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Colorless sulfur oxidizing bacteria from diverse habitats

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ABSTRACT

Colorless sulfur oxidizing bacteria comprise an important part of sulfur cycle in nature and hold significant value for biotechnological applications such as, increasing soil fertility, reduction of environmental pollution by biologically oxidizing toxic sulfides present in waste waters from different industries and sewage, leaching of economically important metals from poor ores. Present article reviews diversity of aerobic sulfur oxidizing bacteria in different habitats and some of their applications.

Keywords: Sulfur, Sulfur oxidizing bacteria, Sulfides, Chemolithoautotrophs, *Beggiatoa*, *Thioploca*

INTRODUCTION

Bacteria capable of using inorganic sulfur compounds, including sulfide ($HS^{- \, -}$), elemental sulfur (S^0), thiosulfate ($HS_2O_3^{- \, -}$), and sulfite ($HSO_3^{- \, -}$), as their energy source are known as sulfur bacteria [1]. The sulfur oxidizing bacteria are found in almost every life-supporting environment where reduced sulfur compounds are available [2].

Sulfur oxidizing bacteria consist of two groups: (i) photosynthetic / colored sulfur oxidizing bacteria and (ii) non-photosynthetic / colorless sulfur oxidizing bacteria. Photosynthetic sulfur oxidizing bacteria are pigmented and therefore tend to form coloured masses when present in large numbers and oxidize sulfur anaerobically in presence of light [3, 4]. Non-photosynthetic sulfur oxidizing bacteria oxidize sulfur compounds aerobically using oxygen or sometimes anaerobically using nitrate as terminal electron acceptor [3].To distinguish them from photolithotrophic sulfur bacteria, chemolithotrophic sulfur bacteria are referred to as colorless sulfur bacteria, the adjective"colorless" is used because of the lack of photopigments in these bacteria [1, 2].

Colorless sulfur bacteria have important economic and environmental applications as they enhance nutrient availability in soil, maintain balance of sulfur cycle, oxidize sulfides and thus reduce toxicity and odours of waste waters. These are some of the applications and many more are to be added to the list as the group is still being explored for diversity and applicability for human welfare.

Colorless sulfur oxidizing bacteria

The term colorless sulfur bacteria, was given by Winogradski to denominate prokaryotic organisms that could use reduced inorganic sulphur compounds as energy source [5]. Members of this group can use a variety of reduced sulfur compounds [6]. The group colorless sulfur bacteria, is a very heterogeneous group, many members of which are not closely related to each other or are not related at all [2]. They are ubiquitous in nature and can be found in almost every environment that provides reduced inorganic sulfur compounds. The habitats for the members of this group include: geothermal springs, oceanic geothermal vents, sulfidic cave systems, sulfide-rich industrial sites, sewage sludge, soil, salt marshes, solfataras and cold springs [3, 7]. The group colorless sulfur bacteria, includes both archaebacteria and eubacteria. Sulfur-oxidizing species of archaea are mainly restricted to the order Sulfolobales of Crenarchaeota [2].

Colorless sulfur bacteria are mostly aerobic, but some members of the group are facultative anaerobes, capable of using nitrogen oxides as the terminal electron acceptor in place of oxygen during denitrification including:

Thiobacillus denitrificans, Sulfurimonas denitrificans, species of *Beggiatoa* and *Thioploca*, *Sulfurovum lithotrophicum*, *Thioalkalivibrio* and *Thiohalomonas* [2, 3, 6].

These are usually found within the sulfide/oxygen interfaces of springs, sediments, soil microenvironments, and the hypolimnion, where both reduced inorganic sulfur compounds and oxygen are available. Colonization of the interface is important since both oxygen and sulfide are needed for growth; and sulfide is rapidly oxidized abiotically in aerobic conditions. Sulfide /oxygen interface makes the availability of both the factors possible [2, 3, 8, 9].

They are also diverse regarding the temperature and pH range they occupy. They can be isolated from habitats with temperatures ranging from 4–95^{0}C. Majority of the well studied members are mesophilic [2, 3, 10, 11]. Some thermophilic members are, *Acidithiobacillus caldus*, *Thermothrix thiopara, Thiofaba tepidiphila, Sulfolobus metallicus*, *Sulfurihydrogenibium yellowstonense*, *Acidianus infernus* [12, 13]. Thermophilic members have been isolated from different habitats including: geothermal springs, solfatara fields and marine hydrothermal systems. Archaeal genera *Sulfolobus* and *Acidianus* represent hyperthermophilic colorless sulfur bacteria. Psychrophilic members *Thiomicrospira arctica* and *Thiomicrospira psychrophila* were isolated from marine habitat growing in a temperature range of -2^{0}C to 20.8^{0}C [10].

Colorless sulfur bacteria encompass members thriving at neutral, acidic and alkaline conditions with majority of well-studied members belonging to neutral pH range. Members that have a low pH optimum include *Sulfolobus*, *Thiobacillus acidophilus*, *Acidithiobacillus ferrooxidans, A. albertensis, A. thiooxidans, A. caldus*, *Sulfurisphaera ohwakuensis*, *Acidianus infernus* and *Sulfurococcus* [14, 15]. Alkaliphilic members *Thioalkalimicrobium*, *Thioalkalivibrio* and *Thioalkalispira* were isolated from soda lakes and are halophilic / halotolerant to varying degrees. They cannot grow at pH lower than 7.5 and salt concentration lower than 0.2 M. *Thioalkalivibrio* is better adapted for living in hypersaline conditions. It includes denitrifying, thiocyanate-utilizing and facultatively alkaliphilic species [16]. The colorless sulfur bacteria occur in two main forms, unicellular and filamentous [4].

Filamentous colorless sulfur chemolithotrophic bacteria
Filamentous members have conspicuous morphology and large cell size as compared to other prokaryotes [3, 17] and contain sulfur and nitrate inclusions. The large cell size gives filamentous colorless sulfur bacteria the competitive advantage for obtaining energy source and electron acceptor, in the environmental conditions that they thrive. The several-cm-long filamentous species can penetrate up through the ca 500 µm-thick diffusive boundary layer and may thereby reach into water, to gain access to the electron acceptor, oxygen or nitrate. These bacteria can thrive even in the conditions when reduced sulfur compounds and electron acceptor do not coexist because of their ability to store large quantities of both nitrate and elemental sulfur in the cells [18].

Beggiatoa and *Thioploca* form motile filaments. Motility helps in finding and reaching the microenvironments with optimal nutrient supply. *Beggiatoa* filaments grow as dense mats while *Thioploca* spp. live as bundles of 15–40 µm thick filaments in a common sheath. They normally escape higher oxygen concentrations [18]. Unusually large polyphosphate inclusions have been observed in the marine *Beggiatoa* strain 35Flor [18]. *Thioploca* filaments can penetrate the anaerobic zone to the depth of 19 cm [20]. *Thiothrix* spp. form sessile filaments and live in environments where oxygen and sulfide are mixed in a turbulent flow, with one end of the filament attached to a solid surface. If the flow or the O_2 and H_2S concentrations change, it can release swarm cells (gonidia) from the unattached end of the filament. These swarm cells enable a *Thiothrix* population to survive in changing environments and to effectively spread to new areas. To overcome their lack of motility they often attach to a living animal that lives in a suitable sulfide-rich environment [18].

Unicellular colorless sulfur bacteria
Unicellular colorless sulfur bacteria include rods (*Thiobacillus* spp., *Titanospirillum*), spirilli (*Thiomicrospira*), cocci (*Thiovulum, Thiomargarita*), vibrioid (*Thiospira*), spirochaete (*Spirochaeta perfilievii*) and coccoid/oval (*Sulfurovum lithotrophicum*) members [18, 21, 22]. Majority of the unicellular members are small cells, with a few exceptions such as *Thiomargarita namibiensis, Titanospirillum* and *Thiovulum,* and are Gram negative. *Thiomargarita namibiensis* is the largest of all known sulfur bacteria. It is non-motile and consists of 98% vacuole, thus have much greater storage capacity for nitrate than filamentous members *Thioploca* and *Beggiatoa*. The enormous cell size of *Thiomargarita* is probably an adaptation to survive long periods of unavailability of electron acceptor [18]. Unicellular members can deposit S^0 extracellularly [3, 4]. *Thiovulum* and *Titanospirillum* are fast swimmers and store sulfur intracellularly [23].

Nutritional types of colorless sulfur bacteria

With respect to nutritional requirements colorless sulfur bacteria are quite diverse and flexible. They can be autotrophs, facultative autotrophs, chemolithoheterotrophs or mixotrophs depending on their ability to utilize inorganic and organic energy sources. They can switch nutritional modes depending on the conditions they are exposed to.

Obligate chemolithoautotrophic colorless sulfur bacteria obtain energy by oxidizing inorganic sulfur compounds and use CO_2 as carbon source; they cannot utilize organic compounds as energy source. Members of genera *Thiomicrospira*, *Acidithiobacillus*, *Halothiobacillus*, *Thermithiobacillus*, *Thioalkalimicrobium* and *Thiohalomonas* belong to this category [1, 3, 5]. *Thioalkalivibrio thiocyanoxidans*, *Thioalkalivibrio paradoxus* are alkaliphilic obligate chemoautotrophs [24].

Facultative chemolithotrophs can grow either autotrophically with an inorganic energy source and CO_2, or heterotrophically by utilizing complex organic compounds as both carbon and energy source. Many species of genus *Thiobacillus* are facultative autotrophs including *T. intermedius, T. novellus* (now *Starkeya novella*), *T. acidophilus, T. perometabolis* and *T. versutus* (now *Paracoccus versutus*). Other members include thermophilic *Thiofaba tepidiphila* isolated from hot spring, *Dyella thiooxidans, Pandoraea thiooxidans* isolated from soil [25], acidothermophilic *Thermothrix thioparus* [13], mesophilic halotolerant *Salinisphaera hydrothermalis* [26].

Chemolithoheterotrophs can generate energy from the oxidation of reduced sulfur compounds, but they cannot fix carbon dioxide such as *Titanospirillum, Beggiatoa alba strain B18LD, Leucothrix mucor DSM 2157* [23, 27]. Mixotrophic colorless sulfur bacteria can use inorganic sulfur compounds and complex organic compounds simultaneously for energy and carbon. *Beggiatoa alba strain B18LD*, *Thioploca* [27]. A few colorless sulfur oxidizing bacteria oxidize sulfur but do not gain energy from oxidation, they use sulfur oxidation as a measure against toxic effect of sulfide and harmful oxygen compounds [2].

Habitats of colorless sulfur oxidizing bacteria

In natural habitats, the reduced sulfur compounds are available either as sulfides (including metallic ores) or sulfur. Due to the activities of sulfate-reducing bacteria, especially in anoxic sediments, hydrogen sulfide is most abundant form of inorganic sulfur. The colorless sulfur bacteria are frequently found in the gradients at the interface between anoxic, sulfide-containing areas and aerobic waters and sediments where, at very low oxygen and sulfide concentrations, they can effectively compete with the spontaneous chemical oxidation. They can be isolated from a variety of habitats including soil, sulfur springs, sewage, acid mine drainage water and hydrothermal vents. The most studied examples of colorless sulfur bacteria are from marine habitat especially from hydrothermal vents. Some members are found living as symbionts with invertebrates mostly around vents [2, 8, 9].

Marine habitat

Thiomicrospira is the most frequently encountered isolate from hydrothermal vents. Kuenen and Veldkamp were first to describe the genus *Thiomicrospira*. They isolated *Thiobacillus thioparus* and autotrophic *Thiomicrospira pleophila* from intertidal mud flats of the shallow Dutch Waddenzee and reported that *T. pleophila* have higher sulphide tolerance as compared to *T. thioparus* and occupy different niches in same habitat [28]. New spp. Including, *Thiomicrospira* sp. strain L-12, *Thiomicrospira crunogena*, *Thiomicrospira* strain, MA-3, *Thiomicrospira chilensis*, *Thiomicrospira kuenenii* sp. nov and *Thiomicrospira frisia* sp. nov. were isolated from different sites [29, 30].

A thermotolerant, chemolithomixotrophic strain of *Thiomicrospira* was identified from a deep-sea hydrothermal fumarole in Western Pacific [31]. Species of *Thiomicrospira* have also been found thriving at low temperatures. *Thiomicrospira arctica* sp. nov. and *Thiomicrospira psychrophila* sp. nov. are psychrophilic members of the genus *Thiomicrospira*, isolated from marine Arctic sediments [10]. *Thiomicrospira species (SP-41)* is capable of oxidizing hydrogen along with inorganic sulfur compounds [16].

Obligately chemoautotrophic way of life is rare in the marine environment and biological oxidation of reduced sulfur compounds in open ocean areas is largely carried out by facultatively autotrophic bacteria. The fact is based on the observation of Tuttle and Jannasch 1972, that out of 136 thiobacillus-like isolates they obtained; 95 % were facultative autotrophs. *Sulfurovum lithotrophicum* gen. nov., sp. nov an obligate chemoautotroph was isolated by Inagaki *et al.* [21]. *Acidianus infernus* is an extreme thermophile from hydrothermal vents [15]. *Salinisphaera hydrothermalis* is a mesophilic, halotolerant, facultatively autotrophic sulfur oxidizer from deep-sea hydrothermal vents [26].

Filamentous *Beggiatoa* species are gradient microorganisms which colonize steep oxygen and sulfide gradients near the sediment/water interface. Studies on *Beggiatoa* by Winogradsky, 1887 led to birth of concept of chemoautotrophy. Unusually large polyphosphate inclusions have been observed in the marine *Beggiatoa* strain 35Flor. The inclusions showed a co-occurrence of polyphosphate [19]. Other important filamentous member is *Thioploca. Thioploca* occur in bundles surrounded by a common sheath.

Acidic mine drainage water

Colorless sulfur bacteria also thrive in acidic conditions in drainage waters of coal mines. Some reported members from acidic waters of coal mine include *Thiobacillus perometabolis, Thiobacillus ferrooxidans*, *Thiobacillus thiooxidans, Burkholderia* and *Sulfolobus* [33, 34]. Many of these bacteria have leaching capability and are implicated in bioleaching of metals. *Thiobacillus ferrooxidans* and *Thiobacillus thiooxidans* are well known for their biotechnological applications in bioleaching.

Sulfur springs

Colorless sulfur bacteria can be isolated from sulfidic springs ranging from cold to mesophilic and geothermal hot sulfur springs. *Thiobacillus, Thiomonas* and mat forming filamentous γ-proteobacteria with *Beggiatoa*-like and/or *Thiothrix*-like cells occur in sulfidic springs in Frasassi cave system. *Beggiatoa* populations thrive in microenvironments with slightly lower oxygen availability than *Thiothrix* [35]. *Themothrix azorensis* an obligately chemolithoautotrophic, thermophile growing in temperature range of 63 to 86^0C, was isolated from a hot spring [36]. *Thiomicrospira psychrophila*, *Thiobacillus* and *Halothiobacillus* sp. strain RA13 were reported from Gypsum Hill and Colour Peak sulfur springs; *Thiomicrospira* was dominant in sediment microbial communities as indicated by DNA based analysis [37, 38]. *Gulbenkiania indica* sp. nov., was reported from a sulfur spring from Athamallik, Orissa [39].

Psychrophilic isolates of *Thiomicrospira* sp., *Sulfuricurvales* and *Sulfurovumales* were obtained from springs located in Borup Fiord Pass, Ellesmere Island; the isolates deposit S^0 extracellularly [40]. Genus *Sulfolobus* was discovered from hot springs and is a thermophilic, acidophilic, facultative autotroph [12]. *Thermothrix thioparus*, a neutrophilic thermophile; capable of depositing sulfur extracellularly and oxidizing sulfur compounds anaerobically using nitrate, was recovered from a New Mexico hot spring [13]. *Sulfurihydrogenibium yellowstonense* sp. nov., is an extremely thermophilic, facultatively heterotrophic sulfur oxidizer recovered from Yellowstone National Park [41]. Occurrence of *Sulfurovum-like* spp. with *Thiothrix* and *Thiofaba* spp. was reported from sulfur springs in USA [42].

Sulphide concentration in the environment also affects diversity of colorless sulfur bacteria. Based on molecular diversity analysis it was evident that *Chloroflexus* was the dominant mat organism in the low-sulfide spring (1 mg / liter) below 70°C and *Aquificales* were dominant in the high-sulfide spring (12 mg / liter) at the same temperature [43].

Soil

Sulfur oxidizing bacteria are crucial to sulfur cycling in soils. They convert inorganic species of sulfur that cannot be used by plants into the forms that are utilized by plants. Colorless sulfur bacteria hold their importance in this habitat also and their diversity and potential applications are being explored. Sulfur oxidizers *Dyella*, *Burkholderia*, *Alcaligenes*, *Microbacterium*, *Leifsonia* and *Pandoraea* have been identified from rhizosphere soils [44, 45].

Applications of colorless sulfur oxidizing bacteria

Waste treatment

Reduced sulfur compounds can occur in industrial wastes in a variety of forms and from a variety of sources. Reduced sulfur compounds present a problem both environmentally, because of their toxicity, and socially, because of their odour. Colorless sulfur bacteria occur in many sewage treatment systems and, in fact, are inadvertently used to oxidize reduced sulfur compounds in the waste water. The end products (sulfur or sulfate) are not hazardous, and sulfate can be discharged directly into the sea or into brackish estuaries (which already are so high in sulfate that the discharge is insignificant) [2]. The potential of activated sludge for the remediation of sludge treatment of sulphur-rich wastewater such as dilute acid mine drainage mixed with municipal wastewater was investigated. A pilot-scale activated sludge plant operated as a flow-through unit; was acclimatised to a low load of sulphide. It was proposed that acclimatisation occurs by changes to the microbial community and is responsible for increased sulphide removal efficiency of the acclimated pilot plant sludge. This pilot plant, being the flow-through system, prevents the process liquor from becoming too acidic and requires no process control to avoid acidic conditions or elevated salt concentrations in the process liquor, as the influent municipal wastewater is slightly alkaline. Therefore there is a potential use for this scheme in remediation of sulphur- rich wastewater added to the influent, by normal activated sludge plants [46].

Bioleaching of metals
Bacterial leaching is used in the recovery of metals from ores that are too poor for conventional metallurgical extraction methods. The mobilization of metal cations from insoluble ores by biological oxidation and complexation processes is termed as bioleaching. Bioleaching technique is mainly employed for extraction of the metals including copper, cobalt, nickel, zinc, and uranium. The predominant leaching bacteria are extremely acidophilic bacteria, thriving at pH values lower than 3. The classical leaching bacteria belong to the genus *Acidithiobacillus* and include *A. thiooxidans*, *A. ferrooxidans* and *A. caldus*. All leaching archaebacteria belong to the order Sulfolobales, including thermophilic genera such as *Sulfolobus*, *Acidianus*, *Metallosphaera*, and *Sulfurisphaera*. *Acidianus* spp. and *A. ferrooxidans* are capable of reducing elemental sulfur during anaerobic hydrogen oxidation (Rohwerder *et al*., 2003). *Acidithiobacillus thiooxidans* named Licanantay strain DSM 17318 was patented for bioleaching processes for sulfured copper minerals [47].

Application in agriculture
Sulphate is the form of sulfur that is utilized by plants and the transformation from inorganic sulphide and other sulfur species to sulphate in soils is primarily brought about by sulfur oxidizing bacteria. Also this transformation is followed by decrease in pH that is development of acidic conditions which helps in solubilization of others nutrients such as phosphate, which can be then utilized by plants. These facts make importance of sulfur oxidizing bacteria in soils evident. *Thiobacilli* play an important role in sulfur oxidation in soil [48]. Vidhyasri and Sridar [49] developed a carrier based formulation of sulphur oxidizing bacteria for enhancing the productivity of crops requiring sulphur nutrition.

Co-inoculation of clay-based pellet formulation of the *Thiobacillus sp.* strain LCH with Rhizobium results in enhanced yield and oil content in groundnut under. Same inoculation in S-deficit soil increased the soil available sulfur [50].

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