Chapter 16

Cyanobacteria From Brazilian Extreme Environments: Toward Functional Exploitation

Diego B. Genuário[1], **Marcelo G.M.V. Vaz**[2], **Suikinai N. Santos**[1], **Vanessa N. Kavamura**[3] **and Itamar S. Melo**[1]

[1]EMBRAPA Environment, Laboratory of Environmental Microbiology, São Paulo, Brazil, [2]Federal University of Viçosa, Department of Plant Biology, Laboratory of Phycology and Molecular Biology, Viçosa, Brazil, [3]Department of Sustainable Agriculture Sciences (SAS), Rothamsted Research, Harpenden, United Kingdom

16.1 INTRODUCTION

Extreme environments exhibit conditions that are beyond those bearable for most known species, which include extremely high or low temperature, pressure, gas content, radiation, pH, water availability, content of solutes and other chemical compounds (Van den Burg, 2003). However, the term "extreme" must be used with caution because it always reflects an anthropocentric point of view since these conditions could be considered completely normal for some macro- and microorganisms (Horikoshi et al., 2011). Currently, the most emblematic examples of extreme environments on Earth include those found on cold and dry deserts, volcanoes, hypersaline lagoons and deep sea sediments; however, these environments could be the most prevailing habitats found in past geological periods (Rampelotto, 2013).

Environments known as extremes were considered lifeless until the late 19th century, when the first report of isolation of organisms from salted fishes was published (Farlow, 1880). Nevertheless, the isolation of microbial strains from high salt-concentrated water in the Dead Sea occurred only in 1936. Nowadays, these environments are recognized as rich habitats with highly adapted species due to their living constraints and long-term evolution (Rampelotto, 2013). In this way, organisms that are able to thrive in these environments and present optimal and suboptimal growth under these conditions are known as extremophiles and extremotrophs, respectively (Horikoshi et al., 2011). Extreme organisms have been mostly investigated under taxonomic and physiological aspects leading to the discovery of novel species/genera and to a better understanding of their metabolic adaptation under environmental pressure (Garland and Carter, 1994).

Among the microorganisms inhabiting extreme environments, the phylum *Cyanobacteria* is considered one of the most ancient, versatile and ecologically successful group, inhabiting several extreme conditions (Abed et al., 2009). They can survive in a range of environments: from oceans to fresh water, soil to bare rocks, deserts to ice shelves, hot springs to Arctic, hypersaline to alkaline lakes, environments with high metal concentrations and low availability of water conditions (xerophilic) through the formation of endolithic communities in desertic regions (Sánchez-Baracaldo et al., 2005; Thajuddin and Subramanian, 2005; Rostagi and Sinha, 2009). They are also known as active biomolecules producers endowed with peculiar biochemical pathways which are of great interest in biotechnological purposes. Therefore, the occurrence and activity of cyanobacteria at extreme conditions make them useful alternatives to the exploration of enzymes, proteins, osmolytes, biopolymers and new drugs (Rampelotto, 2013). In recent years, cyanobacteria have gained attention as a rich source of bioactive compounds, as one of the most promising groups of organisms to produce them (Bhadury and Wright, 2004; Dahms et al., 2006). For example, halophilic cyanobacteria belonging to the species *Aphanothece halophytica, Microcoleus chthonoplastes*, *Phormidium ambiguum*, *Oscillatoria neglecta*, *Oscillatoria limnetica* and *Oscillatoria salina* are source of glycine betaine, trehalose and ectoine, all important osmolytes for agriculture and cosmetics industry (Welsh, 2000; Oren, 2010). Several species of cyanobacteria produce photoprotective metabolites that act as antioxidants, preventing cellular damage from UV-induced reactive oxygen

Microbial Diversity in the Genomic Era. DOI: https://doi.org/10.1016/B978-0-12-814849-5.00016-2

species, and may be used in the development of artificial human sunscreen, such as scytonemin from *Stigonema* sp. (an extremophilic marine cyanobacterium) and mycosporine-like amino acids from endolithic cyanobacteria (Vítek et al., 2014; Singh et al., 2017). The desiccation-resistant genus *Chroococcidiopsis* also exhibits resistance against ionizing radiation probably due to an efficient DNA repair mechanism (Billi, 2009). In addition, cyanobacteria have a relevant potential in producing compounds with medical applications, such as curacin A, produced by *Lyngbya majuscula* and dolastatin 10 which have undergone clinical trials as potential anticancer drugs (antimitotic) (Raja et al., 2014). Calothrixins A and B from *Calothrix* sp. inhibited the growth of the malarial parasite (Xu et al., 2016), whereas the anti-HIV and herpes simplex virus (HSV) compounds extracted from *Microcystis* strains may be important drug candidates for use in humans (Dixit and Suseela, 2013). In the context of extremophilic microorganisms, the number of studies is still low when compared to the great biological diversity harbored by an environment and they are mostly focused on biotechnological and industrial applications (Rampelotto, 2013). However, this is not a result of low biodiversity of extremophiles or rare extreme environments. We can attribute these problems to several factors such as (1) little knowledge on the location of extreme environments, (2) difficulties in accessing these environments and collecting samples and (3) problems in isolating and maintaining the organisms in vitro. In this direction, the main purpose of this chapter was to identify some extreme environments within Brazilian ecosystems based on their peculiar characteristics and on evidences gathered from the literature. Simultaneously to their characterization, it is also presented an overview about the inherent culturable cyanobacterial diversity studied in these environments by polyphasic approach. In the last section, some investigations conducted attempting to explore this cyanobacterial diversity in terms of prospection of new genes, biosynthetic pathways, or products focused on biotechnological application are offered. It is expected that all the information provided in this chapter can encourage researchers to explore the cyanobacterial diversity from some Brazilian extreme environments and use this biodiversity for practical use.

16.2 EXTREMOPHILIC MICROORGANISMS

Extremophiles are organisms that succeed in extreme conditions, which normally is detrimental to most of life forms in Earth. The majority of extremophilic organisms are microorganisms distributed in all domains of life; however, most of them belong to *Archaea* and *Bacteria* (Seckbach and Oren, 2007). Within these domains, some phylogenetic lineages are particularly well adapted to specific extreme conditions, whereas many extremophiles adapted to the same condition are found broadly scattered in the phylogenetic tree (Rampelotto, 2013).

In general, the organisms are classified based on their prevailing physiological characteristics such as the ability to grow in high pH (alkaliphiles) or low pH (acidophiles), beneath rock materials (endolithics), in high salt concentrations (halophiles), under low availability of nutrients (oligotrophics), under low (psychrophiles) or high temperatures (thermophiles), under high levels of radiation (radiophiles), high pressure (piezophiles), under low water activity (xerophiles) (Abe and Horikoshi, 2001; Rothschild and Mancinelli, 2001; Van den Burg, 2003). However, several natural environments present more than one extreme condition associated indicating that some microorganisms, known as polyextremophiles, might display multiple physiological features (Rothschild and Mancinelli, 2001). The alkali-thermophiles and the halophilic alkaliphiles isolated from sediments of soda lakes are good examples of polyextremophiles (Mesbah and Wiegel, 2008). Production of pigments for UV radiation protection, synthesis of thermostable enzymes under high temperatures, accumulation of compatible solutes (osmolytes), production of spores, exopolysaccharides and biofilm under desiccation, and high temperature are among the main characteristics observed in extremophilic microorganisms (Taketani et al., 2017). Within *Bacteria* domain, the phylum *Cyanobacteria* presents diverse species adapted to different extreme conditions, such as those found in desert soils, saline–alkaline lakes, hypersaline ponds, glaciers and hot springs (Ward et al., 1998; Paerl et al., 2000; Jungblut et al., 2005; Sánchez-Baracaldo et al., 2005) and regions with high metal concentrations (Huertas et al., 2014). In general, cyanobacterial species do not tolerate acid environments and rarely grow on pH below 5–6 (Paerl et al., 2000; Duarte et al., 2012).

Cyanobacteria are among the most morphologically diverse group of prokaryotes, currently being dealt in two different Nomenclatural Codes, the International Code of Nomenclature for algae, fungi and plants (McNeill et al., 2012) and the International Code of Nomenclature of Prokaryotes (Castenholz et al., 2001). Within the Bacteriological Code, they have been divided into five different morphological sections with the unicellular groups included in Sections I and II, and the multicellular species comprised in Sections III, IV, and V (Castenholz et al., 2001). Both Sections IV and V evolved cell differentiation (akinetes and heterocytes), and therefore represent the most morphologically complex cyanobacteria (Schirrmeister et al., 2011). According to the International Code of Nomenclature for algae, fungi and plants, and the most recent taxonomic classification using a polyphasic approach, cyanobacterial diversity has been distributed into eight orders (Komárek et al., 2014). The orders Gloeobacterales, Chroococcales, Pleurocapsales, Chroococcidiopsidales comprise exclusively the unicellular forms, while the orders Pleurocapsales, Oscillatoriales and Nostocales accommodate the filamentous ones. Interestingly, the order Synechococcales shelters both the unicellular and filamentous forms (Komárek et al., 2014).

These oxygenic photoautotrophic bacteria play important roles in global carbon and nitrogen cycles (Whitton and Potts, 2000). The first indirect evidence for the presence of cyanobacteria dates back to 2.32–2.45 billion years ago with the rise of oxygen levels in Earth's atmosphere during the Great Oxygenation Event (GOE) (Bekker et al., 2004). Likewise, the variety in shapes, attributed to morphological diversity of cyanobacteria in fossil records, allows a reliable identification of cyanobacterial relatives compared to other prokaryotes (Schirrmeister et al., 2015). Fossil records from all cyanobacterial morphotypes have been found in Mesoproterozoic deposits (Schopf and Blacic, 1971; Horodyski and Donaldson, 1980; Butterfield, 2000). Unicellular forms (Sections I and II) have been recognized in the early Proterozoic period at Duck Creek Dolomite in Australia (Knoll et al., 1988) and Belcher Supergroup in Canada (Hoffmann, 1976), while fossil records from multicellular morphotypes with differentiated cells (Sections IV and V) are extensively found after the GOE, supporting the hypothesis that heterocytes formation evolved as a consequence of an increase in atmospheric oxygen content (Tomitani et al., 2006; Schirrmeister et al., 2015). The differentiation of specialized cells to confine nitrogen fixation spatially apart from the vegetative cells (sites for photosynthesis) has evolved to circumvent the inactivation of the enzymatic complex of nitrogenase by the O_2, which is released during oxygenic photosynthesis (Compaoré and Stal, 2010). In general, the nutritional simplicity of all cyanobacterial strains, associated with the ability to fix carbon, as well as nitrogen, the last one being found in some groups, allowed this phylum of microorganisms to conquer a variety of habitats including the extreme ones mentioned above (Singh et al., 2016). Besides, extreme environments currently found in the Earth might have been the prevailing conditions found in the past in which the cyanobacteria have evolved due to its long evolutionary history. Among its numerous genera, the genus *Chroococcidiopsis* is considered a basal lineage, which is characterized by simple unicellular colonial morphology resembling those microfossils found in Proterozoic records (Schirrmeister et al., 2015). It is considered the prime candidate as pioneer photosynthetic microorganism for terraforming of Mars, since it is one of the most desiccation-resistant groups of microorganisms found in extreme arid habitats (Friedmann and Ocampo-Friedmann, 1995). This genus is also detected from Antarctic rocks to thermal springs and hypersaline habitats, highlighting its remarkable tolerance against environmental extremes (Friedmann and Ocampo-Friedmann, 1995).

16.3 BRAZILIAN EXTREME ENVIRONMENTS

Brazil encompasses 53 major ecosystems (Sayres et al., 2008) and over 600 different terrestrial and aquatic types of habitats. It is considered one of the most important hotspots worldwide, with a rich biodiversity, both in number of individuals as well as in number of endemic species, harboring about 15% of the total diversity of the planet (Bass et al., 2010). Additionally, human activities have promoted a couple of undesired alterations which led to the establishment of novel extreme ecosystems such as areas impacted by heavy metals, oil spills, acid mine drainages, desertified areas and others.

There is still little research on the microbial diversity of all biomes and in the context of extremophiles, the number of studies is even lower. One of the reasons might be the lack of knowledge and information on these environments. Although Brazil is considered a tropical country, it presents some permanent or seasonal extreme environments spread all over the country. Duarte et al. (2012) have described some of these environments in the context of astrobiology, such as mangroves, which are typically anaerobic transitional ecosystems between terrestrial and marine environments with high salt concentrations (up to 30%–37% NaCl); *Caatinga*, which is a very hot and dry ecosystem during the most part of the year, with surface soil temperature reaching up to 60°C; *Cerrado* which presents an extreme acid soil ($pH < 5$) with high aluminum content (Haridasan, 1989). Likewise, there are smaller ecosystems with extreme characteristics such as hot springs, hypersaline lagoons, ultraoligotrophic ecosystems (river, caves, and sea) and deep sea sediments.

This section is an attempt to identify and characterize extreme environments located within the main Brazilian biomes (Fig. 16.1) for the purposes of filling some of the most important gaps in the knowledge of extremophilic conditions. Whatever the situation, these biomes offer remarkable opportunities for exploration and rational exploitation of cyanobacterial biodiversity (Fig. 16.2) and their biotechnological potential.

16.3.1 Brazilian Biomes: Extreme Peculiarities and Cyanobacterial Diversity

16.3.1.1 Amazon Rainforest

The Amazon Rainforest is globally recognized as one of the greatest and richest tropical forests in terms of area and biodiversity (Malhi et al., 2008). It is also known as a myriad of streams and rivers converging to form the Amazon

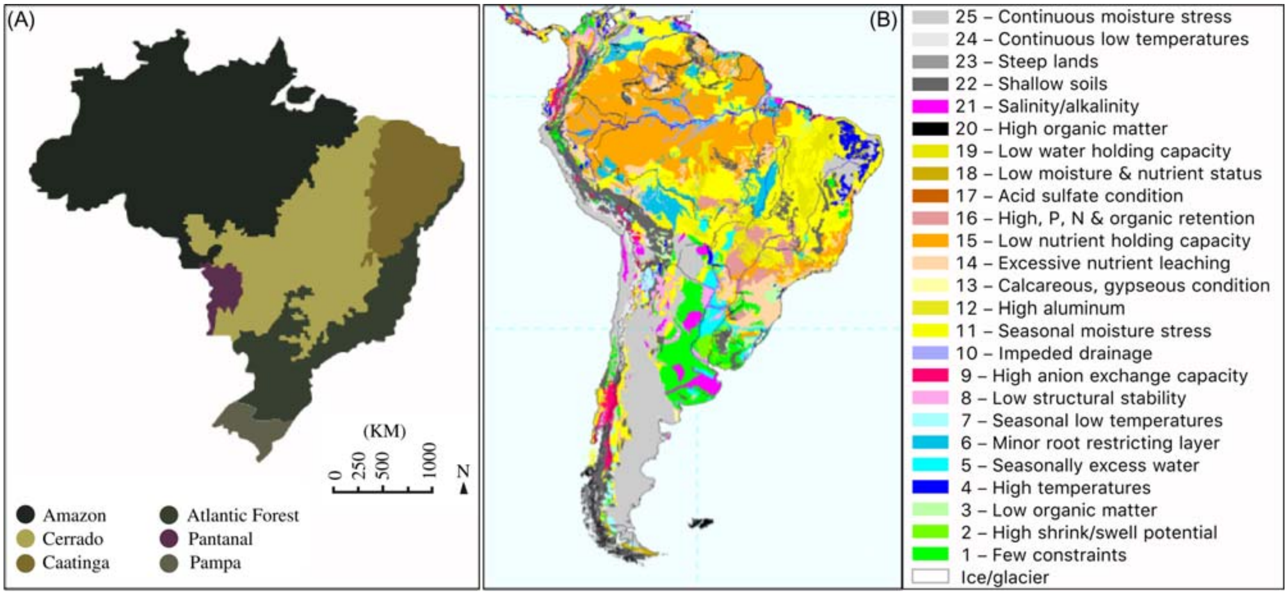

FIGURE 16.1 Representative scheme of Brazilian map showing the main biomes (A) and major land resource stresses (B). *Adapted from Rodrigues, Belmok, Catão, and Kyaw (2016) and US Department of Agriculture, Natural Resources Conservation Service, 1998.*

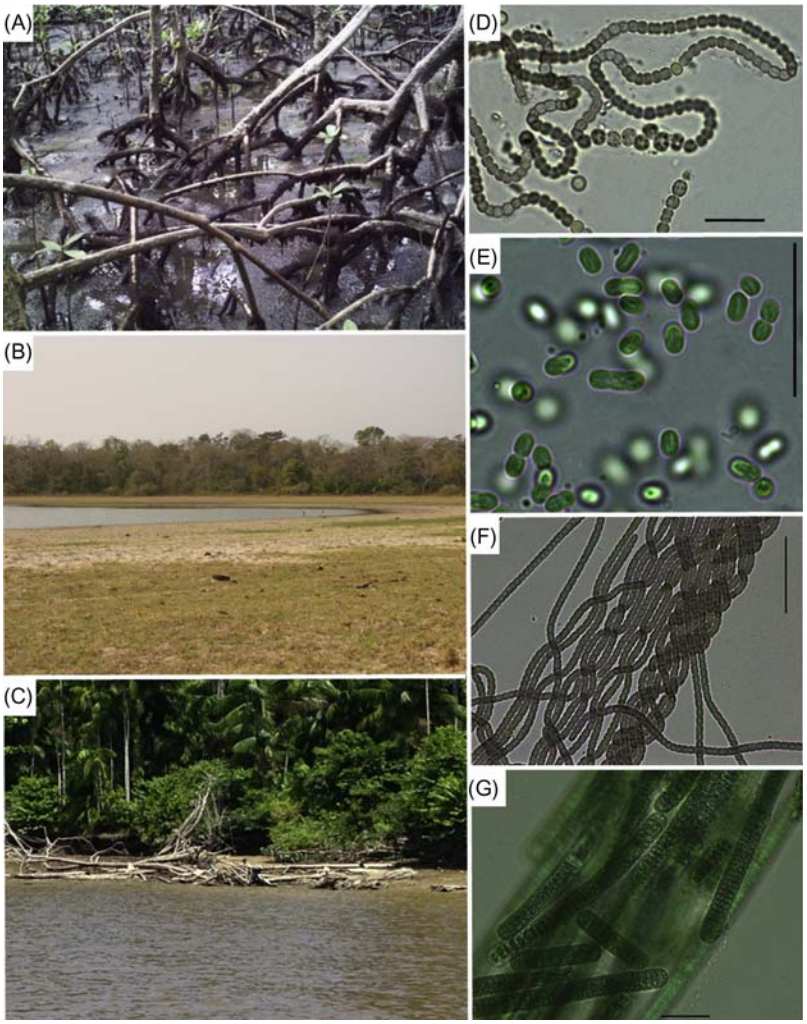

FIGURE 16.2 Extreme environments found in Brazil and examples of cyanobacterial strains isolated from them. (A) Mangrove ecosystems; (B) saline–alkaline lakes in Pantanal wetlands; (C) Amazon Forest; (D) *Halotia branconii* CENA186; (E) *Geminocystis* sp. CENA526; (F) *Pantanalinema rosaneae* CENA516; (G) *Planktothrix mougeotii* CMAA1557.

River, the largest river in the world in terms of water discharge (Gibbs, 1972). It covers almost 25% of South America and it extends into nine countries with about 7.5 million km^2, with more than 70% of tropical rainforest species and one-third of the world's germplasm being restricted to this biome. It is considered one of the last continuous extensions of humid tropical forests of Earth (Fearnside, 2005; Cenciani et al., 2011). In general, the climate is characterized by warm temperatures (ranging from 24 to 27°C all year), high rainfall (around 3200 mm/year) and high relative humidity (from 80% to 94%, throughout the year), being classified as a humid and semihot equatorial biome (FAO, 2015).

The most conspicuous differentiating factor in this biome is the diversity of landscapes modulated by the availability of water, being categorized as dryland forest, swamp and seasonal-swamp forests along the watercourses on the flood plains (Bass et al., 2010; FAO, 2015). This variation on water availability contributes to the emergence of extreme environments and the identification of these zones may reveal hitherto unnoticed aspects of evolutionary processes. Some Amazonian areas have shown soils with high concentration of aluminum (145 mmol/kg), ferrous iron, low chemical fertility and unfavorable physical properties. Those metallic reduced forms become available in the soil as the pH drops below 5, turning them into acidic environments with predominance of podzolic and acrisol soil types, respectively (FAO, 2009). These soils occur mostly along the Negro River (*Rio Negro*) and the northern upper Amazon Basin, surrounding the microregion of Barcelos (mesoregion of *Rio Negro*, Amazônia state—AM) and Tapauá (microregion of Caracaraí, Rondônia state—RO) (Diaz-Castro et al., 2003; FAO, 2015).

Other important factors are the astonishingly high levels of UV radiation and high temperatures that microorganisms colonizing the leaf surfaces of plants have to face (Morton et al., 2016; Saleska et al., 2016). The region of *Conceição do Araguaia municipality*, in the west side of Pará state (S8°15′29″, W49°16′11″), was recorded with the highest levels of UV radiation in Brazil, with extreme values of ca. 6.5 kW h/m^2, coupled with low precipitation between June and August (below 20 mm) (Saleska et al., 2016). Additional elements to be considered are exacerbated rate of deforestation (increased by 29%, FAO, 2015), combined with the progression of fire seasons (1244 fire events were alerted just in January, Global Forest Watch, 2018). These factors have contributed to the emergence of areas under the process of desertification, occurring around the cities of Rio Branco (the capital of Acre state—AC), Rondônia state (RO), Pará state (PA) and Mato Grosso state (MT) (Barber et al., 2014; Global Forest Watch, 2018).

The biodiversity is mainly thought of in terms of animals and plants, but the environmental conditions, such as high temperatures, humidity, solar radiation and precipitation, allow the microbiological diversity to flourish. Among them, the phylum *Cyanobacteria* is notable given its nutritional simplicity and phototrophic metabolism, as well as the possible existence of physiological and morphological mechanisms allowing them to couple with the high solar radiation of Equator over the year. However, studies exploring the diversity of cyanobacteria in the Amazon Rainforest are scarce and most of them were conducted based only on microscopic observations of environmental samples, resulting in pictures, drawings and lists of observed species/morphotypes from specific sites (Vieira et al., 2003, 2005; Aboim et al., 2016). Considering studies dealing with isolation and cultivation, it has been shown that some Amazonian rivers support considerable diversity of homocytous cyanobacteria (Genuário et al., 2017b), with the possibility of discovering new species (Fiore et al., 2005; Genuário et al., 2018). Areas under high UV incidence could potentially be exploited for new cyanobacterial species able to produce pigment molecules like scytonemin that can be used in photoprotection and biomedical research (Rastogi et al., 2015).

The polyphasic approach has been applied for the characterization of isolated cyanobacterial strains in few studies (Fiore et al., 2005; Genuário et al., 2017b, 2018), while culture-independent methodologies have been even less used (Dall'agnol et al., 2012; Pureza et al., 2013). The polyphasic approach was firstly oriented toward the examination of filamentous heterocytous nitrogen-fixing cyanobacterial strains (Fiore et al., 2005) and only lately, the filamentous homocytous forms were also investigated (Genuário et al., 2017b). Likewise, some cyanobacterial strains isolated from several Amazonian habitats have had their whole genome sequenced such as *Cyanobium* (Lima et al., 2014), *Synechococcus* (Guimarães et al., 2015), *Nostoc* (Leão et al., 2016) and *Microcystis* (Castro et al., 2016). However, these cultured cyanobacteria and the genetic information retrieved from their genomes were not further investigated in vitro neither in silico, which could have uncovered the mechanisms involved in the adaptation of this group of microorganisms to high solar radiation and other extreme conditions.

Among the studies in which cyanobacterial strains were sampled, heterocytous strains were isolated from 14 locations along the mainstream of Solimões and Amazon rivers (Fiore et al., 2005). These strains were morphologically identified as belonging to the genera *Nostoc*, *Cylindrospermum* and *Fischerella* (Fiore et al., 2005). However, considering the 16S rRNA gene phylogeny, these morphotypes did not correspond to the typical phylogenetic lineage of their respective genus, indicating the emergence of new phylogenetic lineages reassembling well-known morphotypes (Fiore et al., 2005). On the other hand, the homocytous strains recently identified by morphology as belonging to the genera *Pseudanabaena*, *Leptolyngbya*, *Planktothrix* and *Phormidium* had their 16S rRNA sequences clustered with strong support into the typical phylogenetic clusters of the abovementioned genera, showing a more robust congruence between morphological and molecular data (Genuário et al., 2017b). Despite this, in the same study, some strains morphologically identified as members of the genera *Leptolyngbya* and *Phormidium* were, indeed, related to the phylogenetic clusters of the recently described genera *Pantanalinema*, *Alkalinema* and *Cephalothrix*, respectively (Genuário et al., 2017b). These results demonstrated that Amazonas and Solimões rivers hold a cultured diversity of cyanobacteria similar to those already recorded from other aquatic environments around the world or in Brazil (Genuário et al., 2017b).

In addition, one novel cyanobacterial strain isolated from Solimões river (*Rio Solimões*) was recently described based on a polyphasic approach as a new species, *Cronbergia amazonensis* (Genuário et al., 2018). In addition to the description of this new species, this work also highlighted the existence of three 16S rRNA gene sequences named *Cronbergia siamensis* SAG 11.82 (type-species and reference sequence for the genus Cronbergia), which fall into two distinct phylogenetic lineages (1) one clustered with the typical *Cylindrospermum* cluster and (2) another grouped with the novel Amazonian sequence. In conclusion, this investigation has supported the genus *Cronbergia* as a valid and stable cyanobacterial genus and provided great insights in the *Cronbergia* dilemma (Genuário et al., 2018) (Figs. 16.3–16.5).

16.3.1.2 Cerrado (Brazilian Savanna)

Cerrado is the second biggest Brazilian biome and encompasses 2036,448 km^2 (23.92% of the country's land area), with a vast dry and hot savanna ecoregion, far from being lifeless. It comprises a wide range of biodiversity, described as the richest savanna in the world (Ratter et al., 2003; Lopes and Guilherme, 2016). This neotropical savanna is located in the central portion of the South American continent and northeast and southeast of Brazil. There is a gradient of vegetation cover, which can be divided into different "phytophysiognomies" that range from grasslands (*Campo Limpo* and *Campo Sujo*) to savannas (*Cerrado sensu stricto* and *Cerrado Denso*), as well as riverine forests (*Mata de Galeria*) (Araujo et al., 2012). Approximately 73% of this biome is located between 300 and 900 m of altitude and the incidence of UV radiation is high, with values around 475–500 W/m^2 (WGF, 2018) in soil from open areas, such as *Campo Sujo* and *Cerrado sensu stricto* (Gregoracci et al., 2015; Moreira et al., 2015). Rainfall presents a great variation in precipitation and distribution patterns, with a yearly average of 750–800 mm on the dry side (northeast side) to 2000 mm on the west side. Water deficits can vary from 4 to 791 mm with a very well-defined dry season comprising 5–6 months (from April/May to September) and the occurrence of natural fires (Lopes and Guilherme, 2016). Besides, singular morphoclimatic events are known locally as "veranicos" and they occur due to dry spells during the rainy season, which are often coupled with high solar radiation and high potential evapotranspiration (Haridasan, 1989).

Almost 50% of the soils of this biome are classified as Ferralsol (Latossolos in the Brazilian classification) (FAO, 2009). These soils are poor and present serious limitations in terms of low native-nutrient availability, that is, P, K, Ca, Mg, S, Zn, B, Cu (Walter et al., 2008). The acidity is predominant (pH 4.8–5.1), with high contents of organic matter, very low cation-exchange capacity, high Al saturation and soil temperature regime ranked as isohyperthermic according to the US Taxonomic Criteria (Soil Science Division Staff et al., 2017). All these particular conditions provide physical and geochemical extreme characteristics of temperature, water availability, radiation, salt content, pH and redox potential for the soil and also for the whole environment. In addition, this biome has suffered degradation for decades due to human activities and changes in land use, soil salinity because of deep well drilling for irrigation water, persistently high xenobiotic chemical challenge as a result of industrial pollution and agrochemical use (Horikoshi et al., 2011).

To our knowledge, studies regarding cyanobacterial diversity in this biome are very scarce or even absent making impossible the description of its communities.

16.3.1.3 Pantanal

Pantanal, the largest wetland area in the world, extends over 2×10^5 km^2 in Central-West Brazil, located in the states of Mato Grosso (MT) and Mato Grosso do Sul (MS) (Alho and Silva, 2012). Owing to the strongly marked seasonal distribution of precipitation and the slight grade of the rivers, wide areas are flooded for several months each year (December to May). It consists of many subregions with highly variable hydrological, chemical and edaphic features restricting the gas diffusion in the soil, with depletion of the oxygen, decrease of oxidation–reduction potential (Eh) and prevalence of anaerobic conditions (Cherry, 2011; Pezeshki and DeLaune, 2012). Among them, "Nhecolândia" is a peculiar region with 24,000 km^2, characterized by fine sandy sediments deposited by Taquari River (*Rio Taquari*), housing of approximately 10,000 shallow saline–alkaline and hyposaline lakes that vary greatly in pH, salinity, color and biological parameters and coexist in proximity (Medina-Junior and Rietzler, 2005; Duarte et al., 2012).

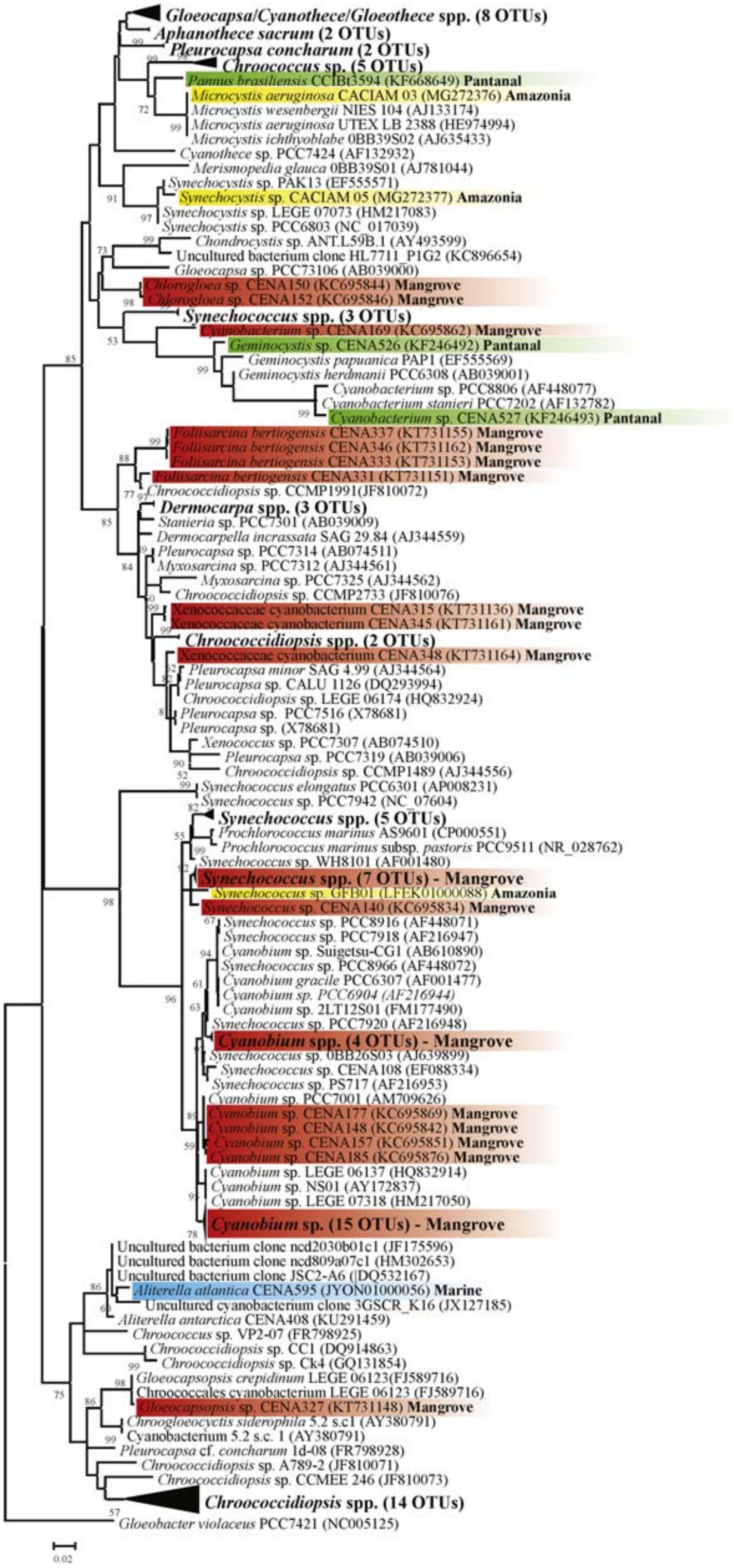

FIGURE 16.3 Maximum likelihood phylogenetic tree based on the 16S rRNA gene sequences of Unicellular cyanobacterial strains. The 16S rRNA gene sequences retrieved from GenBank were aligned using CLUSTAL W from MEGA version 5 and trimmed (16S rRNA gene matrix with a 1447-bp length). A total of 159 sequences were considered and used to infer the phylogeny based on the ML method. The general time reversible evolutionary model of substitution with gamma distribution and with an estimate of proportion of invariable sites (GTR + G + I) was selected as the best fitting model, applying the model-testing function in MEGA version 5. The robustness of the phylogenetic tree was estimated by bootstrap analysis using 1000 replications. *ML*, maximum likelihood.

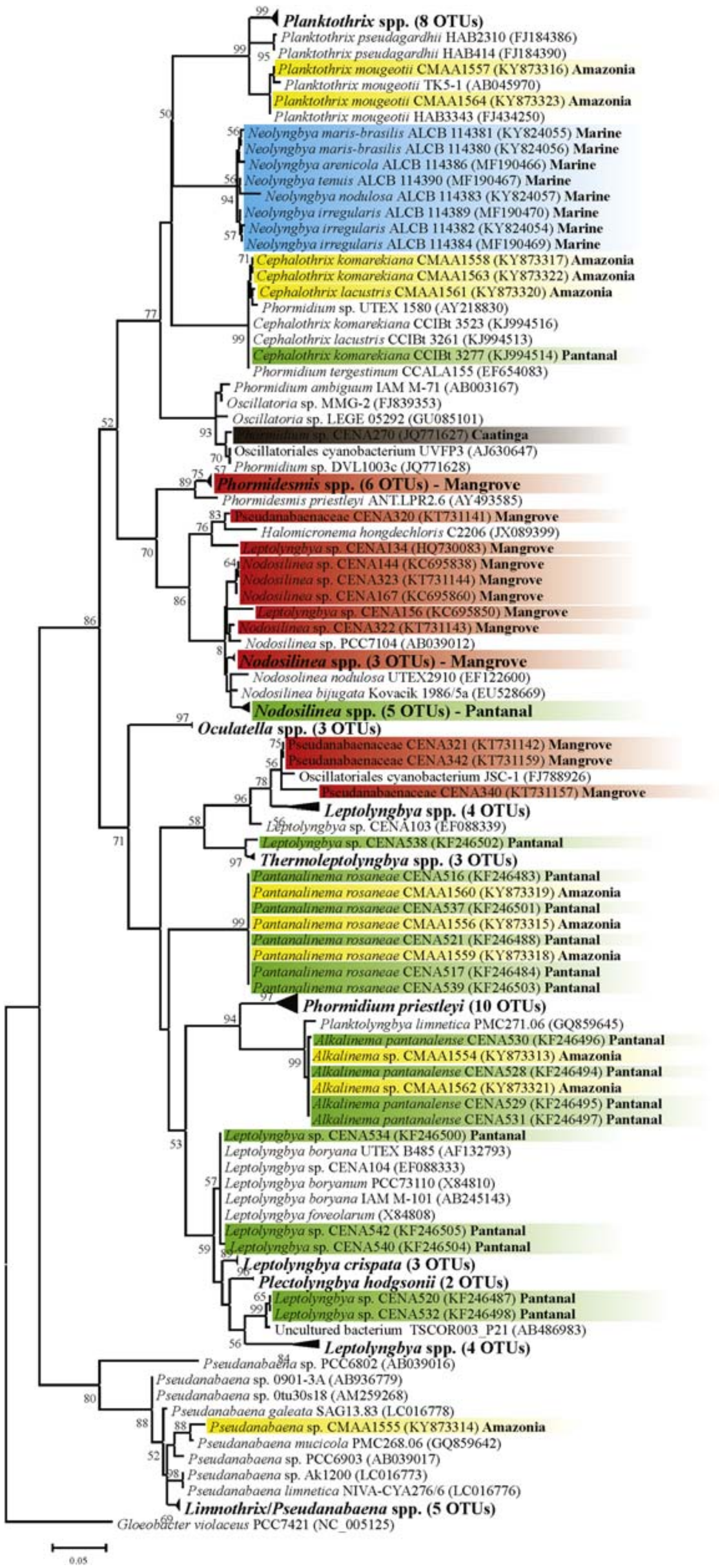

FIGURE 16.4 Maximum likelihood phylogenetic tree based on the 16S rRNA gene sequences of filamentous non-heterocytous cyanobacterial strains. The 16S rRNA gene sequences retrieved from GenBank were aligned using CLUSTAL W from MEGA version 5 and trimmed (16S rRNA gene matrix with a 1452-bp length). A total of 138 sequences were considered and used to infer the phylogeny based on the ML method. The general time reversible evolutionary model of substitution with gamma distribution and with an estimate of proportion of invariable sites (GTR + G + I) was selected as the best fitting model, applying the model-testing function in MEGA version 5. The robustness of the phylogenetic tree was estimated by bootstrap analysis using 1000 replications. *ML*, maximum likelihood.

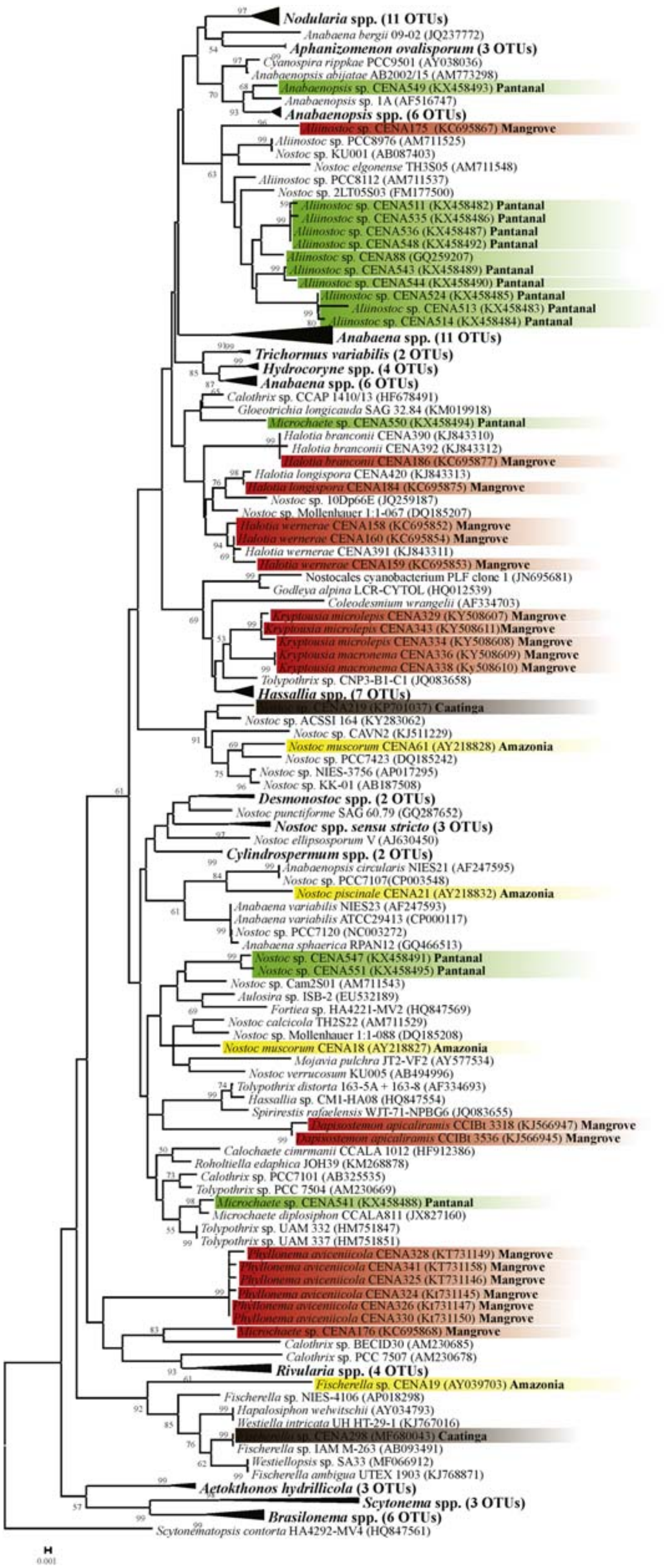

FIGURE 16.5 NJ phylogenetic tree based on the 16S rRNA gene sequences of Filamentous heterocytous cyanobacterial strains. The 16S rRNA gene sequences retrieved from GenBank were aligned using CLUSTAL W from MEGA version 5 and trimmed (16S rRNA matrix with a 1452-bp length). A total of 175 sequences were considered and used to infer the phylogeny based on the NJ method. The Kimura 2-parameter model of substitution with gamma distribution and with an estimate of proportion of invariable sites (K2 + G + I) was selected as the best fitting model, applying the model-testing function in MEGA version 5. The robustness of the phylogenetic tree was estimated by bootstrap analysis using 1000 replications. *NJ*, neighbor-joining.

The hyposaline lakes have variable pH, low-to-very-low salinity, and always lack beaches, whereas the saline–alkaline lakes have high pH (9–10), are often surrounded by sand beaches and rarely become dry across the year. These differences are not well understood, but hydric deficit together with scarcity of Ca^{2+} in surface and ground water may unbalance the Ca^{2+} geochemical cycle and result in increased pH (Almeida et al., 2011). In saline–alkaline lakes, concentration of inorganic ions and electrical conductivity exceed 2.5 g/L and 3 mS/cm, respectively, with pH values above 8.9, while during the dry season these values come up to 50 g/L, 70 mS/cm and 10.5, respectively. The high pH conditions and the $NaHCO_3$ chemical profile are positively correlated with the electrical conductivity (Furian et al., 2013) and high contents of dissolved organic carbon up to 500 mg/L of carbon (Mariot et al., 2007). All indications suggested that Pantanal offers multiple environmental stresses and the organisms from these habitats can be referred as haloalkaliphiles/haloalkalitolerants, having both alkaliphilic and halophilic traits (Bowers et al., 2009).

In the alkaline–saline lakes found in Pantanal wetlands, blooms of microalgae and cyanobacteria occur seasonally or permanently depending on the intensity of the rainfall during the wet season (De-Lamonica-Freire and Heckman, 1996; Santos and Sant'Anna, 2010; Santos et al., 2011) and usually they occur when the electrical conductivity of the water exceeds about 3 mS/cm (Andreote et al., 2014). Although Cyanobacteria is reported as the dominant group in these saline–alkaline lakes during the dry season (De-Lamonica-Freire and Heckman, 1996), very few studies have focused on the occurrence and distribution of this group of microorganisms, and most of them were conducted based only on floristic surveys (De-Lamonica-Freire and Heckman, 1996; Oliveira and Calheiros, 2000; Malone et al., 2007; Santos and Sant'Anna, 2010). It means that the genetic relationships amongst strains retrieved from this ecosystem with regard to other environments remain underexplored. However, the culturable diversity of unicellular, homocytous and heterocytous cyanobacteria from five shallow, nonstratified saline–alkaline lake in Pantanal wetlands at "Nhecolândia" region was recently assessed by morphology and 16S rRNA gene sequences phylogeny (Andreote et al., 2014; Vaz et al., 2015; Genuário et al., 2017a). Based on the polyphasic approach applied to the unicellular and homocytous groups, Andreote et al. (2014) were able to differentiate nonheterocytous cyanobacterial morphotypes as belonging to the genera *Cyanobacterium*, *Geminocystis*, *Phormidium*, *Leptolyngbya*, *Limnothrix* and *Nodosilinea*. Additionally, these authors pointed out that at least five phylogenetic clusters could correspond to new generic units of Pseudanabaenaceae and Phormidiaceae families taking into account their distinct phylogenetic position and the low similarity values (below 95%) found among the novel 16S rRNA sequences and those available in NCBI (Andreote et al., 2014). Posteriorly, Vaz et al. (2015) performed a detailed investigation on the strains resembling *Leptolyngbya* morphotypes falling into two of those phylogenetic lineages which were apart from the typical genus *Leptolyngbya*. Based on a comprehensive analysis of the inter and intraspecific relationship of the selected pseudanabaenacean strains, using the 16S rRNA gene and 16S–23S ITS sequences, as well as their ability to survive and/or grow under different pH conditions, two novel cyanobacterial genera (*Pantanalinema* and *Alkalinema*) were described (Vaz et al., 2015). Moreover, Malone et al. (2015) investigating the evolutionary relationship of some cyanobacterial strains from Phormidiaceae family, by multilocus analyses, described the novel genus *Cephalothrix*. It comprises cyanobacterial strains isolated from diverse environments, from which one was isolated from alkaline–saline lakes located at Pantanal wetlands (Malone et al., 2015). Similarly, one novel species, *Pannus brasiliensis*, was described taking into account one strain isolated from Pantanal wetlands after a detailed morphological and phylogenetic evaluation (Malone et al., 2014). More recently, another study dedicated to the examination of cultured nitrogen-fixing heterocytous cyanobacteria was conducted in the same saline–alkaline lakes examined by Andreote et al. (2014) and Vaz et al. (2015). Fourteen cyanobacterial strains were isolated and morphologically identified as belonging to the genera *Nostoc*, *Anabaenopsis* and *Tolypothrix* (Genuário et al., 2017a). However, according to the phylogenetic tree based on the 16S rRNA gene sequences, only one strain had its phylogenetic placement in accordance with the morphological identification, *Anabaenopsis*. The remaining clusters may represent new genetic lineages since their sequences did not group to the typical phylogenetic lineages of *Nostoc* and *Tolypothrix* genera (Genuário et al., 2017a). Later, one of the clusters described by Genuário et al. (2017a), which harbored nine 16S rRNA sequences retrieved from *Nostoc*-like morphotypes isolated from Pantanal wetlands, was erected as a new genus, *Aliinostoc* gen. nov. (Bagchi et al., 2017).

Similar environments to the saline–alkaline lakes of "Nhecolândia" region at Pantanal wetlands are the soda lakes of the East African Rift Valley (Jones et al., 1998), and a number of heterocytous and nonheterocytous genera have been reported from saline and alkaline lakes around the world (Jones and Grant, 1999; López-Archilla et al., 2004; Foti et al., 2008; Tsyrenova et al., 2011; Dadheech et al., 2012, 2013) (Figs. 16.3–16.5).

16.3.1.4 Caatinga (Brazilian Semiarid Region)

Brazilian semiarid region is located almost exclusively in the northeast of the country. It covers approximately 8% of the Brazilian territory and shows great variation in annual rainfall from the semiarid to coastal zones, ranging from 300 to 2000 mm, respectively (Giulietti et al., 2006). High air temperatures, up to 45°C, in the summer (Kavamura et al., 2013) associated with low rainfall, contribute to the formation of the heterogeneity of this region. Due to high rates of radiation, high temperatures and low rainfall, there is water deficit in almost every month of the year. Most Brazilian semiarid soils also face salinity problems due to the restriction of leaching and transport of soluble salts (as a result of the climate), which is accelerated by inadequate irrigation and poor drainage processes (Gheyi, 2000), as well as use of saline water for irrigation (Lima et al., 2007). Among the Brazilian environments, Caatinga exhibits features that are most similar to those found in extreme environments. Despite that, very few studies have been conducted in this area dedicated to investigate the microbial diversity, especially cyanobacterial communities. It is important to mention that, besides other applications, the investigation of microbes able to tolerate water and osmotic stresses is an important issue once they can be used in agricultural practices in sites facing harsh conditions such as drought (Kavamura et al., 2013) and salinity (Egamberdieva and Lugtenberg, 2014).

Up to now, three main studies aimed to isolate cyanobacterial strains from this biome. Two of them were devoted to study the production of microcystin (hepatotoxin) and antifungal compounds (this issue is discussed below) by strains isolated from freshwater and soil samples collected in Paraiba (PB) and Ceará (CE) states (Shishido et al., 2013, 2015). These authors implemented a polyphasic characterization, describing three new strains from this region, which belongs to the genera *Phormidium*, *Nostoc* and *Fischerella*. In a later study, Borges et al. (2015), aiming to evaluate the production of microcystins and saxitoxins by benthic cyanobacteria, isolated 45 clonal strains, which were characterized applying molecular and morphological data. The isolated strains were placed into eight species, belonging to the Phormidiaceae, Pseudanabaenaceae and Nostocaceae families. According to the phylogenetic analyzes shown in this study, the 16S rRNA gene sequences retrieved from *Geitlerinema* strains were spread in at least three phylogenetic lineages, which possibly correspond to three distinct species (Borges et al., 2015) (Figs. 16.3−16.5).

16.3.1.5 Mangroves Ecosystems

Mangrove is a tropical coastal biome within the Atlantic forest, located at the transition between terrestrial and marine environments, covering around 60%−75% of the world's tropical and subtropical coastlines (Holguin et al., 2006; Santos et al., 2010). Brazilian mangrove ecosystems, which are part of the Atlantic Rain forest biome, are characterized as one of the longest mangrove areas of the world, covering about 25,000 km^2, from north to south coastline, which occur from the border with French Guiana, just above the Equator (04°30′N) to well beyond the Tropic of Capricorn, reaching 28°30′S, near Laguna city, in Santa Catarina (SC) state. The landscapes are coastal wetlands dominated by woody plants, tidal height (<1 to >4 m), geomorphology (oceanic islands to riverine systems), sedimentary environment (peat to alluvial), climate (semiarid to wet tropics) and nutrient availability (oligotrophic to eutrophic) (Schaeffer-Novelli et al., 2000). Their landforms are modeled by the continuous adjustment of forms of water, tidal and wave energies and associated constructive/erosive processes (Walters et al., 2008; Koch et al., 2009; Feller et al., 2010). Mangroves are among the most productive and biologically important environments. They also represent a complex and dynamic ecosystem with harsh settings like high salinity, temperature and sedimentation, extreme tides and muddy anaerobic soils (Thompson et al., 2013). Despite having immense amounts of organic matter, mangroves are also characterized by a low concentration of other nutrients, especially nitrogen (N) and phosphorous (P), which are almost not available to the organisms since the mangrove is usually an anaerobic and reducing environment (Duarte et al., 2012). Furthermore, the synergistic impacts of salinity and aridity can influence species diversity, size and productivity of mangrove forests.

A more thorough description of the bacterial diversity and distribution in a mangrove would improve our understanding of bacterial functionality and microbial interactions found in that ecosystem (Kathiresan and Selvam, 2006). Despite of Brazil having an extensive coastline and a large territorial sea, these areas are still poorly studied in terms of cyanobacterial diversity. Only recently, communities of cyanobacteria collected at different locations along the Brazilian coast (Silva et al., 2014; Hentschke et al., 2016; Alvarenga et al., 2016) and continental shelf in Atlantic Ocean were accessed through isolation and polyphasic characterization (Rigonato et al., 2016; Caires et al., 2018).

In general, research on cyanobacterial diversity in mangroves is scarce, and most of the studies dedicated to investigate cyanobacterial communities have applied mainly optical light microscopic of environmental samples collected in Mexico, India and Brazil (Baeta-Neves and Tribuzi, 1992; Branco et al., 1994, 1996, 1997, 2003; Toledo et al., 1995; Crispino and Sant'Anna, 2006; Nogueira and Ferreira-Correia, 2001; Silambarasan et al., 2012). More recently, the cyanobacterial community of two Brazilian mangrove ecosystems was examined using a culture-dependent strategy and a polyphasic approach to characterize the novel isolates (Silva et al., 2014). In this study, 50 cyanobacterial strains belonging to unicellular, homocytous and heterocytous groups were isolated from soil, water and periphytic samples collected from Cardoso Island (*Ilha do Cardoso*) and Bertioga mangroves. Among them, eight genera were morphologically identified such as *Synechococcus*, *Cyanobium*, *Cyanobacterium*, *Chlorogloea*, *Leptolyngbya*, *Phormidium*, *Nostoc* and *Microchaete*. However, according to the phylogenetic position of their 16S rRNA gene sequences, the novel isolates were not always associated with the type-species from the aforementioned genera (Silva et al., 2014). It demonstrated that several phylogenetic branches were (1) exclusively formed by the novel 16S rRNA gene sequences, suggesting to be endemic, (2) allowed the recognition of some strains into the *Nodosilinea* and *Oxynema* genera, groups genetically derived from *Leptolyngbya* and *Phormidium* genera, respectively, and (3) genotypes resembling *Nostoc* and *Leptolyngbya* morphotypes that might represent new generic entities, since they were distantly affiliated to the true genera phylogenetic clusters. Moreover, the isolation of one cyanobacterial strain from biofilms samples collected on a wood bridge from Cardoso Island mangrove and its phylogenetic characterization supported the description of the novel genus *Dapisostemon* (Hentschke et al., 2016). Yet, Cyanobacteria dwelling on the salt-excreting leaves of the mangrove tree *Avicennia schaueriana* were also accessed through isolation and polyphasic characterization (Alvarenga et al., 2016). Twenty-nine isolated strains belonging to Synechococcales, Nostocales, Pleurocapsales, Chroococcales and Oscillatoriales orders were isolated (Alvarenga et al., 2016). The genetic evaluation of their 16S rRNA sequences indicated that six Rivulariacean and four Xenococcacean strains represented novel taxa, which were described as *Phyllonema* and *Foliisarcina*, respectively. Additionally, the genus *Kryptousia* was described considering cyanobacterial strains isolated from the phyllosphere from *A. schaueriana* and *Merostachys neesii* leaves collected at a mangrove and a mountain area of the Atlantic Forest (Alvarenga et al., 2017). In general, microorganisms inhabiting the phyllosphere experience extreme environmental condition due to the constant and intermittent fluctuations in temperature, UV radiation, wind, moisture and relative humidity (Hirano and Upper, 2000; Schreiber et al., 2004). However, the phyllosphere from *Avicennia* presents a peculiar habitat since these trees eliminate up to 90% of the absorbed salt from seawater through transpiration, forming salt crystals visible to the naked eye in their leaves (Drennan and Pammenter, 1982; Fitzgerald et al., 1992). Morphological and genetic evaluation of cyanobacterial strains isolated from epilithic and epipsammic samples collected in the intertidal zone during low spring tides and in estuaries supported the description of the new genus, *Neolyngbya*, with six novel species *Neolyngbya maris-brasilis*, *Neolyngbya granulosa*, *Neolyngbya irregularis*, *Neolyngbya nodulosa*, *Neolyngbya arenicola* and *Neolyngbya tenuis* (Caires et al., 2018). Similarly, one cyanobacterial strain isolated from the water column in the Atlantic Ocean (ca. 107 m) supported the description of the genus *Aliterella* with two species *Aliterella atlantica* and *Aliterella antarctica* (Rigonato et al., 2016). Besides to the standard molecular approach, these authors also implemented the phylogenomic analysis for the type-species, *A. atlantica* CENA595 based on 21 protein sequences (Rigonato et al., 2016) (Figs. 16.3–16.5).

16.4 BIOTECHNOLOGICAL POTENTIAL OF CYANOBACTERIA FROM BRAZILIAN EXTREME ENVIRONMENTS

Studies dealing with the isolation and characterization of cyanobacterial strains from extreme environments are relatively scarce, and those exploring microbial tolerance to environmental extremes or prospecting new genes, biosynthetic pathways, or products are even scarcer. In general, members of the phylum *Cyanobacteria*, mainly from marine biomes, have attracted interest for their great versatility in terms of production of secondary metabolites, whereas those from terrestrial and freshwater environments have been seen as promising microbial factories for production of renewable chemicals and fuels directly from sunlight and CO_2. Cyanobacteria from extreme environments are potential sources of novel genes, products and important targets for biotechnological application, and once isolated, these strains can be screened for useful metabolites and investigated concerning the mechanisms enabling them to inhabit and/or tolerate such conditions.

In this section, the main goal is to provide a concise overview on how cyanobacterial strains sampled from some of the above-described Brazilian biomes have been screened and explored regarding genes, bioproducts and biofuels. It is worth to mention that the sampling site can provide valuable information on how to cultivate the extreme-isolated strains, facilitating the simulation of the artificial conditions during laboratory cultivation which mimics most properly those found in the original environment. This might help the search for desired bioproducts being produced in their original habitat.

16.4.1 Amazon Rainforest

The Amazon region has been the subject of few studies aiming the isolation of cyanobacterial strains, their cultivation, polyphasic characterization and bioprospection. The first study applying polyphasic approach from Amazon Rainforest was conducted with filamentous heterocytous nitrogen-fixing strains and their nitrogen-fixation capability was investigated (Fiore et al., 2005). Among the strains described by Fiore et al. (2005), *Fischerella* sp. CENA19 was evaluated for algicide production (Etchegaray et al., 2004). Coupling chemical and molecular approaches, these authors were able to demonstrate the production of two fischerellins, which had a potential algicidal activity, identified as aminoacylpolyketide fischerellin A (FsA) and alkaloid 12-epi-hapalindole F (HapF) (Etchegaray et al., 2004). Only lately, the filamentous homocytous forms and one heterocyte-forming strain belonging to the genus *Cronbergia* were polymerase chain reaction (PCR) investigated regarding the genes involved in microcystin biosynthesis without any positive results (Genuário et al., 2017b, 2018). Another recent study focused on the biotechnological potential of cyanobacterial strains from Amazonian region as an alternative source for biodiesel production (Aboim et al., 2016). The authors evaluated unicellular and nonheterocytous strains collected at the hydroelectric plant of Tucuruí Lake (Pará state). According to this screening, the strains that showed better quality of lipids were *Synechocystis* sp. CACIAM05 and *Microcystis aeruginosa* CACIAM03 when grown in BG-11 medium. Despite being obtained in a small laboratory scale, these results are an important and promising achievement of the potential of cyanobacteria for biodiesel production.

Yet, some cyanobacterial strains isolated from several Amazonian habitats have had their whole genomes sequenced such as *Cyanobium* (Lima et al., 2014), *Synechococcus* (Guimarães et al., 2015), *Nostoc* (Leão et al., 2016) and *Microcystis* (Castro et al., 2016); however these authors did not explore those data in terms of the genes which could be involved on their adaptation to harsh conditions found in Amazonian environments. Partial analysis of the draft genome of *Cyanobium* sp. CACIAM 14 (isolated from water sample collected in the Tucuruí Hydroelectric Dam, in Pará state, southeastern Amazonia) revealed the presence of terpene and bacteriocin synthesis clusters reinforcing that Amazonian cyanobacterial strains may be a good source of novel natural products (Lima et al., 2014). In the draft genome of the unicellular *Synechococcus* sp. GFB01 isolated from the surface of the freshwater lagoon "Lagoa dos Índios," located in the municipality of Macapá, Amapá state, northern Brazil, the authors identified several genes involved with heavy metal resistance and natural transformation (Guimarães et al., 2015). The draft genome of the diazotrophic heterocyte-forming cyanobacterium *Nostoc piscinale* CENA21 isolated from the Solimões River (Fiore et al., 2005) was sequenced and investigation of secondary metabolites enabled the detection of at least 16 biosynthetic gene clusters corresponding to bacteriocins, a nonribosomal peptide-synthetase (NRPS), NRPS/polyketide synthases (PKS), biosynthetic gene clusters of terpenes and lantipeptides (Leão et al., 2016). Similarly, the draft genome from the potential-toxigenic bloom-forming strain *M. aeruginosa* CACIAM 03 (isolated from Tucuruí hydroelectric power station reservoir, Pará state) revealed gene clusters involved in the nonribosomal biosynthesis of microcystin, aeruginosin and terpene, as well as gene clusters involved in ribosome synthesis of peptides such as yersiniabactin (bacteriocin), micropeptin (microviridin), microcyclamide (cyanobactin) and microcyclamide (bacteriocin) (Castro et al., 2016).

Additionally, three studies conducted in the Amazonian region reported toxin production by cyanobacterial strains. The production of microcystin (a hepatotoxin) by the genus *Radiocystis* was firstly reported for the species *R. fernandoi* SPC714 isolated from a drinking water reservoir (Utinga Lake) in Belém, Pará state (Vieira et al., 2003). Later, at the same reservoir, Vieira et al. (2005) characterized the cyanobacterial community and evaluated the toxicity of the isolated strains. high-performance liquid chromatography (HPLC) analysis confirmed the production of microcystins by *Microcystis viridis* and *R. fernandoi*.

A deeper chemical characterization of *R. fernandoi* SPC714 confirmed the production of microcystin-LR and three other oligopeptides (Lombardo et al., 2006). Among these oligopeptides, two isomers of aeruginosin and a cyclic cyanopeptolin like micropeptin K139, which is a trypsin inhibitor, were identified (Lombardo et al., 2006).

16.4.2 Caatinga

Very few studies have been conducted in Caatinga, regarding the sampling, isolation and prospection of cyanobacterial strains. Up to now, to our knowledge, only three studies were conducted applying polyphasic approaches for taxonomic classification, coupled with screening for toxins or any other bioactive compounds. The *Phormidium* sp. CENA270, isolated from a pond in Paulista city (Paraíba state, Brazil), was characterized as a microcystin producer with five variants detected (Shishido et al., 2013). *Nostoc* sp. CENA219 (a benthic freshwater strain isolated in Ceará state) and *Fischerella* sp. CENA298 (isolated from soil samples collected in Paraíba state) were able to produce antifungal compounds against *Candida albicans* and *Aspergillus flavus* (Shishido et al., 2015). Fourteen variants of hassallidin, known as a potent antifungal activity, were detected for *Nostoc* sp. CENA219, while those produced by *Fischerella* sp. CENA298 were not correlated with any known compound (Shishido et al., 2015).

Forty-five benthic cyanobacterial strains isolated from rivers and drinking water reservoirs in semiarid region (Mundaú River basin, Pernambuco state and Environmental Protection Area, Ceará state) were examined through molecular and chemical (HPLC) analyzes (Borges et al., 2015). The data showed the production of saxitoxins variants by *Cylindrospermum stagnale*, *Geitlerinema lemmermannii* and *G. amphibium*, confirming the production of this toxin for the first time by *Geitlerinema* and *Cylindrospermum* and the first in Brazil by *Phormidium* (Borges et al., 2015). These authors also PCR-amplified the *myc*E gene fragment, involved in microcystin biosynthesis; however, its production was not detected by HPLC analysis (Borges et al., 2015).

Despite the low number of studies investigating cyanobacterial diversity from Caatinga, these examples show the potential of cyanobacteria isolated from this biome with regards to the production of cyanotoxins and some bioactive compounds.

16.4.3 Pantanal Wetlands

Pantanal wetlands is a promising source for the discovery of novel natural products since many recent studies were oriented through the isolation and polyphasic characterization of cyanobacterial strains, culminating in almost 50 strains from alkaline—saline lakes (Andreote et al., 2014; Malone et al., 2014, 2015; Vaz et al., 2015; Genuário et al., 2017a,b). Some of these isolated strains were submitted to molecular/chemical prospection for bioactive compounds and toxins. Genes involved on the biosynthesis of protease inhibitors (aeruginosin and cyanopeptolin) and cyanotoxins (microcystin and cylindrospermopsin) were investigated by means of PCR from strains belonging to the genera *Cyanobacterium*, *Geminocystis*, *Leptolyngbya*, *Limnothrix*, *Nodosilinea*, *Phormidium* and *Nostoc* (Silva-Stenico et al., 2013). Likewise, their extracts were screened for antimicrobial and antitumoral activities; however, no positive results were observed for these classes of compounds (Silva-Stenico et al., 2013). The extracts obtained from three strains of *Geitlerinema* spp. presented acute effects on mice, and the methanolic extract recovered from the strain CCIBt1044 caused mild and transient symptoms in mice (Rangel et al., 2013). Yet, after 7 days of exposure, the lungs of mice presented hemorrhagic focuses, edema, alveolar collapse and hyperplasia, leading the authors to conclude that this *Geitlerinema* strain produces toxins with different damages than those already known (Rangel et al., 2013). More recently, the filamentous heterocytous cyanobacterial strains isolated by Genuário et al. (2017a) were analyzed in terms of natural products by Jokela et al. (2017) and Shishido et al. (2017). The results from the first study showed that the strain *Nostoc* (*Aliinostoc*) sp. CENA543 produces nodularin-R and pseudospumigins, both synthetized by nonribosomal pathways (Jokela et al., 2017). This was the first report of nodularin-R being produced by a free-living *Nostoc*-like at comparable levels as the toxic strain, *Nodularia spumigena* (Jokela et al., 2017). Yet, pseudospumigin belongs to a novel family of linear tetrapeptide protease inhibitors (Jokela et al., 2017). The simultaneous production of anabaenopeptins and namalides were also detected for this strain (Shishido et al., 2017). Anabaenopeptins are characterized as a group of cyclic peptides, containing an unusual ureido linkage, while namalides are shorter structural homologues of anabaenopeptins, which also contain an ureido linkage. According to the authors, *Nostoc* (*Aliinostoc*) sp. CENA543 synthesizes both novel and already known variants of anabaenopeptins, concomitantly with the production of namalides. Anabaenopeptins were recently characterized as potent inhibitors of blood clot stabilizing carboxypeptidases, indicating their potential use as an alternative anticoagulant. Namalides are cyclic tetrapeptides, similar to anabaenopeptins, but without two amino acids from the macrocycle structure. These cyclic tetrapeptides are carboxypeptidase A inhibitors, and their biosynthetic pathway remains unknown (Shishido et al., 2017). The strains belonging to the novel genera *Pantanalinema* and *Alkalinema* were tested regarding their ability to grow in a wide range of pH values (pH 4—11), and they demonstrated ability to survive and produce biomass in all examined pH and to alter the culture medium to pH values ranging from pH 8.4 to 9.9 (Vaz et al., 2015). These results represent a great potential for large-scale cultivation, once the pH maintenance has high costs in outdoor biomass production. Taken together, these results showed that cyanobacterial strains isolated from saline—alkaline from Pantanal wetlands can be a rich source of bioactive compounds, mainly cyanotoxins and protease inhibitors.

16.4.4 Mangroves

Cyanobacterial communities from Brazilian mangroves have been recently explored in terms of polyphasic approach (Silva et al., 2014; Alvarenga et al., 2016), and besides the taxonomic/phylogenetic characterization of the isolated strains, a comprehensive screening for nonribosomal peptide synthetase, polyketide synthase, microcystin and saxitoxin genes using molecular screening was also performed. Partial sequences of NRPS and PKS domains were PCR-amplified from at least 20.5% of the analyzed strains. Additionally, the *mcy*A and *sxt*I genes involved, respectively, on microcystin and saxitoxin biosynthesis were detected by PCR in six and nine cyanobacterial strains. The strains *Cyanobium* sp. CENA142 and *Oxynema* sp. CENA135 showed amplification of NRPS, PKS, *mcy*A and *sxt*I as well as positive enzyme-linked immunosorbent assay (ELISA) results for toxins, indicating the potential of both strains to produce these toxic natural products (Silva et al., 2014). As highlighted by these authors, picoplanktonic cyanobacteria, as *Cyanobium* morphotypes, are among the most abundant cyanobacteria in marine environments. As consequence, their ability to produce toxins can represent a health risk worldwide, reinforcing the importance of this kind of investigation. In this study, 134 organic extracts obtained from these strains were tested against pathogenic bacteria and yeast. Thirty-four exhibited some antimicrobial activity and 50% and 27% were active against Gram-positive and Gram-negative bacteria, respectively, while 17% were active against *Candida cruzei* (yeast) (Silva et al., 2014). Earlier, Silva-Stenico et al. (2012a) analyzed a subset of these cyanobacteria regarding the aeruginosin and cyanopeptolin production (protease inhibitor). The production of aeruginosin was confirmed for *Cyanobium* sp. CENA166, *Synechococcus* CENA170 and *Nostoc* (*Aliinostoc*) sp. CENA175, and many of the detected variants were novel and with chlorinated molecules which enhance their biological activity (Silva-Stenico et al., 2012a). In addition, Silva-Stenico et al. (2013) performing an evaluation of the effect of some cyanobacterial-organic extracts against cancer cell lines (colon carcinoma CT-26 and lung cancer 3LL) confirmed that the extracts obtained from *Cyanobium* sp. CENA154 and *Oxynema* sp. CENA135 showed antitumor activity against colon carcinoma (CT-26).

The physical and chemical properties of lipids extracted from some cyanobacterial strains were also assessed for biodiesel production (Da-Rós et al., 2013). The biomass and lipid productivity (mg/L/day) of *Synechococcus* sp. CENA170 was 6.8 and 0.9, respectively. According to the authors, these values were low compared to those found in literature for cyanobacteria concluding that these strains were unsuitable as a source of lipid feedstock. However, taking into account the origin of the strain *Synechococcus* sp. CENA170, it presents an opportunity for cultivating and optimizing its growth using nonpotable water, which is a great advantage in terms of costs for lipid production.

Two strains isolated from Brazilian mangroves, *Synechococcus*/*Cyanobium* sp. CENA136 and *Phormidium*/*Oxynema* sp. CENA135, were also analyzed regarding their potential for decolorizing some types of textile dyes (Silva-Stenico et al., 2012b). These strains were able to remove/degrade the tested textile dyes (indigo, palanil yellow, indanthrene yellow, indanthrene blue, dispersol blue, indanthrene red and dispersol red) in a rate higher than 50%. Surprisingly, the strain *Phormidium*/*Oxynema* sp. CENA135 was able to decolorize and completely remove indigo blue, indicating a possible role of cyanobacteria in degrading different textile dyes and their application in bioremediation studies (Silva-Stenico et al., 2012b).

16.5 FUTURE PERSPECTIVE

The physiological, morphological and metabolic characteristics of Cyanobacteria, such as the oxygenic photosynthesis, the nitrogen fixation in some species, and the prolific source of natural products, instinctively make this group of microorganisms suitable for exploration in the energetic and biotechnology fields.

In general, cyanobacteria are considered unique cell factories that combine the cost-effective energy-capturing, and the nonpolluting and environmentally friendly system production, which can optimize the use of renewable energy resources (biodiesel, bioethanol and hydrogen) as well as develop cleaner products and processes slowing down the effects of global warming. The carbon and nitrogen fixation performed by Cyanobacteria allows them to flourish in many extreme environments, and, therefore, strains from different sources can be reintroduced as primary colonizers in degraded and unproductive soils. Furthermore, they can be used as biofertilizers increasing the levels of C, N and P elements, the size of soil aggregates, the water permeability and reduce the compaction and sodicity of soils through improvement of organic carbon content. Likewise, cyanobacterial morphotypes shelter other bacteria associated in their mucilage, forming complex microbial communities which can synergistically contribute to the reestablishment of soil microbiome. In bioremediation, cyanobacteria from extreme environments might be feasible to reduce the contamination in mine drainage areas, wastewater stabilization ponds and polluted water bodies through the sequestration of heavy metals, pesticides, crude oil, naphthalene, phenanthrene, phenol and catechol and xenobiotics. However, the cultivation of cyanobacteria in large scale or their use for production of compounds with biotechnological interest is hampered by their slow growth rates. In this direction, the development of genetic tools has been presented as a reliable option to facilitate metabolic engineering since many cyanobacterial strains are amendable to genetic modification. In addition, the heterologous expression has emerged as an innovative strategy to capture the genetic content from a slow-growing and prolific cyanobacterium and express that biosynthetic gene clusters into fast-growing microorganisms including other cyanobacterial species.

The abovementioned applications could be implemented for those cyanobacterial strains isolated from extreme Brazilian environments which certainly would open new perspectives of exploration of these biomes in different optics not yet explored.

REFERENCES

Abe, F., Horikoshi, K., 2001. The biotechnological potential of piezophiles. Trends Biotechnol. 19 (3), 102−108.

Abed, R.M.M., Dobretsov, S., Sudesh, K., 2009. Applications of cyanobacteria in biotechnology. J. Appl. Microbiol. 106, 1−12.

Aboim, J.B., de Oliveira, D.T., Ferreira, J.E.D., Siqueira, A.S., Dall'Agnol, L.T., Rocha Filho, G.N., et al., 2016. Determination of biodiesel properties based on a fatty acid profile of eight Amazon cyanobacterial strains grown in two different culture media. RSC Adv. 6 (111), 109751−109758.

Alho, C.J., Silva, J.S., 2012. Effects of severe floods and droughts on wildlife of the Pantanal wetland (Brazil)—a review. Animals 2 (4), 591−610.

Almeida, T.I.R., Calijuri, M.C., Falco, P.B., Casali, S.P., Kupriyanova, E., Paranhos Filho, A.C., et al., 2011. Biogeochemical processes and the diversity of Nhecolândia lakes, Brazil. Anais da Academia Brasileira e Ciências 83 (2), 391−407.

Alvarenga, D.O., Rigonato, J., Branco, L.H., Melo, I.S., Fiore, M.F., 2016. *Phyllonemaaviceniicola* gen. et sp. nov. and*Foliisarcinabertiogensis* gen. et. sp. nov., novel epiphyllic cyanobacteria associated with *Avicenniaschaueriana* leaves. Int. J. Syst. Evol. Microbiol. 66 (2), 689−700.

Alvarenga, D.O., Andreote, A.P.D., Branco, L.H., Fiore, M.F., 2017. *Kryptousiamacronema* gen. nov., sp. nov. and *Kryptousiamicrolepis* sp. nov., nostocalean cyanobacteria isolated from phyllospheres. Int. J. Syst. Evol. Microbiol. 67 (9), 3301−3309.

Andreote, A.P.D., Vaz, M.G.M.V., Genuário, D.B., Barbiero, L., Rezende-Filho, A.T., Fiore, M.F., 2014. Nonheterocytous cyanobacteria from Brazilian saline-alkaline lakes. J. Phycol. 50 (4), 675−684.

Araujo, J.F., de Castro, A.P., Costa, M.M., Togawa, R.C., Junior, G.J., Quirino, B.F., et al., 2012. Characterization of soil bacterial assemblies in Brazilian savanna-like vegetation reveals *Acidobacteria* dominance. Microb. Ecol. 64 (3), 760−770.

Baeta-Neves, M.H., Tribuzi, D., 1992. The cyanobacteria from “Ponta do Pai Vitório” mangrove, Cabo Frio, Rio de Janeiro State, Brazil (Lês Cyanophycées de la mangrove de la “Ponta do Pai Vitório” de la région de Cabo Frio, RJ, Brésil). Acta Biol. Leopold. 14, 29−52.

Bagchi, S.N., Dubey, N., Singh, P., 2017. Phylogenetically distant clade of *Nostoc*-like taxa with the description of *Aliinostoc* gen. nov. and *Aliinostocmorphoplasticum* sp. nov. Int. J. Syst. Evol. Microbiol. 67 (9), 3329−3338.

Barber, C.P., Cochrane, M.A., Souza, C.M., Laurance, W.F., 2014. Roads, deforestation, and the mitigating effect of protected areas in the Amazon. Biol. Conserv. 177, 203−209.

Bass, M.S., Finer, M., Jenkins, C.N., Kreft, H., Cisneros-Heredia, D.F., McCracken, S.F., et al., 2010. Global conservation significance of Ecuador’s Yasuní National Park. PLoS ONE 5 (1), e8767.

Bekker, A., Holland, H.D., Wang, P.L., Rumble III, D., Stein, H.J., Hannah, J.L., et al., 2004. Dating the rise of atmospheric oxygen. Nature 427, 117−120.

Bhadury, P., Wright, P.C., 2004. Exploitation of marine algae: biogenic compounds for potential antifouling applications. Planta 219, 561−578.

Billi, D., 2009. Subcellular integrities in *Chroococcidiopsis* sp. CCMEE 029 survivors after prolonged desiccation revealed by molecular probes and genome stability assays. Extremophiles. 13 (1), 49−57.

Borges, H.L.F., Branco, L.H.Z., Martins, M.D., Lima, C.S., Barbosa, P.T., Lira, G.A.S.T., et al., 2015. Cyanotoxin production and phylogeny of benthic cyanobacterial strains isolated from the northeast of Brazil. Harmful Algae 43, 46−57.

Bowers, K.J., Mesbah, N.M., Wiegel, J., 2009. Biodiversity of poly-extremophilic *Bacteria*: does combining the extremes of high salt, alkaline pH and elevated temperature approach a physico-chemical boundary for life?. Saline Syst. 5, 9.

Branco, L.H.Z., Silva, S.M.F., Sant’Anna, C.L., 1994. *Stichosiphon mangle* sp. nova, a new cyanophyte from mangrove environments. Algol. Stud. 72, 1−7.

Branco, L.H.Z., Sant’Anna, C.L., Azevedo, M.T.P., Sormus, L., 1996. Cyanophyte flora from Cardoso Island mangroves, São Paulo State, Brazil. 1. *Chroococcales*. Algol. Stud. 80, 101−113.

Branco, L.H.Z., Sant’Anna, C.L., Azevedo, M.T.P., Sormus, L., 1997. Cyanophyte flora from Cardoso Island mangroves, São Paulo State, Brazil. 2. *Oscillatoriales*. Algol. Stud. 84, 39−52.

Branco, L.H.Z., Moura, A.N., Silva, A.C., Bittencourt-Oliveira, M.C., 2003. Biodiversity and biogeographic considerations of cyanobacteria in a mangrove area of the State of Pernambuco, Brazil. Acta Bot. Bras. 17, 585−596.

Butterfield, N.J., 2000. Paleobiology of the late Mesoproterozoic (ca. 1200 Ma) hunting formation, Somerset Island, Arctic Canada. Precambrian Res. 111 (1−4), 235−256.

Caires, T.A., Lyra, G.M., Hentschke, G.S., Pedrini, A.G., Sant’Anna, C.L., Nunes, J.M.C., 2018. *Neolyngbya* gen. nov. (Cyanobacteria, Oscillatoriaceae): a new filamentous benthic marine taxon widely distributed along the Brazilian coast. Mol. Phylogenet. Evol. 120, 196−211.

Castenholz, R.W., Wilmotte, A., Herdman, M., Rippka, R., Waterbury, J.B., Iteman, I., et al., 2001. Phylum BX *Cyanobacteria* oxygenic photosynthetic bacteria. In: Boone, D.R., Casten- holz, R.W., Garrity, G.M. (Eds.), Bergey’s Manual of Systematic Bacteriology. The Archaea and the Deeply Branching and Phototropic Bacteria. Springer, New York, NY, pp. 473−599.

Castro, W.O., Lima, A.R.J., Moraes, P.H.G., Siqueira, A.S., Aguiar, D.C.F., Baraúna, A.R.F., et al., 2016. Draft genome sequence of *Microcystis aeruginosa* CACIAM 03, a cyanobacterium isolated from Amazonian freshwater environment. Genome Announce. 4 (6), e01299−16.

Cenciani, K., Freitas, S.S., Critter, S.A.M., Airoldi, C., 2011. Enzymatic activity measured by microcalorimetry in soil amended with organic residues. Revista Brasileira de Ciência do Solo 35, 1167−1175.

Cherry, J.A., 2011. Ecology of wetland ecosystems: water, substrate, and life. Nat. Educ. Knowl. 3 (10), 16.

Compaoré, J., Stal, L.J., 2010. Oxygen and the light−dark cycle of nitrogenase activity in two unicellular cyanobacteria. Environ. Microbiol. 2 (1), 54−62.

Crispino, L.M.B., Sant’Anna, C.L., 2006. Marine benthic cyanobacteria in coastal islands of São Paulo, Brazil. Braz. J. Bot. 29 (4), 639−656.

Da-Rós, P.C.M., Silva, C.S.P., Silva-Stenico, M.E., Fiore, M.F., Castro, H.F., 2013. Assessment of chemical and physico-chemical properties of cyanobacterial lipids for biodiesel production. Mar. Drugs 11 (7), 2365−2381.

Dadheech, P.K., Mahmoud, H., Kotut, K., Krienitz, L., 2012. *Haloleptolyngbya alcalis* gen. et sp. nov., a new filamentous cyanobacterium from the soda lake Nakuru, Kenya. Hydrobiologia 691 (1), 269−283.

Dadheech, P.K., Glöckner, G., Casper, P., Kotut, K., Mazzoni, C.J., Mbedi, S., et al., 2013. Cyanobacterial diversity in the hot spring, pelagic and benthic habitats of a tropical soda lake. FEMS Microbiol. Ecol. 85 (2), 389−401.

Dahms, H.-U., Xu, Y., Pfeiffer, C., 2006. Antifouling potential of cyanobacteria: a mini-review. Biofouling 22, 317−327.

Dall’agnol, L.T., Ghilardi-Junior, R., Mcculloch, J.A., Schneider, H., Schneider, M.P.C., Silva, A., 2012. Phylogenetic and gene trees of *Synechococcus*: choice of the right marker to evaluate the population diversity in the Tucuruí Hydroelectric Power Station Reservoir in Brazilian Amazonia. J. Plankton Res. 34 (3), 245−257.

De-Lamonica-Freire, E.M., Heckman, C.W., 1996. The seasonal succession of biotic communities in wetlands of the tropical wet-and-dray climatic zone: III. The algal communities in the Pantanal of Mato Grosso, Brazil, with a comprehensive list of the known species and revision of two desmid taxa. Int. Rev. Hydrobiol. 81 (2), 253−280.

Diaz-Castro, J.J., Souza-Mosimann, R.M., Laudares-Silva, R., Forsberg, B.R., 2003. Composition of the periphytic diatom community of the Jaú river, Amazonas, Brazil. Acta Amazonica 33 (4), 583−606.

Dixit, R.B., Suseela, M.R., 2013. Cyanobacteria: potential candidates for drug discovery. Antonie Van Leeuwenhoek 103, 947−961.

Drennan, P., Pammenter, N.W., 1982. Physiology of salt excretion in the mangrove *Avicennia marina* (Forsk.) Vierh. New Phytol. 91 (4), 597−606.

Duarte, R.T.D., Nóbrega, F., Nakayama, C.R., Pellizari, V.H., 2012. Brazilian research on extremophiles in the context of astrobiology. Int. J. Astrobiol. 11 (4), 325−333.

Egamberdieva, D., Lugtenberg, B., 2014. PGPR to alleviate salinity stress on plant growth. In: Miransari, M. (Ed.), Use of Microbes for the Alleviation of Soil Stresses. Springer, New York, NY, pp. 73−96.

Etchegaray, A., Rabello, E., Dieckmann, R., Moon, D.H., Fiore, M.F., von Döhren, H., et al., 2004. Algicide production by the filamentous cyanobacterium *Fischerella* sp. CENA19. J. Appl. Phycol. 16 (3), 237−243.

FAO/IIASA/ISRIC/ISS-CAS/JRC, 2009. Harmonized World Soil Database (Version 1.1). FAO/IIASA, Rome, Italy/Laxenburg, Austria.

Farlow, W.G. 1880. On the nature of the peculiar reddening of salted codfish during the summer season. In: Report of the Commissioners for 1878. US Commission of Fish and Fisheries, Whashington, DC, pp. 969−974.

Fearnside, P.M., 2005. Deforestation in Brazilian Amazonia: history, rates and consequences. Conserv. Biol. 19 (3), 680−688.

Feller, I.C., Lovelock, C., McKee, K., Berger, U., Joye, S.B., Ball, M., 2010. Biocomplexity in mangrove ecosystems. Ann. Rev. Mar. Sci. 2 (1), 395−417.

Fiore, M.F., Neilan, B.A., Copp, J.N., Rodrigues, J.L.M., Tsai, S.M., Lee, H., et al., 2005. Characterization of nitrogen-fixing cyanobacteria in the Brazilian Amazon floodplain. Water Res. 39 (20), 5017−5026.

Fitzgerald, M.A., Orlovich, D.A., Allaway, W.G., 1992. Evidence that abaxial leaf glands are the sites of salt secretion in leaves of the mangrove *Avicennia marina* (Forsk.) Vierh. New Phytol. 120, 1−7.

Food Agriculture Organization of the United Nations (FAO), 2015. Climate change and food systems: global assessments and implications for food security and trade. ⟨http://www.fao.org/3/a-i4332e.pdf⟩.

Foti, M.J., Sorokin, Y.D., Zacharova, E.E., Pimenov, N.V., Kuenen, J.G., Muyzer, G., 2008. Bacterial diversity and activity along a salinity gradient in soda lakes of the Kulunda Steppe (Altai, Russia). Extremophiles 12 (1), 133−145.

Friedmann, E.I., Ocampo-Friedmann, R., 1995. A primitive cyanobacterium as pioneer microorganism for terraforming Mars. Adv. Space Res. 15 (3), 243−246.

Furian, S., Martins, E.R.C., Parizotto, T.M., Rezende-Filho, A.T., Victoria, R.L., Barbiero, L., 2013. Chemical diversity and spatial variability in myriad lakes in Nhecolândia in the Pantanal wetlands of Brazil. Limnol. Oceanogr. 58 (6), 2249−2261.

Garland Jr., T., Carter, P.A., 1994. Evolutionary physiology. Annu. Rev. Physiol. 56, 579−621.

Genuário, D.B., Andreote, A.P., Vaz, M.G.M.V., Fiore, M.F., 2017a. Heterocyte-forming cyanobacteria from Brazilian saline−alkaline lakes. Mol. Phylogenet. Evol. 109, 105−112.

Genuário, D.B., Vaz, M.G.M.V., Melo, I.S., 2017b. Phylogenetic insights into the diversity of homocytous cyanobacteria from Amazonian rivers. Mol. Phylogenet. Evol. 116, 120−135.

Genuário, D.B., Sant'Anna, C.L., Melo, I.S., 2018. Elucidating the *Cronbergia* (cyanobacteria) dilemma with the description of *Cronbergia amazonensis* sp. nov. isolated from Solimões river (Amazonia, Brazil). Algal Res. 29, 233−241.

Gheyi, H.R., 2000. Problemas de salinidade na agricultura irrigada. In: Oliveira, T.S., Assis Jr., R.N., Romero, R.E., Silva, J.R.C. (Eds.), Agricultura, sustentabilidade e o semi-árido. DCS/UFC, Fortaleza, pp. 329−346.

Gibbs, R.J., 1972. Water chemistry of Amazon river. Geochim. Cosmochim. Acta 36 (9), 1061−1066.

Giulietti, N.A., Harley, R.M., Queiroz, L.P., Rapini, A., 2006. Introduction: Top set the scene. In: Queiroz, L.P., Rapini, A., Giulietti, N.A. (Eds.), Towards Greater Knowledge of the Brazilian Semi-Arid biodiversity. Ministério Ciência e Tecnologia (MCT), Brasília, pp. 15−19.

Global Forest Watch, 2018. World Resources Institute. www.globalforestwatch.org (accessed on Jan 26, 2018).

Gregoracci, G.B., Soares, A.C.D.S., Miranda, M.D., Coutinho, R., Tompson, F.L., 2015. Insights into the microbial and viral dynamics of a coastal downwelling-upwelling transition. PLoS ONE 10 (9), e0137090.

Guimarães, P.I., Leão, T.F., Melo, A.G.C., Ramos, R.T.J., Silva, A., Fiore, M.F., et al., 2015. Draft genome sequence of the picocyanobacterium *Synechococcus* sp. Strain GFB01, isolated from a freshwater lagoon in the Brazilian Amazon. Genome Announce. 3 (4), e00876-15.

Haridasan, M., 1989. Agroforestry systems for the Cerrado region of central Brazil: Potential and constraints. In: Reifsnyder, W.E., Darnhofer, T.O. (Eds.), Meteorology and Agroforestry. ICRAF, Nairobi, pp. 257−272.

Hentschke, G.S., Johansen, J.R., Pietrasiak, N., Fiore, M.F., Rigonato, J., Sant'Anna, C.L., et al., 2016. Phylogenetic placement of *Dapisostemon* gen. nov. and *Streptostemon*, two tropical heterocytous genera (*Cyanobacteria*). Phytotaxa 245 (2), 129−143.

Hirano, S.S., Upper, C.D., 2000. Bacteria in the leaf ecosystem with emphasis on *Pseudomonas syringae*—a pathogen, ice nucleus, and epiphyte. Microbiol. Mol. Biol. Rev. 64 (3), 624−653.

Hoffmann, H.J., 1976. Precambrian Microflora, Belcher Islands, Canada: significance and systematics. J. Paleontol. 50 (6), 1040−1073.

Holguin, G., Zamorano, P.G., Bashan, L.E.D., Mendoza, R., Amador, E., Bashan, Y., 2006. Mangrove health in an arid environment encroached by urban development—a case study. Sci. Total Environ. 363 (1-3), 260−274.

Horikoshi, K., Antranikian, G., Bull, A.T., Robb, F.T., Stetter, K.O., 2011. *Extremophiles Handbook*, vol. 1. Springer, Tokyo.

Horodyski, R.J., Donaldson, A., 1980. Microfossils from the Middle Proterozoic Dismal Lakes Group, Arctic Canada. Precambrian Res. 11 (2), 125–159.

Huertas, M.J., López-Maury, L., Giner-Lamia, J., Sánchez-Riego, A.M., Florencio, F.J., 2014. Metals in cyanobacteria: analysis of the copper, nickel, cobalt and arsenic homeostasis mechanisms. Life 4 (4), 865–886.

Jokela, J., Heinilä, L.M.P., Shishido, T.K., Wahlsten, M., Fewer, D.P., Fiore, M.F., et al., 2017. Production of high amounts of hepatotoxin nodularin and new protease inhibitors *Pseudospumigins* by the Brazilian Benthic *Nostoc* sp. CENA543. Front. Microbiol. 8, 1963.

Jones, B.E., Grant, W.D., 1999. Microbial diversity and ecology of the Soda Lakes of East Africa. In Bell, C.R., Brylinsky, M., Johnson-Green, P. (Eds.), Microbial Biosystems: New Frontiers: Proceedings of the 8th International Symposium on Microbial Ecology. Atlantic Canada Society for Microbial Ecology, Halifax, Nova Scotia, pp. 681–688.

Jones, B.E., Grant, W.D., Duckworth, A.W., Owenson, G.G., 1998. Microbial diversity in soda lakes. Extremophiles 2 (3), 191–200.

Jungblut, A., Hawes, I., Mountfort, D., Hitzfeld, B., Dietrich, D.R., Burns, B.P., et al., 2005. Diversity within cyanobacterial mat communities in variable salinity meltwater ponds of McMurdo Ice Shelf, Antarctica. Environ. Microbiol. 7 (4), 519–529.

Kathiresan, K., Selvam, M., 2006. Evaluation of beneficial bacteria from mangrove soil. Bot. Mar. 49 (1), 86–88.

Kavamura, V.N., Santos, S.N., Silva, J.L., Parma, M.M., Ávila, L.A., Visconti, A., et al., 2013. Screening of Brazilian cacti rhizobacteria for plant growth promotion under drought. Microbiol. Res. 168 (4), 183–191.

Knoll, A.H., Strother, P.K., Rossi, S., 1988. Distribution and diagenesis of microfossils from the lower proterozoic Duck Creek Dolomite, Western Australia. Precambrian Res. 38, 257–279.

Koch, E.W., Barbier, E.B., Silliman, B.R., Reed, D.J., Perillo, G.M.E., Hacker, S.D., et al., 2009. Non-linearity in ecosystem services: temporal and spatial variability in coastal protection. Front. Ecool. Environ. 7 (1), 29–37.

Komárek, J., Kaštovský, J., Mareš, J., Joshansen, J.R., 2014. Taxonomic classification of cyanoprokaryotes (cyanobacterial genera) 2014, using polyphasic approach. Preslia 86, 295–335.

Leão, T., Guimarães, P.I., Melo, A.G.C., Ramos, R.T.J., Leão, P.N., Silva, A., et al., 2016. Draft sequence of the N_2-fixing cyanobacterium *Nostoc piscinale* CENA21, isolated from the Brazilian Amazon Floodplain. Genome Announce. 4, e00189–13.

Lima, A.R.J., Siqueira, A.S., Santos, B.G.S., Silva, F.D.F., Lima, C.P., Cardoso, F.J., et al., 2014. Draft genone sequence of the Brazilian *Cyanobium* sp. strain CACIAM14. Genome Announce. 2, e00669-14.

Lima, C.B., Filho, S.V.S., Santos, M.A., Oliveira, M., 2007. Influência da água salina nas características físico-químicas do solo e no desenvolvimento da mamoneira cultivada em vasos. Revista Caatinga 20 (4), 132–136.

Lombardo, M., Pinto, F.C.R., Vieira, J.M.S., Honda, R.Y., Pimenta, A.M.C., Bemquerer, M.P., et al., 2006. Isolation and structural characterization of microcystin-LR and three minor oligopeptides simultaneously produced by *Radiocystis feernandoi* (Chroococcales, Cyanobacteriae): a Brazilian toxic cyanobacterium. Toxicon 47 (5), 560–566.

Lopes, A.S., Guilherme, L.R.G., 2016. A career perspective on soil management in the Cerrado Region of Brazil. Adv. Agron. 137, 1–72.

López-Archilla, A.E., Moreira, D., López-García, P., Guerrero, C., 2004. Phytoplankton diversity and cyanobacterial dominance in a hypereutrophic shallow lake with biologically produced alkaline pH. Extremophiles 8 (2), 109–115.

Malhi, Y., Roberts, J.T., Betts, R.A., Killeen, T.J., Li, W., Nobre, C.A., 2008. Climate change, deforestation, and the fate of the Amazon. Science 319, 169–172.

Malone, C.F.S., Santos, K.R.S., Neto, M.J., Sakamoto, A.Y., 2007. Gêneros de algas no plâncton de lagoas salinas situadas na fazenda Nhumirim, Pantanal da Nhecolândia, MS. Revista Brasileira de Biociências 5, 588–590.

Malone, C.F.S., Alvarenga, D.O., Fiore, M.F., Sant'Anna, C.L., 2014. Towards a phylogenetic position of the morphologically-defined genus *Pannus* (Cyanobacteria). Nova Hedwigia 99 (3–4), 511–524.

Malone, C.F.S., Rigonato, J., Laughinghouse IV, H.D., Schmidt, E.C., Bouzon, Z.L., et al., 2015. *Cephalothrix* gen. nov. (Cyanobacteria): towards an intraspecific phylogenetic evaluation by multilocus analyses. Int. J. Syst. Evol. Microbiol. 65 (9), 2993–3007.

Mariot, M., Dudal, Y., Furian, S., Sakamoto, A., Valles, V., Fort, M., et al., 2007. Dissolved organic matter fluorescence as a water-flow tracer in the tropical wetland of Pantanal of Nhecolandia, Brazil. Sci. Total Environ. 388 (1), 184.

McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., et al. 2012. International Code of Nomenclature for algae, fungi and plants (Melbourne Code). In: Adopted by the Eighteenth International Botanical Congress Melbourne, Australia. 208 p.

Medina-Júnior, P.B., Rietzeler, A.C., 2005. Limnological study of a Pantanal saline lake. Braz. J. Biol. 65 (4), 651–659.

Mesbah, N.M., Wiegel, J., 2008. Life at extreme limits: the anaerobic halophilic alkalithermophiles. Ann. N. Y. Acad. Sci. 1125, 44–57.

Moreira, A.P.B., Meirelles, P.M., Santos, E.D.O., Amado-Filho, Gilberto, M., Francini-Filho, R.B., et al., 2015. Turbulence-driven shifts in holobionts and planktonic microbial assemblages in St. Peter and St. Paul Archipelago, Mid-Atlantic Ridge, Brazil. Front. Microbiol. 6, 1038.

Morton, D.C., Rubio, J., Cook, B.D., Gastellu-Etchegorry, J.-P., Longo, M., Choi, H., et al., 2016. Amazon forest structure generates diurnal and seasonal variability in light utilization. Biogeosciences 13 (7), 19043–19072.

Nogueira, N.M.C., Ferreira-Correia, M.M., 2001. Cyanophyceae; Cyanobacteria in red mangrove forest at Mosquitos and Coqueiros estuaries, São Luís, State of Maranhão, Brazil. Braz. J. Bot. 61 (3), 347–356.

Oliveira, M.D., Calheiros, D.F., 2000. Flood pulse influence on phytoplankton communities of the south Pantanal floodplain, Brazil. Hydrobiologia 427 (1–3), 101–112.

Oren, A., 2010. Industrial and environmental applications of halophilic microorganisms. Environ. Technol. 31, 8–9.

Paerl, H.W., Pinckney, J.L., Steppe, T.F., 2000. Cyanobacterial–bacterial mat consortia: examining the functional unit of microbial survival and growth in extreme environments. Environ. Microbiol. 2 (1), 11–26.

Pezeshki, S.R., DeLaune, R.D., 2012. Soil oxidation reduction in wetlands and its impact on plant functioning. Biology 1 (2), 196–221.

Pureza, L.M.S., Graças, D.A., Gonçalves, E.C., Correa, J.A.M., Silva, A., Schneider, M.P.C., 2013. Bacterial diversity in an Amazonian mangrove ecosystem. Aquat. Sci. Technol. 1 (1), 66–85.

Raja, R., Hemaiswarya, S., Carvalho, I.S., Ganesan, V., 2014. Therapeutic applications of cyanobacteria with emphasis on their economics. In: Sharma, N.K., Rai, A.K., Stal, L.J. (Eds.), Cyanobacteria: An Economic Perspective. John Wiley, Hoboken, NJ, USA, pp. 93−102.

Rampelotto, P.H., 2013. Extremophiles and extreme environments. Life 3 (3), 482−485.

Rangel, M., Brunetti, R.L., Garcia, A.N., Cambui, C.C.N., Conserva, G.A.A., Neves, A.C., et al., 2013. Acute effects of three *Geitlerinema* spp. (Cyanobacteria) extracts administrated in mice: symptoms and histopathological aspects. Phytochem. Rev. 12 (3), 543−553.

Rastogi, R.P., Sonani, R.R., Madamwar, D., 2015. Cyanobacterial sunscreen scytonemin: role in photoprotection and biomedical Research. Appl. Biochem. Biotechnol. 176 (6), 1551−1563.

Ratter, J.A., Bridgewater, S., Ribeiro, J.F., 2003. Analysis of the floristic composition of the Brazilian cerrado vegetation III: comparison of the woody vegetation of 376 areas. Edinburgh J. Bot. 60 (1), 57−109.

Rigonato, J., Gama, W.A., Alvarenga, D.O., Branco, L.H.Z., Brandini, F.P., Genuário, D.B., et al., 2016. *Aliterella atlantica* gen. nov., sp. nov., and *Aliterella antarctica* sp. nov., novel members of coccoid Cyanobacteria. Int. J. Syst. Evol. Microbiol. 66 (8), 2853−2861.

Rostagi, R.P., Sinha, R.P., 2009. Biotechnological and industrial significance of cyanobacterial secondary metabolites. Biotechnol. Adv. 27, 521−539.

Rothschild, L.J., Mancinelli, R.L., 2001. Life in extreme environments. Nature 6823, 1092−1101.

Saleska, S.R., Wu, J., Guan, K., Araujo, A.C., Huete, A., Nobre, A.D., et al., 2016. Dry-season greening of Amazon forests. Nature 531, E4−E5.

Sánchez-Baracaldo, P., Hayes, P.K., Blank, C.E., 2005. Morphological and habitat evolution in the Cyanobacteria using a compartmentalization approach. Geobiology 3 (3), 145−165.

Santos, K.R., Jacinavicius, F.R., Sant'Anna, C.L., 2011. Effects of the pH on growth and morphology of *Anabaenopsis elenkinii* Miller (Cyanobacteria) isolated from the alkaline shallow lake of the Brazilian Pantanal. Fottea 11 (1), 119−126.

Santos, K.R.S., Sant'Anna, C.L., 2010. Cianobactérias de diferentes tipos de lagoas ("salina", "salitrada" e "baía") representativas do Pantanal da Nhecolândia, MS, Brasil. Braz. J. Bot. 33 (1), 61−83.

Santos, S.N., Kavamura, V.N., Silva, J.L., Melo, I.S., Andreote, F.D., 2010. Plant growth promoter rhizobacteriainplants inhabiting harsh tropical environmentsandits roleinagricultural improvements. In: Maheshwari, D.K. (Ed.), Plant Growth and Health Promoting Bacteria. Springer-Verlag, Berlin, pp. 251−272.

Sayre, R., Bow, J., Josse, C., Sotomayor, L., Touval, J., 2008. Terrestrial ecosystems of South America. In: Campbell, J., Jones, K.B., Smith, J.H., Koeppe, M. (Eds.), North America Land Cover Summit. Association of American Geographers, Washington, DC, pp. 131−152.

Schaeffer-Novelli, Y., Cintrón-Molero, G., Soares, M.L.G., Tognella-de-Rosa, M., 2000. Brazilian mangroves. Aquat. Ecosyst. Health Manage. 3 (4), 561−570.

Schirrmeister, B.E., Anisimova, M., Antonelli, A., Bagheri, H.C., 2011. Evolution of cyanobacterial morphotypes: taxa required for improved phylogenomic approaches. Commun. Integr. Biol. 4 (4), 424−427.

Schirrmeister, B.E., Gugger, M., Donoghue, P.C.J., 2015. Cyanobacteria and the great oxidation event: evidence from genes and fossils. Palaeontology 58 (5), 769−785.

Schopf, J.W., Blacic, J.M., 1971. New microorganisms from the Bitter Springs Formation (Late Precambrian) of the North-Central Amadeus Basin, Australia. J. Paleontol. 45 (6), 925−960.

Schreiber, L., Krimm, U., Knoll, D., 2004. Interactions between epiphyllic microorganisms and leaf cuticles. In: Varma, A., Abbott, L., Werner, D., Hampp, R. (Eds.), Plant Surface Microbiology. Springer, Heidelberg, pp. 145−156.

Seckbach, J., Oren, A., 2007. Oxygenic photosynthetic microorganisms in extreme environments. In: Seckbach, J. (Ed.), Algae and Cyanobacteria in Extreme Environments. Springer, Dordrecht, pp. 4−25.

Shishido, T.K., Kaasalainen, U., Fewer, D.P., Rouhiainen, L., Jokela, J., Wahlsten, M., et al., 2013. Convergent evolution of [D-leucine1] microcystin-LR in taxonomically disparate cyanobacteria. BMC Evol. Biol. 13 (1), 86.

Shishido, T.K., Humisto, A., Jokela, J., Liu, L., Wahlsten, M., Tamrakar, A., et al., 2015. Antifungal compounds from Cyanobacteria. Mar. Drugs 13 (4), 2124−2140.

Shishido, T.K., Jokela, J., Fewer, D.P., Wahlsten, M., Fiore, M.F., Sivonen, K., 2017. Simultaneous production of anabaenopeptins and namalides by the cyanobacterium *Nostoc* sp. CENA543. ACS Chem. Biol. 12 (11), 2746−2755.

Silambarasan, G., Ramanathan, T., Kathiresan, K., 2012. Diversity of marine cyanobacteria from three mangrove environment in Tamil Nadu Coast, South East Coast of India. Curr. Res. J. Biol. Sci. 4 (3), 235−238.

Silva, C.S.P., Genuário, D.B., Vaz, M.G.M.V., Fiore, M.F., 2014. Phylogeny of culturable cyanobacteria from Brazilian mangroves. Syst. Appl. Microbiol. 37 (2), 100−112.

Silva-Stenico, M.E., Rigonato, J., Leal, M.G., Vaz, M.G.M.V., Andreote, A.P.D., Fiore, M.F., 2012a. Non-ribosomal halogenated protease inhibitors from cyanobacterial isolates as attractive drug targets. Curr. Med. Chem. 19 (30), 5205−5213.

Silva-Stenico, M.E., Vieira, F.D.P., Genuário, D.B., Silva, C.S.P., Moraes, L.A.B., Fiore, M.F., 2012b. Decolorization of textile dyes by Cyanobacteria. J. Braz. Chem. Soc. 23 (10), 1863−1870.

Silva-Stenico, M.E., Kaneno, R., Zambuzi, F.A., Vaz, M.G.M.V., Alvarenga, D.O., Fiore, M.F., 2013. Natural products from cyanobacteria with antimicrobial and antitumor activity. Curr. Pharm. Biotechnol. 14 (9), 820−828.

Singh, J.S., Kumar, A., Rai, A.N., Singh, D.P., 2016. Cyanobacteria: a precious bio-resource in agriculture, ecosystem, and environmental sustainability. Front. Microbiol. 7 (12), 529.

Singh, R., Parihar, P., Singh, M., Bajguz, A., Kumar, J., Singh, S., et al., 2017. Uncovering potential applications of cyanobacteria and algal metabolites in biology, agriculture and medicine: current status and future prospects. Front. Microbiol. 8, 515.

Soil Science Division Staff, 2017. Soil survey manual. In: Ditzler, C., Scheffe, K., Monger, H.C. (Eds.), USDA Handbook 18. Government Printing Office, Washington, DC.

Taketani, R.G., Kavamura, V.N., Santos, S.N., 2017. Diversity and technological aspects of microorganisms from semiarid environments. In: de Azevedo, J., Quecine, M. (Eds.), Diversity and Benefits of Microorganisms from the Tropics. Springer International Publishing, Switzerland, pp. 3–19.

Thajuddin, N., Subramanian, G., 2005. Cyanobacteria biodiversity and potential applications in biotechnology. Curr. Sci. 89, 47–57.

Thompson, C.E., Beys-da-Silva, W.O., Santi, L., Berger, M., Vainstein, M.H., Guimarães, J.A., et al., 2013. A potential source for cellulolytic enzyme discovery and environmental aspects revealed through metagenomics of Brazilian mangroves. AMB Express 3 (1), 65.

Toledo, G., Bashan, Y., Soeldner, A., 1995. Cyanobacteria and black mangroves in Northwestern Mexico: colonization and diurnal and seasonal nitrogen fixation on aerial roots. Can. J. Microbiol. 41 (11), 999–1011.

Tomitani, A., Knoll, A.H., Cavanaugh, C.M., Onho, T., 2006. The evolutionary diversification of cyanobacteria: molecular-phylogenetic and paleontological perspectives. Proc. Natl. Acad. Sci. U.S.A. 103 (14), 5442–5447.

Tsyrenova, D.D., Bryanskayab, A.V., Namsaraevc, Z.B., Akimovd, V.N., 2011. Taxonomic and ecological characterization of cyanobacteria from some brackish and saline lakes of Southern Transbaikal Region. Microbiology 80 (2), 216–227.

Van den Burg, B., 2003. Extremophiles as a source for novel enzymes. Curr. Opin. Microbiol. 6 (3), 213–218.

Vaz, M.G.M.V., Genuário, D.B., Andreote, A.P.D., Malone, C.F.S., Sant'Anna, C.L., Barbiero, L., et al., 2015. *Pantanalinema* gen. nov. and *Alkalinema* gen. nov.: novel pseudanabaenacean genera (Cyanobacteria) isolated from saline–alkaline lakes. Int. J. Syst. Evol. Microbiol. 65 (1), 298–308.

Vieira, J.M.S., Azevedo, M.T.P., Oliveira, S.M.F., Honda, R.Y., Corrêa, B., 2003. Microcystin production by *Radiocystis fernadoi* (Chroococcales, Cyanobacteria) isolated from drinking water reservoir in the city of Belém, PA, Brazilian Amazonia region. Toxicon 42 (7), 709–713.

Vieira, J.M.S., Azevedo, M.T.P., Oliveira, S.M.F., Honda, R.Y., Corrêa, B., 2005. Toxic cyanobacteria and microcystin concentration in a public water supply reservoir in the Brazilian Amazonia region. Toxicon 45 (7), 901–909.

Vítek, P., Jehlička, J., Ascaso, C., Mašek, V., Gómez-Silva, B., Olivares, H., et al., 2014. Distribution of scytonemin in endolithic microbial communities from halite crusts in the hyperarid zone of the Atacama Desert, Chile. FEMS Microbiol. Ecol. 90 (2), 351–366.

Walter, B.M.T., Carvalho, A.M. De, Ribeiro, J.F.O., 2008. Conceito de Savana e de seu Componente Cerrado. In: Sano, S.M., Almeida, S.P. De, Ribeiro, J.F. (Eds.), Cerrado: Ecologia e Flora. Embrapa Informação Tecnológica, Brasília, DF, pp. 19–45.

Walters, B.B., Ronnback, P., Crona, B., Kovacs, J.M., Hussain, S.A., Badola, R., et al., 2008. Ethnobiology socio-economics and management of mangrove forests: a review. Aquat. Bot. 89 (2), 220–236.

Ward, D.M., Ferris, M., Nold, S.C., Bateson, M.M., 1998. A natural view of microbial biodiversity within hot spring cyanobacterial mat communities. Microbiol. Mol. Biol. Rev. 62 (4), 1353–1370.

Welsh, D.T., 2000. Ecological significance of compatible solute accumulation by micro-organisms: from single cells to global climate. FEMS Microbiol. Rev. 24, 263–290.

Whitton, B.A., Potts, M., 2000. The ecology of cyanobacteria, their diversity in time and space. Boston Kluwer Academic, Netherlands.

Xu, S., Nijampatnam, B., Dutta, S., Velu, S., 2016. Cyanobacterial metabolite calothrixins: recent advances in synthesis and biological evaluation. Mar. Drugs 14, 17. 12.

FURTHER READING

Catão, E., Castro, A.P., Barreto, C.C., Kruger, R.H., Kyaw, C.M., 2013. Diversity of archaea in Brazilian savanna soils. Arch. Microbiol. 195 (7), 507–512.

Grimm, A.,M., 2011. Interannual climate variability in South America: impacts on seasonal precipitation, extreme events and possible effects of climate change. Stochastic Environ. Res. Risk Assess. 25 (4), 537–554.

Gromov, B.V., Vepritskiy, A.A., Titova, N.N., Namkayeva, K.A., Alexandrova, O.V., 1991. Production of the antibiotic cyanobacterin LU-1 by Nostoc linckia CALU 892 (cyanobacterium). J. Appl. Phycol. 3, 55–59.

Hirata, K., Nakagami, H., Takashina, J., Mahmud, T., Kobayashi, M., In, Y., et al., 1996. Novel violet pigment, nostocine A, an extracellular metabolite from the cyanobacterium *Nostoc spongiaeforme*. Heterocycles 43, 1513–1519.

Karthikeyan, N., Prasanna, R., Lata, D.P., Kaushik, B.D., 2007. Evaluating the potential of plant growth promoting cyanobacteria as inoculants for wheat. Eur. J. Soil Biol. 43, 23–30.

Kaushik, B.D., 2012. Developments in cyanobacterial biofertilizer. Proc. Natl. Acad. Sci. U.S.A. 80, 379–388.

Quintana, N., Van der Kooy, F., Van de Rhee, M.D., Voshol, G.P., Verpoorte, R., 2011. Renewable energy from Cyanobacteria: energy production optimization by metabolic pathway engineering. Appl. Microbiol. Biotechnol. 91 (3), 471–490.

Rajeev, K.J., Xu, Z., 2004. Biomedical compounds from marine organisms. Mar. Drugs 2, 123–146.

Shimizu, Y., 2003. Microalgal metabolites. Curr. Opin. Microbiol. 6, 236–243.

Wilansky, B., 1936. Life in the Dead Sea. Nature 138, 467.