered the course of evolution on Earth (Soo et al. 2017). Surprisingly, the fossilized forms of cyanobacteria showed similarity to the cyanobacterial species of the present times, hence indicating the slow pace of evolutionary advancement in cyanobacteria (Henson et al. 2002). During their course of evolution, cyanobacteria became one of the most widely distributed and diverse prokaryotes, which occupy several niches within aquatic, benthic, and terrestrial habitats (Rastogi et al. 2012; Pathak et al. 2017; Walter et al. 2017; Gaysina et al. 2019).

Cyanobacteria have been named according to the Botanical Code as they share similar features with eukaryotic algae (Kauff and Büdel 2010; Walter et al. 2017). Currently, there is no consensus regarding taxa nomenclature of cyanobacteria and this has long been a topic of discussion (Hoffmann et al. 2005; Oren and Tindall 2005; Oren et al. 2009; Schirrmeister et al. 2011a; Oren and Ventura 2017; Singh 2017). Owing to their photosynthetic ability, the presence of chlorophyll *a* and distinct cell wall cyanobacteria have been grouped with plants and classified as
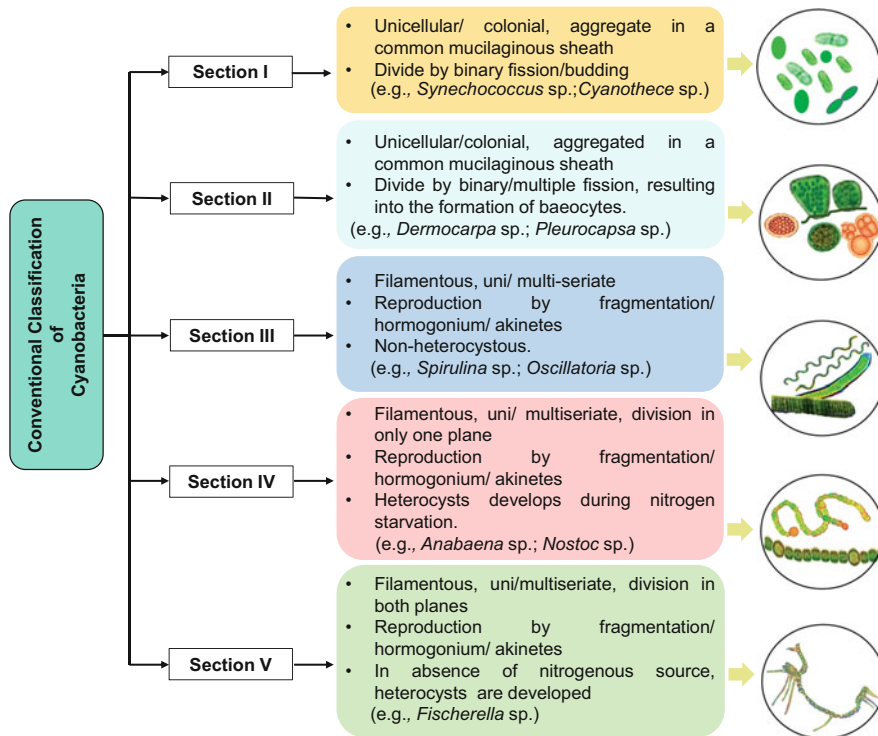
Fig. 1.1 Conventional classification of cyanobacteria. (For details, see the Refs. Rippka et al. 1979; Schirrmeister et al. 2016)

algae. The prime basis of this classification design was their morphological attributes and the developmental characteristics (Rippka et al. 1979; Rippka 1988; Rippka and Herdman 1992; Castenholz 2001). According to this classification design, cyanobacteria were formally recognized into five sections (Fig. 1.1).

Section I constitutes unicellular cyanobacteria in which division takes place by binary fission or budding, whereas in Section II division takes place by multiple fission, resulting in the development of baeocytes. Sections III, IV, and V constitute the filamentous forms of cyanobacteria. In Section III, members were filamentous but nonheterocystous that proliferated by trichome breakage. Sections IV and V represented the heterocystous cyanobacteria having ability to develop akinetes and heterocysts, and hormogonia formation was their main mode of reproduction. These two sections were further subdivided into two subsections, viz. Stigonematales and Nostocales on the basis of the plane of division. Section IV consisted of the nostocalean members, which comprised of the cyanobacterial strains that divided in only one plane, while the stigonematalean line represented by Section V constituted cyanobacteria, which have the ability to divide in more than one plane (Rippka et al. 1979; Rippka 1988).

Another remarkable feature of cyanobacteria is its capacity to form stable symbiotic interactions with different eukaryotic hosts, and this has led to the plastid, i.e., chloroplasts, and this eventually resulted in plant dominated biosphere of the Earth (Moreira et al. 2000; Reyes-Prieto and Bhattacharya 2007). These eukaryotic hosts range from the amoeboid *Paulinella chromatophora* (harboring unicellular endosymbiotic cyanobacterium), to several plant species found within the plant kingdom (Marin et al. 2005; Usher et al. 2007; Reyes-Prieto et al. 2010). The flexibility and adaptability of cyanobacteria are because of their highly diverse morphology (unicellular, multicellularity, and filamentous) and their self-sufficiency in terms of physiological capabilities (photosynthesis and nitrogen fixation), which allows them to occupy wide range of habitats on a global scale (soils/freshwater/marine), including extreme environments (from desert regions, hot springs to cold arctic) (Larsson et al. 2011; Rastogi et al. 2012; Gaysina et al. 2019).

Cyanobacteria show diversity at the genomic level also. Sequencing data revealed significant variation in the genomes within the cyanobacterial phylum in different aspects such as size of genome (~1.4–9.1 Mbp), number of coding nucleotide proportion (52–94%), G + C content (31–63%), and number of protein-coding genes (1214–8446) (Meeks et al. 2001; Welsh et al. 2008; Ran et al. 2010; Tripp et al. 2010). Cyanobacteria are equally diverse with respect to size and protein-coding capacity. In the history of evolution of cyanobacteria, two routes of genome development have been suggested on the basis of multicopy gene abundance and different rates of genome size evolution, which are as follows (Larsson et al. 2011):

1. The genome expansion
2. The genome streamlining

The genome expansion is achieved by gene family enlargement and develops a broad adaptive potential, whereas the genome streamlining imposes adaptations to highly specific niches and is also indicated in their different functional capacities (Larsson et al. 2011). Based on *16S rRNA* gene sequences, 170 genera of cyanobacteria have been proposed (Kozlov et al. 2016). Farrant et al. (2016) delineated 15 *Synechococcus* and 121 *Prochlorococcus* ecologically significant taxonomic units in the marine ecosystems utilizing single-copy petB sequences (encoding cytochrome b6) and different environmental cues. Cyanobacteria constitute a challenging group for the ecologists and microbiologists. Traditional taxonomy based on only morphologic traits does not completely reflect the results of phylogenetic analyses in cyanobacteria (Singh 2017). The *16S rRNA* gene sequences can be a useful data in characterizing and charting microbial communities, but it lack the sensitivity for evolutionary changes that take place in ecological dynamics, where physicochemical parameters determine the microbial diversity (Choudoir et al. 2012; Becraft et al. 2015; Kozlov et al. 2016). The long history of cyanobacteria provided them with a broad heterogeneity comprising multicellular and unicellular with genomes sizes ranging from 1 to 10 Mb, nonphotosynthetic (*Melainabacteria*) and photosynthetic, symbiotic, free-living, toxic, and predatory organisms (Schirrmeister et al. 2011b; Di Rienzi et al. 2013; Shih et al. 2013; Soo

et al. 2014, 2015). The processes that shaped cyanobacterial communities over time and space are still not very clear, and this chapter endeavors to decipher the complex evolutionary pattern in this group of oxygenic photoautotrophs along with their mesmerizing diversity in a wide range of habitats.

1.2 Evolution of Cyanobacteria

It is believed that the first cyanobacteria could have appeared ~2.7–2.6 billion years ago in local warm shallow water bodies that formed small oxygen "oases" within the biosphere, which was anoxygenic (Buick 2008; Blank and Sanchez-Baracaldo 2010). In Archean sediments, microfossils morphologically similar to filamentous cyanobacteria were found (Schopf 1993; Buick 2008). Previously, carbonate stromatolites were considered as analogs of modern cyanobacterial mats, which were dated back ~3.5–3.2 billion years old. In later studies, it was found that both ancient mats and microfossils were probably formed by filamentous anaerobic bacteria and not by cyanobacteria (Brasier et al. 2006; Fedonkin 2006; Bosak et al. 2013). Among some eukaryotic clades, oxygenic photosynthesis spread at least 1.05 Ga ago, which resulted in diverse types of algae and plants (Fig. 1.2) (Demoulina et al. 2019).

This crucial evolutionary process was because of the primary endosymbiosis of a cyanobacterium within a unicellular eukaryote and subsequent endosymbiotic events of higher order (Sagan 1967; Delwiche 1999; Schirrmeister et al. 2011b). Despite the importance of cyanobacteria in the early evolution of life on Earth, basic questions remain about the origin of these ancient groups of photoautotrophs, origin of oxygenic photosynthesis, and pattern and timing of diversification of cyanobacteria, in the time range from the Archean to the GOE (Fischer et al. 2016). Discrepancy between the unambiguous record of cyanobacterial fossil (starting at 1.9 Ga, the GOE at 2.4 Ga), and several older geochemical data suggestive of oxygenic photosynthesis, is one crucial problem, which needs to be addressed carefully (Rosing and Frei 2004; Shen and Buick 2004). For reconstructing the fossil record of cyanobacteria, several types of evidence are used but all have their challenges and limitations (Demoulina et al. 2019). Cyanobacterial fossil stromatolites are usually associated with cyanobacterial activity; however, although conical stromatolites seem indicate for oxygenic photosynthesis, microbially induced sedimentary structures (MISSs) and other types of stromatolites may have been produced by noncyanobacterial lineages such as anoxygenic phototrophs and their association with methanotrophs (Noffke et al. 2001; Bosak et al. 2009, 2013; Heubeck 2009; Slotznick and Fischer 2016; Homann et al. 2018). These studies indicate that MISS and stromatolites do not reflect cyanobacterial activity and not even photosynthesis by cyanobacteria (Suosaari et al. 2016). Direct evidence for cyanobacteria may be provided by microfossils, but because of their ambiguous identification they are not very reliable (Demoulina et al. 2019). Presently, identity of only three cyanobacterial fossil taxa is not debated namely *Polybessurus*, *Eohyella,* and *Eoentophysalis*. The oldest cyanobacterial
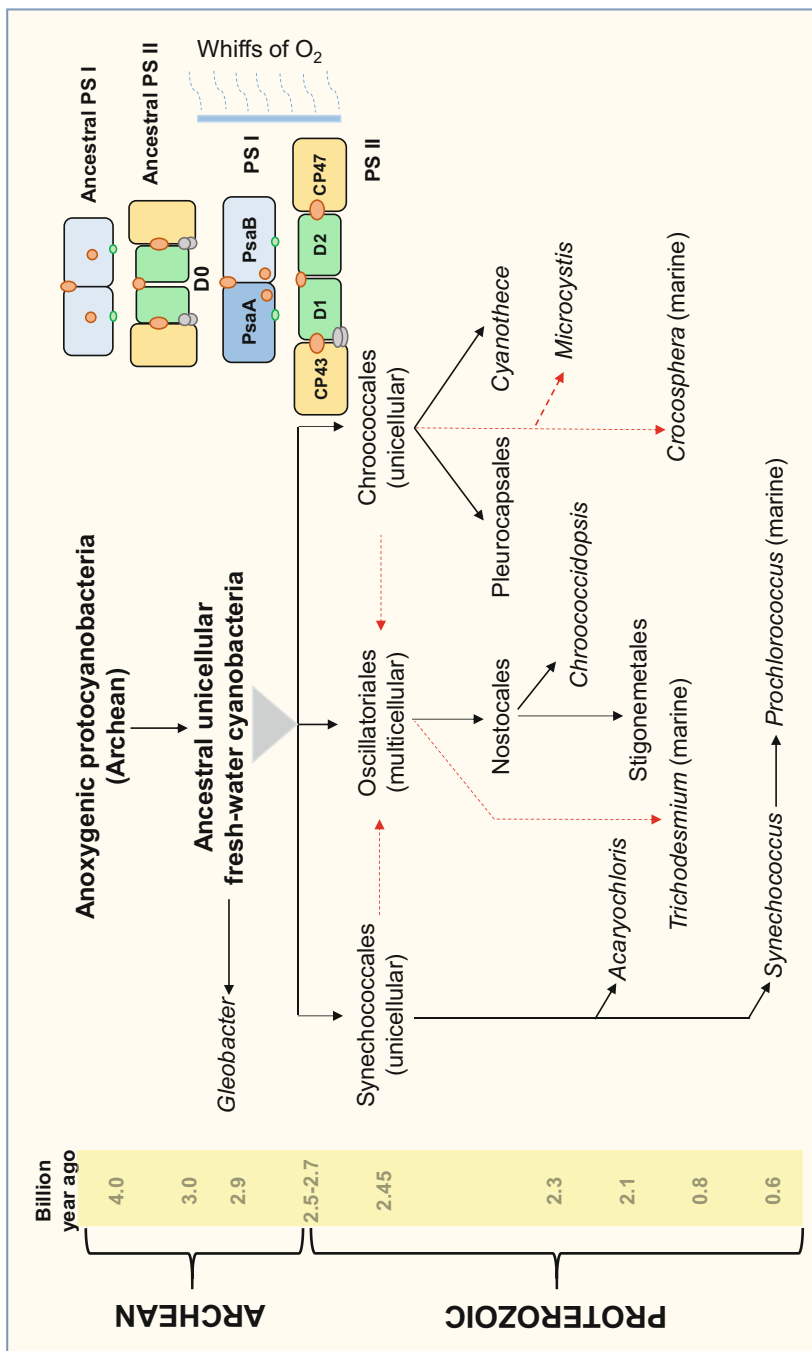
Fig. 1.2 Chronology of the evolution and origin of the cyanobacterial orders and some families in the geological scale of the Earth's history. Timeline of the appearance of photosystem (PS) I, PSII, and cyanobacterial lineages has been shown. D0 depicts an ancestral core subunit before the gene duplication that led to evolution of D1 and D2 proteins. (For details, see the Refs. Shestakov and Karbysheva 2017; Sánchez-Baracaldo and Cardona 2020)

microfossil interpreted with certainty as a cyanobacterium is *Eoentophysalis belcherensis,* which is silicified stromatolites of the Belcher supergroup found from Hudson Bay, Canada, and dates back to 1.89–1.84 Ga (Hofmann 1976).

Biomarkers (fossil molecules) can also serve as indicator of oxygenic photosynthesis, but these biomolecules are present only in the well-preserved unmetamorphosed rocks and their contamination is a big challenge to study these fossil molecules (Alleon and Summons 2019). Among such biomarkers, pigments such as porphyrins with N isotope composition and lipids such as 2-methyl-hopanes are produced by some cyanobacteria (Rashby et al. 2007; Schinteie and Brocks 2017; Gueneli et al. 2018). The fossilized porphyrins exhibit a specific fractionation of N isotope reflecting a cyanobacterial source and also indicate that in mid-proterozoic oceans cyanobacteria were the main primary producers (Gueneli et al. 2018). Ultraviolet-absorbing (sunscreen) pigments/compounds such as the mycosporine-like amino acids (MAAs), and two pigments specific to cyanobacteria, i.e., scytonemin and gloeocapsin, may be used as biosignature for bacterial life (Rastogi and Sinha 2009; Rastogi et al. 2013; Pathak et al. 2015; Demoulina et al. 2019).

Scytonemin, the novel multipurpose pigment, is a sun-screening molecule composed of phenolic and indolic subunits and is specific to cyanobacteria (Proteau et al. 1993; Rastogi et al. 2013; Pathak et al. 2020). It is biosynthesized in several species of cyanobacteria having exopolysaccharide sheaths (Rastogi et al. 2013; Pathak et al. 2017; Pandey et al. 2020) including benthic filaments of *Calothrix* sp. (Lepot et al. 2014), *Hyella* sp., and *Solentia* sp. (the endolithic cyanobacteria) from coastal carbonates (Storme et al. 2015). Scytonemin may be a promising biosignature of cyanobacterial presence given that it can be fossilized (Fulton et al. 2012; Lepot et al. 2014). Carotenoids and derivatives of scytonemin can be extracted from 125,000 years BP sediments in older deposits from Antarctica (Hodgson et al. 1997). However, there is scarce information about the preservation potential of scytonemin in older rocks. The recalcitrance of filamentous polysaccharide sheaths, possibly helped by the presence of pigments, was observed by artificial taphonomic experiments of decaying cyanobacterial cultures (Bartley 1996). However, both transparent (scytonemin-poor) and brown (scytonemin-rich) filamentous sheaths were found to be well preserved in lake sediments from Antarctica; hence, it was found that scytonemin probably was not the factor responsible for their preservation (Lepot et al. 2014).

For piecing together the events that occurred around the Earth's oxygenation, understanding of the origins of cyanobacteria and oxygenic photosynthesis is required (Sánchez-Baracaldo and Cardona 2020). It is believed that evolution of photosynthesis occurred within bacterial lineages, which are not extant; hence, studying the early history of photosynthesis becomes challenging. Our knowledge about the evolution of cyanobacteria and evolution of photosynthetic reaction centers has changed significantly due to recent findings on molecular and genomic and evolution (Sánchez-Baracaldo and Cardona 2020). In cyanobacteria, the photosynthetic apparatus was optimized and various strategies for protection against the lethal effects of the oxygen produced from cyanobacteria were developed during the

slow evolution of these ancient photoautotrophs, which lasted for hundreds of millions of years (Garcia-Pichel 1998). After oxidation of the oceans which occurred for a long time cyanobacteria relatively and rapidly occupied the photic zone on surface of the oceans, whereas oxygenation of deeper layers of oceans occurred much later (Johnston et al. 2009). As mentioned previously, these ancient photoautotrophs changed the ecological and geochemical parameters of the planet *via* production of oxygen and played crucial role in the evolution of the aerobic atmosphere, which led to the formation of complex communities and eukaryotes (Shestakov and Karbysheva 2017). Combination of paleobiological and geological approaches aids in better understanding of microbiology of modern cyanobacteria (Demoulina et al. 2019). Estimation of the origin of the oxygenic photosynthesis and the origin of phylum cyanobacteria can be better understood through the increasing cyanobacterial genetic data, which allow molecular clock analyses and phylogenetic reconstructions (Demoulina et al. 2019). However, these estimates are quite variable because of the contamination of genetic sequences, lack of tree calibrations from the fossil record, chosen dataset, and differences/limitations in models (Schirrmeister et al. 2016). Thus, there are discrepancies between the fossil and geological records and molecular phylogenies and the origin and evolution of oxygenic photosynthesis, cyanobacteria, and chloroplast are still debated (Demoulina et al. 2019).

1.2.1   Structural Evolution

Phylogenetic relationship based on conservative housekeeping genes and *16S rRNA* gene sequences reveals the relationship between the cyanobacterial taxa but does not give a complete picture of the evolutionary relationships between different taxa reflecting the pathways of losses and acquisitions of ecologically crucial properties such as halophility, thermophility, production of toxins, and motility (Shestakov and Karbysheva 2017). These properties can be expressed independently in cyanobacteria, which are phylogenetically distant due to duplication, horizontal gene transfer (HGT), genome rearrangements, and neofunctionalization, which affect the regulation of cellular metabolism (Shestakov and Karbysheva 2017).

Certain tendencies of cyanobacteria such as their ability of aggregation and colonies formation, specialized cells, and multicellular filaments increase adaptation to varying environmental conditions due to enhancement in the reliability of metabolic cooperation and functions. Initially, it was believed that multicellular blue-green appeared from anoxygenic nitrogen-fixing heterotrophic bacteria during the earliest stages of evolution on Earth (Gupta 1982). These multicellular forms could have evolved simultaneously with the unicellular forms, which evolved from photoautotrophic bacterium. Molecular phylogenetics studies suggested that phylum cyanobacteria have monophyletic origin (Shestakov and Karbysheva 2017). Phylogenetic data indicate that multicellular cyanobacteria evolved from small unicellular coccoid cyanobacteria inhabiting aquatic (freshwater) habitats (Blank and Sanchez-Baracaldo 2010; Larsson et al. 2011). The phylogenetic trees constructed with different methods revealed that bacterium *Gloeobacter violaceus* (living fossil),

which possessed a photosynthetic apparatus of primitive organization, occupies a root position distant from other cyanobacteria (Shi and Falkowski 2008; Gupta and Mathews 2010; Nguyen et al. 2012; Shih et al. 2013).

During early stages of evolution, different groups of both unicellular and multicellular families of cyanobacteria originated from ancestral unicellular form (related to protocyanobacterium) (Schirrmeister et al. 2013). Polyphasic analysis revealed representatives of phylogenetically related families Leptolyngbyaceae and Pseudoanabaenaceae forming linear filaments composed of identical cells belonged to the polyphyletic order Synechococcales, which earlier included unicellular species of *Acaryochloris*, *Prochlorococcus*, *Synechococcus*, and other cyanobacteria, which divide by binary fission (Komarek et al. 2014). Order Chroococcales consisted of other unicellular cyanobacteria (*Aphanothece*, *Microcystis*, and *Crocosphaera*) that are able to form colonies and cellular aggregates. Chroococcales is phylogenetically distant from Synechococcales and more related to Pleurocapsales, which is characterized by baeocytes formation and irregular multiple fission. Chroococcales is more close to the recently separated order Spirulinales, which consists of cyanobacteria having spiral filaments. *Spirulina platensis* was excluded from this group (Spirulinales) as molecular biological and phylogenetic tree studies revealed that it belonged to the genus *Arthrospira* of the order Oscillatoriales, which lies in between Chroococcales and Synechococcales (unicellular) (Komarek et al. 2014).

Families differing in thylakoid structure and cell division type such as multicellular filamentous Microcoleaceae and unicellular Cyanothecaceae belonged to the order Oscillatoriales (polyphyletic). *Oscillatoria limnetica* (filamentous cyanobacterium), which can use H_2S as instead of H_2O as electron donor, was previously considered as an evidence of phylogenetic relationship between green sulfur bacteria and cyanobacteria. However, it was found that under selective environmental conditions, cyanobacteria gained the capability for sulfide oxidation later through HGT as revealed by the data of comparative ecological genomics (Sanchez-Baracaldo et al. 2005). *Trichodesmium erythraeum*, the marine nitrogen-fixing cyanobacterium, which is phylogenetically related to *Arthrospira* and *Lyngbya*, belonged to the family Microcoleaceae, but specificities of physiological, cytological, and biochemical properties of this cyanobacterium make the issue of its origin debatable. It differs from other nitrogen-fixing cyanbacteria of the monophyletic cluster Nostocales, which is capable of differentiation of specialized cells such as akinetes and heterocysts, which allow them to survive under unfavorable environmental conditions. Several members of order Nostocales inhabiting different environments live in symbiosis with different plants. The origin of symbiotic cyanobacteria imprinted on the genomic structure, which occurred during the late stages of evolution. For example, *Anabaena azollae* (obligate symbiont) is characterized by presence of a high number of pseudogenes and genome reduction indicating the incompleteness of the evolutionary optimization of the cyanobacterial species (Larsson et al. 2011).

Among prokaryotes, multicellular cyanobacteria of the family Stigonematales such as *Scytonema hofmanii*, *Mastigocladus laminosus*, *Fischerella thermalis*, and

others forming branched trichomes possess the most complex morphology. These cyanobacteria having branched filamentous were previously kept under a separate morphotypes V, but the modern taxonomy included them in the order Nostocales, as they were found to have the same ancestors (Rippka et al. 1979; Komarek et al. 2014). Their proteomes contained only few specific proteins coding for the capability of "branching," and these findings suggest that functioning of certain regulatory genes encoding for intercellular communications and cell division determines branching in these cyanobacteria (Dagan et al. 2013; Nürnberg et al. 2014).

Phylogenetic analysis of large number of cyanobacterial species belonging to different orders suggested that cyanobacterial evolution was not in a unidirectional pathway from unicellular forms to multicellular taxa. The process of loss of multicellularity was going simultaneously along with complications of morphotypes in cyanobacteria (Schirrmeister et al. 2011b). Secondary transitions from unicellular forms to multicellular taxa occurred during the course of evolution as indicated by the polyphasic analysis, and this probably occurred during the appearance of the cyanobacterial genus *Spirulina* (Schirrmeister et al. 2011b). Thus, in order to evaluate phylogenetic relationships between different cyanobacterial taxa the morphological properties such as cell shape, size, and cell division type are taxonomically important but insufficient to reach at any reliable conclusion as morphologically taxa could be formed due to a convergence of phylogenetically different cyanobacteria for allowing them to adapt to the same environmental conditions/ecological habitats (Dvořák et al. 2015). Variability in cyanobacterial phylogeny is typical of certain crucial physiological property such as nitrogen fixation, which is specific to many multicellular and some unicellular cyanobacteria. During the course of cyanobacterial evolution, they were selected on the basis of the possession of the "nitrogenase gene cluster" and different strategies for protection of nitrogenase enzyme from oxygen, whereas selection of symbiotic forms was on the basis of their ability to interact with their host organism/partner. The enzyme complex "nitrogenases" appeared for the first time in archaea in anoxygenic bacteria and later on through HGT it could be transferred in cyanobacteria (Raymond et al. 2004).

1.2.2 Genome Evolution

The enormous biodiversity of phylum cyanobacteria is also reflected in the sizes of their genomes, which range from 1 to 13 Mb (Larsson et al. 2011). The combination of various genetic processes forms the evolutionary trajectories of cyanobacterial genomes (Fig. 1.3) as these trajectories are not constituted by simple bifurcation schemes (Zhaxybayeva et al. 2006; Shestakov 2007; Shi and Falkowski 2008).

Discovery of new cyanobacterial species and strains and increasing data of their genome sequencing have resulted in continuously change in the sizes of pangenomes of the phylum cyanobacteria along with its taxonomic groups. Recently, significant progress in this field of research has been observed owing to metagenomic studies and the advancements in the methods/techniques for the analysis of genomes of
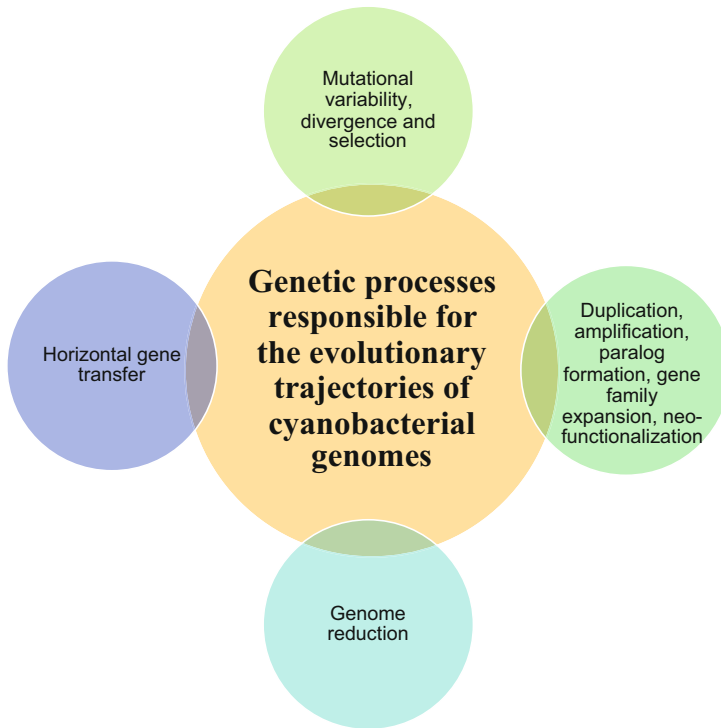
Fig. 1.3 The evolutionary trajectories of cyanobacterial genomes. (For details, see the Ref. Shestakov and Karbysheva 2017)

noncultivated cyanobacteria. Decrease in the size of the general cyanobacterial core genome has been observed as studies showed that the core set comprised 1044 genes in 2006, whereas it included only 559 genes in 2015 showing a significant decrease (Mulkidjanian et al. 2006; Simm et al. 2015). On the basis of genomic analyses of 60 cyanobacterial species and strains, two main trajectories of cyanobacterial genomic transformations have been suggested (Sun and Blanchard 2014):

1. Reduction in genome size
   It is achieved through deletion along the entire genome sequence and fixed by stabilizing selection.
2. Increase genome size
   It occurs *via* gene family expansion and the presence of repeated sequences, plasmids, and mobile elements.

Majority of cyanobacterial species having a large number of mobile elements show low gene polymorphism and their genomes evolution occurred primarily *via* genomic rearrangements through site-specific transposases and integrases responsible for movements, which altered the nature of regulation of genes responsible for

expression of ecologically significant characters. This enhancement in the number of genes is related not only to extension of the adaptive responses range but is also associated with construction of genome-scale metabolic networks of complex nature, which aids in cell differentiation, toxin synthesis, symbiogenesis, and operation of alternative metabolic pathways in cyanobacteria (Larsson et al. 2011). Simultaneously, trend toward genome reduction may operate along with the tendency of gene families to expand (Ran et al. 2010). Different studies suggest that ~10–50% of the genes in the genomes of cyanobacteria were transferred *via* the process of HGT, which made significant contribution in the evolutionary processes of cyanobacteria by helping in the rapid acquisition of valuable characters in cyanobacteria (Zhaxybayeva et al. 2006; Shi and Falkowski 2008; Yerrapragada et al. 2009). It is believed that majority of these gene transfers occurred during intensive diversification of the cyanobacterial families in the earliest stages (Puigbò et al. 2014). It was found that the probability of acquisition of novel gene from another phylum (phylogenetically distant donor) is less in comparison with probability of transfer of gene within the cyanobacteria phylum itself. Homologous recombination results in the highest frequency of genetic exchange at intraspecific (between the strains) and interspecific levels and helps in selecting more valuable variants by the replacement of orthologs (Shestakov and Karbysheva 2015). In representatives of *Synechococcus/Prochlorococcus* group, *psbAD* genes of photosystem II, genes of photosystem I, plastocyanin, ferredoxin, and other components of energy metabolism have been transferred horizontally (Lindell et al. 2004; Millard et al. 2004). During the interaction of cyanobacteria with cyanophages, the factors which determine strain specificity (such as formation of light-proof Hli proteins and proteins contributing in the cell surface formation) were acquired by the process of HGT (Shestakov and Karbysheva 2015). Still, the mechanisms involved in the process of HGT in cyanobacteria are not very clear. In the evolution of cyanobacteria, cyanophages have thought to play a crucial role as they control the number of natural populations and providing preservation of their gene pool during unfavorable environmental conditions (Shestakov and Karbysheva 2015). Although the involvement of cyanophages in gene transfer between cyanobacteria is obvious, reproducible transduction systems have not yet been developed (Lindell et al. 2004; Dammeyer et al. 2008; Ignacio-Espinoza and Sullivan 2012; Shestakov and Karbysheva 2015). However, recent large-scale genome sequencing studies suggested that the viruses such as Chlorovirus, Coccolithovirus, Pandoravirus, Marseillevirus, and Tupanvirus have played crucial role in the evolution of microalgae (Nelson et al. 2021).

1.3   Diverse Habitats of Cyanobacteria

Cyanobacteria can be found in diverse and extreme habitats ranging from the very extreme hot springs to extremely cold deserts of the Arctic and Antarctic Zones and thus represent an interesting and diverse form of life in a variety of terrestrial and aquatic environments (Whitton and Potts 2000a, b; Mataloni and Komarek 2004;

Rastogi et al. 2012; Gaysina et al. 2019). A wide range of symbiotic relationships are formed by cyanobacteria (nitrogen fixing) with almost all groups of plant such as *Geosiphon pyriforme* (fungi) with *Nostoc*, *Hemiaulus hauckii* (algae) with *Richelia intracellularis*, *Anthoceros* (bryophyte) with *Nostoc*, *Azolla* (pteridophyte) with *Anabaena*, *Cycas* (gymnosperm) with *Nostoc*, and *Gunnera* (angiosperm) with *Nostoc* (Morot-Gaudry and Touraine 2001). Their enormous physiological flexibility and plasticity enable them to be present in almost all geographical regions of the earth (Castenholz 1973; Whitton 1973; Skulberg 1994; Laamanen 1996; Gaysina et al. 2019). Figure 1.4 depicts the wide distribution of cyanobacteria in different habitats on Earth.

1.3.1   Terrestrial Habitats

Cyanobacteria constitute the major microorganisms in the biological soil crusts (Büdel et al. 2009). In different regions of India, biological soil crusts constitute genera with sheath such as *Plectonema*, *Lyngbya,* and *Scytonema,* which were found to be dominant, whereas *Phormidium*, *Oscillatoria*, *Nostoc*, *Microcoleus*, *Aulosira*, *Calothrix*, *Westiellopsis*, *Hapalosiphon,* and *Fischerella* were also found frequently (Tirkey and Adhikary 2005). In Baja California Desert in Mexico, *Desmonostoc muscorum* (*Nostoc muscorum*) and *Schizothrix calcicola* were found to be the dominant taxa (Flechtner et al. 1998). Cyanobacteria *Chroococcidiopsis* sp., *Microcoleus paludosus*, *Phormidium* spp., *Pseudanabaena* spp., *Nostoc* spp., and *Leptolyngbya* spp. were detected frequently in biological soil crusts in four biomes in Africa (Büdel et al. 2009). *Microcoleus*, *Scytonema*, *Nostoc*, *Lyngbya,* and
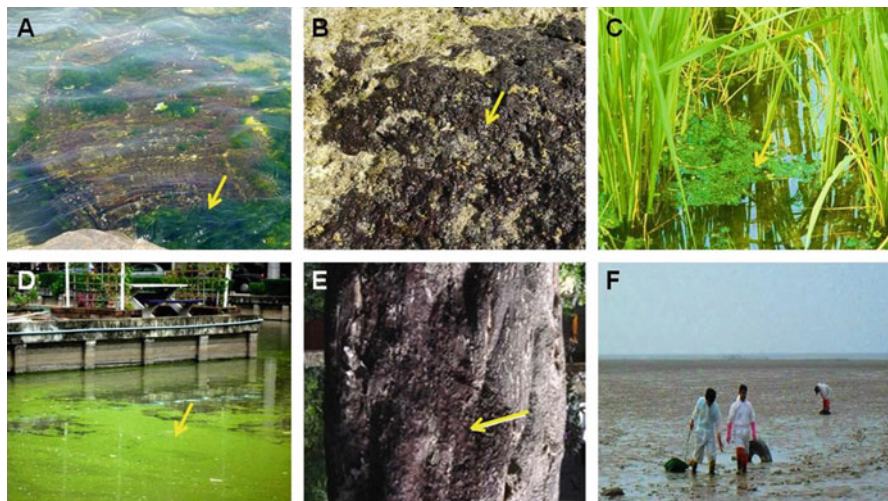

Fig. 1.4   Distribution of cyanobacteria in different habitats on Earth such as marine water (**A**), rock surface (**B**), rice paddy field (**C**), fresh water (**D**), tree bark (**E**) and mudflatS (**F**)

Phormidium were also found frequently (Issa et al. 1999). In biological crusts around the world, *Microcoleus vaginatus* was found to be the most dominant and ecologically important cyanobacteria (Johansen and Shubert 2001). In soils of North American deserts together with the cyanobacterium, *Microcoleus vaginatus*, *Nostoc commune*, *Schizothrix calcicola*, *N. paludosum*, *N. punctiforme*, *N. muscorum*, *Leptolyngbya tenuis* (as *Phormidium tenue*), *Trichormus variabilis* (as *Anabaena variabilis*), *Phormidium minnesotense,* and *Tolypothrix tenuis* have been found in the biological crusts (Johansen 1993). *Microcoleus vaginatus*, *Scytonema* sp., and *Nostoc* spp. were the dominant cyanobacteria found in the desert crusts of Southeastern Utah (Garcia-Pichel and Belnap 1996). In steppes and semideserts in the territory of USSR, *Scytonema ocellatum*, *Nostoc commune*, and *Microcoleus vaginatus* formed *Nostoc–Scytonema* communities (Gollerbach and Shtina 1969). *Scytonema* sp., *Scytonema* cf. *ocellatum*, *Microcoleus* cf. *paludosus*, *M.* cf. *sociatus*, *Calothrix* cf. *marchica*, *Calothrix* cf. *elenkinii*, *Phormidium* sp., and *Nostoc* cf. *microscopicum* were detected in microbiotic crusts in eroded soils of a tropical dry forest in Mexico (Maya et al. 2002). *Xenococcus lyngbyae*, *Microcoleus paludosus*, and *M. vaginatus* were the most dominant cyanobacteria in the biological soil crusts in the Gurbantunggut Desert in Western China (Chen et al. 2007). Several cyanobacteria including *Microcoleus vaginatus* were detected in the microbiotic crusts on sand dunes (artificially stabilized) in Tengger Desert, China, during first stages of dune stabilization (after 0–8 years); however, in stylized dune after 24 years, these species were not found (Li et al. 2002). *Anabaena azotica*, *Jaaginema pseudogeminatum* (as *Oscillatoria pseudogeminata*), *Limnoraphis cryptovaginata* (as *Lyngbya cryptovaginata*), *Oscillatoria obscura*, *O. subbrevis*, *Leptolyngbya tenuis* (as *Phormidium tenue*), *Leptolyngbya lurida* (as *Phormidium luridum*), *Microcoleus autumnalis* (as *Phormidium autumnale*), *Schizothrix rupicola*, *Scytonema javanicum,* and *S. millei* were also found together with *Microcoleus vaginatus*. Filamentous cyanobacteria *Scytonema* sp. and *Sypmplocastrum purpurascens* were found to be the dominating cyanobacteria in the dry savanna ecosystem in Australia (Büdel et al. 2018).

In temperate forest soils, *Nostoc punctiforme*, *Desmonostoc muscorum* (*Nostoc muscorum*), *Leptolyngbya foveolarum* (*Phormidium foveolarum*), and *Microcoleus autumnalis* (*Phormidium autumnale*) were the dominant cyanobacterial species (Aleksakhina and Shtina 1984). *Microcoleus autumnalis* (*Phormidium autumnale*) and *Leptolyngbya foveolarum* were detected in the algal flora of unlimed and limed forest soils in the Ardennes (Belgium) (Hoffmann et al. 2007). *Symplocastrum friesii* was detected in the soils of the northern part of the Great Smoky Mountains National Park, USA (Khaybullina et al. 2010). Several cyanobacterial species such as *Aphanothece stagnina*, *Leptolyngbya* cf. *nostocorum*, *Leptolyngbya* cf. *hansgirgiana*, *Hormoscilla pringsheimii*, *Kamptonema laetevirens*, *Kamptonema animale*, *Oxynema* cf. *acuminatum*, *Phormidium* cf. *retzii*, *Phormidium aerugineo-caeruleum*, *Phormidium uncinatum*, *Phormidium tergestinum,* and *Nostoc* cf. *ellipsosporum* were reported only in the boreal forest zone. In the broad-leaved forest zone, cf. *Trichocoleus hospitus* was the widely distributed cyanobacteria.

Chroococcus varius and *Myxosarcina* cf. *tatrica* were found only in this type of environment (Gaysina et al. 2018). In flood plain forest having trees *Padus avium* Mill. and *Alnus glutinosa* (L.) Gaertn., a maximum number of cyanobacteria were found namely *Borzia trilocularis*, *Cylindrospermum* sp., *Cylindrospermum majus*, *Leptolyngbya voronichiniana*, *Leptolyngbya foveolarum*, *Microcoleus vaginatus*, *Nostoc* cf. *calcicola*, *N.* cf. *punctiforme*, *Phormidium ambiguum*, *P. breve*, *P. corium*, *P. dimorphum*, *Roholtiella bashkiriorum*, *Trichormus variabilis,* and cf. *Trichocoleus hospitus* (Gaysina et al. 2018). In the Yuraktau and Tratau Mounts in the forest steppe zone of Bashkiria, 56 species of cyanobacteria were reported, among which dominant species were *Phormidium jadinianum*, *Leptolyngbya foveolarum*, *Microcoleus autumnalis* (*Phormidium autumnale*), and *Nostoc punctiforme* (Bakieva et al. 2012). Unique cenoses in the arid regions were created by *Nostoc commune*, *Microcoleus vaginatus,* and *Scytonema ocellatum* (Gollerbach and Shtina 1969). In a forb–grass steppe near Sibay town and a sand savanna of Northwestern Ohio, *Cyanothece aeruginosa* was found in the biological soil crusts (Neher et al. 2003; Gaysina et al. 2018).

Filamentous cyanobacteria like *Anabaena* and *Tolypothrix* were dominant in the restoration of soils damaged by volcano eruption (Treub 1888). Cyanobacteria were dominant only near lava flows after volcanic activity in Surtsey Island (Schwabe 1972). Several *Nostoc* Vausher species and *Anabaena variabilis* Küzting were reported (Henriksson et al. 1972). On the volcanic ash of Kuril–Kamchatka arcs, inside the edge of the crater nine cyanobacterial taxa were found namely *Aphanocapsa muscicola* (*Microcystis muscicola*), *Synechocystis aquatilis*, *Desmonostoc muscorum* (*Nostoc muscorum*), *Mastigocladus laminosus*, *Aphanothece castagnei*, *Nostoc gelatinosum*, *N. humifusum*, *Oscillatoria geminata* f. *sulphurea*, *Leptolyngbya* (*Plectonema nostocorum*), and *Leptolyngbya gracillima* (*Plectonema gracillimum*) (Shtina et al. 1992). *Mastigocladus laminosus* Cohn is usually found in the hot springs (Shtina et al. 1992). Phylogenetic analysis of cyanobacterial strains through *16S rRNA* gene sequencing was done for the cyanobacteria isolated from hot springs in Rajgir, India. These cyanobacteria were identified as *Cyanothece* sp. strain HKAR-1, *Nostoc* sp. strain HKAR-2, *Scytonema* sp. strain HKAR-3, and *Rivularia* sp. strain HKAR-4 (Rastogi et al. 2012).

Reclamation of the highly alkaline "usar" soil in India by blue-green algae with the dominance of *Nostoc commune* was detected by Singh (1950). In deserts of USSR, cyanobacteria were extensively grown in the wet period on "takyr" soils having pH 9–10 and *Nostoc commune* (*Desmonostoc commune*), *Microcoleus,* and *Phormidium* were the dominant species (Gollerbach et al. 1956). It was found that *Microcoleus vaginatus* crusts started to grow in liquid media after cultivation in salt solutions (Bolyshev et al. 1965). In halophytic solonchaks (salted soils) of the Sahara–Gobi desert area, cyanobacteria *Anabaena*, *Anabaenopsis*, *Aulosira*, *Calothrix*, *Nostoc*, and *Tolypothrix* were found to be widely distributed. In various types of salted soils and vegetation true solonchak, saline steppes, meadow halophilous 49 cyanobacterial species were reported and the dominant genera were *Calothrix*, *Leptolyngbya*, *Lyngbya*, *Phormidium*, *Anabaena*, *Jaaginema,* and *Nostoc*. *Nostoc linckia*, *Leptolyngbya fragilis,* and *L. tenuis* were the most dominant

species. *Phormidium paulsenianum*, *Leptolyngbya fragilis,* and *Nostoc linckia* were reported to grow on soils covered by meadow halophilous vegetation (Vinogradova and Darienko 2008).

Different cyanobacteria such as *Phormidium paulsenianum*, *P. jadinianum*, *P. breve* (*Oscillatoria brevis*), and *Leptolyngbya foveolarum* (*Phormidium foveolarum*) were found to be grown in all types of solonchaks, and *Microcoleus autumnalis* (*Phormidium autumnale*) was typically found in the meadow solonetz (Khaibullina and Gaisina 2008). Recently, for examining the cyanobacterial community structure, pooled mat sample was studied from the Rann of Kachchh, India, which is desert area on the western part of India and is exposed to dynamic environmental changes such as temperature, salinity, and nutrients (Patel et al. 2019). Taxonomic profiling revealed that the mats predominately contained the members of Pseudanabaenales and Oscillatoriales. Other abundant cyanobacterial orders were Nostocales, Chroococcales, and unclassified cyanobacteria (Patel et al. 2019).

Cyanobacteria also play an important role in the restoration of disturbed ecological areas by colonizing the lifeless substrates left after anthropogenic degradation such as mine spoils, heavy metals, and contaminated soils. Such degraded habitats are characterized by lack of water high concentrations of heavy metals, deficient nutrient contents, and high levels of isolation (Trzcińska and Pawlik-Skowrońska 2008). Cyanobacterial species such as *Lyngbya*, *Microcoleus*, *Nostoc edaphicum*, *Nostoc* sp., *Oscillatoria* sp., and *Phormidium* sp. were present in the soils polluted with heavy metal contaminations (García-Meza et al. 2006; Trzcińska and Pawlik-Skowrońska 2008; Cabala et al. 2011). In reclaimed soils in brown coal and lignite postmining area of Czech Republic and Germany, *Microcoleus vaginatus*, *M. autumnalis*, *Nostoc muscorum*, *N.* cf. *calcicola,* and representatives of the genera *Phormidium*, *Leptolyngbya*, *Pseudophormidium,* and *Schizothrix* were found (Lukešová 2001). The cyanobacterial genera *Microcoleus*, *Oscillatoria*, and *Phormidium* were reported as dominant taxa in the spoils of age 1–2 years of coal deposits of Russia where as on the spoils of age 5–9 years, *Pseudophormidium*, *Phormidium*, and *Oscillatoria* were reported as dominant genera (Kabirov 1997).

The polar region of Earth comprises the Antarctic and Arctic regions and constitutes about 14% of the Earth's biosphere (Rampelotto 2014). In these ecosystems, cyanobacteria have been reported as dominant phototrophs because of their ability to tolerate the abiotic stresses such as low temperature and ultraviolet radiation in these regions of Earth (Vincent 2007). Cyanobacterial species such as *Aphanocapsa fusco-lutea*, *A. grevillei*, *Chroococcus cohaerens*, *C. spelaeus*, *Desmonostoc muscorum*, *Gloeocapsa ralfsii*, *G. sanguinea*, *G. violacea*, *Kamptonema animale*, *Leptolyngbya boryana*, *L. foveolarum*, *Microcoleus autumnalis*, *Nostoc commune*, *N. punctiforme*, and *Phormidium ambiguum* were reported from aerophytic habitats in Hypoarctic and Arctic regions, and these were on the soil surface and inside the soil layer (Davydov and Patova 2018). Cyanobacterial diversity in the Arctic was found to be higher as compared to the Antarctic regions (dry valleys) (Zakhia et al. 2008). *Chroococcus* and *Gloeocapsa* were found to be dominant in the crust in the Arctic conditions, whereas *Stigonema*

ocellatum, *S. minutum*, and *S. informe* with associated *Gloeocapsopsis magma* and *Gloeocapsa violascea* were found to be most frequent species in crusts in hypoarctic regions (Davydov and Patova 2018). *Gloeocapsopsis magma*, *Leptolyngbya foveolarum*, *Nostoc commune*, *Scytonema hofmannii*, *Stigonema minutum,* and *S. ocellatum* were reported as permanent species of BSC in the mountain tundras of the Polar and Subpolar Urals (Patova et al. 2018). Several cyanobacterial taxa such as *Microcoleus autumnalis*, *Merismopedia tenuissima*, *Nostoc punctiforme*, *N. commune*, *Pseudanabaena frigida*, and *Schizothrix* cf. *calcicola* were identified in the Hornsund area, Spitsbergen (Matuła et al. 2007). On wet soils in Antarctica, wide distribution of filamentous cyanobacteria from the order Oscillatoriales, especially *Microcoleus autumnalis,* was found (Strunecký et al. 2012).

1.3.2 Aquatic Habitats

Cyanobacteria inhabiting aquatic habitats can be divided into two broad ecological groups (Fogg et al. 1973):

1. Planktonic cyanobacteria (float freely in the water column)
2. Benthic cyanobacteria (adhere to submerged solid surfaces)

In many ocean regions, cyanobacteria genera such as *Cyanobium*, *Prochlorococcus, Synechococcus,* and *Synechocystis* are widely distributed as marine planktonic communities (Flombaum et al. 2013; Costa et al. 2014). Some filamentous genus such as *Romeria* also inhabits oceans as marine plankton (Komárek 2001). During favorable environmental conditions, cyanobacteria form blooms as a result of their rapid growth (Sellner 1997; De Figueiredo et al. 2006; Sciuto and Moro 2015). The colonial filamentous cyanobacteria *Trichodesmium* is one of the most abundant bloom-forming genus in the marine pelagic zone and is distributed panglobally in subtropical and tropical oceans having oligotrophic environments (Capone et al. 1997; LaRoche and Breitbarth 2005). Cyanobacterium *Crocosphaera watsonii* contributes significantly to oceanic nitrogen fixation, and *Crocosphaera* also inhabit regions having low iron content due to its ability to reduce its iron metalloenzyme inventory (Zehr et al. 2001; Montoya et al. 2004; Moisander et al. 2010; Saito et al. 2011). In the Baltic Sea, cyanobacterial genera *Anabaena*, *Aphanizomenon,* and *Nodularia* are found as the most important bloom-forming cyanobacteria (O'Neil et al. 2012). Worldwide, filamentous cyanobacteria *Lyngbya* are commonly found as benthic communities (Paul et al. 2005; Jones et al. 2011; O'Neil et al. 2012). The cyanobacterial genus *Lyngbya majuscule* belongs to the benthic zones forming dense mats and is widely distributed in tropics in reef and lagoons (Whitton and Potts 1982, 2000a, b; Hoffmann 1994; Thacker and Paul 2004). Another filamentous genus *Moorea* belongs to a cosmopolitan pantropical ecological group, which is abundant in the marine benthos. In intertidal flats of the German Wadden Sea, the cyanobacterial genera *Coleofasciculus*, *Hydrocoleum,* and *Lyngbya* are dominant in all the sediment types in cyanobacterial populations (Vogt

et al. 2018). Common cyanobacterial species in marine littoral and intertidal habitats are constituted by *Microcoleus ethnoplasts* and representatives of the genera *Oscillatoria* sp. and *Spirulina* (Kulasooriya 2011). In the Portugal coast, the filamentous cyanobacterial genus *Leptolyngbya*, *Nodosilinea*, *Pseudanabaena*, and *Romeria* constitute a large group of the marine cyanobacterial strains (Costa et al. 2014). Among the most widely distributed cyanobacterial mangrove dwellers worldwide, *Aphanocapsa*, *Calothrix*, *Chroococcus*, *Coleofasciculus*, *Lyngbya*, *Oscillatoria*, and *Schizothrix* constitute the most important genera (Alvarenga et al. 2015).

In the oceans and large transparent lakes, the autotrophic picoplanktons constitute the major primary producers (Callieri and Stockner 2002; Ting et al. 2002). The phycoerythrin-rich freshwater cyanobacteria *Synechococcus* is the dominant genus among the autotrophic picoplanktons in oligotrophic lakes (Fahnenstiel and Carrick 1992; Ting et al. 2002). The cyanobacterial genera *Cyanobium* and *Synechocystis* are also very important plankton in freshwater ecosystems (Stockner 1988; Albertano et al. 1997; Komárek 2003). In freshwater bodies, large populations are formed by the genus *Aphanothece* (Mur et al. 1999). In freshwater ecosystems, common cyanobacterial genera are *Chroococcus*, *Coelosphaerium*, *Coelomoron*, *Cyanodictyon*, *Gomphosphaeria*, *Rhabdoderma*, *Merismopedia,* and *Snowella* (Komárek and Anagnostidis 1999; Komárek 2003). Ecostrategists focusing on scum formation constitute large colonies of filaments or coccoid cells and genera *Anabaena*, *Aphanizomenon,* and *Microcystis* belong to such ecological group. In freshwater habitats, the genus *Microcystis* is one of the most widely distributed microcystin-producing cyanobacteria, which forms blooms in eutrophic lakes and springs of the temperate zone (Reynolds et al. 1981; Kurmayer et al. 2002; Rastogi et al. 2014, 2015). Filamentous cyanobacterial species such as *Limnothrix redekei* and *Planktothrix agardhii* inhabit eutrophic and hypertrophic shallow (<3 m depth) lakes (Mur et al. 1999). *Aphanothece*, *Oscillatoria*, and *Phormidium* constitute benthic mats, which usually grow on the sediments of ponds and lakes (Komárek 2003). Among epilithic cyanobacteria, *Aphanocapsa*, *Aphanothece*, *Chroococcus*, *Nostoc,* and *Leptolyngbya* are the most distributed cyanobacterial genera from freshwater streams of India (Saha et al. 2007). *Oscillatoria*, *Phormidium*, *Lyngbya*, *Leptolyngbya*, *Microcoleus*, *Tychonema*, and *Schizothrix* are usually found as benthic cyanobacteria (Steppe et al. 1996; Mez et al. 1997, 1998; Hitzfeld et al. 2000; Aboal et al. 2005; Gugger et al. 2005). In freshwater habitats, *Aphanothece* and *Synechococcus* along with nitrogen-fixing cyanobacteria *Anabaena* and *Scytonema* are usually found as toxic cyanobacteria (Krienitz et al. 2003; Dasey et al. 2005; Mohamed et al. 2006; Mohamed 2008; Smith et al. 2011). Macroscopic colonies forming cyanobacteria of order Nostocales namely *Nostoc caeruleum*, *N. commune*, *N. microscopicum*, *N. parmelioides*, *N. pruniforme*, *N. verrucosum*, and *N. zetterstedtii* have been found from inland aquatic habitats (Mollenhauer et al. 1999).

1.3.3 Symbiotic Associations

Corals, diatoms, dinoflagellates, seagrass, and sponges are the common marine organisms, which form associations with cyanobacteria. Colonies of the coral *Montastraea cavernosa* form endosymbiotic association with cyanobacteria, which express nitrogenase and thus also provide fixed nitrogen to the host coral (Lesser et al. 2007). *Calothrix rhizosoleniae* and *Richelia intracellularis* (heterocystous cyanobacteria) form symbiotic relationship with diatoms such as *Chaetoceros, Hemiaulus,* and *Rhizosolenia* (Foster et al. 2011). A unicellular nitrogen-fixing cyanobacterium is present as endosymbiont in diatoms belonging to the family *Epithemiaceae* (DeYoe et al. 1992). In sponges, *Synechococcus* sp. is commonly found in symbiotic association, and *Oscillatoria spongeliae* has also been reported to form association with sponges over a wide geographic range in oceans (Usher 2008). The leaves of the seagrass *Cymodocea rotundata* bear cyanobionts as small attached patches of thin biofilms having pigmented microbial aggregates. The cyanobacterium *Nostoc* is a prolific symbiotic partner, which forms association with several eukaryotic organisms such as protists, fungi, plants, and animals (Rai et al. 2002). Nostocacean cyanobacteria form the symbiotic association with members of the plant kingdom ranging from bryophyta to pteridophyta (*Azolla*) and from gymnosperms (family Cycadaceae) to angiosperms (family Gunneraceae). High strain diversity has been observed both among and within different host species as revealed by most of the studies on identification and diversity of the cyanobionts from the individual hosts except *Azolla* (West and Adams 1997; Rasmussen and Svenning 1998; Nilsson et al. 2000; Costa et al. 2001; Guevara et al. 2002; Rasmussen and Nilsson 2002). *Nostoc muscorum* and *N. punctiforme* have been identified as cyanobionts, which form symbiotic relationship with *Cycas* (Costa et al. 1999). Approximations of these cyanobionts have been assigned to the genera *Anabaena*, *Nostoc*, and *Trichormus*, or all of these symbionts have been shifted to a new separate genus, but all of these cyanobionts certainly belong to the order Nostocales (Komárek and Anagnostidis 1989; Plazinski et al. 1990; Gebhardt and Nierzwicki-Bauer 1991; Caudales et al. 1995; Baker et al. 2003; Pabby et al. 2003; Svenning et al. 2005).

1.4 Perspective and Conclusion

Undoubtedly, the ancient photoautotrophs cyanobacteria have played crucial role in the evolution of early Earth and its biosphere and are also responsible for the oxygenation of the oceans and atmosphere. Diversity of cyanobacteria is expressed by their morphological, physiological, and biochemical properties, which enable them to survive and sustain in diverse range of ecological niches ranging from the polar regions to the hot springs, thus representing life in almost every possible environments on Earth. Their success in acclimatizing such wide range of diverse habitats can be attributed to their long course of evolutionary process. Despite the important role of cyanobacteria in the early evolution of life and Earth, fundamental

questions still remain unanswered about the origin, timing, and pattern of diversification of cyanobacteria. Hence, it is required to define new biosignatures, which could serve as indicator of cyanobacteria in order to reassess their fossil record and could aid in providing new calibration points for molecular clocks. These biosignatures will help in combining analyses of the ultrastructure, morphology, and ecology of cyanobacterial microfossils with their biomolecular (pigments and lipids), metal, and isotopic composition. Identification of these promising fossils, not only as cyanobacteria, but of specific clades within this ancient group of photoautotrophs will improve the understanding of the diversification record of cyanobacteria.

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