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Peptide and Amino Acid Oxidation in the Presence of Thiosulfate by Members of the Genus *Thermoanaerobacter*

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Abstract. *Thermoanaerobacter brockii*, *T. ethanolicus*, *T. thermohydrosulfuricus*, *T. finnii*, and *Thermoanaerobacter* strain SEBR 5268 (an isolate from an oil-producing well) were studied for their ability to oxidize proteinaceous compounds that included gelatin, peptides, and casamino acids. All bacteria tested used peptides and amino acids, but only slightly. However, in the presence of thiosulfate all the *Thermoanaerobacter* species showed a substantial improvement in growth and/or the production of acetate, isovalerate, isobutyrate, and sulfide. Propionate was a minor product of peptide or amino acid oxidation. The reduction of thiosulfate during growth on peptides by members of the *Thermoanaerobacter* species is a trait that closely resembles that of archaeal hyperthermophiles during growth on peptides and amino acids with elemental sulfur as electron acceptor.

In the past two decades, novel thermophilic microbes, which include members of the domains *Archaea* and *Bacteria*, have been isolated from a variety of thermal environments [17, 24]. In the case of members of the domain *Bacteria*, a great deal of attention has been focused on thermoanaerobes, e.g., *Clostridium thermohydrosulfuricum*, *Thermoanaerobacter* species, and *Thermoanaerobium* species as they have potential in the fuel and enzyme industries [17, 27]. On the basis of the current knowledge, strains of *Clostridium thermohydrosulfuricum* and *Thermoanaerobium brockii* have recently been reclassified and are all now included as members of the genus *Thermoanaerobacter* [16]. *Thermoanaerobacter* species are thermophilic, heterotrophic, saccharolytic anaerobes and have the ability to reduce thiosulfate to sulfide. Their habitat is soil, sugar beet extraction juices, sugar cane juices, thermal volcanic hot springs, and oil-producing wells [9, 16, 21]. In the domain *Archaea*, numerous studies have been undertaken on the novel and presumably archaeal nature of their physiology, which includes growth on peptides and/or amino acids and the concomitant reduction of sulfur in order to gain energy for growth [1, 18]. Proteolytic, peptidolytic or aminolytic activities have also been demonstrated in the mesophilic and thermophilic anaerobes in the *Bacteria* domain. Of these, mesophilic bacteria belonging to the genera *Clostridium* and *Bacteroides* have been the most intensively studied with respect to their role in mineralizing proteins [8, 11]. *Thermobacteroides proteolyticus* [20], recently renamed as *Coprothermobacter proteolyticus* [22], and *T. leptospartum* [25] account for the strict thermophiles fermenting proteins and peptides, but not amino acids. These microorganisms also use carbohydrates as an energy source.

Thermoanaerobacter thermohydrosulfuricus is the only species in the genus *Thermoanaerobacter* known to produce H_2S from peptide metabolism [12, 26], and amino acid oxidation has never been demonstrated within this genus. In this paper we first report on the utilization of amino acids by *Thermoanaerobacter* species and extend the ability to oxidize peptides to other members within this genus, particularly in the presence of thiosulfate. This observation can be regarded as analogous to the situation in which there is growth on amino acids and/or polypeptides in the presence of sulfur by some archaeal hyperthermophiles.

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Table 1. Effect of thiosulfate on peptide and amino acid oxidation by SEBR 5268

Treatment	O.D. 580 nm	Acetate (mM)	Propionate (mM)	Isobutyrate (mM)	Isovalerate (mM)	H_2 (mM)	H_2S (mM)
M	0.228	6.50	0.00	0.00	0.00	0.00	1.60
M+Thio	0.180	6.88	0.00	0.00	0.51	0.00	1.31
Casa	0.209	6.31	0.06	0.14	1.55	5.98	1.82
Casa+Thio	0.293	11.87	0.00	1.37	6.28	0.42	6.02
Biot	0.140	5.51	0.42	0.13	1.51	1.45	1.45
Biot+Thio	0.323	13.63	0.12	1.93	8.62	0.54	6.88
Pap	0.258	6.60	0.05	0.00	0.48	0.00	1.65
Pap+Thio	0.335	11.95	0.15	0.44	2.68	0.00	5.75
Pan	0.215	6.62	0.23	0.00	0.51	3.84	1.33
Pan+Thio	0.349	11.76	0.37	0.52	2.18	0.43	5.19
Bact	0.160	6.66	0.45	0.00	0.96	6.34	1.66
Bact+Thio	0.330	10.32	0.39	0.45	2.48	0.00	3.95
Biogel	0.180	7.18	0.18	0.00	0.44	7.10	0.56
Biogel+Thio	0.290	13.48	0.14	0.47	2.25	0.00	6.11
Gel	0.200	5.56	0.09	0.00	0.13	1.66	1.90
Gel+Thio	0.260	7.52	0.06	0.00	0.74	0.00	2.27

Results after 3 days of incubation at 60°C. Peptides, casamino acids and gelatin were added at 5 g/liter. M: basal medium containing 1 g/liter yeast extract; Thio: thiosulfate (20mM); Casa: casamino acids; Biot: bio-Trypcase; Pap: Soja bean papainic peptone; Pan: pancreatic peptone; Bact: bactopeptone; Biogel: bio-gelytone; Gel: gelatin.

Table 2. Effect of thiosulfate on peptide and amino acid oxidation by *T. finnii*

Treatment	O.D. (580 nm)	Acetate (mM)	Propionate (mM)	Isobutyrate (mM)	Isovalerate (mM)	H_2 (mM)	H_2S (mM)
M	0.113	5.10	0.06	0.00	0.00	0.43	0.96
M+Thio	0.116	6.98	0.03	0.00	0.30	0.00	1.08
Casa	0.160	6.08	0.05	0.00	0.70	4.60	1.25
Casa+Thio	0.180	10.29	0.05	1.25	6.43	0.23	5.30
Biot	0.100	6.50	0.06	0.00	0.72	2.76	1.00
Biot+Thio	0.197	9.18	0.09	0.75	5.12	0.94	4.95
Pap	0.110	10.21	0.06	0.00	0.31	6.02	1.01
Pap+Thio	0.350	15.20	0.06	0.44	2.82	0.19	8.30
Pan	0.180	5.46	0.07	0.00	0.11	3.25	1.00
Pan+Thio	0.185	10.02	0.24	0.29	1.70	0.00	2.50
Bact	0.125	6.55	0.45	0.00	0.23	10.17	1.10
Bact+Thio	0.130	8.66	0.40	0.17	1.66	0.19	3.70
Biogel	0.130	6.13	0.07	0.00	0.15	1.27	1.10
Biogel+Thio	0.115	8.36	0.28	0.05	1.14	0.10	1.50
Gel	0.080	5.70	0.06	0.00	0.00	0.79	1.01
Gel+Thio	0.090	6.60	0.07	0.00	0.36	0.00	1.65

Results after 3 days of incubation at 60°C. Peptides, casamino acids and gelatin were added at 5g/liter. M: basal medium containing 1g/liter yeast extract; Thio: thiosulfate (20 mM); Casa: casamino acids; Biot: bio-Trypcase; Pap: Soja bean papainic peptone; Pan: pancreatic peptone; Bact: bactopeptone; Biogel: bio-gelytone; Gel: gelatin.

Table 3. Effect of thiosulfate on peptide and amino acid oxidation by *Thermoanaerobacter* species

Treatment	O.D. 580nm	Acetate (mM)	Propionate (mM)	Isobutyrate (mM)	Isovalerate (mM)	H_2 (mM)	H_2S (mM)
T. ethanolicus							
M	0.052	4.58	0.00	0.00	0.00	0.25	0.42
M+Thio	0.024	6.28	0.00	0.00	0.00	0.00	0.50
Casa	0.033	6.63	0.05	0.60	0.83	1.21	0.14
Casa+Thio	0.017	7.25	0.07	1.16	2.03	1.50	1.06
Biot	0.030	6.55	0.06	0.39	0.81	1.61	0.64
Biot+Thio	0.077	7.60	0.12	0.97	2.33	0.71	2.35
Gel	0.038	6.28	0.05	0.65	0.00	0.79	0.21
Gel+Thio	0.033	6.73	0.06	0.31	0.50	0.23	0.84
T. thermohydrosulfuricus							
M	0.056	5.61	0.037	0.53	0.00	0.34	0.45
M+Thio	0.044	6.39	0.044	0.53	0.00	0.00	0.46
Casa	0.067	7.00	0.047	0.49	0.60	1.86	0.45
Casa+Thio	0.060	7.20	0.065	0.62	1.84	3.32	1.00
Biot	0.035	6.51	0.054	0.32	0.52	1.71	0.82
Biot+Thio	0.100	9.00	0.088	1.19	2.50	3.41	1.80
Gel	0.057	5.88	0.042	0.45	0.00	0.64	0.39
Gel+Thio	0.040	6.65	0.043	0.24	0.00	0.00	1.05
T. brockii							
M	0.039	6.13	0.051	0.00	0.00	0.00	0.41
M+Thio	0.050	7.60	0.053	0.450	0.00	0.00	0.34
Casa	0.066	7.17	0.074	0.200	0.38	1.48	0.21
Casa+Thio	0.110	9.20	0.110	1.400	2.53	0.18	3.83
Biot	0.057	7.42	0.094	0.140	0.42	1.35	0.37
Biot+Thio	0.189	10.00	0.183	1.030	2.85	0.00	4.50
Gel	0.061	6.35	0.074	0.046	0.00	0.68	0.30
Gel+Thio	0.050	6.65	0.029	0.028	0.29	0.00	1.10

Results after 7 days incubation at 60°C; bio-Trypcase, casamino acids and gelatin were added at 5 g/liter; M: Basal medium containing 1g/liter yeast extract; Thio: thiosulfate (20mM); Casa: casamino acids; Biot: bio-Trypcase; Gel: gelatin.

Materials and Methods

Organisms. *Thermoanaerobacter thermohydrosulfuricus* (DSM No. 567), *T. brockii* (DSM No. 1457), *T. finnii* (DSM No. 3389), and *T. ethanolicus* (DSM No. 2246) were obtained from DSM (Deutsche Sammlung von Mikroorganismen, Braunschweig, Germany). Strain SEBR 5268 was isolated from an oil-producing well in France; the characteristics were reported previously [3, 9].

Culture medium. All experiments were performed at 60°C in the basal medium that was supplemented with yeast extract ($1gL^{-1}$) as described previously [9]. Thiosulfate, casamino acids (DIFCO, USA), gelatin (Sigma, USA) and the following peptones from different sources were added from separately autoclaved stock solutions: bio-Trypcase (bioMérieux, France), pancreatic Peptone (PROLABO, France), Bactopeptone (DIFCO, USA), bio-Gelytone (bioMérieux, France), Soja bean papainic peptone (Institut Pasteur Production, France). The anaerobic techniques of Hungate [14] were used throughout this work. After preparing the anaerobic medium, we dispensed this liquid medium into Hungate tubes (5 ml) or serum bottles (50 ml) under a stream of oxygen-free nitrogen gas.

Analytical techniques. Duplicate vessels were used during the course of this work. Optical density, dissolved hydrogen sulfide, hydrogen, and volatile fatty acids were analyzed as previously described [9].

Results and Discussion

The physiology and metabolism of the members of the genus *Thermoanaerobacter* are poorly understood. They have been classified as carbohydrate-fermenting bacteria, which typically produce ethanol, acetate, lactate, hydrogen, and carbon dioxide as end-products [16]. None of the members of the genus *Thermoanaerobacter* are reported to oxidize peptides or amino acids with the exception of *T. thermohydrosulfuricus*, which has been shown to use peptides but not amino acids [12, 16, 26]. Furthermore, *Thermoanaerobacter brockii* (previously classified as *Thermoanaerobium brockii*) has been described as not using these organic compounds (e.g., tryptone and casamino acids, [28]). Recent physiological studies have shown that *Thermoanaerobacter finnii* and *Thermoanaerobac-*

ter strain SEBR 5268 oxidized H_2 in the presence of thiosulfate [9]. We now provide evidence that in the case of these two strains, amino acids and peptides from different biological sources (Tables 1 and 2) are utilized more efficiently if thiosulfate is added to the medium. In the presence of thiosulfate, there is an increase in optical density and/or the production of volatile fatty acids, viz. acetate, iso-butyrate, iso-valerate, and propionate, whereas in the absence of thiosulfate these activities are limited (Tables 1 and 2). In contrast, only an insignificant increase in the growth of the two strains of *Thermoanaerobacter* species was noted on gelatin as an energy source (Tables 1 and 2). This slight increase in growth may be due to weak proteolytic activities by *Thermoanaerobacter* species studied or to the presence of contaminating small peptide residues in gelatin preparation. Indeed, when bio-Gelytone, which is a tryptic digest of gelatin, was used in the presence of thiosulfate, very good growth and a significant volatile fatty acid production was observed, in particular with *Thermoanaerobacter* SEBR 5268 (Table 1).

The three remaining *Thermoanaerobacter* species, namely, *T. ethanolicus*, *T. thermohydrosulfuricus*, and *T. brockii*, were also tested for growth on casamino acids and bio-Trypcase (Table 3). In the presence of thiosulfate, the three species were also able to use the peptides and amino acids significantly, but not gelatin.

The results provided in Tables 1, 2, and 3 indicate for the first time that all the *Thermoanaerobacter* species tested utilize peptides and amino acids more efficiently when thiosulfate is added as an electron acceptor. However, the efficiency with which these compounds are used is species/strain dependent. The most efficient utilizers are *T. finnii*, *T. brockii*, and *Thermoanaerobacter* SEBR 5268, while *T. ethanolicus* and *T. thermohydrosulfuricus* are poor utilizers. In all five *Thermoanaerobacter* strains, together with improved growth and/or an improved production of volatile fatty acids, sulfide is also produced, while a decrease in hydrogen levels is observed, in particular with *T. brockii*, *T. finnii*, and *Thermoanaerobacter* SEBR 5268 (Tables 1, 2, and 3). The production of hydrogen and volatile fatty acids during bio-Trypcase fermentation in the presence and in the absence of thiosulfate by *T. brockii*, a proficient user of peptides, and *T. ethanolicus*, a poor utilizer of peptides, is shown in Figures 1 and 2.

This is the first report on amino acid oxidation by members of the *Thermoanaerobacter* genus, particularly in the presence of thiosulfate as electron acceptor. We also show the ability of this genus to produce

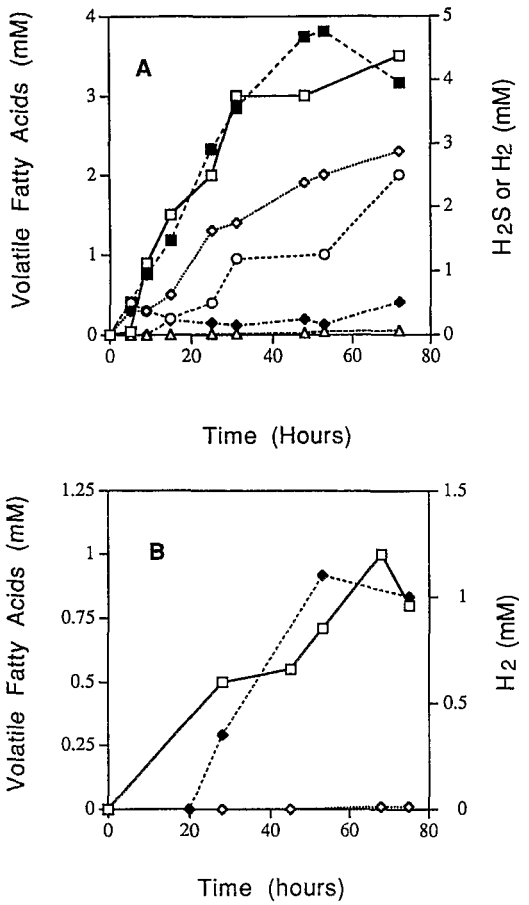

Fig. 1. Metabolite production from bio-Trypcase oxidation by *T. brockii*, in the presence (**A**) and in the absence (**B**) of thiosulfate: acetate, □; isobutyrate, ○; isovalerate, ◇; propionate, △; H_2, ◆; H_2S, ■.

propionate even though it is a minor product from peptide metabolism as described within the sulfur reducers, hyperthermophilic *Archaea* [4]. The other volatile fatty acids produced such as acetate, iso-butyrate, and iso-valerate are typical end-products obtained from amino acid or peptide oxidation by a variety of mesophilic anaerobes [15, 19, 23], but also by several hyperthermophilic *Archaea* [4].

The ability of *Thermoanaerobacter* species to grow on amino acids and/or peptides while being stimulated by thiosulfate indicates that they may be growing by mixotrophy. There is no direct evidence of this hypothesis as we have not studied enzymes involved in this process. However, indirect evidence does suggest this, as all the members are stimulated by the presence and subsequent reduction of thiosulfate during amino acid and/or peptide oxidation, resulting in an increase in hydrogen sulfide. It has also been reported that members of the genus *Thermo-*

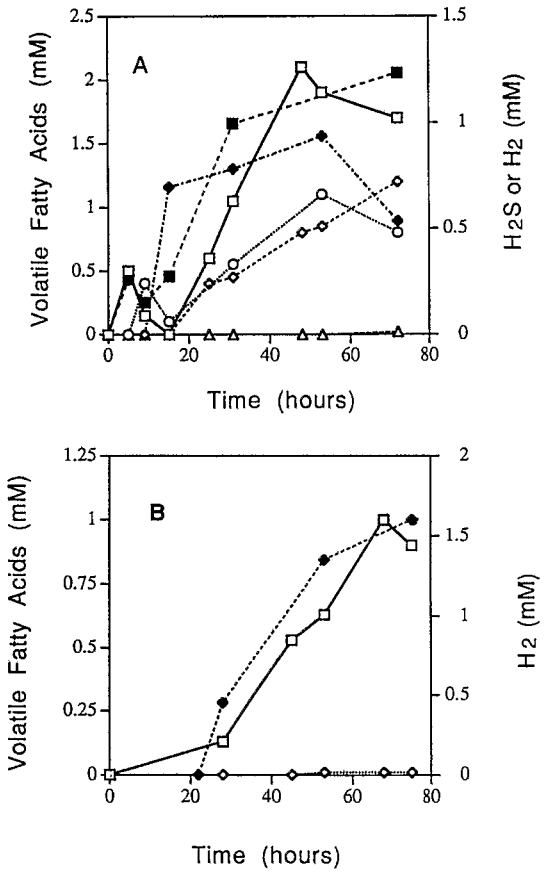

Fig. 2. Metabolite production from bio-Trypcase oxidation by *T. ethanolicus*, in the presence (**A**) and in the absence (**B**) of thiosulfate: acetate, □; isobutyrate, ○; isovalerate, ◇; propionate, △; H_2, ◆; H_2S, ■.

anaerobacter are able to oxidize hydrogen in the presence of thiosulfate [9, 10], indicating there could be a role played by hydrogenases in the process of thiosulfate reduction. The members of the genus *Thermoanaerobacter* can be considered similar to some of the facultative autotrophic hyperthermophilic belonging to the *Archaea* domain (e.g., *Pyrobaculum*, *Thermococcus*, *Staphylothermus*, and *Pyrococcus* species), which are able to grow by heterotrophic mode on yeast extract or cell extracts in the presence of added mineral electron acceptors such as elemental sulfur [1, 4, 13]. Further phenotypic similarities between the genus *Thermoanaerobacter* and the hyperthermophilic sulfur reducers *Archaea* are evidenced by the typical end-products obtained from peptide oxidation as discussed above [4].

Members of the genus *Thermoanaerobacter* to date have been considered to be important only in sugar fermentation. However, the results presented here indicate that they also have an equally important role to play in degradation of proteinaceous compounds such as peptides or amino acids. They must play a very important role in the overall decomposition processes in the hot spring ecosystem where organic matter and thiosulfate are present. Thiosulfate can be formed by chemical oxidation of sulfides [2, 6, 7] and is known to exist in some hot springs but absent in others [5].

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Literature Cited

1. Adams MWW (1990) The metabolism of hydrogen by extremely thermophilic, sulfur-dependent bacteria. FEMS Microbiol Rev 75:219–238
2. Barrett EL, Clark MA (1987) Tetrathionate reduction and production of hydrogen sulfide from thiosulfate. Microbiol Rev 51:192–205
3. Bernard FP, Connan J, Magot M (1992) Indigenous microorganisms in connate water from many oil fields: a new tool in exploration and production techniques. Proceedings of the 67th Annual Conference and exhibition of the Society of Petroleum Engineers. Richardson, TX, Society of Petroleum Engineers Inc., pp. 467–476
4. Bonch-Osmolovskaya EA, Stetter KO (1991). Interspecies hydrogen transfer in cocultures of thermophilic *Archaea*. Syst Appl Microbiol 14:205–208
5. Brock TD, Brock ML, Bott TL, Edwards MR (1971) Microbial life at 90°C: the bacteria of Boulder Spring. J Bacteriol 107:303–314
6. Crolet JL, Daumas S, Magot M (1993) pH regulation by sulfate-reducing bacteria. In: Corrosion 93. Houston, TX: NACE, paper No. 303
7. Cypionka H, Widdel F, Pfennig N (1985) Survival of sulfate-reducing bacteria after oxygen stress, and growth in sulfate-free oxygen-sulfide gradients. FEMS Microbiol Ecol 31:39–45
8. Dowell VR, Lombard GL (1981) Pathogenic members of the genus *Bacteroides*. In: Starr MP, Stolp H, Trüper HG, Balows A, Schlegel HG (eds) The Prokaryotes, Vol 2. Berlin, Heidelberg, New York: Springer Verlag, pp. 1425–1449
9. Fardeau ML, Cayol JL, Magot M, Ollivier B (1993) H_2 oxidation in the presence of thiosulfate by a *Thermoanaerobacter* strain isolated from an oil-producing well. FEMS Microbiol Lett 113:327–332
10. Fardeau ML, Cayol JL, Magot M, Ollivier B (1994) Hydrogen oxidation abilities in the presence of thiosulfate as electron acceptor within the genus *Thermoanaerobacter*. Curr Microbiol 29:269–272
11. Gottschalk G, Andreesen JR, Hippe H (1981) The genus *Clostridium* (nonmedical aspects). In: Starr MP, Stolp H, Trüper HG, Balows A, Schlegel HG. (eds) The Prokaryotes, Vol 2. Berlin, Heidelberg, New York: Springer Verlag, pp. 1767–1803
12. Hollaus F, Sleytr U (1972) On the taxonomy and fine structure of some hyperthermophilic saccharolytic clostridia. Arch Mikrobiol 86:129–146
13. Huber R, Kristjansson JK, Stetter KO (1987) *Pyrobaculum* gen. nov., a new genus of neutrophilic, rod shaped archaebacteria from continental solfataras growing optimally at 100°C. Arch Microbiol 149:95–101

14. Hungate RE (1969) A roll tube method for cultivation of strict anaerobes. In: Norris JR, Ribbons DW (eds), Methods Microbiol 3B:117–132
15. Jain MK, Zeikus JG (1989) Bioconversion of gelatin to methane by a coculture of *Clostridium collagenovorans* and *Methanosarcina barkeri*. Appl Environ Microbiol 55:366–371
16. Lee YE, Jain MK, Lee C, Lowe SE, Zeikus JG (1993) Taxonomic distinction of saccharolytic thermophilic anaerobes: description of *Thermoanaerobacterium xylanolyticum* gen. nov., sp. nov., and *Thermoanaerobacterium saccharolyticum* gen. nov., sp. nov.; reclassification of *Thermoanaerobium brockii*, *Clostridium thermosulfurogenes*, and *Clostridium thermohydrosulfuricum* E100-69 as *Thermoanaerobacter brockii* comb. nov., *Thermoanaerobacterium thermohydrosulfugenes* comb. nov., and *Thermoanaerobacter thermohydrosulfuricus* comb. nov., respectively; and transfer of *Clostridium thermohydrosulfuricum* 39E to *Thermoanaerobacter ethanolicus*. Int J Syst Bacteriol 43: 41–51
17. Lowe SE, Mahendra KJ, Zeikus JG (1993) Biology, ecology, and biotechnological applications of anaerobic bacteria adapted to environmental stresses in temperature, pH, salinity, or substrates. Microbiol Rev 57:451–509
18. Ma K, Schicho RN, Kelly M, Adams MWW (1993) Hydrogenase of hyperthermophile *Pyrococcus furiosus* is a elemental sulfur reductase or sulfhydrogenase: evidence for a sulfur-reducing hydrogenase ancestor. Proc Natl Acad Sci USA 90:5341–5344
19. Mc Sweeny CS, Allison MJ, Mackie RI (1993) Aminoacid utilization by the ruminal bacterium *Synergystes jonesii* strain 78-1. Arch Microbiol 159:131–135
20. Ollivier B, Mah RA, Ferguson TJ, Boone DR, Garcia JL, Robinson R (1985) Emendation of the genus *Thermobacteroides*; *Thermobacteroides proteolyticus* sp. nov., a proteolytic acetogen from a methanogenic enrichment. Int J Syst Bacteriol 35:425–428
21. Patel BKC, Skerratt JH, Nichols PD (1991) The phospholipid ester-linked fatty acid composition of thermophilic bacteria. Syst Appl Microbiol 14:311–316
22. Rainey FA, Stackebrandt E (1993) Transfer of the type species of the genus *Thermobacteroides* to the genus *Thermoanaerobacter* as *Thermoanaerobacter acetoethylicus* (Ben-Bassat and Zeikus 1981) comb. nov., description of *Coprothermobacter* gen. nov., and reclassification of *Thermobacteroides proteolyticus* as *Coprothermobacter proteolyticus* (Ollivier et al. 1985) comb. nov. Int J Syst Bacteriol 43:857–859
23. Stams AJM, Hansen TA (1984) Fermentation of glutamate and other compounds by *Acidaminobacter hydrogenoformans* gen. nov., an obligate anaerobe isolated from black mud. Studies with pure cultures and mixed cultures with sulfate-reducing and methanogenic bacteria. Arch Microbiol 137:329–337
24. Stetter KO, Fiala G, Huber G, Huber R, Segerer A (1990) hyperthermophilic microorganisms. FEMS Microbiol Rev 75: 117–124
25. Toda Y, Saiki T, Uozumi T, Beppu T (1988) Isolation and characterization of a protease producing, thermophilic, anaerobic bacterium, *Thermobacteroïdes leptospartum* sp. nov. Agric Biol Chem 52:1339–1344
26. Wiegel J, Ljungdahl LS, Rawson JR (1979) Isolation from soil and properties of the extreme thermophile *Clostridium thermohydrosulfuricum*. J Bacteriol 139:800–810
27. Zeikus JG (1979) Thermophilic bacteria: ecology, physiology and technology. Enzyme Microbiol Technol 1:243–252
28. Zeikus JG, Hegge PW, Anderson MA (1979) *Thermoanaerobium brockii* gen. nov. and sp. nov., a new chemoorganotrophic, caldoactive, anaerobic bacterium. Arch Microbiol 122:41–48