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EXPERIMENTAL ARTICLES

Physiology of Organotrophic and Lithotrophic Growth of the Thermophilic Iron-Reducing Bacteria *Thermoterrabacterium ferrireducens* and *Thermoanaerobacter siderophilus*

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Abstract—Growth physiology of the iron-reducing bacteria *Thermoterrabacterium ferrireducens* and *Thermoanaerobacter siderophilus* was investigated. The stimulation of the organotrophic growth of *T. ferrireducens* and *T. siderophilus* in the presence of Fe(III) was shown to be due to the utilization of ferric iron as an electron acceptor in catabolic processes and not to the effect exerted on the metabolism by Fe(II) or by changes in the redox potential. It was established that Fe(III) reduction in *T. ferrireducens* is not a detoxication strategy. In *T. siderophilus*, this process is carried out to alleviate the inhibitory effect of hydrogen. *T. ferrireducens* was shown to be capable of lithoautotrophic growth with molecular hydrogen as an electron donor and amorphous ferric oxide as an electron acceptor, in the absence of any organic substances. The minimum threshold of H_2 consumption was 3×10^{-5} vol % of H_2. The presence of CO dehydrogenase activity in *T. ferrireducens* suggests that CO_2 fixation in this organism involves the anaerobic acetyl-CoA pathway. *T. siderophilus* failed to grow under lithoautotrophic conditions. The fact that *T. ferrireducens* contains *c*-type cytochromes and *T. siderophilus* lacks them confirms the operation of different mechanisms of ferric iron reduction in these species.

Key words: dissimilatory Fe(III) reduction, thermophilic microorganisms, lithoautotrophic growth, *Thermoterrabacterium ferrireducens*, *Thermoanaerobacter siderophilus.*

Microorganisms that reduce inorganic electron acceptors under anaerobic conditions represent an important link of the biogeochemical carbon cycle in diverse ecosystems. Prokaryotes inhabiting thermal niches include organisms that reduce nitrates, CO_2, and various Mn(IV), Fe(III), and sulfur compounds [1].

Fe(III)-reducing thermophiles are widespread in the sediments of hot freshwater springs [2, 3], in deep marine hydrotherms [4], and in the subterranean hydrosphere [5, 6]. The functions of thermophilic iron reducers in microbial communities are still poorly understood; so far, the data on their growth and metabolic properties are confined to the information given in the works describing new taxa [7–10].

The goal of this work was to elucidate the mechanism of the influence of Fe(III) on the organotrophic growth of thermophilic iron-reducing microorganisms and to examine their capacity to grow lithoautotrophically. The subjects of our study were the iron-reducing bacteria *Thermoterrabacterium ferrireducens* [9] and *Thermoanaerobacter siderophilus* [10].

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MATERIALS AND METHODS

Microorganisms. *Thermoterrabacterium ferrireducens* (DSM 11255) and *Thermoanaerobacter siderophilus* (DSM 12299) were obtained from the Deutsche Sammlung von Mikroorganismen und Zellkulturen (Braunschweig, Germany).

Medium composition and cultivation conditions. Microbial cultures used in studies on the Fe(III) effect on organotrophic growth were maintained in an earlier described [9] anaerobic medium with 90 mM amorphous Fe(III) oxide under a gas phase of 100% CO_2. The main carbon and energy sources were peptone (10 g/l) or glycerol (3 g/l) for *T. ferrireducens* and peptone (10 g/l) for *T. siderophilus*. The cell number in the inoculum (grown with amorphous ferric oxide) was about (3.5–5.0) $\times$ 10^8 cells/ml for both cultures.

Studies with bacteria grown under lithotrophic conditions with molecular hydrogen were conducted in the same medium, but no organic substrates, yeast extract, or vitamin solution were added. CO_2 gas as the sole carbon source was passed through the medium during its preparation. The gas phase volume was filled with 100% H_2.

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Studies with cultures grown organotrophically without iron compounds and studies on the effect of Fe(III) on the metabolism used media that were analogous to media with amorphous Fe(III) with respect to their composition and preparation method, but no amorphous ferric oxide was added. Four variants of the medium were used: (I) without additions; (II) medium reduced by the addition of 0.7 g/l $Na_2S \cdot 9H_2O$ and containing 0.5 ml/l of 0.01% resazurin solution; (III) medium containing 5 mM $FeSO_4 \cdot 7H_2O$; and (IV) medium containing chemically synthesized magnetite (20 mM). Magnetite was prepared by adding 5 g of $FeSO_4 \cdot 7H_2O$ to 1 l of a suspension of amorphous Fe(III) oxide (90 mM); the mixture was sterilized in an autoclave at 2 atm.

The metabolic effects of molecular hydrogen were investigated in two media without iron that contained 100% H_2 and 100% N_2 in the gas phase.

Cultures grown in a Fe(III)-free, sulfide-reduced medium (with cell concentrations of 1.5×10^8 and 1.0×10^8 cells/ml for *T. siderophilus* and *T. ferrireducens*, respectively) were used as inocula in studies of organotrophic growth without Fe(III). The following inocula were employed in studies with cultures grown organotrophically in medium variant IV: the first subculture of *T. siderophilus* (2.4×10^8 cells/ml) in the medium containing chemically synthesized magnetite and a *T. ferrireducens* culture grown with amorphous Fe(III) oxide.

The pH value in all media was 6.5–6.8.

All studies were conducted in Hungate tubes with a liquid phase volume of 10 ml and a gas phase volume of 7 ml at 65°C. Culture transfers were performed anaerobically using sterile syringes. The inoculum volume was 10% in studies on lithotrophic growth and 5% in all other experiments.

Growth estimation. Cell numbers were determined by counting the cells under a light phase-contrast microscope (Amplival, Carl Zeiss, Jena). Before counting the cells grown in media with amorphous Fe(III) oxide or chemically synthesized magnetite, the samples (0.1 ml) were diluted threefold with an ammonium oxalate (28 g/l)–oxalic acid (15 g/l) solution (pH 3.5) to dissolve the sediment consisting of iron compounds; this dilution step was taken into account when calculating cell concentrations.

Analytical methods. The concentrations of Fe(II) and metabolic products were determined by the methods we described earlier [2]. The concentration of molecular hydrogen was determined on a Chrom 5 gas chromatograph equipped with a katharometer as the detector. Nitrogen was the carrier gas, and AG3 charcoal served as the stationary phase. The sensitivity threshold for hydrogen was 2×10^{-5} vol %.

Preparation of cell-free extracts. Microorganisms were grown in the medium that was used for maintaining the cultures, but amorphous Fe(III) oxide was replaced by Fe(III) citrate (20 mM); glycerol (*T. ferrireducens*) or peptone (*T. siderophilus*) served as electron donors. The cells were harvested at the end of the exponential growth phase under nitrogen, centrifuged at 5400 g for 40 min, resuspended in an aqueous solution of 20 mM morpholinoethanesulfonic acid (pH 6.5), and stored under N_2 at 4°C under anaerobic conditions. Cell-free extracts were obtained by ultrasonic disintegration of the harvested biomass.

Determination of CO dehydrogenase activity. CO dehydrogenase activity was determined from the rate of methyl viologen reduction in anaerobic thermostated cuvettes with a Specord UV-VIS spectrophotometer at 65°C. The composition of the incubation mixture was as follows: 960 μl of 50 mM HEPES (pH 6.7), 10 μl of 0.5 M methyl viologen in 50 mM HEPES (pH 6.7), and 10 μl of 4.6 mM dithionite. The gas phase contained CO (100%). The reaction was started by adding 5 μl of cell-free extract (12 mg/ml protein).

Cytochrome determination. The cytochrome content in cell-free extracts was determined from the difference spectra of dithionite-reduced vs. air-oxidized samples. The spectra in the 300- to 700-nm range were recorded at room temperature with an SF-56 (LOMO) two-beam spectrophotometer using 1-cm cuvettes.

RESULTS

Organotrophic growth with and without Fe(III) and Fe(II). The growth curves of *T. ferrireducens* and *T. siderophilus* obtained in the presence of amorphous Fe(III) oxide and the soluble and insoluble forms of ferrous iron and in iron-free media are given in Figs. 1 and 2. The maximum concentration of cells of both microorganisms was attained in the Fe(III)-containing medium. Fe(II) compounds did not increase cell numbers to a comparable extent (against the background of iron-free media). Moreover, virtually no growth of *T. ferrireducens* occurred in a medium with chemically synthesized magnetite. The addition of Na_2SO_4 to an iron-free medium, so that the sulfate concentration equaled that in $FeSO_4$-containing media (in order to estimate the possible effect of sulfate on the growth of the culture), failed to yield any detectable changes in the parameters of growth (data not shown). Growth was stimulated somewhat by decreasing the redox potential of the medium by the addition of 0.7 g/l $Na_2S \cdot 9H_2O$, but the cell concentration attained was significantly below that observed with Fe(III).

Growth and formation of metabolic products on peptone. The growth of *T. ferrireducens* and *T. siderophilus* was stimulated by Fe(III) in a medium containing peptone as the main energy and carbon source; the maximum cell concentration increased three- and twofold with *T. ferrireducens* and *T. siderophilus*, respectively (Table 1 and 2). In the presence of Fe(III), *T. ferrireducens* oxidized peptone to ethanol and acetate; *T. siderophilus* oxidized it to ethanol, acetate, propionate, isobutyrate, isovalerate, and molecular hydrogen. *T. ferrireducens* did not form ethanol in the pres-

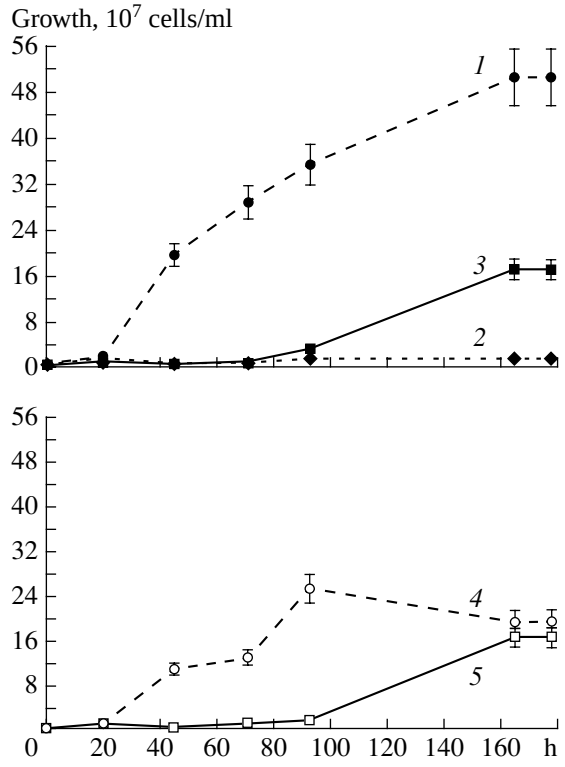

Fig. 1. Growth of *T. ferrireducens* in various media with glycerol as the electron donor: (*1*) medium with amorphous Fe(III) oxide; (*2*) medium with chemically synthesized magnetite; (*3*) medium with $FeSO_4$; (*4*) sulfide-reduced medium without ferric or ferrous iron; (*5*) iron-free medium without reducing agent.

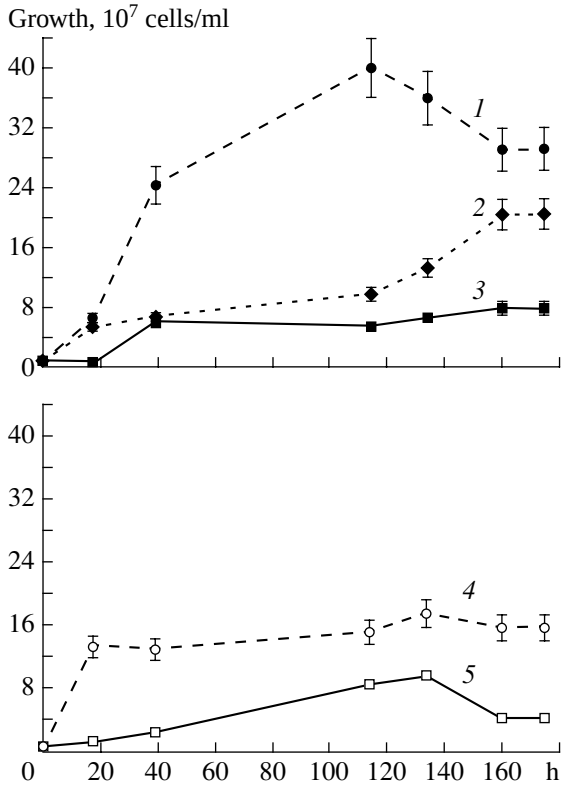

Fig. 2. Growth of *T. siderophilus* in various media with peptone as the electron donor: (*1*) medium with amorphous Fe(III) oxide; (*2*) medium with chemically synthesized magnetite; (*3*) medium with $FeSO_4$; (*4*) sulfide-reduced medium without ferric or ferrous iron; (*5*) iron-free medium without reducing agent.

ence of Fe(III), and the amount of acetate formed per one cell decreased twofold. In the presence of ferric iron, *T. siderophilus* formed neither ethanol nor acetate and the amount of molecular hydrogen formed per one cell decreased approximately threefold.

Effect of molecular hydrogen on organotrophic growth without Fe(III). Without Fe(III), the organotrophic growth of *T. ferrireducens* was virtually independent of the presence of molecular hydrogen in the gas phase (Fig. 3). The growth of *T. siderophilus* without ferric iron was inhibited by hydrogen; the growth rate and the maximum cell concentration significantly decreased in the atmosphere of pure H_2 (Fig. 4).

Table 1. Growth and formation of metabolic products by *T. ferrireducens* in the presence and absence of amorphous Fe(III) oxide

Cultivation conditions	Growth,* 10^7 cells/ml	Products, mM		Fe(II), mM
		ethanol	acetate	
Peptone	7.7 ± 0.8	1.8	3.1	–
Peptone + Fe(III)	23.5 ± 2.4	0.0	4.1	11.8 ± 0.8

* The maximum cell concentration after 180 h of cultivation (cells were counted at 24-h intervals).

Capacity for lithoautotrophic growth. *T. ferrireducens* was found to be able to grow in a medium containing amorphous Fe(III) oxide, molecular hydrogen, and CO_2 as the sole carbon source (Fig. 5). Sustainable growth occurred under these conditions in at least four consecutive subcultures (the inoculum dose was 10%). The increase in cell number corresponded to the extent of iron reduction, and the maximum cell concentration did not exceed 6.0×10^7 cells/ml. The mean stoichiometric ratio of Fe(II) to H_2 was 2.4. The minimum threshold of H_2 consumption in seven-day-old cultures was 3×10^{-5} vol %, and this value did not subsequently decrease. Amorphous Fe(III) oxide was reduced to a black, strongly magnetic sediment that most probably was magnetite. In the absence of molecular hydrogen (100% N_2 as the gas phase) or CO_2/$NaHCO_3$ (pH 6.8, 100% H_2 as the gas phase), growth and Fe(III) reduction did not occur (data not shown). No growth, molecular hydrogen consumption, or Fe(III) reduction occurred in *T. siderophilus* cultures under the tested conditions. However, *T. siderophilus* consumed H_2 and

Table 2. Growth and formation of metabolic products by *T. siderophilus* in the presence and absence of amorphous Fe(III) oxide

Cultivation conditions	Growth,* 10^7 cells/ml	Products, mM						Fe(II), mM
		ethanol	acetate	propionate	isobutyrate	isovalerate	H_2	
Peptone	16.7 ± 1.7	1.9	1.7	0.7	0.7	1.9	1.7	–
Peptone + Fe(III)	39.2 ± 3.9	0	0	0.2	1.2	4.7	1.4	15.8 ± 0.8

* The maximum cell concentration after 180 h of cultivation (cells were counted at 24-h intervals).

reduced iron in the presence of 100 mg/l yeast extract in the medium (data not shown).

CO dehydrogenase activity. Cell-free extracts of *T. ferrireducens* contained CO dehydrogenase that catalyzed CO oxidation by methyl viologen at 65°C. The maximum specific activity of CO dehydrogenase was 0.867 μmol CO/(min mg protein). Cell-free extracts of *T. siderophilus* lacked CO dehydrogenase activity.

Cytochrome detection. The examination of the absorption spectra of the cell-free extract of *T. ferrireducens* revealed peaks at 423, 526, and 552 nm, which are characteristic of *c*-type cytochromes (Fig. 6). As for the absorption spectra of the cell-free extract of *T. siderophilus* with the same protein concentration as *T. ferrireducens* (1.4 mg/ml), we failed to detect any absorption peaks in the 300- to 700-nm range (data not shown).

DISCUSSION

The stimulation of the organotrophic growth of microorganisms in the presence of Fe(III) can be due, apart from the redistribution of energy among catabolic processes, to an intensification of metabolic processes that is caused by assimilation of large amounts of Fe(II) formed by the reduction of Fe(III). Data on the stimulatory effect of Fe(II) (which is a component in a large number of enzymes and cofactors) on the growth of some thermophiles were reported earlier [11, 12]. In addition, the reduction of ferric iron to ferrous iron results in a decrease in the redox potential of the medium, which may also exert an influence on microbial growth.

The results of our study indicate that stimulation of the organotrophic growth of *T. ferrireducens* and *T. siderophilus* in the presence of Fe(III) is due to the functioning of ferric iron as an electron acceptor, and it does not involve the influence of Fe(II). The Eh value of the medium containing amorphous Fe(III) oxide that we used in our study changed from +370 to 0 mV during the process of iron reduction [13]. Because no significant growth stimulation occurred in the medium reduced with sodium sulfide (Eh < –110 mV), we can rule out the explanation of our data based on the suggestion that the Eh value was not sufficiently low to enable the operation of some of the enzymes. Hence, Fe(III) reduction by both tested microorganisms growing on organic substances is linked to catabolic processes and represents a dissimilatory process.

It should be noted that by dissimilatory Fe(III) reduction we mean any consumption of ferric iron as an external electron acceptor in metabolic processes [14], and not only the iron respiration process, during which the cell obtains ATP only via the operation of the electron transfer chain.

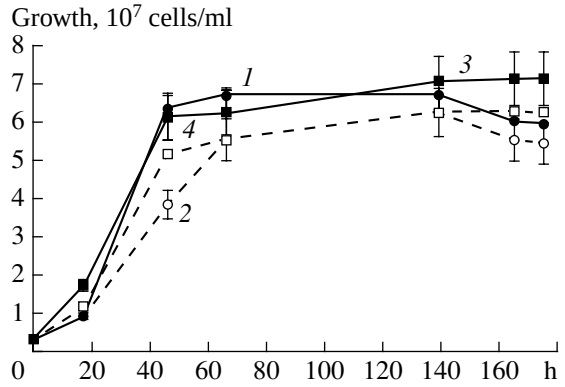

Fig. 3. Growth of *T. ferrireducens* in Fe(III)-lacking media with or without molecular hydrogen in the gas phase, with peptone or glycerol serving as electron donors: (*1*) peptone is the donor, and the gas phase is nitrogen; (*2*) peptone is the donor, and the gas phase is hydrogen; (*3*) glycerol is the donor, and the gas phase is nitrogen; (*4*) glycerol is the donor, and the gas phase is nitrogen.

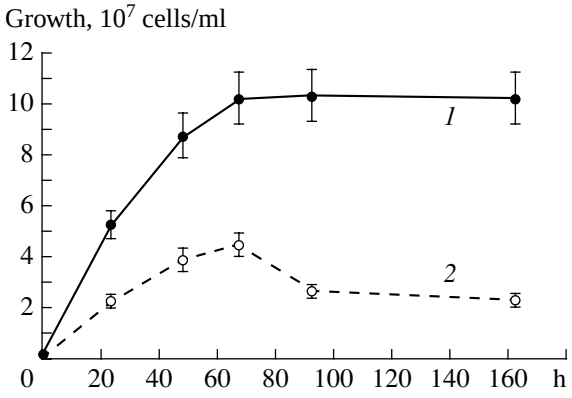

Fig. 4. Growth of *T. siderophilus* with or without molecular hydrogen in the gas phase in a Fe(III)-lacking medium with peptone as the electron donor: (*1*) the gas phase is nitrogen; (*2*) the gas phase is hydrogen.

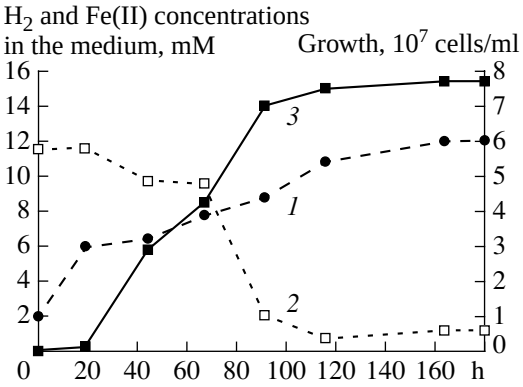

Fig. 5. Growth of *T. ferrireducens* in a medium with amorphous Fe(III) oxide, molecular hydrogen, and CO_2 as the sole carbon source: (*1*) growth; (*2*) hydrogen; (*3*) Fe(II).

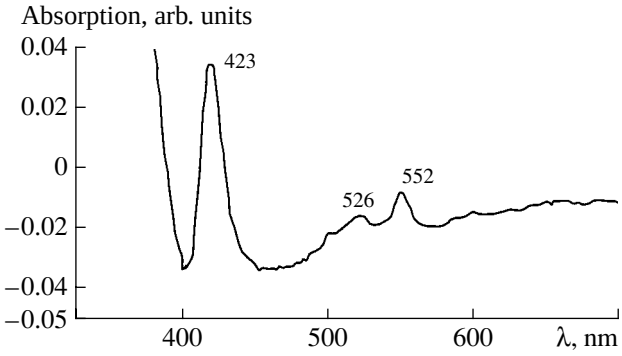

Fig. 6. Reduced vs. oxidized absorption spectrum of the cell-free extract of *T. ferrireducens.*

According to the original description of *T. ferrireducens* and *T. siderophilus* given in the literature, both microorganisms grow and reduce Fe(III) in a medium with complex organic substrates such as peptone [9, 10]; however, no qualitative and quantitative data on the oxidation products were obtained, and the dependence of their formation on the availability of Fe(III) in the medium was not elucidated. Our results indicate that, both with and without Fe(III), peptone is not completely oxidized and energy is probably obtained by the tested microorganisms in the fermentation process. With ferric iron added, this kind of metabolism can be regarded as fermentation with an exogenous electron acceptor. However, the ratio between the concentrations of the metabolic products and the cell yield considerably decreases in the presence of Fe(III), suggesting a possible linkage between the oxidation of some peptone components and the electron flow to Fe(III) via the electron transfer chain. The tested organisms differ in that the oxidation of organic substances by *T. siderophilus* results in the formation of molecular hydrogen, whereas this process is not accompanied by the evolution of detectable amounts of H_2 in *T. ferrireducens.* The data obtained indicate that molecular hydrogen inhibits the growth of *T. siderophilus*, in contrast to *T. ferrireducens*, whose growth is not influenced by the hydrogen content in the gas phase. Obviously, Fe(III) reduction in *T. siderophilus* is aimed at alleviating the inhibitory effect of hydrogen, either via its oxidation by exogenous Fe(III) or by influencing the flow of reducing equivalents [15]. Hence, the metabolism of *T. siderophilus* in the presence of Fe(III) is similar to that of other representatives of the genus *Thermoanaerobacter* growing with an exogenous electron acceptor, such as thiosulfate and elemental sulfur [16–18]. Fe(III) reduction by *T. ferrireducens* does not represent a detoxication strategy, and it is most probably related to the supplementary energy production in the electron transfer chain.

A large number of iron-reducing microorganisms can grow lithotrophically with molecular hydrogen and Fe(III), but there are only fragmentary data on the autotrophic growth of iron reducers [19]. The results of our research indicate that *Thermoterrabacterium ferrireducens* is capable of lithoautotrophic growth with molecular hydrogen as the electron donor, amorphous ferric oxide as the electron acceptor, and CO_2 as the carbon source in the absence of any organic substances in the cultivation medium. Hence, this organism can potentially perform the function of a primary producer of organic substances in thermal systems that contain ferric compounds and are situated in the gas discharge zone. The minimum threshold of H_2 consumption in mature cultures was 3×10^{-5} vol %. Although the thresholds of hydrogen consumption by thermophilic anaerobes of various physiological groups have not yet been determined, we suggest that iron-reducing microorganisms can successfully compete for molecular hydrogen with other anaerobic hydrogenotrophs in thermal ecosystems, as has been shown for mesophilic habitats [20]. The detection of CO dehydrogenase activity revealed that CO_2 fixation in *T. ferrireducens* proceeds via the anaerobic acetyl-CoA pathway, which is characteristic of many anaerobic bacteria [21]. In contrast to *T. ferrireducens*, *T. siderophilus* failed to grow lithoautotrophically; this microorganism required organic substances in order to use molecular hydrogen with Fe(III) as the electron acceptor. *T. ferrireducens* contains cytochromes, and *T. siderophilus* lacks them, which also suggests differences between the biochemical mechanisms of ferric iron reduction in these species. Iron-reducing activity is known to involve cytochromes in some microorganisms [22].

Therefore, the two tested microorganisms possess distinct biochemical mechanisms of ferric iron reduction, even though they belong to one phylogenetic group (the gram-positive bacteria), share the same ecological niche (continental hydrotherms), and grow at similar temperatures.

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