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SCAN ME

Review Paper

MAT FORMING CYANOBACTERIA: A REVIEW ON EARLY PHOTOAUTOTROPHS IN EVOLUTION

Vijay W. Lande

National Environmental Enginnering Research Institute,
Nehru Mar Nagpur-440020,,
India.

Abstract

Cyanobacteria mat forming reported from early Silurian black radiolarian charts (Paleozoic-464-416Ma) and even in recent this group of prokaryotic organisms are being known to perform for oxygenic photosynthesis, nitrogen fixation (diazotrophy).Cyanobacterial bloom have increased in response to global warming,occur due to climate change.Cyanobacterial mats have sustained these characteriestics in high latitude Lakes, Rivers and Seas(shallow ponds and a Lake from Alaska, Antarctic stream,high Arctic Canada and low Arctic (Sub-Arctic) Canada.Exopolysaccharide (EPS-a heteropolymer) in varying compositionis very widely distributed in cyanophyceae.Anastomosing network of mats have provided conduits for nutrient transferinOscillatoriales (filamentous cyanobacteria) andbacteria incertae sedis/or Archaea bacteria.Phylogenetic sequences of the 16S rRNA genes and the adjacent intergenic transcribed specer (ITS) have shown signifcant advancement in cyanobacteria taxa identification.Exclusive use of phenotypic (morphology and pigments) traits presence in cyanobacterial and variable phenotypes based on historical evolutionary relationships is defined as problematic.Cyanobacteria in fossil recovered were exclusively fromin various regions of Russia and Australia.Phylogeny based on 5 groups of morphological cyanobacteria records in preserved fossil illustrated with mat forming cyanobacteria alnong with early origin of Archaea bacteraial taxa ~3.5Ga old Apex chert is described in this review.Formation of $CaCO_3$ rich lime stones, as resultant of two product of cyanobacterial photosynthesis i.e organic matter and O_2...Cyanobacteria have shown presenceas evidenceofKerosenebanded iron formations (BIFs), andUranium-rich pyritic in early history of atmosphere.

Key words: Cyanobacterial mats, High latitude Lakes, EPS, Cyanobacterial lineage, Fossil cyanobacteria.

INTRODUCTION

The abundance of mat forming cyanobacteria were usually observed from highlatitude Lakes, Rivers and Seas. Filamentous cyanobacterial species were embedded within a polymeric gel matrixi.e. exopolysaccharide secreted that bind together the assemblage forming attached or free floating colonies in high latitude areas. The electron and confocal microscopy showed cyanobacterial architecture of these biofilms have an anastomosing network of holes and chennels which may provide conduits for nutrient transfer in Chroococcaceae species and bacteria even sometimeschannels for the movement of gliding filamentous cyanobacteria, [1]. Coloration and pigment content of cyanobacteria include phycocyanin and phycoerythrin,photo-protective molecules helps in light harvesting. The intriguing feature about non toxic and toxic cyanobacteria depend on presence or absence cyanotoxin producing genes. Benthic *Phormidium* spp.The exudates of anatoxin-a, homoanatoxin-a, and degradation products such as dihydroanatoxin-a and dihydrochemoanatoxinwere characterized using liquid chromatography - mass spectrometry (LC-MS) and 16S r-RNA gene sequences used for differentiating anatoxin and nonanatoxin producing stains followed by separation into two subclades during phylogenetic analyzedat 3-different sites in New Zealand [2].

CYANOBACTERIAL MATS IN HIGH LATITUDE LAKES, RIVERS AND SEAS

It is typically dominated highest in the basal stratum of the total ecosystem pigment stocks at High arctic Canada and low Arctic (Sub-Arctic) Canada. The chlorophyll 'a' and carotenoid content of the mats (mg m^{-2}) were more than 100 times than that of the phytoplankton in overlying water column in shallow ponds and a Lake from Alaska[3]. In Antarctic stream, a Cyanobacteria with *Nostoc commune* look like golden, brown, olive green or black in appearance as a result of high concentrations of the UV screening pigment Scytonemin [4]. The mats and crusts of *Calothrix* (e.g Antarctic stream bed communities and the green land ice cap cryoconite assemblages) are also black pigmented due to scytonemin[5], [6]. The luxuriant Oscillatorian mat communities and living stromatolites was observed at the bottom of Antarctic ice capped lakes e.g McMurdo Dry Valley lakes, and Lake Untersee [7]. Interestingly,five types of microbial mats were initially identified in Antarctic ice capped Lakes (i) moat mats that occur around the edge of the Lake where the ice melts in summer (ii) lift off mats,that trap-bubbles of nitrogen and oxygen in upright columnar structure up to icon in diameter and that may eventually detach from the sediment to the surface (iii) pinnacle mats that

form small cone shaped structures (iv) aerobic prostate mats (v) anaerobic prostate mats [8],[9]. The most commonly orange, pink or purple color depending on presence of carotenoids Oscillatorian mat communities were observed throughout both polar regions in shallow waters. Black colonies of *Tolypothrix* sp. were observed in shallow waters of Ward Flunt Lake at the northern limit of high Arctic Canada.*Leptolyngbya*, *Pseudoanabaena* and colonies of *Nostoc* species appear as pink layer and blue-green layer ofoscillatoriales were comprised ofembeded with small diatoms such as *Achnanthes* sp., *Cymbella* sp., and chlorophytes such as *Mougeotia* sp., *Closterium* sp. in both pink and blue green layer. Ratio of total carotenoid to chlorophyll 'a'and Scytonemin to chlorophyll 'a' in mat algal species were maximum in the upper mat surface. Many carotenoids forms canthaxanthin, echinenone, myxoxanthophyll and related glycoside closely resembling 4-keto-myxoxanthophyll were characterized in mats. Highest concentrations of violaxanthin and chl 'b' in blue-green layer indicated increased importance in the lower community of algae [10]. Figure-1 has shown details of mat of Phormidium lucidium (Kutz) isolated from stream near the Iron ore mine at Dilli Rajhara, Dist. Durg, (C.G.)[11].

ENVIRONMENTAL FACTORS IMPACT AND COMPOSITION OF EPS OF CYANOBACTERIA

The Cyanobacterial bloom is ever increasing in response to global warming climate [12] [13] [14],[15]. The percentage of cyanobacteria increasing with temperature and total nitrogen have observed in Danish lakes [16], [17]. The sucession of algal dominance shift due to maximum nutrient enrichment as towards abundance of chlorophyta rather than by cyanophyta were seen in temperate shallow lakes [18]. Cyanobacteria cause toxin producing bloom, dissolved oxygen depletion problems in lakes and reservoirs [19]. Other variables responsible to cause cynobacterial bloom are nutrients concentration [20], TN: TP ratios [21], pH and CO_2 concentrations [22],[23], Stratification [24],[25],[26], Salinity [27] and Light [28],[29].

Understanding the influence of environmental stressors on cyanotoxin production in cyanobacteria is essential for effective water management.Variability in *Phormidium* mats have produced greater percentage cover in summer months correlated with stable water flows and when it increases in excess 3-times flow andwater temperature (above 13.4°C) wereresulted in removal of *Phormidium* mats and toxin [30]. Studies on Six cyanobacterial strains were isolated and recovered using-Conway culture medium and

harvested in laboratory's closed photobioreacters, from"Kopara" shallow brackish to marine ponds of Rangiroa atoll, Tuamotar archipelago, French Polynesia. Under unbalance environment capsular and released EPS were produced by these filamentous and unicellular cyanobacteria, [31]. Half of the cyanobacteria were filamentous species as *Geitlerinema* (Oscillatoria) sp. strain FE, *Plectonema* (Leptolyngbya) cf. golenkinianum Gomont strain FF, and *Plectonema* (Leptolyngbya) cf. battersii, Gomont GF, and rest of the other unicellular strains *Chroococcus submarinus* (Hansgirg) Kovàčik strain BM, *Johannesbaptistia pellucida* (Dickie), Taylor and Dronet strain GC, and *Rabdoderma* cf. rubrum (Åivik) Komárek and Anagnostidis strain CH. Cyanobacterial filamentous species FF,GF and unicellular BM,GC produced much more CEPS than REPS whereas filamentous strain FE and unicellular strain CH producedd equal amounts of CEPS and REPS. The yield EPS produced (mg/g biomass) 7.7-124.0mg/g comprised ofneutral sugars 42-84%, Uronic acid 2-11% protein 7-24% and sulfates 0-19% in varying concentration from above mentioned six strains of cynobacteria.

Three different type of polysaccharide are known to produce in cyanobacteria (i) endogeneous polysaccharides: that serve as storage compounds is so-called α – granules a branched glycogen-like polymer α (1-4) and α (1-6) linked glucose molecules. Second one is cell envelope polysaccharide i.e. cell wall polysaccharides and external layers of glycocalyx. Two fractionsare further subdivided in (i) the wall structured polysaccharide sheath and is less structured (ii) a polysaccharide capsule which extends outsidethe cell as capsules/or extracellular slime or mucilage polysaccharides.Glycocalyx is considered as Extracellular poly saccharide (EPS) released may suspended or colloidal molecules form of 6-sugars or more monosaccharides suite of at least 12 sugars in varying compositions in different algae. Ten monosaccharides in cyanobacterial RPSs are the hexoses: glucose, galactose, and mannose, the pentoses: ribose, arabinose and xylose, the deoxyhexoses: fucose and rhamnose and the acidic hexoses:glucuronic acid and galacturonic acid.

The matrix producing cyanobacteria in which filaments are found embedded. This matrix is also involved in attachment of cyanobacteria. The molecular weight is often more than 100,000Da. anionic nature glucose,in RPSis being abundant in 60% of the cases. Half of the strains were studied represent about 90% polymers being characterized by the presence of uronic acids.It exceeds 20% of the RPSs-dry weight

and contribute to the anionic EPS which determines the sticky properties of these molecules.In addition significant amount of sulphate and keto linked pyruvic acid have been found in many cyanobacterial RPSs [32],[33]. Significant amount of sulphate groups are also present in *Gloeothece* sp., *Spirulina* and *Aphanocapsa* sp.and revealed antiviral activities,[34]. EPS (a heteropolymer) very widely distributed and vary in composition among different Cyanobacteria [35]. It has physcial and chemical properties known for stabilizing, suspending, thickening, gelling and water retention capability.This has functional application in textile, adhesives, paints, food and breverage industries [36],[37]. In pharmaceuticals EPS of *Cyanospira capsulata* [38] and *Aphanothece halophtica*GRO2 (32) which display similar viscosity behavior as xanthan [39]. The metal ion binding capacity of EPSs produced by Anabaena sp. (Choi et al., 1998) and *Cyanothece* spp. [40], may find useful applications in waste water treatment whereas the water holding capacity of EPS produced by *Nostoc muscorum* [41] may be used as a soil conditioner EPS produced by *Cyanospira capsulata* strain Mag I 50 ATCC43193 is of great interest for oil recovery [42].

PHYLOGENETIC CLASSIFICATION OF CYANOBACTERIA LINEAGE

In taxonomy of cyanobacteria, *Phormidium* group sensu Gomont represents taxa forming, divergent phylogenetic clusters and taxa comprised of a number of different genera based on Random Amplified Polymormhic DNA (RAPD) genotypes, Restriction Fragment Length Polymorphism (RFLP) profiles and pigment composition. The following clusters defined

1. Species pragmatic concept designed where a species are a cluster of similar strains that have recognizable discontinuities with other known clusters [43].
2. Polyphasic approach is combining morphological, ultrastructural, biochemical characteristics data set, [44],[45].
3. Bacteria species have splited into smalller more meaningful units as “ecotype” which provide a rational basis for demarcating bacterial taxa

Relationship among *Phormidium* strains and with other cyanobacteria from different geographical places have reflected in their morphology and most pronounced in pigment composition, [46]. Komarek & Anagnostidis (1999) supported this view partly, of thecosmopolitan distribution of cyanobacteria and emphasised many taxa have present in narrowly defined ranges of distribution[47]. In other studies, distribution patternscyanobacteria correlatedwith ecological determinantsrather than formal

morphotypic description of genus "Phormidium" [48], [49] i.e. group of *Arthrospira* and *Phormidium retzii* strains are more localized than having spatial distributed. Similar results were obtained based on sequences of the 16S rRNA genes and the adjacent intergenic transcribed specer (ITS) [50]. There is a clear relationship between the strains original environmental habitat and specific subtrees on the phylogenetic trees. These results were consistent with formal genus *Oscillatoria*, which also proved to be polyphyletic in a predictable studies i.e. nutritional and other environmental impacts that changes in enviromental conditions and sustained modified phenotypes [51]. Other studies were carried out under light-microscope and ultrastructures were also defined insufficient tocorrelate between positions of cyanobacterial strains in the phylogenetic tree.Two conclusion were drawn (i) Some phylogenetically distant members were also showed similar morphological traits (ii) Similar strains came from similar ecosystems and were similar in cell size and shape, [52]. Several individual clade are restricted to marine, freshwater or terrestrial, and /or these clades themselves have a mixed distribution overall in the inferred trees. However, *Phormidium* spp. in the ice free regions of Nizzara Desert, an extreme terrestrial habitat of Antarctic that have similar strains clustered together with *Phormidium automnale* (CCAP 1462/10) from-Antarctica ice zone.

Exclusive use of phenotypic (morphlogy and pigments) traits to determine a natural system of the cyanobacteria that is based on historical evolutionary relationships is problematic even more so because phenotypes might change under variable environmental conditions or after extended cultivation.Cyanobacteria synthesize the same carotenes as the higher plants, and are known to produce unique type of Xanthophylls e.g. Echienone. Although Chlorophyll 'a' amount and has traditionally been used as a surrogate measure for cyanobacterial abundance and/or bimass in culture as well as in Marine, Freshwater and Terrestrial habitats [53].The mycosporine-gutaminol-amycosporine so far considered characteristics for terrestrial fungi and a secondary metabolite of terrestrial *Phormidium* sp. which function is still unknown.In cyanobacteria morphological character have a chemical basis but chemical characters frequently donot have a morphological expression [54]. Palinska et al., (2011) investigated 29 cyanobactrial strains belong to *Oscillatoria-Leptolynbya-Phormidium* group represented only eight major carotenoids, and three mycosporines (also present in terrestrial fungi). It also suggesed early diversion of algae- fungi and protists. In other

study about cyanobacteria, 15 common cyanobacterial carotenoids were observed [55]. That is qualitative carotenoid composition is a suitable biochemical criteria to support classification of cyanobacteria.Uniform feature of all *Phormidium* like isolates were observed with presence of zeaxanthin and β-carotene, and also proved *Oscillatoria* (CCMEE416) difffer in their carotenoid pattern from the isolates belonging to the *Phormidium* sp. Some isolates assigned to the genera, *Leptolyngbya*, *Oscillatoria* and *Phormidium* have shown difference in their carotenoid patterns e.g. Myxoxanthophyll is strongly light dependent. The percentage of chlorophyll 'a' in comparison to all pigments varies from 30.9 to 82.7%.

STRATEGY FOR SURVIVAL OF CYANOBACTERIA

EPS (a heteropolymer) very widely distributed, it contains repeating units of sugar, acetyl group, peptide group, and sulphate group and uronic acid. EPS often contains D-glucuronic acid, D-galactouronic acid and D-mannuronic acid its carboxy groups binds with metal ions. Cyanobacteria contain EPS in hydrophobic and hydrophilic nature. Presences of hydrophobic groups , ester linked methyl groups ranging up to 12% of RPS dry wt. together with peptides and deoxysugars which also determine the emulsifying properties and the rheological properties [56]. Cohesive gel or in a colloidal form tertiary structure of EPS not only depends on the chemical composition but also strongly on temperature. Cyanobacteria in intertidal mudflats where it also affect cohesiveness and rheological properties of the sediments. Some cyanobacteria are capable of modifying EPS from hydrophobic to hydrophilic and they get detach from colony to surface and sink down in water column when conditions become adverse [57].This phenomenanis also observed in benthic phototrophic diatoms [58]. EPS of Cyanobacteria has protective function against desiccation, grazing and from toxic substances, scavenging of trace metals and (anti-) calcification. It also help cyanobacteria to overcome long periods of drought by forming hydrogen bonds with proteins, membrane, lipids and DNA and replacing the water shell surrounding these cell constituents [59],. The cyanobacterial EPS have following distinct characteristics

(1) The capacity of cell to store glycogen is enough within cell and additional synthesis of polysaccharide excreted as mucilage in old starved cultures.

(2) Most of the polysaccharides in EPS are heteropolysaccharides that are composed of variety of different monosaccharides, arranged in repeating units. RPS often contains uronic acids such as D- glucuronic acid, D-galacturonic acid and D-

mannuronic acid, carboxyl group responsible for interactions with other EPS molecules or the binding of metals. Extra cellular poly meric substances may be hydrophilic or hydrophobic, (hydrophylic charged groups: Uronic acid, Pyruvate) and(Sulfate hydrophobic groups: deoxy-sugar, acetate and peptidic moiety).

(3) Cyanobacteria grouped with respect to type of polymer accumulated in response to osmotic stress [60],[61].

(a) Halotolerant freshwater Cyanobacteria e.g. *Oscillatoria* sp. EPS contains disaccharides sucrose or trehalose).While typical organism in established microbial matcontains trehalose.

(b) Marine Cyanobacteria EPS have the heterocyclicglucosylglycerol: 2-O-α-D glucopyranosyl-glycerole.g..*Microcoleus chthonoplastes* contains glucosylglycerol.

(c) Hypersaline Cyanobacteria accumulate quaternary ammonium compounds (glycine betaine and in one case glutamate betaine) e.g. *Aphanthece halophytica* contains sucrose and betaine.

(4) Although Cyanobacteria normally accumulate a low molecular weight organic compound inresponse to osmotic stress, many species may produce a secondary compound. The synthesis of disaccharide is much faster than Glucosyl glycerol (within 8 h as compare to24- 48h in response to osmotic upshock after storage product pool reached 90% of its maxima) [62].

(5) Betaine may serve as Substrate for Sulfate-reducing bacteria and the product of its metabolism, Trimethylamine (TMA) is known as a substrate for methanogenic bacteria [63].

(6) Microbial mats have often been found to evolve dimethyl sulfide (DMS), sulphur containing organic volatile compound, it is known that DMS can be produced from Dimethyl sulfoniopropionate (DMSP) by microbial activity or by chemical decomposition at high pH [64].

(7) DMSP occurs in number of eukaryotic algae where it most likely function is that it serves as an Osmoprotectant[65] .

CYANOBACTERIA: FOSSIL TO RECENT FORMS

Cyanobacteria are monophyletic group but morphologically classified in to five groups. Representative of all five groups are known from the fossil record. The classification of cyanobacterial fossils is done based on morphology not on their original biochemistry. Two principal processes preserve organic wall cyanobacterial fossils (i) Compression

(ii) Permineralization compression preserve microorganisms occur and pressed and flattened along bedding planes as the sediment lithified in fine-grained detrital sediments such as shales and silt stones.microbes are rarely known from Phanerozoic Eon (Comprised of Paleozoic, Mesozoic and Cenozoic era) when the palaeontologists focus on megascopic fossilized remains.

Phylogeny consideration is based on molecular "clock" by which date time of lineage emergence and closeness might be established. Taxa classified on the basis of morphological and anatomical characteristics also provide time of evolutionary relationship. The molecular clock method uses molecular data by comparing the sequence of aminoacids in proteins of the same families in diverse groups of organisms. It took into account fast and slowly evolving lineages and compared 531 aminoacid sequences in 57 families of enzymatic proteins from 15 major groups of organisms. Their analysis yielded an internally consistent aminoacid based tree in which the branches are all more or less the same length and have a branching order in good agreement with the rRNA Universal tree of life of lineage emergence [66]. Perhaps ancient fossils life originated, become extinct, then originated a second time a ~2000 Ma ago or perhaps, like the rRNA trees, the aminoacid data yield reliable evidence only of the branching order of evolution, not the timing of that branching (Precambrian to Proterozoic Eon).In general, taxa included in (ii) Pleurocapsaceae,(iv) Nostocaceae and (v) Stigonemataceae consistent with biochemically based phylogenies, and monophyletic whereas the cyanobacteria of (i) Chroooccaceae (iii) Oscillatoriaceaewere polyphyletic lineage (In genealogy, a group that is monophyletic consists of all of the descendants of its most recent common ancestor and a polyphyletic group is one in which there are two or more separate groups, each with a separate common ancestor).

(i) Chroococcaceae: family identification chacteristics comprised of predominantly spheroidal, solitary and colonial unicellular Cyanobacteria that reproduced by fission or by budding (e.g. Gloeacapsa). Fossil species record was ~1000Ma old Sukhaya Tunguska formation of Siberia Russia; ~800Ma old bitter Springs formation of Central Australia: ~1500Ma old Satka formation of Bashkiria, Russia and ~775 Ma old Chichkan formation of Siberia, Russia (Precambrian to Proterozoic Eon). (ii) Pleurocapsaceae: family consists of unicellular or pseudofilamentous forms that by multiple fission giverise to small daughter cells known as baeocytes (e.g Pleurocapsa). Fossil species Paleopleurocapsa reniforma compared with Pleurocapsa a petrographc thin section

from the ~775Ma old Chichkan formation of southern Kazakhstan andSkillogalee formation of Australia. It living morphological counterpart Polybessurus bipartitus first reported from other site ~775 Ma old stromatolites of River Wakefield formation of South Australia (Precambrian to Proterozoic Eon). (iii) Oscillatoriaceae: family encompasses uniseriate cyanobacterial filaments that lack cellular differentiation (e.g Oscillatoria and Spirulina). Two techniques confocal laser scanning Microscope (CLSM) and Raman imagery have recently introduced to such studies. Compared to photomicrographa of modern *Oscillatoria* with that of its fossil equivalent *Oscillatoriopsis media* reported in a thin section of chert (an 100 μm thick petrographic thin section) from the ~775 Ma-old chichksn formation of Southern Kazakhstan [67],[68],[69] and ~800 Ma-old Bitter Springs formation of Central Australia (Precambrian to Proterozoic Eon). (iv) Nostocaceae: family includes simple uniseriate filaments that exhibit cellular differentiation in to akinetes and heterocysts (e.g Nostoc). Such differentiated cells Bing first known from the Devonian period of Paleozoic era Rhynine Chert [70]. Nostocaceans are also represented in the Precambrian record by elongate spore like cells such as *Archaeoellipsoides.* Dateback to ~2100Ma ago and closely resemble the reproductive akinetes of extent members of the family [71],[72] (v) Stigonemataceae: family is composed of morphologically more compex heterocystous cyanobacterial filaments that exhibit true branching. Fossil forms of Stigonemataceae was found in ~400Ma (Devonian period of Paleozoic era) old Rhynie chert of Scotland [70]. *Entophysalis belcherensis* ~2100 Ma old fossil of Kasegalik formation of Canada was compared with living *Entophysalis* sp.

There is ample evidence of the reactant of photosynthesis and formation of $CaCO_3$ rich limestones were as result of aqueous reaction between Ca_2^+ derived from weathering of land surface, reaction with bicarbonate (HCO_3^-), produced bydissolution of atmospheric CO_2. The two product of cyanobacterial photosynthesis organic matter and O_2 are also evidenced as Kerogen (organic matter) ~0.5 to ~0.8% by weight was found in fossils [73]. Carbonaceous cell wall and least small amount of O_2 in petrified stata reflected by the occurrence of iron oxide rich sedimentary units known as banded iron formations (BIFs), the world's major source of iron oxide ore during older but not younger than about 2000Ma (Precambrian to Proterozoic Eon) and together with Uranium-rich pyritic conglomerates, provide evidence of the early history of the atmosphere.

EVIDENCE FROM THE ~3.5GA OLD APEX CHERT- FOSSIL RECORD ARE ALSO KNOWN FOR TWO CLASS OF BACTERIA

Bacteria incertae sedis (i) Prokaryotes of uncertain systematic relations

Archaea of the groups (i) Sulphate-reducing bacteria (ii) Methane producing archaens

Beside Cyanobacteria, biochemical components of such microbes are geochemically labile-converted over geological time scale in to coaly kerogen, a geochemically stable complex mix of interlinked polycyclic aromatic hydrocarbons. The Archean fossil microbes were identified from ~3465 Ma-old Apex chert (Precambrian to Proterozoic Eon) of north western of Western Australia [74],[75],[76], [77]. Fossil Specimens of *Primaevifilum conicoterminatum* and *P. amoenum* two of 11 taxa of filamentous microorganism identified based on *sterane* biomarker date to ~2700 Ma ago. The era is well before the great oxidation event of the early Proterozoic and microorganism biomarkers represent strong presumptive evidence of O_2 producing Photoautotrophy during Archean Earth history.

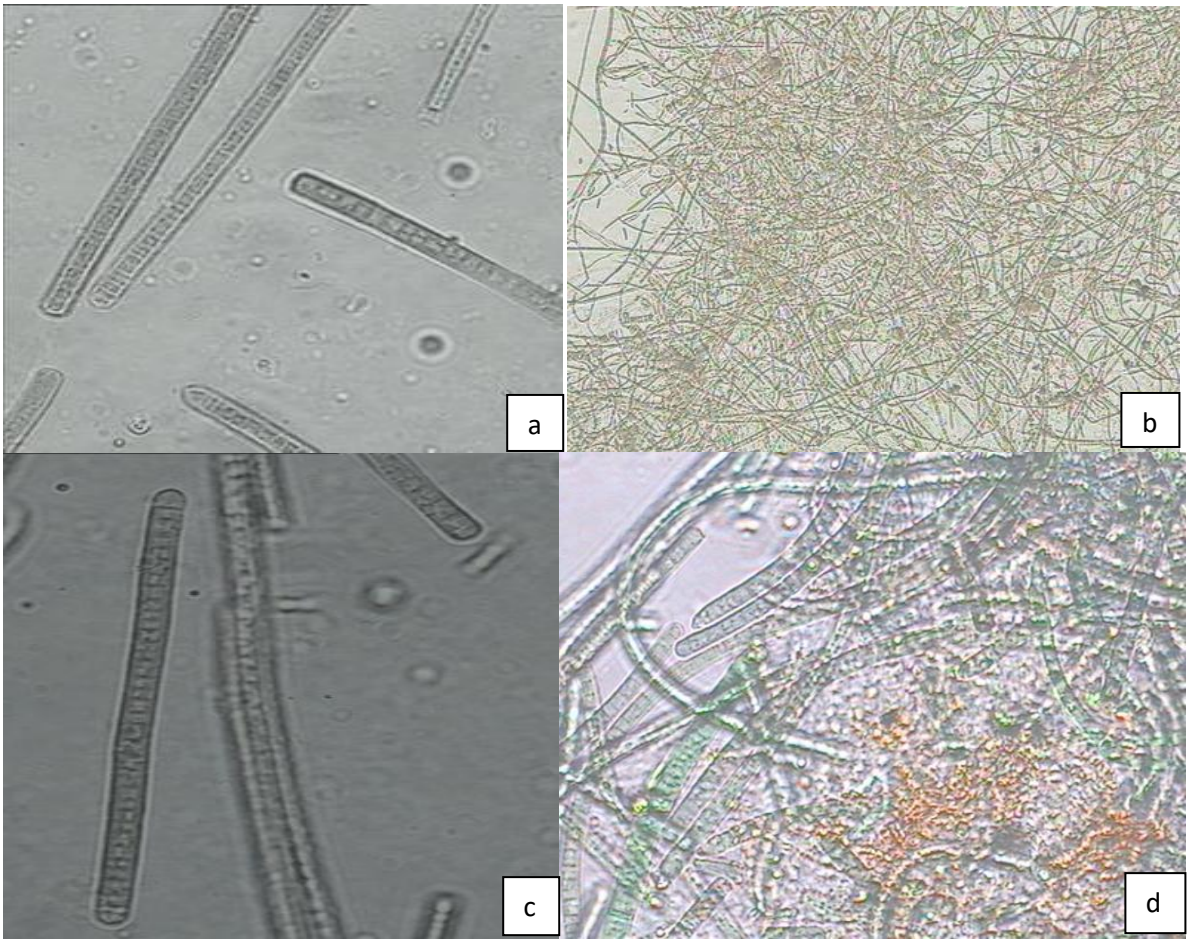

Figure-1: (a) *Phormidium lucidium*(Kutz) Gomant (b) Cyanobacterial mat (c)Akinete of *Phormidium lucidium*(Kutz) Gomant (d) Released Exopolysaccride matrix of Cyanobacteria

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