Description of *Thermoanaerobacter brockii* subsp. *lactyiethicus* subsp. nov., Isolated from a Deep Subsurface French Oil Well, a Proposal To Reclassify *Thermoanaerobacter finnii* as *Thermoanaerobacter brockii* subsp. *finnii* comb. nov., and an Emended Description of *Thermoanaerobacter brockii*

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A strictly anaerobic, thermophilic, gram-positive, spore-forming catabacterium designated strain SEBR 5268T (T = type strain) was isolated from an oil field at a depth of 2,100 m, where the temperature was 92°C. The cells of this organism were gram-positive, straight, motile rods (0.5 by 2 to 3 μm) with peritrichous flagella. The cells occurred singly or in pairs during the logarithmic growth phase, but were pleomorphic and filamentous (length, 15 μm) in old cultures. Growth occurred at temperatures of 40 to 75°C, and optimum growth occurred at temperatures between 55 and 60°C. The fermentable substrates included glucose, fructose, galactose, mannose, cellobiose, maltose, sucrose, lactose, D-xylose, D-ribose, mannitol, pyruvate, and starch. The products of fermentation of glucose were lactate, acetate, ethanol, H2, and CO2. The DNA base composition was 35 mol% G+C. The results of 16S rRNA sequence comparisons indicated that strain SEBR 5268T was closely related to *Thermoanaerobacter brockii* and *Thermoanaerobacter finnii*, and these three organisms exhibited levels of ribosomal DNA sequence homology of 98% to 99%. The results of DNA-DNA hybridization studies performed with the three organisms confirmed this close affiliation, and as base pairing values of >70% were obtained, these organisms belong to the same species. Therefore, we propose that *T. finnii* should be reclassified as a subspecies of *T. brockii*, *Thermoanaerobacter brockii* subsp. *finnii* comb. nov. This automatically creates *Thermoanaerobacter brockii* subsp. *brockii*. We also propose that strain SEBR 5268T should be classified as a member of a new subspecies of *T. brockii*, *Thermoanaerobacter brockii* subsp. *lactyiethicus*. The latter differs from *T. brockii* subsp. *brockii* and *T. brockii* subsp. *finnii* by its 16S rRNA sequence, DNA sequence diversity, lower temperature optimum, G+C content, and carbohydrate utilization spectrum. Strain SEBR 5268T has been deposited in the Deutsche Sammlung von Mikroorganismen as strain DSM 9801T.

In the past two decades, workers have performed intensive studies to isolate thermophilic, anaerobic, carbohydrate-fermenting catabacteria from marine and terrestrial volcanic hot springs (24, 41), and have studied these organisms with a view toward using these microbes and their enzymes for biotechnological applications (24). Because of the large number of new isolates of thermophilic strains that belong to the genus *Thermoanaerobacter* has been reclassified (24, 37), and these three organisms exhibited levels of ribosomal DNA sequence homology of 98% to 99%. The results of DNA-DNA hybridization studies performed with the three organisms confirmed this close affiliation, and as base pairing values of >70% were obtained, these organisms belong to the same species. Therefore, we propose that *T. finnii* should be reclassified as a subspecies of *T. brockii*, *Thermoanaerobacter brockii* subsp. *finnii* comb. nov. This automatically creates *Thermoanaerobacter brockii* subsp. *brockii*. We also propose that strain SEBR 5268T should be classified as a member of a new subspecies of *T. brockii*, *Thermoanaerobacter brockii* subsp. *lactyiethicus*. The latter differs from *T. brockii* subsp. *brockii* and *T. brockii* subsp. *finnii* by its 16S rRNA sequence, DNA sequence diversity, lower temperature optimum, G+C content, and carbohydrate utilization spectrum. Strain SEBR 5268T has been deposited in the Deutsche Sammlung von Mikroorganismen as strain DSM 9801T.

**MATERIALS AND METHODS**

**Origins of strains.** Strain SEBR 5268T (= *T. brockii* type strain) was isolated from a French oil field, whereas strains SEBR 7311 and SEBR 7312 were isolated from African oil fields in Cameroon. In the in situ temperature of the wells was 92°C, but the temperatures were 51 to 53°C by the time that the samples were collected at the wellhead. The method of sampling used has been described elsewhere (3). *Thermoanaerobacter finnii* AKQ-1T (= DSM 33899) and *Thermoanaerobacter brockii* HTD4T (= DSM 14577) were obtained from the Deutsche Sammlung von Mikroorganismen, Braunschweig, Germany. All strains were routinely cultured in the glucose-based growth medium described below.

**Culture medium.** A glucose-based medium was used to culture the strains. This medium contained (per liter) 1.0 g of NH4Cl, 0.3 g of K2HPO4, 0.3 g of KH2PO4, 1.3 g of MgCl2 · 6H2O, 0.1 g of CaCl2 · 2H2O, 2.0 g of KCl, 2.0 g of NaCl, 0.5 g of CH3CONa, 5.0 g of tryptone (BioMérieux, Craponne, France), 5.0 g of yeast extract (Difco Laboratories, Detroit, Mich.), 10.0 g of glucose, 1 ml of 0.1% resazurin, and 10 ml of a trace element solution (1). Unless indicated otherwise, the anaerobic technique of Hungate was used throughout.
this study (17, 25, 27). Portions (20 ml) of the anaerobic medium were dispensed into 50-ml serum bottles under a stream of oxygen-free N₂-CO₂ (80:20). The medium dispensed in this way was sterilized for 45 min at 110°C. Just prior to inoculation, 0.2 ml of 2% Na₂S - 9H₂O, 0.1 ml of 10% NaHCO₃, 0.2 ml of a vitamin solution (31), and 0.1 ml of a 0.2% sodium dithionite solution (from sterilized anaerobic stock solutions) were injected into each bottle. For enrichment cultures 2 ml of a sample was injected, and the preparation was incubated at 60°C for 24 h without shaking. Pure cultures were obtained by repeatedly using the agar shake dilution method with glucose-based medium that was supplemented with 0.5% Noble agar.

**Nutritional characterization.** Basal medium containing 1 g of yeast extract per liter and 1 g of tryptose per liter but no glucose was used for nutritional characterization. This medium was prepared as described above, and 5-ml portions were distributed into Hungate tubes. Just prior to inoculation, 0.05 ml of a 2% Na₂S - 9H₂O sterile anaerobic stock solution and 0.25 ml of a 10% NaHCO₃ sterile anaerobic stock solution were injected into each tube. Substrates were injected from sterile anaerobic stock solutions to give final concentrations of 20 mM thiosulfate with H₂-CO₃ (2 × 10⁻³ Pa) as the gas phase. Only limited genotypic studies were performed with strains SEBR 7311 and SEBR 7312, whereas strain SEBR 5268 was studied in greater detail.

**Cellular features.** Cells of strain SEBR 5268T were straight rods (Fig. 1) that were 0.5 μm in diameter and 2 to 3 μm long during the exponential growth phase. They occurred singly and in pairs in young cultures. However, pleomorphic forms, including filaments up to 15 μm long, developed in old cultures. Strain SEBR 5268T was motile and possessed peritrichous flagella (data not shown). Sessile were never observed on rich medium containing glucose and in the presence of thiosulfate, but were observed after 48 h of incubation at 60°C (Fig. 1) in a medium containing D-xylene and thiosulfate. In addition, growth was observed after the culture was pasteurized at 90°C for 20 min on glucose-thiosulfate medium. Cells of all phases of growth were gram positive. Electron microscopy also revealed a gram-positive type of cell wall (data not shown).

**Growth and nutritional properties.** Strain SEBR 5268T required yeast extract for growth during the exponential growth phase. They occurred singly and in pairs in young cultures. However, pleomorphic forms, including filaments up to 15 μm long, developed in old cultures. Strain SEBR 5268T was motile and possessed peritrichous flagella (data not shown). Sessile were never observed on rich medium containing glucose and in the presence of thiosulfate, but were observed after 48 h of incubation at 60°C (Fig. 1) in a medium containing D-xylene and thiosulfate. In addition, growth was observed after the culture was pasteurized at 90°C for 20 min on glucose-thiosulfate medium. Cells of all phases of growth were gram positive. Electron microscopy also revealed a gram-positive type of cell wall (data not shown).

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**DNA base composition.** The DNA base composition of strain SEBR 5268T was 35 mol% G+C.

**16S rRNA sequence analysis.** Comparisons of partial 16S rRNA gene sequences (500 nucleotides) revealed that strains SEBR 5268T, SEBR 7311, and SEBR 7312 were closely related as they exhibited a level of sequence similarity of 99% (data not shown). Therefore, the complete sequence of only strain SEBR 5268T (1,507 bases) was determined. This sequence
Isolation of members of various physiological groups of thermophilic bacteria from deep subsurface environments has been reported previously, and the organisms isolated include methanogens and sulfur- or sulfate-reducing bacteria (11, 28, 37). To date, no formal characterization of fermentative bacteria isolated from such environments has been published, although short descriptions of strains SEBR 5268T and Gluc 1 have appeared previously (12, 38). Our formal description of strain SEBR 5268T obtained from an oil field in this paper extends the physiological diversity and taxonomic diversity of thermophiles found in deep subsurface environments.

Strain SEBR 5268T did not grow at temperatures above 75°C, although the in situ temperature of the oil well from which it was isolated was 92°C, indicating that this microbe may colonize the cooler parts of the reservoir. However, we cannot eliminate the possibility that thermophilic anaerobic heterotrophs may have been introduced during sample collection. Interestingly, strain SEBR 5268T cells sporulated when they were grown with D-xylose as an electron donor and thiosulfate as an electron acceptor; thus, this organism is able to survive but not necessarily grow at temperatures higher than 75°C.

Strain SEBR 5268T has been reported to utilize thiosulfate as an electron acceptor and to produce sulfide (12). When yeast extract was used as a growth substrate, H2 was oxidized to H2S by this isolate in the presence of thiosulfate. H2 oxidation took place mainly after the exponential growth phase. These physiological features (H2 consumption and sulfide production) make strain SEBR 5268T a potential biocorrosive agent in oil petroleum fields in the presence of thiosulfate (12-14).

The diversity and role in pipeline corrosion and biofouling of fermentative bacteria similar to strain SEBR 5268T are currently being examined by workers in our laboratories.

Strain SEBR 5268T is a sporulating, anaerobic, rod-shaped thermophile which ferments a variety of sugars and produces ethanol, acetate, lactate, CO2, and H2. In this respect strain SEBR 5268T is similar to numerous thermoanaerobes belonging to the domain Bacteria. However, phylogenetically, strain SEBR 5268T is clearly related to *Thermoanaerobacter* species, including *T. finnii* and *T. brockii* (average level of similarity,
with strain SEBR 5268<sup>T</sup> (13). Strain SEBR 5268<sup>T</sup> is not related to <i>T. acetethylicus</i> as the latter organism is a gram-negative nonsporulating bacterium that cannot produce lactate from fermentation of glucose (2, 32). Furthermore, <i>T. acetethylicus</i> does not use pyruvate and D-xylose, whereas strain SEBR 5268<sup>T</sup> does. Although strain Gluc 1, a partially characterized isolate obtained from a 6,779-m-deep Swedish bore hole, is morphologically and phylogenetically similar to strain SEBR 5268T<sup>T</sup>, it produces ethanol, lactate, CO<sub>2</sub>, and H<sub>2</sub> from fermentation of glucose (38), whereas strain SEBR 5268<sup>T</sup> produces acetate in addition to these products. The phenotypically most closely related <i>Thermoaerobacter</i> species is <i>T. finnii</i>. However, strain SEBR 5268T<sup>T</sup> differs from <i>T. finnii</i> in its optimum temperature and pH for growth and uses melibiose. Furthermore, when <i>T. finnii</i> is cultured under the same growth conditions as strain SEBR 5268<sup>T</sup>, it produces ethanol as the major end product of glucose metabolism, whereas strain SEBR 5268<sup>T</sup> produces equal amounts of lactate and ethanol. However, it is possible that varying culture conditions may affect the end product profile, as has been reported for <i>T. ethanolicus</i> (39).

A comparison of the 16S ribosomal DNA sequence of strain SEBR 5268<sup>T</sup> with the sequences of <i>Thermoaerobacter</i> spe-

![FIG. 3. Dendrogram showing the position of strain SEBR 5268<sup>T</sup> among representatives of the genus <i>Thermoaerobacter</i> and related genera. The dendrogram was derived from the evolutionary distance matrix shown in Table 1.](image)

### TABLE 1. Evolutionary distance matrix determined from a comparison of the 16s rRNA sequences of carbohydrate-fermenting thermoaerobes by using the method of Jukes and Cantor<sup>a</sup>

| Strain | Thermoaerobacter sp. strain SEBR 5268<sup>T</sup> | Thermoaerobacter sp. strain ATCC 3326ST | Thermoaerobacter sp. strain ATCC 31550<sup>T</sup> | Thermoaerobacter DSM 567<sup>T</sup> | Thermoaerobacter DSM 1457<sup>T</sup> | Thermoaerobacter DSM 203<sup>T</sup> | Thermoaerobacter DSM 567<sup>T</sup> | Thermoaerobacter DSM 7097<sup>T</sup> | Thermoaerobacter DSM 263<sup>T</sup> | Thermoaerobacter DSM 7097<sup>T</sup> | Thermoaerobacter DSM 42<sup>T</sup> | Thermoaerobacter DSM 263<sup>T</sup> | Thermoaerobacter DSM 7097<sup>T</sup> | Thermoaerobacter DSM 263<sup>T</sup> | Thermoaerobacter DSM 7097<sup>T</sup> | Thermoaerobacter DSM 263<sup>T</sup> | Thermoaerobacter DSM 7097<sup>T</sup> | Thermoaerobacter DSM 263<sup>T</sup> | Thermoaerobacter DSM 7097<sup>T</sup> | Thermoaerobacter DSM 263<sup>T</sup> | Thermoaerobacter DSM 7097<sup>T</sup> | Thermoaerobacter DSM 263<sup>T</sup> | Thermoaerobacter DSM 7097<sup>T</sup> | Thermoaerobacter DSM 263<sup>T</sup> | Thermoaerobacter DSM 7097<sup>T</sup> | Thermoaerobacter DSM 263<sup>T</sup> | Thermoaerobacter DSM 7097<sup>T</sup> |
|--------|-----------------------------------------------|----------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|
| 0.1    |                                               |                                        |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |                                               |

<sup>a</sup> See Materials and Methods. The sequences used in this analysis were obtained from the Ribosomal Database Project, version 4.0 (21). Only 1,320 unambiguous nucleotides were used.
cies also revealed that strain SEBR 5268T is more closely related to \textit{T. brockii} and \textit{T. finnii} (level of similarity, 98.3\%) than to \textit{T. thermohydrosulfuricas} (level of similarity, 95.7\%), \textit{T. ethanolicus} (level of similarity, 95.6\%), \textit{Thermoanaerobacter kivui} (level of similarity, 96.3\%), or \textit{Thermoanaerobacter thermocaprinus} (level of similarity, 94.7\%). It has been proposed that if the level of 16S rRNA similarity is more than 97\%, it should not be used to distinguish taxonomically related strains (35), and therefore DNA-DNA hybridization experiments were performed. Our DNA-DNA hybridization data confirmed that strain SEBR 5268T could not be classified as a member of a new \textit{Thermoanaerobacter} species. \textit{T. brockii} and \textit{T. finnii} are also closely related to each other (level of similarity, 98.9\%). On the basis of our DNA-DNA hybridization data, it is evident that these organisms should not be distinguished at the species level (Table 2). This is in contrast to the results of Schmid et al. (35), who obtained values low enough to place \textit{T. finnii} and \textit{T. brockii} strains in separate species. This discrepancy in results can be explained by the fact that two different methods were used for DNA-DNA hybridization experiments.

The DNA-DNA hybridization method has been refined, and now the data include \(\Delta T_m\) values for improved sensitivity; the \(\Delta T_m\) should be >5°C to differentiate species. The \(\Delta T_m\) value obtained in most hybridization experiments performed with \textit{T. brockii}, \textit{T. finnii}, and strain SEBR 5268T was 0°C; the only exception was the value obtained in the experiment performed with a \textit{T. brockii} strain and strain SEBR 7311 (\(\Delta T_m\) 1°C), which indicated that these organisms should be considered strains rather than members of distinct species. DNA-DNA hybridization studies performed with two other oil field \textit{Thermoanaerobacter} strains (SEBR 7311 and SEBR 7312) also gave similar results. On the basis of the results described above, we propose that \textit{T. finnii} should be reclassified in the species \textit{T. brockii} since the latter bacterium was described first (42). Therefore, \textit{T. finnii} becomes a new subspecies of \textit{T. brockii}, \textit{T. brockii} \textit{subsp. finnii} comb. nov. We also propose that strain SEBR 5268T should be classified as a member of a new subspecies of \textit{T. brockii}, \textit{T. brockii} \textit{subsp. lactiethylicus}. The description of the genus \textit{Thermoanaerobacter} is the description given previously by Lee et al. (22).

Our results also indicate that \textit{T. brockii} strains are widely distributed in nature as they have now been isolated from soil, lake sediments, volcanic hot springs, and subsurface terrain, such as oil fields and deep bore holes. As these organisms are sporulators, their distribution in such a diverse range of ecosystems is perhaps not surprising.

**Emendation of the species description of \textit{Thermoanaerobacter brockii} Zeikus, Hegge, and Anderson 1979; Lee, Jain, Lee, Lowe, and Zeikus 1993.** \textit{Thermoanaerobacter brockii} (brock'i.i. M. L. gen. n. brockii, of Brock, named for Thomas Dale Brock, who performed pioneering studies on the physiological ecology of extreme thermophiles). Rods are 0.4 to 1.0 by 1 to 20 \(\mu\)m. Cells occur singly, in pairs, in short chains, and in filaments. Gram positive. Heat-resistant terminal endospores are formed. Colonies are circular and 0.2 to 4 mm in diameter. Thermophilic. The optimum growth temperature is 55 to 70°C; the temperature range for growth is 35 to 85°C. The optimum pH is 6.5 to 7.5. Obligate anaerobe. Chemooxygenotrophic. Ferments hexoses and pyruvate. The end products of glucose fermentation are ethanol, lactate, acetate, \(H_2\), and \(CO_2\). Reduces thiosulfate to hydrogen sulfide. The G+C content of the DNA is 30 to 35 mol\%. Isolated from the sediment of lakes, hot springs, and oil wells.

**Description of \textit{Thermoanaerobacter brockii} \textit{subsp. brockii} Zeikus, Hegge, and Anderson 1979; Lee, Jain, Lee, Lowe, and Zeikus 1993.** \textit{Thermoanaerobacter brockii} \textit{subsp. brockii} (brock'i.i. M. L. gen. n. brockii, of Brock, named for Thomas Dale Brock, who performed pioneering studies on the physiological ecology of extreme thermophiles). Short rods are 1.0 by 2 to 20 \(\mu\)m. Cells frequently vary in length (minicells) and occur in pairs, chains, and filaments. Gram positive. Round, heat-resistant terminal endospores are formed. Cytochrome pigments and catalase are absent. Colonies are circular, 0.2 to 0.3 mm in diameter, flat, mucoid, and nonpigmented. Monolayer cell wall architecture without an outer wall membrane. Growth is inhibited by penicillin, cycloserine, streptomycin, tetracycline, and chloramphenicol. Thermophilic. The optimum growth temperature is 65 to 70°C; the temperature range for growth is >35°C to <85°C. The pH range for growth is 5.5 to 9.5; the optimum pH is 7.5. Obligate anaerobe. Chemooxygenotrophic. Ferments glucose, maltose, sucrose, lactose, cellobiose, starch, and pyruvate. Does not use xylose, cellulose, arabinose, mannose, lactate, tartrate, ethanol, trypoline, Casamino Acids, and pectin. The end products of glucose fermentation are ethanol, lactate, acetate, \(H_2\), and \(CO_2\). Reduces thiosulfate to hydrogen sulfide. The G+C content of the DNA is 30 to 31 mol\%. Isolated from a thermal spring sediment in Yellowstone National Park.
The type strain is HTD4 (= DSM 1457 = ATCC 33075).

Description of Thermoaerobacter brockii subsp. finni

Schmid, Giesel, Schobert, and Sahm 1986. Thermoaerobacter brockii subsp. finni (fin'ni.i. M. L. gen. n. finni, of Finn, named for Robert K. Finn, who made important contributions to the development of the ethanol vacuum fermentation process). Short rods are 0.4 to 0.6 by 1 to 4 µm. Cells occur singly, in pairs, and in short chains and are motile. Occasionally coccolid cells are found. Heat-resistant terminal endospores are contained. Colonies are circular, 1 to 3 mm in diameter, smooth, and white. Contains peptidoglycan of the meso-diaminopimelic acid type. Susceptible to penicillin G and tetracycline. Thermonaerobacter brockii subsp. finni is a mesophilic, obligate anaerobe. Chemoorganotrophic. Ferments products of glucose and xylose fermentation are ethanol and CO₂. The optimum pH is 6.5 to 6.8. Obligate anaerobe. Chemoorganotrophic. Ferments lactic acid and ethanol. Cells are straight rods (0.5 by 2 µm) that are motile by means of peritrichous flagella and occur singly or in pairs in young cultures. Pleomorphic filaments (length, 15 µm) occur in old cultures. Gram positive. Spores are formed in medium containing D-xylose as an electron donor and thiosulfate as an electron acceptor. Anaerobic dehydrogenase activities towards ethanol, acetaldehyde, hydrogen sulfide. The type strain is KO-1 (= DSM 9801).

Thermonaerobacter brockii

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Titre original : Description of *Thermoanaerobacter brockii* subsp. *lactiethylicus* subsp. nov., isolated from a deep subsurface french oil well, a proposal to reclassify *Thermoanaerobacter finnii* as *Thermoanaerobacter brockii* subsp. *finnii* comb. nov., and an amended description of *Thermoanaerobacter brockii*


Titre en Français : Description de *Thermoanaerobacter brockii* subsp. *lactiethylicus* subsp. nov., isolé d'un puits de pétrole français, une proposition de reclassement de *Thermoanaerobacter finnii* en *Thermoanaerobacter brockii* subsp. *finnii* comb. nov., et une description modifiée de *Thermoanaerobacter brockii*

Mots-clés matières : *Thermoanaerobacter* - réduction du thiosulfate - (10 au plus) puits de pétrole - Anaérobiose - Taxonomie

Résumé en Français :
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Plan de classement : Monde végétal et Animal - Fermentations