

# 32 The Family *Thermoanaerobacteraceae*

Erko Stackebrandt

Leibniz Institute DSMZ-German Collection of Microorganisms and Cell Cultures GmbH,  
Braunschweig, Germany

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## Abstract

The family *Thermoanaerobacteraceae* is a family of the order *Thermoanaerobacterales*, phylum Firmicutes, comprising several genera of strictly anaerobic, rod-shaped, spore-forming bacteria which were mostly isolated from hot springs. The metabolism is variable, ranging from carbohydrate fermentation to chemolithoautotrophy. Reduction of thiosulfate varies. This brief overview concentrates on genera and species described since 2006, and which are not covered in the chapter *Thermoanaerobacteraceae* in *Bergey's Manual of Systematic Bacteriology*, 2nd edition.

## Taxonomy

The family *Thermoanaerobacteraceae* (Wiegel 2009) encompasses the genera *Ammonifex*, *Brockia*, *Caldanaerobacter*, *Caldanaerobius*, *Caloribacterium*, *Carboxydotherrmus*, *Desulfoviregula*, *Gelria*, *Moorella*, *Tepidanaerobacter*, *Thermacetogenium*, *Thermanaeromonas*, and the type genus *Thermoanaerobacter*. The genus list of Euzéby (<http://www.bacterio.net/>) lists a few more genera though the type species were transferred to other genera; as the taxa were validly published, they did keep their taxonomic status: *Acetogenium kivui* was reclassified as *Thermoanaerobacter kivui* (Collins et al. 1994), *Carboxydibrachium pacificum* as *Caldanaerobacter subterraneus* subsp. *pacificum* (Fardeau et al. 2004), *Thermoanaerobium acetigenum* as *Caldicellulosiruptor acetigenus* (Onyenwoke et al. 2006), *Thermoanaerobium brockii* as *Thermoanaerobacter brockii* subsp. *brockii* (Lee et al. 1993), and species of *Thermobacteroides* to *Thermoanaerobacter* (Rainey and Stackebrandt 1993), *Clostridium* (Fardeau et al. 2001), and *Coprothermobacter* (Rainey and Stackebrandt 1993).

The last comprehensive coverage of the family *Thermoanaerobacteraceae* has been presented by 2009 in *Bergey's Manual of Systematic Bacteriology*, 2nd ed (Wiegel 2009), covering descriptions since 2006. Since then, new genera and new species of genera described until 2006 were proposed. This

communication concentrates on recently described genera and species, and the reader should consult the chapter of 2009 for obtaining a more comprehensive overview of the biology of family members. ♦ [Table 32.1](#) is a list of species belonging to genera described until 2006, together with some of the salient feature of these taxa. ♦ [Table 32.2](#) compiles recently described genera of *Thermoanaerobacteraceae*.

The family contains anaerobic, mainly heterotrophic, but also chemolithoautotrophic members. Cells are mainly Gram positive, rod shaped, and spore forming, though some species stain Gram negatively, while no spores have been reported for other species. The family is phylogenetically heterogeneous, forming individual clades which are related to other families according to the ML tree (♦ [Fig. 32.1](#)). The heterogeneity has been observed by Sekiguchi et al. (2006), while other species description exclusively included members of the family as reference strains in depicting phylogenetic dendrograms. *Thermoanaerobacter* and *Caldanaerobacter* are closely related and group adjacent to a clade consisting of *Coprothermobacter*, *Dictyoglomus*, and other *Thermoanaerobacteraceae* members such as *Ammonifex*, *Tepidanaerobacter*, and *Brockia*. *Desulfoviregula* and *Thermanaeromonas* form a third clade. A fourth clade is phylogenetically heterogeneous in itself as it embraces authentic clostridia, symbiotic and syntrophic taxa, *Heliobacteriaceae* and *Peptococcaceae*, as well as the *Thermoanaerobacteraceae* members *Caldanaerobius*, *Caloribacterium*, *Symbiobacterium*, *Gelria*, and *Moorella*. *Syntrophaceticus schinkii* and *Symbiobacterium thermophilum*, not reported to be members of *Thermoanaerobacteraceae*, cluster closely with *Thermacetogenium schinkii* and *Gelria glutamica*, respectively. A fifth clade consists of *Carboxydotherrmus*. This family is certainly in need of a taxonomic revision.

## Genome Sequences

Several representatives of *Thermoanaerobacteraceae*, especially from the type genus, were subjected to the analysis of genome sequences. Only a few examples of published or deposited sequences of strains of the various genera are given in ♦ [Table 32.3](#). More information is available in the GOLD database ([genomes.org/cgi-bib/Gold/Search.cgi](http://genomes.org/cgi-bib/Gold/Search.cgi)).

■ Table 32.1  
Species published since 2006, for genera described before 2006

Genus	<i>Moorella</i>		<i>Carboxydotherrmus</i>	
Species	<i>humiferrea</i>	<i>pertinax</i>	<i>islandicus</i>	<i>siderophilus</i>
Gram-stain	Positive	n.r.	Positive	Positive
Motility	Peritrichous flagella	Peritrichous flagella	Peritrichous flagella	Lateral flagella
Morphology	Straight rods, singly or short chains	Rods	Short, slightly curved rods	Short, straight rods
Spore formation	+ in terminal swollen sporangia	n.r.	n.r.	–
Growth range °C optimum	46.0–70.0 (65.0)	50.0–70.0 (65.0)	50.0–70.0 (65.0)	40.0–78.0 (70.0–72.0)
pH range optimum	5.5–8.5 (7.0)	4.6–8.6 (6.0–6.5)	5–8 (5.5–6.0)	6.6–8.0 (7.0)
Metabolism	Lactate, malate succinate, glycerol, YE as electron donors, 9,10-anthraquinon-2,6-disulfonate as electron shuttle to Fe(III) oxide. Various hexose, pyruvate, and peptone are fermented	YE, peptone, pyruvate, glucose, or chemolithoautotrophic on CO as electron donor, and ferric citrate, amorphous Fe (III) oxide, and 9,10-anthraquinon-2,6-disulfonate as electron acceptors. CO + H <sub>2</sub> O → CO <sub>2</sub> + H <sub>2</sub>	YE, lactate, pyruvate, or chemolithoautotrophic on CO as electron donor, 9,10-anthraquinon-2, 6-disulfonate as electron acceptor. CO + H <sub>2</sub> O → CO <sub>2</sub> + H <sub>2</sub>	Chemoheterotrophic with glucose, xylose, lactate, or YE; chemolithotrophic with CO, in the presence of Fe(III) or 9,10-anthraquinon-2,6-disulfonate hydrogen, CO <sub>2</sub> and Fe(II), or AQDSH <sub>2</sub> , respectively, are produced
Endproducts of carbohydrate fermentation	Fructose: acetate	Check	Pyruvate: acetate, CO <sub>2</sub> , H <sub>2</sub>	None
Sulfur metabolism	Thiosulfate reduced to sulfide	Thiosulfate and elemental sulfur not reduced	Thiosulfate and elemental sulfur not reduced	Thiosulfate and elemental sulfur not reduced
Major fatty acids >10 %	n.r.	iso-C <sub>15:0</sub> , C <sub>15:0</sub> , C <sub>15:0</sub> DMA and/or C <sub>14:0</sub> 3-OH	C <sub>14:0</sub> , iso-C <sub>15:0</sub> , C <sub>16:0</sub>	n.r.
Mol% G+C	51	42.2	37.7	41.5
Type strain	64-FGQ <sup>T</sup>	Ug1 <sup>T</sup>	SET IS-9 <sup>T</sup>	1315 <sup>T</sup>
Habitat	Terrestrial hypothermic spring, Kamchatka, Russia	Hot spring, Kyushu Island, Japan	Hot spring, Iceland	Hot spring, Kamchatka, Russia
Publication	Nepomnyashchaya et al. 2012	Yoneda et al. 2012	Novikov et al. 2011	Slepova et al. 2009
Genus	<i>Thermoanaerobacter</i>			<i>Ammonifex</i>
Species	<i>pseudethanolicus</i> <sup>a</sup>	<i>thiophilus</i>	<i>uzonensis</i>	<i>pentosaceus</i>
Gram stain	Positive	Positive	Type positive, stain negative	Stain negative
Motility	+	Peritrichous flagella	Peritrichous flagella	–
Morphology	Rods, older cells form chains of coccoid cells to long filamentous cells	Rods, singly or pairs	Straight to slightly curved rods	Rods, single, pairs, short chains
Spore formation	Round, terminal	Round, terminal	Oval, subterminal	Terminal

■ Table 32.1 (continued)

Genus	<i>Thermoanaerobacter</i>			<i>Ammonifex</i>
	<i>pseudethanolicus</i> <sup>a</sup>	<i>thiophilus</i>	<i>uzonensis</i>	<i>pentosaceus</i>
Growth range °C optimum	37.0–76.0 (65.0–70.0)	60.0–82.0 (75.0)	32.5–69.0 (61.0)	50.0–80.0 (70.0)
pH range optimum	5.8–8.5	6.0–7.5 (6.8–7)	4.2–8.9 (7.1)	5.4–8.9 (7.0)
Metabolism	Chemoorganotroph. Fermentation of glucose, fructose, mannose, galactose, ribose, xylose, lactose, sucrose, maltose, cellobiose, starch, and pyruvate in the presence of YE	Autotrophic growth with CO <sub>2</sub> as carbon source and H <sub>2</sub> or formate as electron donors. Facultative chemolithoautotrophic	Chemoorganotroph. YE, various hexoses, cellobiose, inulin, mannitol, pyruvate, crotonate	Chemoorganotroph. YE, various hexoses, pectin, starch, xylose
Endproducts of carbohydrate fermentation	Hexoses, starch: ethanol and CO <sub>2</sub> ; lactate and acetate in minor amounts	Not fermentative	Glucose: acetate, ethanol, CO <sub>2</sub> , H <sub>2</sub>	Xylose: ethanol, H <sub>2</sub> , lactate, acetate. Presence of thiosulfate shifts the endproducts toward acetate, sulfite enhances formation of ethanol
Sulfur metabolism	Thiosulfate and sulfite reduced to H <sub>2</sub> S	Weak growth with sulfate, sulfur, thiosulfate reduced	Thiosulfate reduced to sulfide. In the presence of YE, glucose, and thiosulfate, H <sub>2</sub> S and elemental sulfur are formed	Sulfite and thiosulfate reduced
Major fatty acids >10 %	n.r.	n.r.	iso-C <sub>15:0</sub> , C <sub>15:0</sub>	iso-C <sub>15:0</sub> , iso-C <sub>14:0</sub> 3-OH, iso-C <sub>17:0</sub>
Mol% G+C	32–34.4	56.2	33.6	34.2
Type strain	39E <sup>T</sup>	SR <sup>T</sup>	JW/IWO10 <sup>T</sup>	DTU01 <sup>T</sup>
Habitat	Octopus spring, Yellowstone, USA	Hot spring, Kamchatka, Russia	Hot spring, Kamchatka, Russia	Household waste reactor
Publication	Onyenwoke et al. 2007	Miroshnichenko et al. 2008	Wagner et al. 2008	Tomas et al. 2013

n.r. not recorded, n.a. not applicable, YE yeast extract

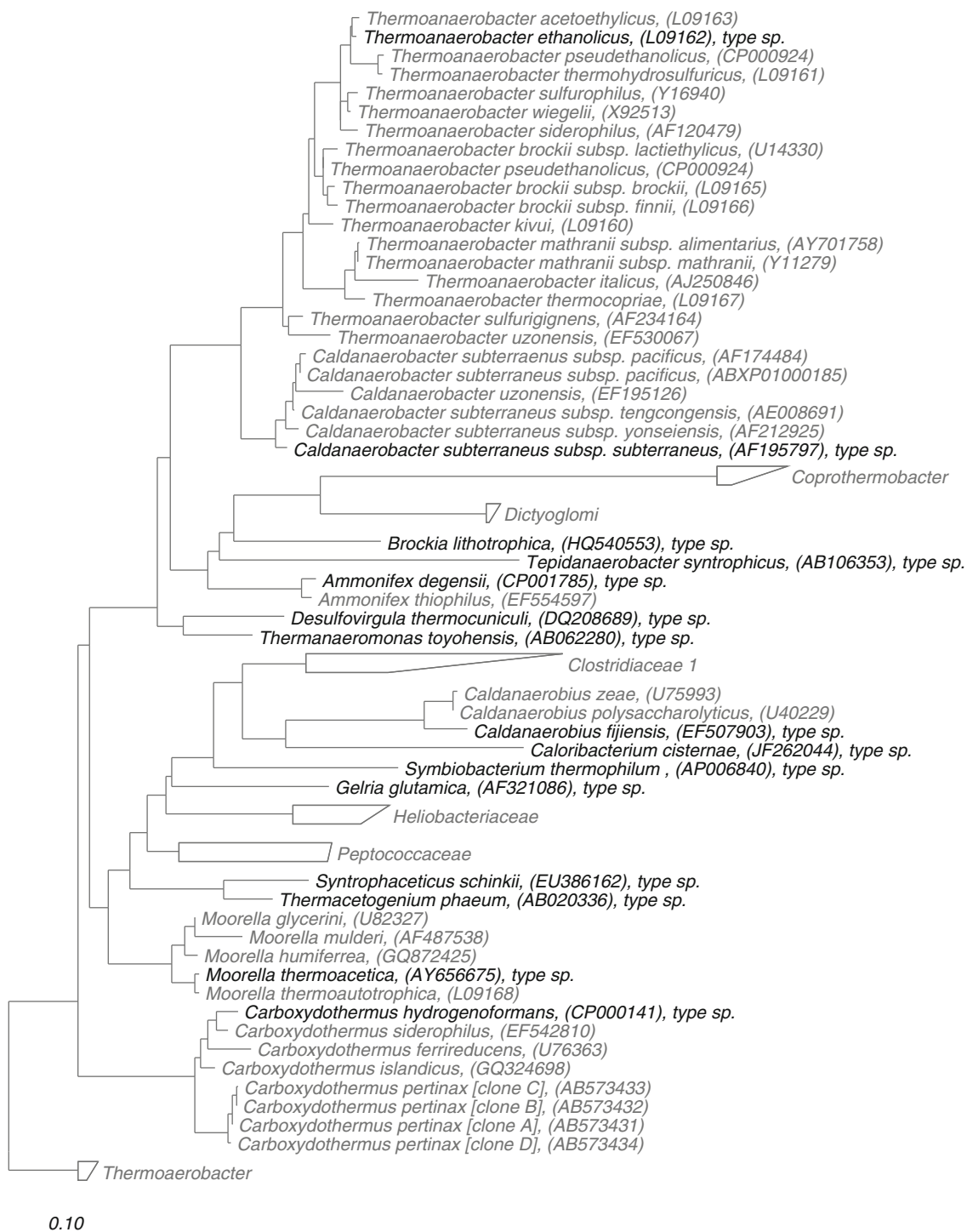
<sup>a</sup>According to Hollaus and Sleytr (1972) based upon *Clostridium thermohydrosulfuricum* ATCC 7956<sup>T</sup> and on *Thermoanaerobacter ethanolicus* (Wiegel and Ljungdahl 1981; Lee et al. (1993))

■ Table 32.2

New genera of *Thermoanaerobacteraceae* and their species, described since 2006

Genus	<i>Caldanaerobius</i>	<i>Brockia</i>	<i>Caloribacterium</i>	<i>Tepidanaerobacter</i>
Species	<i>fijiensis</i>	<i>lithotrophica</i>	<i>cisternae</i>	<i>syntrophicus</i>
Gram type/ stain	Type positive, stain negative	Type positive	Type positive	Type positive, stain negative
Motility	Peritrichous flagella	Peritrichous flagella	Nonpolar flagella	—
Morphology	Straight to slightly curved	Thin regular rods, singly or pairs	Straight rods, singly or pairs	Irregular rods
Spore formation	Spherical, terminal		—	—
Growth range °C (optimum)	40.0–67.0 (60.0–63.0)	46.0–78.0 (60.0–65.0)	28.0–65.0 (50.0)	25.0–60.0 (45.0–50.0)
pH range (optimum)	4.5–8.4 (6.8)	5.5–8.5 (6.5)	5.5–8.0 (7–7.5)	5.5–8.5 (6–7)
Substrates used	YE, various pentoses, hexoses, cellobiose	H <sub>2</sub> , formate as electron donors, elemental sulfur, thiosulfate, polysulfide as electron acceptors	YE, peptone, various hexoses, pyruvate, citrate	YE, various riboses, hexoses, starch, pectin, crotonate. In coculture with <i>Methanothermobacter thermoautotrophicus</i> , ethanol, glycerol, and lactate are utilized
Endproducts of glucose fermentation	Ethanol, acetate formate	Not applicable	Acetate, hydrogen, CO <sub>2</sub>	(Plus YE), acetate, H <sub>2</sub>
Sulfur metabolism	Thiosulfate reduced to elemental sulfur	H <sub>2</sub> -sulfur metabolism	Thiosulfate reduced to sulfide	Thiosulfate reduced
Major fatty acids >10 %	n.r.	C <sub>16:0</sub> , iso-C <sub>16:0</sub> , C <sub>18:0</sub> , iso-C <sub>17:0</sub>	iso-C <sub>15:0</sub> , C <sub>16:0</sub> , iso-C <sub>17:1</sub> ω8, C <sub>18:0</sub>	iso-C <sub>15:0</sub> , C <sub>16:1</sub> ω9C, C <sub>15:1</sub>
Mol% G+C	37.6	63	43.1	37–38
Habitat	Sediment hot spring, Fiji	Sediment hot spring, Kamchatka, Russia	Underground gas storage reservoir, Siberia, Russia	Thermophilic sludge digester, Japan
Type strain	JW/YJL-F3 <sup>T</sup>	Kam1851 <sup>T</sup>	SGL43 <sup>T</sup>	JL <sup>T</sup>
Publication	Lee et al. 2008	Perevalova et al. 2013	Slobodkina et al. 2012	Sekiguchi et al. 2006

For abbreviations see ▶ Table 32.1



■ Fig. 32.1

Neighbor-joining genealogy reconstruction based on the RAxML algorithm (Stamatakis 2006) of the sequences of members of the family *Thermoanaerobacteraceae* and some neighboring taxa present in the LTP\_106 (Yarza et al. 2010). The tree was reconstructed by using a subset of sequences. Representative sequences from closely relative genera were used to stabilize the tree topology. In addition, a 40 % maximum frequency filter was applied to remove hypervariable positions from the alignment. Scale bar indicates estimated sequence divergence

■ Table 32.3

Examples of complete, incomplete, and draft genome sequences of *Thermoanaerobacteraceae* members as listed in the GOLD genome database

Taxon	Strain number	GOLD identification	Status
<i>Ammonifex degensii</i>	KC4	Gc02209	Complete, unpublished
<i>Caldanaerobacter subterraneus</i>	MB4 <sup>T</sup>	Gc00086	Bao et al. 2002
Sequenced as <i>Thermoanaerobacter tengcongensis</i>			
<i>Caldanaerobius polysaccharolyticum</i>	DSM 13641 <sup>T</sup>	Gi02942	Incomplete, unpublished
<i>Carboxydothemus ferrireducens</i>	DSM 11255 <sup>T</sup>	Gr00123	Permanent draft, unpublished
<i>Carboxydothemus hydrogenoformans</i>	DSM 6008 <sup>T</sup>	Gc00307	Wu et al. 2005
<i>Desulfoviregula thermocuniculi</i>	DSM 16036 <sup>T</sup>	Gi11444	Permanent draft, unpublished
<i>Moorella thermoacetica</i>	ATCC 39073	Gc00397	Pierce et al. 2008
<i>Tepidanaerobacter acetatoxydans</i>	Re1	Gc02475	Manzoor et al. 2013
<i>Thermacetogenium phaeum</i>	PB	Gc0028002	Oehler et al. 2012
<i>Thermanaeromonas toyohensis</i>	DSM 14490	Gi04363	Incomplete, unpublished
<i>Thermoanaerobacter mathranii</i>	DSM 11426 <sup>T</sup>	Gc01347	Complete, unpublished
<i>Thermoanaerobacter thermocopriae</i>	ATCC 51646	Gi22384	Complete, unpublished
<i>Thermoanaerobacter pseudethanolicus</i>	ATCC 33223 <sup>T</sup>	Gc00718	Hemme et al. 2011

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