Oxidation of Thiosulfate by a New Bacterium, *Bosea thiooxidans* (strain BI-42) gen. nov., sp. nov.: Analysis of Phylogeny Based on Chemotaxonomy and 16S Ribosomal DNA Sequencing

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A gram-negative bacterium which was capable of oxidizing reduced inorganic sulfur compounds was isolated from agricultural soil and designated BI-42. This new isolate grew on a wide range of organic substrates but was not able to grow autotrophically and lacked ribulose 1,5-bisphosphate carboxylase, a key enzyme of carbon dioxide fixation. These results suggested that strain BI-42 was a chemolithoheterotroph. Ammonia and nitrate were not used as sole nitrogen sources for growth, and strain BI-42 lacked glutamate synthase activity, which resulted in glutamate auxotrophy. The glutamate dehydrogenase activity of this organism was apparently insufficient for ammonia assimilation. On the basis of the results of additional biochemical tests, the G+C content of the DNA, the results of a respiratory ubiquinone analysis, the results of a 16s ribosomal DNA sequence analysis, the fatty acid composition, and the results of a membrane lipid analysis, strain BI-42 was identified as a phylogenetically and physiologically distinct taxon belonging to the alpha subclass of the *Proteobacteria*. *Bosea thiooxidans* gen. nov., sp. nov. is the name proposed for this taxon.

Because of the potential importance of chemolithoheterotrophs in soil, attempts were made to isolate chemolithoheterotrophic bacteria from soil by enrichment culture techniques. A single strain was isolated from an agricultural field soil, and this strain was designated BI-42T. Strain BI-42 oxidizes reduced inorganic sulfur compounds only in the presence of some organic substrates. In this paper we describe the isolation of this organism, its morphological and biochemical characteristics, its phylogenetic position based on the results of a 16S ribosomal DNA (rDNA) sequence analysis, its chemotaxonomic properties, and its mode of thiosulfate utilization. In addition, we studied the properties of the nitrogen-metabolizing enzymes of strain BI-42, including glutamine synthetase (GS), glutamate dehydrogenase (GDH), and glutamate synthase (GOGAT), in order to characterize the glutamate auxotrophy of this organism.

**MATERIALS AND METHODS**

**Chemicals.** All of the chemicals used were analytical grade and were purchased from Sigma Chemical Co., St. Louis, Mo., E. Merck, Darmstadt, Germany, and SRL Pvt., Ltd., Bombay, India. Yeast extract, tryptone and agar-agar were obtained from Difco Laboratories, Detroit, Mich., and Dowex-I-chloride (50-100 dry mesh) was obtained from Aldrich Chemical, Inc. NaH14CO3 was purchased from Bhabha Atomic Research Centre, Trombay, India.

**Enrichment and isolation.** Soil samples were collected from different agricultural fields around Calcutta, India. The soil samples (25 g) were moistened with 5 ml of sterile distilled water and enriched by adding sodium thiosulfate (100 mg), sodium sulfite (50 mg), or elemental sulfur (25 mg). After thorough mixing, the preparations were incubated in petri dishes at 30°C for 10 days. Further enrichment was carried out in mineral salts broth (pH 8.0) supplemented with phenol red (0.02 g/liter) and either Na2S2O3 · 5H2O (5 g/liter) or thiosulfate plus yeast extract (5 g/liter). Portions (1 g) of the enriched soil samples were transferred into 250-ml conical flasks containing 50 ml of enrichment medium, and the resulting preparations were incubated in a gyratory water bath shaker (model G76; New Brunswick) at 220 rpm and 30°C. After 2 days of incubation, one flask turned yellow, indicating that acid was formed. Serial dilutions of the contents of this flask were plated onto mineral salts-thiosulfate agar and onto mineral salts-thiosulfate-yeast extract agar plates. These colonies were purified by repeated streaking on the same medium. Thus, a purified culture was obtained, and this culture was designated strain BI-42.

**Medium and growth conditions.** The mineral salts medium contained (per liter) 4.0 g of NaHPO4, 1.5 g of KH2PO4, 0.1 g of MgCl2 · 6H2O, 1.0 g of...
NH₄Cl, and 2 ml of a trace metal solution (53). The pH was adjusted to 8.0 with 4 N NaOH. Glutamate-yeast-extract-mineral salt (GYM) medium (per liter) contained 4.0 g of NaH₂PO₄, 1.25 g of KH₂PO₄, 0.1 g of MgCl₂-6H₂O, 0.5 g of sodium glutamate, and 0.1 g of yeast extract; the pH of this medium was 8.0. GYM medium was used as the basic medium unless stated otherwise. Mixed-substrate medium was GYM medium supplemented with Na₂SO₄, H₂O, and an organic substrate. The media were sterilized by autoclaving them at 103 kPa for 15 min.

For solid media 20.0 g of agar per liter was added.

The denitrifying activity of strain BI-42 was determined under microaerobic conditions by adding KNO₃ (1.0 g/liter) to GYM medium containing organic substrates (5 g/liter) or thiosulfate (5 g/liter) or both. Inverted Durham tubes were placed in the culture media to determine whether gas was formed. Whether anaerobic growth occurred, was determined with the BBL GasPak system (Becton Dickinson and Co., Cockeysville, Md.). Crossed-pool aerography was performed as described by Holliday (10). All other routine biochemical tests and procedures were performed as described previously (3, 43).

Utilization of amino acids as sole nitrogen sources or sole nitrogen and carbon sources was determined in mineral salts medium lacking NH₄Cl. Utilization of organic compounds other than amino acids was determined in GYM medium containing substrates at concentrations of 1 to 5 g/liter.

Utilization of inorganic sulfur compounds was determined in GYM medium containing thiosulfate or both thiosulfate and succinate.

For the GS, GDH, and GOGAT assays cells were grown in GYM medium supplemented with sodium acetate (10 g/liter). NH₄Cl (1 g/liter) was added at the mid-log phase for induction, and the preparations were incubated for an additional 3 h. Ribulose 1,5-bisphosphate (RuBP) carboxylase activity was assayed by using intact cells of exponential-phase cells grown in GYM medium supplemented with thiosulfate or both thiosulfate and succinate.

Flagella staining and electron microscopy. The presence of flagella was determined by using cells that were negatively stained with 2% phosphotungstic acid (pH 6.5). The flagella were observed on a carbon-coated grid (300 mesh; diameter, 3 mm) and examined with a JEOL model JEM 200 CX electron microscope at an accelerating voltage of 80 kV (36).

Susceptibility tests. Antibiotic resistance and the MICS of different antibiotics were determined as described.

The MIC of 5-fluorouracil (5-FU) was determined by making a series of 10-fold dilutions in GYM medium with 10 ml of exponentially growing cells was treated with cetyltrimethylammonium bromide (0.1 g/liter) and then shaken thoroughly for 3 min. The treated cultures were sonicated immediately at 4°C. After sonication, the resulting suspensions were washed and resuspended in 1 ml of an ice-cold KCl solution (10 g/liter). These cell suspensions were used for the GS activity assay.

Enzyme assays. GDH activity was measured by the method of Maulick and Ghosh (26). The 1 ml reaction mixture used for the NADH-dependent assay contained the following: 0.1 M Tris-HCl buffer (pH 8.5), 50 mM NaHCO₃, 0.5 mM NADH, and 0.1 mM NADP, and the cell extract. The assay was performed at 30°C by measuring the rate of oxidation of NADPH at 340 nm with a Shimadzu UV-visible recording spectrophotometer (model UV 240). Similarly, the NADH-dependent GDH activity was measured by replacing NADPH with 1 mM NADH and increasing the concentration of 2-oxoglutarate to 10 mM. After incubation for 3 min at 30°C, the reaction was stopped by adding 6.5 ml of 100 mM NaOH, and the A₅₆₂nm was determined. The oxidative deamination of glutamate by GDH was assayed by measuring the formation of NADPH at 340 nm by using an assay mixture containing 100 mM Tris-HCl (pH 6.8), 25 mM glutamate, and 0.5 mM NADP in a final volume of 1 ml.

GOGAT activity was measured by using 2-ketoglutarate and determining glutamine-dependent oxidation of NADPH as described by Meers et al. (27). GS activity was measured by the y-glutamyl transferase method described by Miller et al. (28). In every case, the y-glutamyl transferase activities in the presence and absence of 60 mM MgCl₂ were measured to determine the active state of the enzyme. The reaction mixture was incubated for 10 min at 30°C, and the amount of y-glutamyl hydroxamate formed was determined at 535 nm by using a reagent blank for comparison. Specific activity was expressed as the amount of enzyme which catalyzed the formation or disappearance of 1 μmol of product or substrate per minute.

The RuBP carboxylase activity in the cell extract was determined as described by Kelly et al. (16). The final volume of the assay mixture, which contained cell extract (0.1 to 0.4 g of protein), was 0.3 ml. The reaction was initiated with RuBP and was terminated after 0.5, 1, 1.5, 2, 3, and 4 min by adding 0.2 ml of acetic acid. Zero-time and RuBP-free controls were included. Each reaction mixture was dried in its vial, 5 ml of scintillation fluid, which contained 10 g of 2,5-di-phenyloxazole per liter, 0.25 g of 1,4-bis(5-phenyl-2-oxazolyl)benzene (POPOP) per liter, and 100 g of naphthalene per liter in 1,4-dioxane, was added, and 14CO₂ incorporation was determined by a liquid scintillation counter.

Analytical methods. DNA base composition was determined by the thermal denaturation method of Marmur and Doty (25). The growth of cells was monitored by measuring optical density at 600 nm. Protein contents were estimated by using the method of Lowry et al. (22) and bovine serum albumin as the standard. The concentrations of thiosulfate and tetrathionate in culture filtrates were determined as described by Kelly et al. (15). The sulfate content was determined by the method of Truper and Schlegel (49), as modified by Suzuki and Silver (45). The sulfate content was determined by the method of Berglund and Silver (45). The sulfite content was determined by the method of Marmur and Doty (25). The growth of cells was monitored by monitoring cell concentrations by measuring optical density at 600 nm. Protein contents were estimated by using the method of Lowry et al. (22) and bovine serum albumin as the standard. The concentrations of thiosulfate and tetrathionate in culture filtrates were determined as described by Kelly et al. (15). The sulfate content was determined by the method of Truper and Schlegel (49), as modified by Suzuki and Silver (45). The sulfate content was determined by the method of Berglund and Silver (45). The sulfite content was determined by the method of Marmur and Doty (25). The growth of cells was monitored by monitoring cell concentrations.
RESULTS

Morphological and biochemical features of strain BI-42. Colonies of the organism which we isolated grown on Luria agar or on thiosulfate-yeast extract agar were circular, 1 to 1.5 mm in diameter, smooth, mucoid, round, and creamy colored. Single colonies appeared within 4 days at 30°C. The cells stained gram negative and were motile, rod shaped, 0.85 μm wide, and 1.4 to 1.6 μm long. The cells occurred mostly singly, did not form spores, and were motile by means of a single polar flagellum (Fig. 1). Cells grown on GYM medium containing thiosulfate and yeast extract or on mixed-substrate agar containing thiosulfate and succinate did not form sulfur deposits on the colony surfaces. The isolate which we obtained was designated BI-42.

Strain BI-42 was not able to grow without small amounts of yeast extract when sugars, amino acids, and tricarboxylic acid cycle intermediates were used as the sole sources of carbon and energy. Crossed-pool auxanography revealed that nicotinic acid (0.001 g/liter) partially replaced the requirement for 0.1 g of yeast extract per liter. Strain BI-42 also was not able to grow in a chemically defined medium containing the inorganic nitrogen compounds NH₄Cl, KNO₃, and (NH₄)₂SO₄ as sole nitrogen sources. Growth was observed when these nitrogen compounds were replaced by glutamate (0.5 g/liter). These observations led to the formulation of GYM medium.

Strain BI-42 did not grow anaerobically in the presence or absence of nitrate with any of the substrates tested. However, under microaerobic conditions, strain BI-42 formed gas in GYM medium containing malate, succinate, glucose, or sucrose. When thiosulfate was added to the media, gas was not produced. The gas produced was not absorbed by NaOH. Thus, the gas was identified as N₂ or N₂O, the products of denitrification. Strain BI-42 exhibited catalase, oxidase, and nitrate reductase activities and could grow on Simmons citrate agar and MacConkey agar. Methyl red, urease, starch hydrolysis, indole production, H₂S production, Voges-Proskaeur, gelatin hydrolysis, and pigment production tests were negative. The optimum temperature for growth was 30 to 32°C. The pH range for growth was 6.0 to 9.0, and the optimum pH was 7.5 to 8.0.

Utilization of organic compounds. Glutamate, glutamine, proline, cysteine, aspartic acid, serine, asparagine, alanine, and lystine were used as both nitrogen and carbon sources, while arginine and histidine were used as nitrogen sources. In contrast, leucine, glycine, isoleucine, methionine, tyrosine, tryptophan, and phenylalanine did not support growth.

Strain BI-42 grew heterotrophically in GYM medium supplemented with glucose, fructose, rhamnose, xylose, sorbose, ribose, galactose, citrate, gluconate, acetate, pyruvate, arabinose, succinate, and malate. Glycerol, raffinose, mannitol, formate, lactate, glyoxylate, propionate, salicylate, butyrate, cyclohexanol, p-aminobenzoate, and methanol did not support the growth of this organism.

Growth and oxidation of sulfur compounds. In GYM medium supplemented with thiosulfate the growth yield of strain BI-42 was almost the same as the growth yield in GYM medium alone. No stimulation of growth occurred, although a considerable amount of thiosulfate was consumed (data not shown). However, marked stimulation of growth was observed when GYM medium was supplemented with sodium succinate in addition to thiosulfate. The growth yield varied with the concentration of thiosulfate (Fig. 2); the greatest growth (A₆₆₀: 1.2 to 1.3) was observed at a concentration of 5 g/liter. Under these conditions, conversion of thiosulfate to sulfate was stoichiometric, and the pH of the medium decreased from 8.0 to 6.6 (Fig. 3). Thiosulfate added to the medium was almost produced. The gas produced was not absorbed by NaOH. Thus, the gas was identified as N₂ or N₂O, the products of denitrification. Strain BI-42 exhibited catalase, oxidase, and nitrate reductase activities and could grow on Simmons citrate agar and MacConkey agar. Methyl red, urease, starch hydrolysis, indole production, H₂S production, Voges-Proskaeur, gelatin hydrolysis, and pigment production tests were negative. The optimum temperature for growth was 30 to 32°C. The pH range for growth was 6.0 to 9.0, and the optimum pH was 7.5 to 8.0.
entirely consumed within 36 h. Interestingly, the pH of the medium increased after 36 to 40 h of growth. Like thiosulfate, tetrathionate also stimulated growth in the presence of succinate, but NaSCN, Na,SO₄, and Na₂SO₄ inhibited growth (data not shown).

CO₂ fixation. No RuBP carboxylase activity was detected in strain BI-42.

Susceptibility to antibiotics. The MICs of several antibiotics for strain BI-42 were determined. Growth of this organism was not inhibited even at a concentration of 200 µg/ml. Ampicillin did not inhibit growth even at a concentration of 200 µg/ml. NADPH was added to a concentration of 0.1% during the exponential phase of growth. The preparation was incubated for 3 h, and then the enzyme activities were measured. The GS activity measured in the presence of both Mn²⁺ and Mg²⁺. NADP+- and NADH-dependent GDH activities were not detected. However, considerable activity in the assimilatory direction was observed when NADPH was the cofactor. Addition of ammonium chloride did not influence the GDH activity (Table 1). GOGAT activity was not observed in this organism.

DNA base composition. The G+C content of the DNA of strain BI-42 was 68.2 mol%.

Ubiquinones. Ubiquinone was the sole respiratory quinone present. The major ubiquinone contained 10 isoprenoid units (ubiquinone 10).

Fatty acid composition. The cellular fatty acid composition of strain BI-42 is shown in Table 2. The fatty acids identified were the saturated straight-chain acids C₁₂:0, C₁₆:0, C₁₇:0, C₁₈:0, and C₁₉:0 10-methyl; the unsaturated straight-chain acids C₁₆:1 ω7c, C₁₇:1 ω8c, and C₁₈:1 ω7c; and the nonhydroxy acids C₁₇:1 cyclopropane and C₁₉:1 ω8c. cis-Octadec-9-enoic acid (C₁₈:1 ω7c) was the predominant compound among the other nonhydroxy acids. The major hydroxylated fatty acids found were C₁₅:0 3-OH, C₁₆:0 3-OH and C₁₇:0 3-OH.

Hydroxyacids. 3-Hydroxyoctadecanoic acid, 3-Hydroxyheptadecanoic acid, and 3-Hydroxyheptadecanoic acid were detected. Hydroxyacids were the saturated straight-chain acids C₁₅:0, C₁₆:0, C₁₇:0 10-methyl; the unsaturated straight-chain acids C₁₆:1 ω7c, C₁₇:1 ω8c, and C₁₈:1 ω7c; and the nonhydroxy acids C₁₇:1 cyclopropane and C₁₉:1 ω8c. cis-Octadec-9-enoic acid (C₁₈:1 ω7c) was the predominant compound among the other nonhydroxy acids. The major hydroxylated fatty acids found were C₁₅:0 3-OH, C₁₆:0 3-OH and C₁₇:0 3-OH.

Polar lipids. The polar head groups consisted of phosphatidylglycerol, phosphatidylethanolamine, phosphatidylcholine, diphosphatidylglycerol, and an unidentified amino lipid.

Phospholipids. The phospholipids found in strain BI-42 were phosphatidylglycerol, phosphatidylethanolamine, phosphatidylcholine, diphosphatidylglycerol, and an unidentified amino lipid.

Sulfur compounds (µg atoms of S/ml)

![Sulfur compounds graph](image)

FIG. 3. Time course of utilization of thiosulfate (C), release of sulfate (△), and change in pH (inset) during growth of strain BI-42 in GYM medium containing thiosulfate (5.0 g/liter) and sodium succinate (5.0 g/liter).

**TABLE 1.** Effect of NH₄⁺ on GS, GDH, and GOGAT activities of strain BI-42

<table>
<thead>
<tr>
<th>Addition to medium</th>
<th>Sp act (mol/min/mg of protein)</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>GS</td>
</tr>
<tr>
<td></td>
<td>Mn²⁺</td>
</tr>
<tr>
<td>None</td>
<td>1,347</td>
</tr>
<tr>
<td>NH₄⁺</td>
<td>827</td>
</tr>
</tbody>
</table>

* NH₄⁺ was added to a concentration of 0.1% during the exponential phase of growth. The preparation was incubated for 3 h, and then the enzyme activities were determined.
or mixotrophic growth conditions (19). However, it has also been reported that *Thiobacillus* sp. strain Q (8) and *C. thiocyclus* (39) oxidize sulfur compounds to yield metabolically useful energy under lithotrophic growth conditions. In this context, the stimulation of strain BI-42 growth by thiosulfate observed in an organic culture medium is very similar to the chemolithotrophic growth of *Thiobacillus* sp. strain Q described by Gommers and Kuenen (8).

The following major physiological characteristics of strain BI-42 distinguish it from similar gram-negative bacteria, including *Thiobacillus novellus* (13), *Thiobacillus versutus* (46), *Thiobacillus* sp. strain Q (8), *Thiosphaera pantotropha* (32), *Pseudomonas aeruginosa* (35), *Achromobacterbutzeri* (41), and *Pseudomonas* sp. strain 16B (50), which are capable of oxidizing inorganic sulfur compounds: (i) strain BI-42 cannot grow in chemically defined medium containing ammonia or nitrate as the sole nitrogen source; (ii) strain BI-42 requires trace amounts of yeast extract as a growth factor; and (iii) strain BI-42 is autotrophic for glutamate.

A large number of organic compounds supported heterotrophic growth of strain BI-42 but this organism was not able to utilize aromatic compounds and alcohol. Unlike *Thiobacillus* sp. strain Q (8), strain BI-42 grown on mixed-substrate agar did not produce sulfur deposits on the colony surfaces. Even though both strain BI-42 and *Thiobacillus versutus* (46) denitify under heterotrophic growth conditions, the absence of denitrification under mixed-substrate growth conditions differentiates strain BI-42 from *Thiosphaera pantotropha* and *Thiobacillus versutus* (32). This may be due to the inhibitory effect of thiosulfate for denitrifying activity under mixed-substrate growth conditions.

Despite the presence of an assimilatory GDH, strain BI-42 was not able to grow in culture medium containing ammonia as the sole nitrogen source. Thus, the assimilatory GDH may not have been sufficient for assimilation of ammonia.

The fatty acid composition of BI-42 was distinct from the fatty acid compositions of other autotrophic and facultatively chemolithoautotrophic sulfur oxidizers (14). The uniqueness of this isolate was supported by the presence of hydroxy fatty acids along with 10-methyl and cyclic fatty acids, which are not found in any other species belonging to the alpha subclass of the class *Proteobacteria* (4, 23, 33).

The respiratory quinone present in strain BI-42 was a ubiquinone with 10 isoprenoid units (ubiquinone 10), which indicates that this organism is closely related to members of the alpha subclass of the *Proteobacteria*. The lipids of the polar head groups of strain BI-42 were not unique but were similar to those found in the obligate or restricted facultative methylotrophs (11). The presence of ubiquinone 10 and phosphatidylcholine and the high level of the unsaturated nonhydroxy fatty acid C<sub>18:1</sub> ω7C resembles characteristics of the genus *Methylobacterium* (9, 11).

Oxidation of thiosulfate in GYM medium was gratuitous since it did not increase the growth yield. Despite thiosulfate oxidation, the low cell yield clearly indicated that like other chemolithoheterotrophic sulfur oxidizers, strain BI-42 could not assimilate carbon dioxide (8, 31). The failure to detect RuBP carboxylase is consistent with this conclusion. In contrast, the increased growth yield obtained with thiosulfate and succinate implies that thiosulfate oxidation is used to enhance heterotrophic carbon assimilation. Under these growth conditions, the stoichiometry for thiosulfate oxidation to sulfate by strain BI-42 is very similar to the stoichiometry reported for *Thiobacillus thioparus* (52) and *Thiobacillus novellus* (34).

As determined by a 16S rDNA sequence analysis, biochemical tests, and a chemical composition analysis, strain BI-42 represents a novel genus and species in the alpha subclass of the *Proteobacteria*, for which the name *Bosea thiooxidans* is proposed.

**Description of Bosea gen. nov. Bosea** (Bos' e.a. M. L. gen. n. *Bosea*, of J. C. Bose the founder of the Bose Institute, where the organism was isolated). Cells are gram-negative rods that occur mostly as single cells. Strictly aerobic. The optimum temperature for growth is 30 to 32°C. No growth occurs at temperatures below 20°C and above 37°C. Oxidase and catalase positive. Reduced inorganic sulfur is oxidized in the presence of organic carbon sources. No autotrophic growth occurs.

Phosphatidylglycerol, phosphatidylethanolamine, phosphatidylcholine, diposphatidylglycerol, and an amino lipid are the major lipid constituents of the polar head groups. The abundant fatty acids are cis-octadec-9-enoic acid (C<sub>18:1</sub> ω7C), cis-cyclo-10,11-methylene octadecanoic acid (C<sub>18:0</sub> cyclo ω8C), and hexadecenoic acid (C<sub>16:1</sub>). Hydroxylated fatty acids are also present. A 16S rDNA sequence analysis of strain BI-42 revealed that the genus branches intermediate to the genus *Methylobacterium*, the genus *Beijerinckia*, *R. palustris*, and related taxa. The type species is *Bosea thiooxidans*.

**Description of Bosea thiooxidans** sp. nov. *Bosea thiooxidans* (thio.o'xi.dans. Gr. n. thion, sulfur; M.L.v. oxido, make acid, oxidize; M.L. part. adj. thiooxidans, oxidizing sulfur). This bacterium was isolated from agricultural soil. Cells are straight rods that are 0.85 μm wide by 1.4 to 1.6 μm long. Cells occur singly. Motile by means of a single polar flagellum. Strictly aerobic. Spores are not formed. Colonies on agar containing thiosulfate and succinate or yeast extract are smooth, mucoid, round, and cream colored; these colonies are about 1 to 1.5 mm in diameter after 4 days of incubation. No sulfur deposition occurs on the colony surfaces. Glutamate, glutamine, and aspartate, but not NH₄⁺, NO₃⁻, and urea, can serve as nitrogen sources. This organism can denitrify and produce gas only in heterotrophic growth medium containing nitrate. It has glutamate autotrophy and requires yeast extract (0.1 g/liter) as a
growth factor. The pH range for growth is 6.0 to 9.0, and the optimum pH is 7.5 to 8.0. A variety of organic compounds support heterotrophic growth in GYM medium. These compounds include glucose, fructose, rhamnose, xylose, sorbose, ribose, arabinose, galactose, citrate, gluconate, succinate, malate, acetate, glutamate, glutamine, proline, cysteine, aspartic acid, serine, asparagine, alanine, lysine, common hexoses, pentoses, and organic acids, pyruvate, and some amino acids.

This species is a chemolithoheterotroph. Thiolsulfate stimulates growth in the presence of succinate. Tetrathionate is not support growth. The pH range for growth is 6.0 to 9.0, and the ubiquinone.

REFERENCES