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REVIEWS

Microbial Diversity of Methanogenic Communities in the Systems for Anaerobic Treatment of Organic Waste

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Abstract—Methane production via anaerobic degradation of organic-contaminated wastewater, semiliquid, or solid municipal waste of complex composition by methanogenic microbial communities is a multistage process involving at least four groups of microorganisms. These are hydrolytic bacteria (polysaccharolytic, proteolytic, and lipolytic), fermentative bacteria, acetogenic bacteria (syntrophic, proton-reducing), and methanogenic archaea; complex trophic interactions exist between these groups. The review provides information concerning the diversity of the major microbial groups identified in the systems for wastewater and concentrated waste treatment, solid-phase anaerobic fermentation, and landfills for disposal of municipal solid waste, and also specifies the sources of isolation of the type strains. The research demonstrates that both new microorganisms and those previously isolated from natural habitats may be found in waste treatment systems. High microbial diversity in the systems for organic waste treatment provides for stable methanogenesis under fluctuating environmental conditions.

Keywords: anaerobic bacteria and archaea, methanogenic microbial communities, methanogenesis, organic waste

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INTRODUCTION

Anaerobic microbial degradation of organic matter (OM) is a multistage process of OM conversion into biogas, containing mainly methane and CO_2. At least four groups of microorganisms are involved in this process: hydrolytic bacteria (polysaccharolytic, proteolytic, and lipolytic), fermentative bacteria, acetogenic bacteria (syntrophic, proton-reducing), and methanogenic archaea. Since every group of microorganisms in methanogenic communities has specific substrates and products of metabolism, this community is able to switch between different pathways of OM decomposition, acting as a self-regulating system maintaining the optimal values of pH, Eh, and other environmental parameters [1].

The electron acceptor used for anaerobic OM decomposition is OM carbon, which is reduced to methane via a sequence of intermediate stages. OM carbon oxidized to CO_2 is used as the electron donor for this process. Thus, anaerobic microbial degradation results in OM conversion from the solid (liquid) phase to the gas phase. This pattern is the basis of the biotechnology for utilization of almost all kinds of organic waste [2]. Relatively low production of microbial biomass, applicability for concentrated wastewater and solid waste, as well as production of a renewable energy source (methane) are the advantages of anaerobic OM treatment [3]. This biotechnology is considered reliable and is used in full-scale treatment facilities in many countries of Europe, Asia, and America. New technologies aimed at more efficient water treatment, accelerated utilization of solid organic waste, and increased yield of methane are being developed under laboratory conditions [4].

Since the understanding of specifics of microbial activity is important for high efficiency of waste treatment, determination of the structure of microbial communities in anaerobic reactors is of importance for engineering. Thus, knowledge of the responses of methanogenic communities to varying conditions in the system is essential for stable and efficient operation

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Abbreviations: ARDRA, amplified ribosomal DNA restriction analysis; ASBR, anaerobic sequencing batch reactor; CSTR, continuously stirred tank reactor; CFSTR, continuous-flow stirred-tank reactor; DGGE, denaturing gradient gel electrophoresis; EGSB, anaerobic expanded granular sludge bed reactor; FISH, fluorescence in situ hybridization; LB, batch leach bed reactor; MAR-FISH, microautoradiography-fluorescence in situ hybridization; MSW, municipal solid waste; OM, organic matter; PB, packed-bed reactor; qPCR, quantitative PCR; RT-PCR, real-time PCR; SSCP, single strand conformation polymorphism; T-RFLP, terminal restriction fragment length polymorphism; VFA, volatile fatty acids; UAF, up-flow anaerobic filter reactor; UASB, up-flow anaerobic sludge blanket reactor.

of an anaerobic reactor. A number of works dealt with determination of the diversity and activity of methanogens in the reactors treating, municipal, and industrial wastewater of complex composition, as well as simple soluble substrates (mostly synthetic ones). There are, however, relatively few works dealing with the structure of methanogenic communities in the systems of solid-phase fermentation [5]. Development of culture-independent molecular biological techniques of the 16S rRNA gene analysis facilitated investigations of microbial communities, including the communities of waste treatment systems, where microbial diversity is extremely high. Application of molecular approaches to anaerobic reactors and municipal solid waste (MSW) landfills resulted in detection of the organisms related to both cultured and uncultured microorganisms, as well as some unknown organisms with unclear function.

Detailed information concerning the trophic relations and biochemical characteristics of the major microbial groups within methanogenic communities has been provided in numerous publications [1, 6–12]. The present review characterizes organic waste and briefly describes the fundamental basics of anaerobic OM decomposition and of the functioning of methanogenic communities. Specific attention is paid to phylogenetic diversity of microorganisms (hydrolytics, fermenters, syntrophs, and methanogens) in laboratory and full-scale systems for wastewater treatment, solid-phase anaerobic fermentation, and at the landfills. The microorganisms initially isolated from waste treatment facilities, as well as those detected in these systems by molecular genetic techniques and related to known species isolated from natural habitats, are listed in the text and in the tables.

COMPOSITION OF ORGANIC WASTE

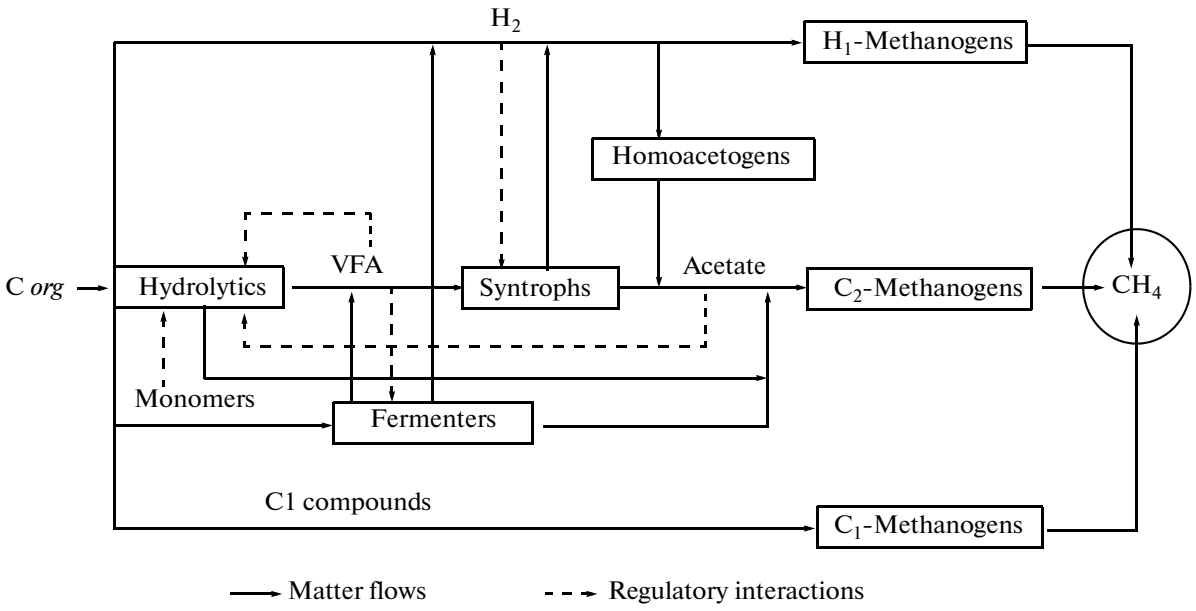
Organic waste is classified according to its origin (as municipal, industrial, and agricultural) or according to its physical state as liquid (wastewater), semiliquid (sewage sludge and semiliquid manure), and solid (MSW, food waste, agricultural waste, and dunnage manure) [3]. The waste contains the whole spectrum of simple and complex OM. Depending on their source (municipal and industrial waste, animal husbandry and agricultural waste), specific organic compounds may predominate, although exact composition of the waste is often unknown. Chemical analysis of the waste, while possible, provides little information useful for development of the technological approaches to waste treatment. Organic waste is therefore conditionally classified according to predominance of one of the three components—carbohydrates, proteins, and fats.

Carbohydrate-rich waste. Carbohydrates are present in all waste, albeit in different proportions. Food waste, as well as waste of the sugar industry or fruit and vegetable processing, is enriched with simple sugars and disaccharides, which are easily decomposed by methanogenic communities with formation of volatile fatty acids (VFA). High levels of simple sugars may result in rapid VFA accumulation in the reactor, decreased pH, and suppression of methanogenesis. For balanced operation of anaerobic reactors, mixing the feedstock containing high amounts of simple carbohydrates with waste with lower content of easily degradable organic components is recommended [13].

The wastes of pulp-and-paper and woodworking industries, MSW, and straw or silage rich in polysaccharides (cellulose and hemicellulose) are difficult to hydrolyze by microorganisms under anaerobic conditions. Physicochemical or biological pretreatment of this material is required for its efficient anaerobic fermentation. Pretreatment is aimed at modification of the structure of hemicellulose or lignin, decreasing the crystallinity of cellulose, and increasing the substrate surface area [4]. Application of agricultural waste without pretreatment results in low biogas yield due to the high values of C/N ratio and lignin content. Moreover, this material may be contaminated by pesticide and herbicide residues, which may affect the kinetics of the process [13, 14].

Protein-rich waste. Similar to carbohydrates, proteins are present in all organic waste. Slaughterhouse waste, pig and poultry manure, and stillage from the ethanol industry are examples of waste with high protein content. Domestic wastewater and food waste also contain proteins, albeit in lower amounts. Microbial degradation of proteins results in release of ammonium ions, which are strong inhibitors of methanogenic communities and may cause reactor malfunction [13].

Fat-rich waste. Waste and wastewater of slaughterhouses, as well as waste from the diary industry and oil production are typical materials with high fat content used for biogas production by anaerobic fermentation. Microbial degradation of fats results in high production of methane-rich biogas. High fat content in the waste may, however, cause reactor malfunction. Thus, degradation of triglycerides produces long-chain fatty acids (over 12 carbon atoms) and glycerol. Glycerol is rapidly converted to biogas, while decomposition of long-chain fatty acids is a more complex process carried out by a syntrophic association of bacteria and hydrogenotrophic methanogens. These acids may be accumulated in the system. Some long-chain fatty acids in high concentrations may inhibit activity of anaerobic microorganisms, including methanogens. Oleic and stearic acids have a negative effect on methanogens at 0.2–0.5 g L^{-1} [14, 15]. Long-chain fatty



Trophic relations in a methanogenic community, from Zavarzin [16].

acids possess also detergent properties, which may cause foaming, especially at elevated temperatures.

Co-fermentation of mixed feedstock. Co-fermentation of mixure of different input materials usually provides better results than fermentation of homogenous substrates. Mixed feedstock probably contains more components required for microbial growth or has the C/N ratio closer to the optimal value. Complex substrates provide for development of various microbial groups, thus increasing the stability of the process and making the system more resistant to toxic compounds. Co-fermentation of various substrates may be used to improve the performance of the reactor, e.g., simplifying the pumping and mixing of the input [13]. Full-scale industrial systems of solid-phase anaerobic fermentation use a mixture of food and agricultural waste, MSW organic fraction, and sewage sludge.

MICROBIAL DIVERSITY IN THE SYSTEMS OF ANAEROBIC WASTE TREATMENT

For fermentation of polymer-containing waste, hydrolysis and VFA decomposition to the substrates of methanogenesis are the key reactions determining the rate of the entire process. Hydrogen is the central metabolite responsible for the regulation of methanogenic communities. When hydrogen partial pressure is maintained at a low level, interspecies hydrogen transfer becomes possible, which affects the metabolism of hydrolytic and fermenting microorganisms and enables the reactions of VFA and alcohol degradation by acetogenic (syntrophic) bacteria (figure). Microbial abundance and diversity in methanogenic communities depends on the composition of degraded OM and on the conditions developing in the system. Apart from the major microbial groups, methanogenic communities contain the microorganisms not involved directly in OM degradation but playing an important role in providing the growth factors for other bacteria, removal of the toxic products of anaerobic metabolism, and maintaining anoxic conditions [1, 16, 17].

Hydrolytic Bacteria

Hydrolysis is the first stage of OM decomposition, determining the overall rate of the process. Most anaerobic hydrolytic bacteria synthesize cell-bound enzymes or specific enzyme complexes (cellulosomes); they usually carry out the process in direct contact with the surface of hydrolyzed materials. Hydrolytics thrive under conditions of substrate excess; this unhydrolyzed substrate is unavailable to other organisms. According to the substrates used, hydrolytics fall into the groups of polysaccharolytic, proteolytic, and lipolytic organisms, which utilize preferentially the polymers of carbohydrates, nitrogenous compounds, and lipids, as well as the products of their hydrolysis. Hydrolysis is closely associated with the fermentative stage (acidogenesis), with polymer-hydrolyzing microorganisms often fermenting the monomeric products of hydrolysis, thus carrying out both phases [1, 6].

Polysaccharolytic bacteria. Organic waste contain various polysaccharides: cellulose, hemicellulose,

starch, xylan, pectin, etc. Cellulolytic clostridia play the major role in anaerobic degradation of such waste. Molecular genetic techniques (FISH, qPCR, T-RFLP, and cloning) revealed the predominance of *Clostridium* spp. in laboratory and full-scale anaerobic reactors treating wastewater of various industries, landfill leachates, reactors fermenting the organic fraction of MSW, sewage sludge, and silage [18–20]. Apart from clostridia, members of the genera *Acetovibrio, Ruminococcus, Fibrobacter, Bacteroides*, and *Spirochaeta* are involved in polysaccharide degradation at landfills and mesophilic reactors operating at 30–35°C [18–25]. These organisms are the typical rumen inhabitants and are known to be capable of efficient cellulose degradation. Cellulolytic anaerobic fungi of the order *Neocallimastigales* involved in polysaccharide degradation were also found at landfills [20, 25].

Analysis of experimental works on the composition of microbial communities in various systems of anaerobic waste treatment revealed that most polysaccharolytic bacteria identified by molecular genetic techniques in mesophilic reactors were closely related to the species isolated from anthropogenic systems (sewage sludge, anaerobic reactors, landfill soil, cereal debris, rumen, and human and animal feces) (Table 1 [19, 21–24, 26–42]). The polysaccharolytics identified in thermophilic reactors operating at 50–55°C were related to the species isolated from both anthropogenic (digested sludge, compost, fermented manure, and contaminated soils) and natural habitats (water, mud and sediments of geothermally heated pools and thermal springs). *Clostridium* species prevailed in the first case, while *Petrotoga* and *Thermoanaerobacterium* species were found in the second case (Table 2 [18, 27, 32, 36, 38, 41–51]). Polysaccharolytics identified in hydrogen bioreactors operating at temperatures above 65°C were related to extremely thermophilic members of the genera *Caloramator, Caldanaerobacter, Thermoanaerobacter*, and *Thermoanaerobacterium*, which have been isolated mostly from natural habitats (geothermally heated streams and thermal springs) (Table 3 [18, 36, 38, 40, 42, 45, 52, 53]).

In reactors operating at 30–35°C, both mesophilic and moderately thermophilic polysaccharolytics occur. Thus, predominance of thermotolerant clostridia *C. thermocellum* and *C. stercorarium* was revealed by FISH in various mesophilic laboratory and industrial reactors [18]. Similarly, mesophilic cellulolytic clostridia with growth optimum at 20–40°C have often been identified in thermophilic reactors (>50°C) [32, 36, 38] (Table 1).

It was suggested that the species composition of cellulolytic bacteria has no effect on the rate and stability of cellulose degradation in anaerobic reactors. The overall rate of cellulose decomposition depends on the rate and degree of substrate colonization, rather than on the presence of specific cellulolytic microbial species [27]. Colonization of the surface of an insoluble substrate is the strategy of cellulolytics, and their metabolism is proportional to available area [1]. Homogenization of solid waste prior to their fermentation in anaerobic reactors or landfilling is therefore desirable, since it promotes increased rates of OM degradation and development of conditions for formation of microbial biofilms over the surface of the decomposed material [25].

Proteolytic and lipolitic bacteria. Diversity of proteolytic and lipolytic bacteria in the systems of anaerobic waste treatment is poorly studied. *Butyrivibrio proteoclasticus* isolated from cattle manure [54] and the moderately thermophilic halotolerant *Anaerosalibacter bizertensis* isolated from the sludge of storage tanks holding wastes generated by the recycling of discarded motor oils [55] are bacteria exhibiting proteolytic activity. The thermophilic proteolytic *Caloramator proteoclasticus* isolated from the mesophilic granular methanogenic sludge of a whey-treating UASB reactor [56] was subsequently identified by DGGE in an ASBR reactor treating the palm oil mill effluent [32]. A thermophilic proteolytic *Coprothermobacter platensis* was isolated from a mesophilic UASB reactor treating wastewater of a baker's yeast production facility [57]. Another species *Coprothermobacter proteolyticus*, which was isolated from a thermophilic reactor fermenting tannery waste and cattle manure [58], is most often detected by molecular techniques in various waste treatment systems [36, 45, 59]. Many proteolytic bacteria are also capable of carbohydrate fermentation.

A mesophilic species *Selenomonas lipolytica* isolated from an anaerobic lagoon receiving wastewater from an edible oil mill possesses lipolytic activity [60]. An organism closely related to a thermophilic lipolytic *Bacillus coagulans* was identified by DGGE in enrichment cultures on cellulose from thermophilic compost of solid waste management facility [45].

Fermentative Bacteria

Fermentative bacteria are responsible for the acidogenic (hydrogen) stage of anaerobic OM decomposition. Their substrates—various sugars, higher fatty acids, peptides, amino acids, and other products of polymer hydrolysis—are fermented to hydrogen, CO_2, and lower fatty acids and alcohols depending on their type of metabolism and environmental conditions. Some fermenters are also able to metabolize phenolic and nitrogen- or sulfur-containing compounds of the waste. Activity of fermentative bacteria results in a drastic decrease of carbohydrate content in

Table 1. Mesophilic polysaccharolytic bacteria detected in waste treatment systems

Species*	Site of identification (feedstock)	Identification technique	References	Source of type strain isolation**
Acetivibrio cellulolyticus	Municipal sewage sludge, sludge of a two-stage anaerobic reactor (pretreated cornstalks)	Cultivation, DGGE	[21, 23]	Municipal sewage sludge
A. cellulosolvens	Municipal sewage sludge	Cultivation	[22]	"
Bacteroides cellulosolvens	Municipal sewage sludge, laboratory reactor inoculated with an enriched on microcrystalline cellulose landfill leachate microbial consortium	Cultivation, FISH	[26, 27]	Municipal sewage sludge
Cellulomonas fermentans	Landfill soil; laboratory chemolithotrophic denitrifying UASB reactor inoculated with methanogenic sludge from a full-scale reactor (paper waste)	Cultivation, cloning	[28, 29]	Landfill soil
Clostridium acetobutylicum	CSTR (suluble condensed molasses), anaerobic completely mixed tank reactors (whey permeate)	RT-PCR; DGGE	[30, 31]	Cereal crops, soil, lake sediments
C. cellobioparum	Laboratory LB reactors (silage)	T-RFLP-cloning	[19]	Rumen
C. cellulolyticum	Thermophilic H_2-ASBR (palm oil mill effluent)	DGGE	[32]	Decomposing grass
C. cellulovorans	Methanogenic reactor (finely divided hybrid poplar wood)	Cultivation	[33]	"
C. lentocellum	River sediment containing paper-mill waste	Cultivation	[34]	"
C. leptum	Cattle manure; thermophilic CFSTR (artificial garbage slurry); laboratory LB reactors (silage)	Cultivation; T-RFLP, cloning	[19, 35, 36]	Human feces
C. populeti	Methanogenic reactor (woody-biomass); thermophilic CFSTR (artificial garbage slurry)	Cultivation, cloning	[36, 37]	Methanogenic reactor fermenting finely divided hybrid poplar wood
C. roseum	Thermophilic H_2-UASB reactor (wheat straw hydrolysate)	DGGE	[38]	Corn (soil may be the habitat)
C. ramosum	Cattle manure	Cultivation	[35]	Human clinical material
C. spiroforme				Human, chicken, and rabbit feces
C. sufflavum	Methanogenic digester (cattle waste)	Cultivation	[39]	"
Halocella cellulosilytica	Thermophilic solid-state anaerobic digester (paper waste)	Cloning	[40]	Anaerobic sediments of Lake Sivash hypersaline lagoon (Crimea)
Ruminococcus flavefaciens	Anaerobic reactor (MSW organic fraction)	DGGE	[24]	Cattle and sheep rumen
Soehngenia saccharolytica	UASB reactor (potato starch wastewater)	Cultivation	[41]	"

* Closely related microorganisms were identified by molecular techniques.

** According to Bergey's Manual [42] and original publications.

Table 2. Moderately thermophilic polysaccharolytic bacteria detected in waste treatment systems

Species*	Site of identification (feedstock)	Identification technique	References	Source of type strain isolation**
Clostridium amygdalinum	UASB reactor (potato starch wastewater)	Cultivation	[41]	"
C. cellulosi	Cattle manure compost; enrichment cultures obtained on cellulose from thermophilic compost of a biowaste treatment plant	Cultivation, DGGE	[43–45]	Cattle manure compost
C. caenicola	Digested sludge from methane-tank (MSW); enrichment cultures obtained on cellulose from thermophilic compost of a biowaste treatment plant	Cultivation, DGG	[45, 46]	Sludge from an MSW-digesting methane-tank
C. clariflavum	Digested sludge from methane-tank (MSW)	Cultivation	[46]	
C. isatidis	H_2-UASB reactor (wheat straw hydrolysate)	DGGE	[38]	Woad vat
C. straminisolvens	Compost from feces of domestic animals, poultry, rice straw, and sugarcane waste; CFSTR (artificial garbage slurry)	Cultivation, cloning	[36, 47]	Compost from feces of domestic animals, poultry, rice straw, and sugarcane waste
C. thermoamylolyticum	H_2-ASBR (palm oil mill effluent); enrichment cultures obtained on cellulose from thermophilic compost of a biowaste treatment plant	DGGE	[32, 45]	Mud of hot springs in Hveragerdi (Iceland)
C. thermocellum	Fermented manure; H_2-ASBR (palm oil mill effluent); consortium isolated from compost on an artificial medium (cellulose); CFSTR (artificial garbage slurry); solid-phase anaerobic digestor (paper waste); laboratory reactor inoculated with an enriched on microcrystalline cellulose landfill leachate microbial consortium; mesophilic anaerobic acidogenic digestor (raw sewage)	Cultivation, DGGE, FISH, cloning	[18, 27, 32, 36, 40, 44, 48]	Fermented manure
C. thermopalmarium	Enrichment cultures obtained on cellulose from thermophilic compost of a biowaste treatment plant	DGGE	[45]	Palm wine (Senegal)
Petrotoga mobilis	CFSTR (artificial garbage slurry)	Cloning	[36]	Hot oilfield water of a North Sea oil reservoir
Thermoanaerobacterium aotearoense	H_2-producing sludge from a fermentor (cellulose-containing wastewater); solid-phase fermentor (fruit and vegetable waste)	DGGE, cloning	[49, 50]	Water and sediments of geothermally heated pools (New Zealand)
T. thertnosaccharolyticum	Consortia from thermophilic composts on cellulose, including those from a biowaste treatment plant; H_2-ASBR (palm oil mill effluent)	DGGE	[32, 44, 45, 51]	Contaminated soil

* Closely related microorganisms were identified by molecular techniques.

** According to Bergey's Manual [42] and original publications.

Table 3. Extremely thermophilic polysaccharolytic bacteria detected in waste treatment systems

Species*	Site of identification (feedstock)	Identification technique	References	Source of type strain isolation**
Caloramator fervidus	H_2-UASB reactor (wheat straw hydrolysate containing mainly hemicellulose)	DGGE	[38]	Geothermal spring (New Zealand)
Thermoanaerobacter wiegelii				Freshwater pool formed by a water outlet of a heat exchanger (New Zealand)
Caldanaerobacter subterraneus				Oilfield (France)
C. subterraneus susbsp. *subterraneus*	Enrichment cultures from cattle manure	DGGE	[52]	Oilfield (France)
C. subterraneus subsp. *tengcongensis*				Hot spring (China)
C. subterraneus subsp. *yonseiensis*				Geothermal hot stream at Sileri (Jawa)
Clostridium stercorarium	Mesophilic laboratory and industrial reactors; CFSTR (artificial garbage slurry); solid-phase anaerobic digestor (paper waste); enrichment cultures obtained on cellulose from thermophilc compost of a biowaste treatment plant	Cloning; DGGE; FISH	[18, 36, 40, 45]	Plant debris from a compost heap decomposing at 70°C
Thermoanaerobacter italicus	Enrichment cultures obtained on cellulose from thermophilc compost of a biowaste treatment plant	DGGE	[45]	Thermal spa (Italy)
T. mathranii subsp. *mathranii*				Hot spring (Iceland)
Thermoanaerobacterium polysaccharolyticum	Leachate of a waste pile from a canning factory (sweet corn and other vegetables)	Cultivation	[53]	"
Thermoanaerobacterium zeae				

* Closely related microorganisms were identified by molecular techniques.

** According to Bergey's Manual [42] and original publications.

the medium and an increase in the concentrations of lower fatty acids (formic, acetic, propionic, and butyric) CO_2, H_2, and alcohols (ethanol, propanol, and butanol). Mutual dependence exists between hydrolytic and fermenting bacteria: hydrolytics provide oligomeric substrates, while fermenters maintain the concentrations of hydrolysis products below the threshold level required for hydrolase synthesis; the latter is under metabolic control [1].

Fermentative bacteria developing in waste treatment systems are highly diverse. Fermenters of the classes *Clostridia—Acetanaerobacterium elongatum* (paper mill wastewater) [61], *Acetivibrio multivorans* (oil refinery wastewater) [62], *Anaerofilum pentosovorans* (industrial wastewater) [63], *Ethanoligenens harbinense* (molasses wastewater) [64], and *Saccharofermentans acetigenes* (brewery wastewater) [65]; *Bacteroidia—Bacteroides paurosaccharolyticus* (cattle farms wastewater) [66]; and *Actinobacteria—Bifidobacterium thermacidophilum* (wastewater from a beancurd farm) [67] were originally obtained in pure cultures from anaerobic reactors treating wastewaters of various industries.

Acid-producing clostridia were identified in anaerobic reactors by molecular genetic techniques. In a laboratory CSTR inoculated with activated sludge from a municipal wastewater treatment facility and used for hydrogen production from soluble condensed molasses, mesophilic clostridia *C. saccharobutylicum, C. sporosphaeroides*, and *C. pasteurianum* were identified by RT-PCR [30]. The species *C. pasteurianum* and *C. tyrobutyricum* were detected by DGGE in H_2-producing acidogenic granular sludge from a reactor treating sucrose-containing synthetic wastewater [68]. Clostridia closely related to the psychrophilic species *C. bowmanii* isolated from Lake Fryxell (Antarctica) were detected by cloning in a methanogenic sludge from a full-scale UASB bioreactor treating recycle paper factory waste [29]. In completely mixed mesophilic laboratory reactors for treatment of synthetic glucose wastewater, whey permeate, and liquefied sewage sludge, clostridia related to *C. propionicum, C. tertium, C. sticklandii*, and *C. magnum* were identified by RT-PCR and DGGE. Apart from clostridia, fermentative bacteria closely related to *Streptococcus bovis, Aeromonas hydrophila*, and *Anaerofilum agile* were revealed in these reactors [31]. The species *A. agile* was originally isolated from a methanogenic reactor treating acidic whey and inoculated with activated sludge from a wastewater treatment plant [63].

Lactobacilli closely related to the mesophilic species *Lactobacillus hammesii, L. parabrevis, L. sakei, L. spicheri*, and to the psychrophilic species *L. fuchuensis* were identified by DGGE in reactors of full-scale municipal biogas plant. The biological fraction of MSW, agricultural waste, free flowing commercial waste, liquid manure, and bio-waste requiring sanitation (waste from grease separators and canteen kitchens) were processed in this plant under thermophilic conditions (55°C). These reactors also contained fermentative organisms closely related to mesophilic *Enterococcus faecalis, Pseudoramibacter alactolyticus*, and moderately thermophilic *Anaerobaculum mobile, Sporanaerobacter acetigenes* [69]. The species *A. mobile* isolated from an anaerobic lagoon receiving wastewater from a wool-processing factory [70] was detected by cloning in a thermophilic laboratory CSTR using artificial garbage slurry as a feedstock [36]. The species *S. acetigenes*, originally isolated from a mesophilic commercial UASB reactor treating wastewater contaminated by diverse OM [71], was subsequently identified by cloning in the laboratory-scale reactors fermenting thermally hydrolysed waste activated sludge [72].

In general, fermentative bacteria are relatively resistant to the fluctuating conditions inside a reactor due to their high species diversity and capacity for fermentation of a broad spectrum of organic compounds. The acidogenic stage of OM decomposition is therefore highly efficient and may be used for production of considerable amounts of biohydrogen as a fermentation product, especially in the case of decomposition of semiliquid or solid organic waste.

Acetogenic (Syntrophic or Proton-Reducing) Bacteria

In methanogenic communities, the products of the acidogenic stage (VFA and alcohols), as well as some amino acids and aromatic compounds, are oxidized syntrophically to H_2, CO_2, formate, and acetate (the substrates for methanogenesis). It was shown that VFA oxidation becomes exergonic, so that bacteria may obtain sufficient energy for growth, only when the concentrations of the products of this process (hydrogen and formate) are maintained at low levels [9]. Syntrophic bacteria are therefore dependent on their hydrogen/formate-utilizing partners. At this stage, the concentration of the carrier (hydrogen or formate) is the key problem, since it should be below the inhibitory level for the hydrogen/formate-producing organism and sufficiently high for the hydrogen/formate-utilizing one. Partial hydrogen pressure for syntrophic VFA decomposition should not exceed 10^{-4} bar [7]. Malfunctioning of anaerobic reactors, e.g., in the case of overloading, results in a sharp increase of higher VFA concentrations, probably associated with increased hydrogen partial pressure. Removal of produced acetate is also important for stable decomposition of VFA and alcohols [73].

Syntrophic associations of bacteria and hydrogen/formate-utilizing methanogenic archaea have certain specific characteristics: (1) while VFA decom-

position is coupled to growth, neither bacteria, nor methanogens alone are able to degrade these compounds; (2) intercellular distance affects the rate of the process and specific growth rates, resulting in formation of aggregates of bacteria and archaea, one of the reasons for formation of granular sludge in anaerobic digesters; and (3) syntrophic associations exist under conditions close to thermodynamic equilibrium, and special biochemical mechanisms are required in order to distribute the chemical energy between the members of the community [8]. Aggregation of the consortia of syntrophic bacteria and methanogenic archaea is highly important for high rates of methanogenesis via VFA decomposition. Formation of granular sludge in anaerobic reactors is one of the necessary conditions for efficient wastewater treatment [74]. Inside microbial granules, the optimal conditions for interspecies hydrogen transfer and for biomass accumulation are maintained, which makes it possible to isolate syntrophic bacteria and methanogenic archaea from anaerobic reactors and to investigate their physiology.

Dependence of syntrophic bacteria upon the hydrogen/formate-utilizing partner has been long considered obligatory. By now, however, almost all bacteria capable of syntrophic metabolism have been isolated in pure cultures with the carbon sources more oxidized than those utilized during syntrophic growth (e.g., crotonate for VFA-utilizing bacteria or fumarate, for propionate-utilizing ones). Only several species are known to be obligate syntrophic bacteria: *Syntrophomonas zehnderi, S. sapovorans, Pelotomaculum schinkii*, and *P. isophthalicicum* [9, 75].

Analysis of the 16S rRNA gene sequences of bacteria capable of syntrophic metabolism revealed many of them to belong to the class *Deltaproteobacteria* (to the genera *Syntrophus, Syntrophobacter, Desulfoglaeba, Geobacter, Desulfovibrio*, and *Pelobacter*). Two other groups of synrophs are low-G + C gram-positive bacteria. The first one contains members of the genera *Desulfotomaculum, Pelotomaculum, Sporotomaculum*, and *Syntrophobotulus*. The second group forms the family *Syntrophomonadaceae* comprising the genera *Syntrophomonas, Syntrophothermus*, and *Thermosyntropha* [9].

Syntrophic bacteria are most often isolated from anaerobic reactors treating various types of wastewater. *Syntrophomonas wolfei*, the first described bacteria capable of syntrophic VFA oxidation in co-culture with a hydrogen-utilizing methanogen, was isolated from anaerobic digestor sludge [76]. Six more mesophilic *Syntrophomonas* species degrading butyrate and more long-chained VFA were isolated from anaerobic reactors treating municipal wastewater and wastewater of various industries [77–82]. An organism closely related to *S. sapovorans*, identified by cloning in a full-scale anaerobic plant, digests the excess sludge of the domestic wastewater treatment facility [83]. Thermophilic *Syntrophothermus lipocalidus*, another member of the family *Syntrophomonadaceae*, was isolated from granular sludge of a thermophilic UASB reactor which had been fed with an artifcial wastewater containing sucrose, acetate, and propionate as the major carbon sources [84].

Syntrophus aciditrophicus, isolated from a benzoate-degrading enrichment culture obtained from secondary anaerobic digestor sludge of a municipal sewage treatment plant, is capable of syntrophic oxidation of butyrate, longer-chain VFA, and benzoate [85]. *Syntrophus buswellii*, isolated from the municipal primary anaerobic sewage digestor, is also capable of syntrophic benzoate utilization [86].

Syntrophobacter wolinii, isolated from the primary anaerobic digestor sludge, was the first described syntroph degrading propionate [87]. A closely related organism was identified by cloning in an UASB reactor treating brewery wastewater [88]. Three more propionate-degrading, sulfate-reducing *Syntrophobacter* species were isolated from anaerobic sludge: *S. pfennigii* from the anoxic sludge of the municipal sewage plant [89], *S. fumaroxidans* from granular sludge of an UASB reactor treating sugar refinery wastewater [90], and *S. sulfatireducens* from the sludge of UASB reactors treating brewery and bean curd wastewater [91]. The presence of *S. fumaroxidans, S. wolinii*, and *S. pfennigii* was revealed by membrane hybridization in reactors treating MSW and sewage sludge [92]. A species closely related to *S. fumaroxidans* was identified by DGGE in enrichment cultures obtained on propionate from mesophilic granular sludge of a full-scale reactor treating paper mill wastewater [93]. The thermophilic *Desulfotomaculum thermobenzoicum* subsp. *thermosyntrophicum* is another sulfate-reducing bacterium capable of syntrophic propionate degradation. It was isolated from granular sludge of a laboratory-scale UASB reactor operated at 55 C with a mixture of VFA as feed, which was inoculated with mesophilic granular sludge from a potato-processing factory [94].

Mesophilic *Pelotomaculum schinkii, P. propionicum*, and thermophilic *P. thermopropionicum*, which were isolated from methanogenic sludge of UASB reactors [95–97], are also capable of propionate decomposition in syntrophic associations with hydrogenotrophic methanogens. *P. thermopropionicum*, apart from propionate, is capable of syntrophic degradation of lactate and various alcohols. Two other *Pelotomaculum* species, *P. terephthalicicum* and *P. isophthalicicum*, were isolated from granular sludge of a UASB reactor treating wastewater from manufacturing of terephthalic and isophthalic acids. These species syntrophically decompose various phthalate isomers and other aromatic compounds [98]. Although

they are incapable of sulfate reduction, these *Pelotomaculum* species—as well as benzoate-degrading syntroph *Sporotomaculum syntrophicum* isolated from methanogenic sludge of a reactor treating terephtalate manufacturing wastewater [99]—are closely related to sulfate-reducing *Desulfotomaculum* spp. according to their 16S rRNA gene sequences.

Mesophilic *Smithella propionica* isolated from an anaerobic UAF reactor inoculated with digested domestic sewage sludge and operated with propionate as the major feedstock [100] is another propionate-degrading syntroph. In a co-culture with methanogens, *S. propionica* decomposes propionate to acetate, small amounts of butyrate, CO_2, and methane. In co-cultures it can also grow and produce methane from crotonate, butyrate, malate and fumarate; in pure culture, it only grows on crotonate. Closely related organisms were detected by cloning and membrane hybridization in reactors digesting excess sludge of domestic wastewater treatment facility and MSW [83, 92].

Mesophilic *Clostridium ultunense* isolated from a laboratory reactor fed with pig manure is capable of syntrophic acetate oxidation [101]. *C. ultunense*, was subsequently revealed by DGGE in thermophilic reactors of a full-scale municipal biogas plant utilizing different solid organic waste [69]. Predominance of syntrophic acetate oxidizers *C. ultunense*, *Tepidanaerobacter acetatoxydans*, and *Syntrophaceticus schinkii* at the ammonia level above 0.8–6.9 g NH_4-N L^{-1} was revealed by qPCR in laboratory-scale mesophilic reactors with gradually increasing ammonium load. It indicates resistance of these syntrophs to high concentrations of toxic ammonium ions [102]. Another acetate oxidizing syntroph, thermophilic *Thermacetogenium phaeum*, was isolated from a methanogenic reactor treating kraft-pulp wastewater [103]. The organisms exhibiting 93% similarity of 16S rRNA gene sequence to *T. phaeum* and 96% similarity to *Tepidanaerobacter syntrophicus* were detected by cloning in a UAF reactor treating awamori distillery wastewater [104]. *T. syntrophicus* isolated from sludge of thermophilic digesters that decomposed either MSW or sewage sludge is capable of syntrophic oxidation of lactate and some alcohols [104].

Thermotoga lettingae isolated from an anaerobic thermophilic sulfate-reducing reactor is capable of syntrophic decomposition of methanol to CO_2 and H_2 in association with hydrogenotrophic methanogens. In pure culture this organism ferments methanol to acetate, CO_2, and H_2, but the process is slower than under syntrophic conditions or in the presence of electron acceptors (thiosulfate, S_0, Fe(III), or antraquinone-2,6-disulfonate). In the presence of thiosulfate or elemental sulfur, methanol is converted to CO_2 and partially to alanine. The organism is able to grow on acetate in the presence of thiosulfate or a methanogen [105].

Organisms closely related to a rumen inhabitant *Syntrophococcus sucromutans*, which is capable of syntrophic fructose decomposition in association with hydrogen/formate-utilizing microorganisms, were revealed by DGGE in thermophilic reactors of a full-scale municipal biogas plant utilizing different solid organic waste [69, 107].

Although over 25 new species of syntrophic bacteria have been isolated from anaerobic reactors, quantitative in situ data obtained by molecular genetic techniques (FISH, MAR-FISH, and membrane hybridization) revealed low abundance of metabolically active syntrophs in a number of laboratory and full-scale reactors. In these systems, the contribution of syntrophic bacteria to the total microbial number or total rRNA (in the case of membrane hybridization) usually does not exceed 5% [75]. Since syntrophic VFA oxidation is the key stage limiting OM decomposition, anaerobic reactors should provide conditions favoring accumulation of bacteria carrying out syntrophic metabolism.

Methanogenic Archaea

The complex process of anaerobic OM decomposition is completed by methanogenic archaea, which use H_2/CO_2, acetate, and methylated compounds as the major substrates for methanogenesis. Some of them are able to use formate and carbon monoxide as well. Acetate is the most important substrate for methanogenesis, responsible for production of up to 70% methane in the course of mesophilic decomposition of complex OM [108]. In mesophilic reactors fermenting the feedstock with high protein content, ammonium is accumulated and syntrophic acetate oxidation commences. In such reactors, syntrophic bacteria and hydrogenotrophic methanogens predominate, since they are more resistant to toxic effects of ammonium than aceticlastic methanogens [102].

Analysis of experimental works on methanogenesis in laboratory and full-scale reactors revealed certain patterns of methanogen development in these systems. First, *Methanosaeta* spp. usually predominate in the reactors where low acetate concentrations are maintained (e.g., sewage sludge digestion). Abundance of *Methanosaeta* spp. is also higher in reactors with granular sludge than in those with flocculating sludge. Predominance of *Methanosarcina* spp. occurs at high concentrations of acetate and other VFA (e.g., manure fermentation) [5]. These results agree perfectly with the physiological characteristics of the genera *Methanosaeta* and *Methanosarcina*. *Methanosaeta* spp. exhibit high affinity to acetate (the minimal threshold of 7–70 μM) and low growth rates, while *Methano-*

Table 4. Mesophilic methanogenic archaea detected in waste treatment systems

Species*	Site of identification (feedstock)	Identification technique	References	Source of type strain isolation**
Aceticlastic methanogens (acetate)				
Methanosaeta concilii	Digested sewage sludge, fermented manure, mesophilic and thermophilic anaerobic reactors (wastewater of soy protein and molasses production, potato processing, sugar plant, paper mill, ets; solid paper, food, agricultural waste), MSW landfill	Cultivation, immunofluorescence, T-RFLP, cloning, DGGE, ARDRA, SSCP, membrane hybridization	[29, 88, 92, 93, 112, 114–123]	Digested sludge from the sewage treatment plant
Hydrogenotrophic methanogens (H_2/CO_2, in some cases formate)				
Methanobacterium bryantii	MSW landfill; high-rate anaerobic bioreactor (sulfite evaporator condensate); granular sludge of an UASB reactor (2,4-dichlorophenol)	Cultivation; immunofluorescence	[124–126]	Anaerobic digestor
Methanobacterium beijingense	Granular sludge of an UASB reactor (brewery wastewater); laboratory LB reactors (silage)	Cultivation; T-RFLP-cloning	[19, 127]	Granular sludge of a mesophilic UASB reactor (brewery wastewater)
Methanobacterium congolense	Anaerobic reactors (raw cassava-peel waste, MSW organic fraction); laboratory LB reactors (silage)	Cultivation; DGGE, T-RFLP-cloning	[19, 24, 128]	Anaerobic reactor processing raw cassava-peel waste
Methanobacterium espanolense	Primary sludge (kraft pulp mill wastewater)	Cultivation	[129]	″
Methanobacterium formicicum	MSW landfills; mesophilic and thermophilic anaerobic reactors (wastewater of soy protein production, paper mill wastewater, starch-, VFA-, and 2, 4-dicholrophenol-containing wastewater; solid food waste, MSW organic fraction, sewage sludge, sulfite evaporator condensate)	T-RFLP, DGGE, immunofluorescence, SSCP, cultivation; cloning	[24, 93, 117, 119, 123–126, 130]	Sewage sludge
Methanobacterium subterraneum	UASB reactor (brewery wastewater)	Cloning	[88]	Groundwater from deep subterranean granitic aquifers
Methanobrevibacter arboriphilus	Mesophilic reactors (wastewater of sugar and potato-processing plants; wastewater containing whey permeate, VFA; sulfite evaporator condensate)	Cultivation, immunofluorescence	[116–118, 125]	Wetwood enrichment cultures
Methanobrevibacter cuticularis	Full-scale anaerobic reactor (food waste)	T-RFLP	[119]	Hindgut of the termite *Reticulitermes flavipes*
Methanobrevibacter curvatus				

Table 4. (Contd.)

Species*	Site of identification (feedstock)	Identification technique	References	Source of type strain isolation**
Methanobrevibacter smithii	Mesophilic and thermophilic anaerobic reactors (wastewater of soy protein production, potato processing, whey permeate-, VFA-, and 2,4-dicholrophenol-containing wastewater; solid food waste, sewage sludge)	Immunofluorescence, SSCP, cultivation	[117, 118, 123, 125, 126]	Enrichment culture from sewage sludge on formate; human feces
Methanococcus voltae	Granular sludge of a UASB reactor (2,4-dichlorophenol)	Cultivation	[126]	River sediments (United States)
Methanocorpusculum bavaricum	Wastewater pond (sugar factory wastewater)	Cultivation	[131]	"
Methanocorpusculum parvum	Methanogenic digestor (sour whey); laboratory reactor (synthetic wastewater, VFA, sucrose); granular sludge of a hybrid reactor (wastewater of molasses production); sludge from a wastewater pond (paper mill wastewater); solid-phase reactor (MSW)	Cultivation T-RFLP-cloning, ARDRA, DGGE	[113, 120, 121, 132, 133]	Anaerobic sour whey digester, originally inoculated with sewage sludge
Methanocorpusculum sinense	Pilot plant (distillery wastewater)	Cultivation	[131]	"
Methanoculleus olentangyi	MSW landfills; mesophilic and thermophilic anaerobic reactors (awamori distillery and brewery wastewater, wastewater containing 2,4-dichlorophenol, tannery waste, MSW organic fraction, agricultural waste, liquid manure, biowaste)	Cultivation, T-RFLP, cloning, DGGE	[69, 88, 104,112, 126, 130, 134]	River sediments (United States), reactor fermenting tannery waste initially inoculated with digested sewage sludge
Methanoculleus palmolei	Anaerobic digestor (palm oil plant wastewater), MSW landfill	Cultivation, cloning	[122, 135]	Anaerobic digestor treating wastewater of palm oil plant
Methanofollis liminatans	Effluent of an anaerobic reactor (industrial wastewater); MSW landfills	Cultivation, T-RFLP, cloning	[112, 122, 136]	Effluent of a reactor treating industrial wastewater
Methanogenium cariaci (psychrotolerant species, t_{opt} 20–25°C)	High-rate turbulent reactors (whey-permeate containing wastewater); sludge from an UASB reactor (potato processing wastewater, VFA)	Immunofluorescence	[117, 118]	Marine sediments (Cariaco Trench)
Methanospirillum hungatei	Mesophilic and thermophilic anaerobic reactors (sugar plant, molasses production, potato processing, palm oil mill, and brewery wastewater; VFA-, ethanol-, sucrose-, 2,4-dichlorophenol-containing wastewater; food waste, sewage sludge)	Cultivation, immunofluorescence T-RFLP-cloning, ARDRA, SSCP, DGGE	[88, 116, 118, 120, 121. 123, 126, 137, 138]	Sewage sludge

Table 4. (Contd.)

Species*	Site of identification (feedstock)	Identification technique	References	Source of type strain isolation**
Methanospirillum stamsii (psychrotolerant species, t_{opt} 20–25ºC)	Granular sludge from a low-temperature (3–8°C) laboratory EGSB reactor (VFA)	Cultivation	[139]	"
Methanogens utilizing all substrates (acetate, methylamines, methanol, H_2/CO_2, CO)				
Methanosarcina barkeri	MSW landfills; mesophilic anaerobic reactors (wastewater of sugar plant, soy protein production; whey-, ethanol-, VFA-, sucros-containing wastewater; solid food waste, MSW, sewage sludge)	Cultivation, immunofluorescence, T-RFLP, cloning, DGGE	[112, 113, 116,117, 119. 120, 122, 124, 140]	Enrichment culture on butyrate from sewage sludge digestor
Methanosarcina lacustris (t_{opt} 20–25°C)	Laboratory reactor (fermented manure); sludge from a wastewater pond (paper mill wastewater)	Cultivation	[133]	Anaerobic lake sediments (Switzerland)
Methanosarcina mazeii	Mesophilically fermented cattle manure; mesophilic and thermophilic anaerobic reactors (sewage sludge, wastewater containing whey-permeate, 2,4-dichlorophenol; solid food waste, MSW organic fraction, wheat straw hydrolysate, sulfite evaporator condensate)	Cultivation, T-RELP, DGGE, immunofluorescence	[24, 38, 113, 115, 117,119, 125, 126, 141]	Methane-tank
Methanosarcina siciliae	Full-scale reactor (food waste); laboratory LB reactors (silage)	T-RFLP, cloning	[19, 119]	Marine sediments, oil well
Methanosarcina vacuolata	Methane-tank sludge	Cultivation	[142]	"
Methylotrophic methanogens (methanol or methylamines, some also utilize acetate, methanethiol, and dimethyl sulfide)				
Methanomethylovorans hollandica	Thermophilic laboratory reactor (methanol); UASB reactor (brewery wastewater); MSW landfill	ARDRA, DGGE, cloning	[88, 122, 143]	Sediments of a eutrophic freshwater pond (The Netherlands)
Methanosarcina semesiae	MSW landfill	Cloning	[122]	Mangrove sediment
Methanosarcina acethorans	Granular sludge from a UASB reactor (2,4-dichlorophenol); full-scale reactor (food waste)	T-RFLP, cultivation	[119, 126]	Littoral marine sediments (United States)

Table 4. (Contd.)

Species*	Site of identification (feedstock)	Identification technique	References	Source of type strain isolation**
Methanosphaera stadtmanae	Thermophilic reactors of full-scale municipal biogas plant (MSW organic fraction, agricultural waste, free flowing commercial waste, liquid manure, bio-waste)	DGGE	[69]	Human feces
Methanimicrococcus blatticola				Hindgut of a cockroach *Periplaneta americana*

* Closely related microorganisms were identified by molecular techniques.

** According to Bergey's Manual [42] and original publications.

sarcina spp. have low affinity to acetate (the minimal threshold of 0.2–1.2 mM) and high growth rates [110]. Successful start-up of laboratory anaerobic co-digesters treating MSW and sewage sludge occurred when the content of archaeal rRNA was high, with predominance of aceticlastic methanogens *Methanosaeta concilii*. In contrast, digesters that experienced a difficult start-up period and VFA accumulation had lower levels of archaeal rRNA with proportionally more abundant *Methanosarcina* spp. and *Methanobacteriaceae* [92]. Aceticlastic *Methanosaeta* species (*M. concilii* and *M. thermophila*), as well as *Methanosarcina* species (*M. barkeri, M. mazeii*, and *M. thermophila*), which utilize a variety of substrates (acetate, methylamines, methanol, and H_2/CO_2), are most often found at MSW landfills and in mesophilic or thermophilic anaerobic reactors treating wastewater of various industries, sewage sludge, MSW, manure, etc. (Tables 4 and 5).

Moreover, the species diversity of methanogens is higher in mesophilic reactors than in thermophilic ones. The number of mesophilic methanogenic species detected in various reactors and at landfills (Table 4) is more than twice higher than the number of thermophilic species found in the same systems (Table 5). Hydrogenotrophic methanogens predominate in thermophilic reactors [5]. Nine out of twelve species of methanogens detected in various thermophilic reactors were hydrogenotrophic (*Methanoculleus* spp., *Methanothermobacter* spp.) (Table 5).The prevalence of hydrogenotrophic methanogenesis over aceticlastic under thermophilic conditions was confirmed for bottom sediments of a contaminated lake by the radioisotope method [109]. Quantitative data obtained by FISH revealed, however, the predominance of hydrogenotrophic methanogens only during the start-up of thermophilic laboratory CSTR fermenting MSW. When the reactor reached the steady-state conditions they were replaced by the acetotrophic methanogens [111]. On the contrary, at landfills hydrogenotrophic methanogens prevailed over aceticlastic ones in the course of time [25]. At the sites with fresh waste (about 2 years old), hydrogenotrophic, aceticlastic, and Cl-utilizing methanogens of the orders *Methanobacteriales, Methanomicrobiales*, and *Methanosarcinales* developed, while at "older" sites (~6 years old), hydrogenotrophic methanogens of the orders *Methanobacteriales* and *Methanomicrobiales* prevailed (according to cloning and RFLP) [112]. Similar results have been obtained by DGGE and cloning for laboratory reactors simulating waste decomposition at the MSW landfills [113].

Thus, anaerobic methanogenic communities are ensembles of interacting groups of microorganisms forming an integrated trophic system. In this system, the microorganisms experience competition for the common substrates or cooperation in their utilization. Application of molecular genetic techniques to waste treatment systems reveals both new anaerobic microorganisms and those previously isolated from natural environments. These findings improve our understanding of biodiversity and ecology of the microorganisms in methanogenic communities. Knowing the biodiversity and physiological characteristics of the components of methanogenic communities, it is possible to optimize the technological parameters of the operation of full-scale anaerobic reactors, to increase the efficiency and rate of OM conversion and methane

Table 5. Moderately thermophilic methanogenic archaea detected in waste treatment systems

Species*	Site of identification (feedstock)	Identification technique	References	Source of type strain isolation**
Aceticlastic methanogens (acetate)				
Methanosaeta thermophila	Digested sewage sludge from a thermophilic methane-tank, thermophilically fermented cattle manure	Cultivation	[115, 144, 145]	Mud of a hydrothermal chloride lake (Kamchatka); digested sewage sludge from a thermophilic methane-tank
Hydrogenotrophic methanogens (H_2/CO_2, in some cases formate)				
Methanobacterium thermaggregans	UASB reactor (brewery wastewater)	Cloning	[88]	Mud sample from a cattle pasture
Methanoculleus receptaculi	Thermophilic laboratory reactor (food waste, sewage sludge)	SSCP	[123]	Shengli oil field (China)
Methanoculleus thermophilicus	Thermophilic CSTR (artificial garbage slurry), MSW landfills; thermophilic granular sludge from a hybrid reactor (molasses production wastewater)	Cloning, T-RFLP, ARDRA	[36, 112, 121, 130]	Sediments underlying high-temperature effluent from a coastal nuclear power plant
Methanolinea tarda	Anaerobic prodionate-degrading enrichment culture isolated from mesophilic methanogenic sludge (municipal wastewater)	Cultivation	[146]	"
Methanothermobacter defluvii	Sludge from an anaerobic reactor (methacrylate-containing wastewater); thermophilic UASB reactor (wheat straw hydrolysate containing mainly hemicellulose)	Cultivation, DGGE	[38, 147]	Sludge from an anaerobic reactor treating methacrylate-containing wastewater
Methanothermobacter marburgensis	Digested sewage sludge from mesophilic methane-tank	Cultivation	[148]	"
Methanothermobacter thermautotrophicus	Digested sewage sludge, thermophilically fermented cattle manure; thermophilic anaerobic reactors (potato processing and molasses production wastewater; VFA-containing wastewater, wheat straw hydrolysate)	Cultivation, immunofluorescence, DGGE, ARDRA	[38, 115, 118, 121, 149, 150]	Digested sewage sludge
Methanothermobacter thermoflexus	Sludge from an anaerobic reactor (methacrylate-containing wastewater)	Cultivation	[147]	"
Methanotherm obacter thermophilus	Digested sewage sludge from a thermophilic methane-tank	Cultivation	[151]	"
Methanothermobacter wolfeii	Enrichment cultures from a mixture of sewage sludge and river sediment, full-scale thermophilic anaerobic reactors (domestic and livestock waste, sewage sludge)	Cultivation, cloning	[152, 153]	Enrichment cultures from a mixture of sewage sludge and river sediment

Table 5. (Contd.)

Species*	Site of identification (feedstock)	Identification technique	References	Source of type strain isolation**
Methylotrophic methanogens (methanol or methylamines, some also utilize acetate)				
Methanomethylovorans thermophila	UASB reactor (methanol)	Cultivation	[154]	"
Methanosarcina thermophila	Mesophilic and thermophilic anaerobic reactors (sulfite evaporator condensate; potato processing and awamori distillery wastewater; food waste, sewage sludge); MSW landfill	Cultivation, immunofluorescence, SSCP, T-RFLP, cloning	[36, 104, 118, 119, 123, 125, 130, 155]	Laboratory thermophilic reactor inoculated with the sewage sludge from a municipal wastewater treatment plant

* Closely related microorganisms were identified by molecular techniques.

** According to Bergey's Manual [42] and original publications.

yield in the biogas, and to develop new technologies for solid waste utilization.

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REFERENCES

1. Zavarzin, G.A., Lektsii po prirodovedcheskoi mikrobiologii, (Lectures in Environmenal Microbiology), Moscow: Nauka, 2003.
2. Kalyuzhnyi, S.V., Danilovich, D.A, and Nozhevnikova, A.N., Anaerobic biological wastewater treatment, *ITOGI nauki i tekhniki, Ser. Biol.,* Moscow: VITNITI, 1991, vol. 29.
3. Nozhevnikova, A.N., Microbial processes in environmental biotechnology. Biological treatment of organic waste, in *Ekologiya mikroorganizmov* (Microbial Ecology), Netrusov, A.I., Ed., Moscow: Nauka, 2004, pp. 175–199.
4. Li, Y., Park, S.Y., and Zhu, J., Solid-state anaerobic digestion for methane production from organic waste, *Renew. Sustain. En. Rev.*, 2011, vol. 15, pp. 821–826.
5. Demirel, B. and Scherer, P., The roles of acetotrophic and hydrogenotrophic methanogens during anaerobic conversion of biomass to methane: a review, *Rev. Environ. Sci. Biotechnol.*, 2008, vol. 7, pp. 173–190.
6. Lynd, L.R., Weimer, P.J., van Zyl, W.H., and Pretorius, I.S., Microbial cellulose utilization: fundamentals and biotechnology, *Microbiol. Mol. Biol. Rev.*, 2002, vol. 66, no. 3, pp. 506–577.
7. Schink, B. and Stams, A.J.M., Syntrophism among prokaryotes, in *The Prokaryotes: an Evolving Electronic Resource for the Microbiological Community*, Dworkin, M., Falkow, S., Rosenberg, E., Schleifer, K.-H., and Stackebrandt, E., Eds., New York: Springer, 2006, pp. 309–335.
8. Stams, A.J.M. and Plugge, C.M., Electron transfer in syntrophic communities of anaerobic bacteria and archaea, *Nat. Rev. Microbiol.*, 2009, vol. 7, pp. 568–577.
9. McInerney, M.J., Struchtemeyer, C.G., Sieber, J., Mouttaki, H., Stams, A.J.M., Schink, B., Rohlin, L., and Gunsalus, R.P., Physiology, ecology, phylogeny, and genomics of microorganisms capable of syntrophic metabolism, *Ann. New York Acad. Sci.*, 2008, vol. 1125, pp. 58–72.
10. McInerney, M.J., Sieber, J.R., and Gunsalus, R.P., Syntrophy in anaerobic global carbon cycles, *Curr. Opin. Biotechnol.*, 2009, vol. 20, pp. 623–632.
11. Ferry, J.G., Methanogenesis biochemistry, in *Encyclopedia of Life Sciences*, Macmillan, 2002. www.els.net
12. Thauer, R.K., Kaster, A-K., Seedorf, H., Buckel, W., and Hedderich, R., Methanogenic archaea: ecologically relevant differences in energy conservation, *Nat. Rev. Microbiol.*, 2008, vol. 6, pp. 579–591.
13. Schnurer, A. and Jarvis, A., *Microbiological Handbook for Biogas Plants*, Swedish Waste Management, U2009:03, Swedish Gas Centre Report 207, 2010.
14. Chen, Y., Cheng, J.J., and Creamer, K.S., Inhibition of anaerobic digestion process: a review, *Biores. Technol.*, 2008, vol. 99, pp. 4044–4064.
15. Angelidaki, I. and Ahring, B.K., Effects of free long-chain fatty acids on thermophilic anaerobic digestion, *Appl. Microbiol. Biotechnol.*, 1992, vol. 37, pp. 808–812.
16. Zavarzin, G.A., Biogas and small-scale energetics, *Priroda* (Moscow), 1987, no. 1, pp. 66–79.
17. Nozhevnikova, A.N., Growth and interaction of anaerobic bacteria in methanogenic associations and mixed cultures, *Itogi nauki i tekhniki, Ser. Microbiol.*, Moscow: VINITI, 1991, vol. 24, pp. 123–148.
18. O'Sullivan, C., Burrell, P.C., Clarke, W.P., and Blackall, L.L., A survey of the relative abundance of specific groups of cellulose degrading bacteria in anaerobic environments using fluorescence in situ hybridization, *J. Appl. Microbiol.*, 2007, vol. 103, pp. 1332–1343.
19. Wang, H., Vuorela, M., Keränen, A.-L., Lehtinen, T.M., Lensu, A., Lehtomäki, A., and Rin-

tala, J., Development of microbial populations in the anaerobic hydrolysis of grass silage for methane production, *FEMS Microbiol. Ecol.*, 2010, vol. 72, pp. 496–506.

20. McDonald, J.E., Houghton, J.N., Rooks, D.J., Allison, H.E., and McCarthy, A.J., The microbial ecology of anaerobic cellulose degradation in municipal waste landfill sites: evidence of a role for fibrobacters, *Environ. Microbiol.*, 2012, vol. 14, no. 4, pp. 1077–1087.
21. Patel, G.B., Khan, A.W., Agnew, B.J., and Colvin, J.R., Isolation and characterization of an anaerobic, cellulolytic microorganism, *Acetiuibrio cellulolyticus* gen. nov., sp. nov., *Int. J. Syst. Bacteriol.*, 1980, vol. 30, pp. 179–185.
22. Khan, A.W., Meek, E., Sowden, L.C., and Colvin, J.R., Emendation of the genus *Acetivibrio* and description of *Acetivibrio cellulosolvens* sp. nov. a nonmotile cellulolytic mesophile, *Int. J. Syst. Bacteriol.*, 1984, vol. 34, pp. 419–422.
23. Lu, Y., Zhang, C., Zhao, H., Ma, K., Zhao, Z., Chen, H., Liu, D., and Xing, X-H., Characteristics of hydrogen and methane production from cornstalks by an augmented two- or three-stage anaerobic fermentation process, *Biores. Technol.*, 2009, vol. 100, pp. 2889–2895.
24. Trzcinski, A.P., Ray, M.J., and Stuckey, D.C., Performance of a three-stage membrane bioprocess treating the organic fraction of municipal solid waste and evolution of its archaeal and bacterial ecology, *Biores. Technol.*, 2010, vol. 101, pp. 1652–1661.
25. Semrau, J.D., Current knowledge of microbial community structures in landfills and its cover soils, *Appl. Microbiol. Biotechnol.,* 2011, vol. 89, pp. 961–969.
26. Murray, W.D., Sowden, L.C., and Colvin, J.R., *Bacteroides cellulosolvens* sp. nov. a cellulolytic species from sewage sludge, *Int. J. Syst. Bacteriol.*, 1984, vol. 34, pp. 185–187.
27. O'Sullivan, C.A., Burrell, P.C., Clarke, W.P., and Blackall, L.L., Structure of a cellulose degrading bacterial community during anaerobic digestion, *Biotechol. Bioeng.*, 2005, vol. 92, pp. 871–878.
28. Bagnara, C., Toci, R., Gaudin, C., and Belaich, J.P., Isolation and characterization of a cellulolytic microorganism, *Cellulomonas fermentans* sp. nov., *Int. J. Syst. Bacteriol.*, 1985, vol. 35, pp. 502–507.
29. Fernandez, N., Sierra-Alvarez, R., Field, J.A., Amils, R., and Sanz, J.L., Microbial community dynamics in a chemolithotrophic denitrification reactor inoculated with methanogenic granular sludge, *Chemosphere*, 2008, vol. 70, pp. 462–474.
30. Lay, C-H., Wu, J-H., Hsiao, C-L., Chang, J-J., Chen, C-C., and Lin, C-Y., Biohydrogen production from soluble condensed molasses fermentation using anaerobic fermentation, *Int. J. Hydrogen Energy*, 2010, vol. 35, pp. 13445–13451.
31. Kim, J., Shin, S.G., Han, G., O'flaherty, V., Lee, C., and Hwang, S., Common key acidogen populations in anaerobic reactors treating different wastewaters: molecular identification and quantitative monitoring, *Wat. Res.*, 2011, vol. 45, pp. 2539–2549.
32. Prasertsan, P., O-Thong, S., and Birkeland, N.-K., Optimization and microbial community analysis for production of biohydrogen from palm oil mill effluent by thermophilic fermentative process, *Int. J. Hydrogen Energy*, 2009, vol. 34, pp. 7448–7459.
33. Sleat, R., Mah, R.A., and Robinson, R., Isolation and characterization of an anaerobic, cellulolytic bacterium, *Clostridium cellulovorans* sp. nov., *Appl. Environ. Microbiol.*, 1984, vol. 48, pp. 88–93.
34. Murray, W.D., Hofmann, L., Campbell, N.L., and Madden, R.H., *Clostridium lentocellum* sp. nov., a cellulolytic species from river sediment containing papermill waste, *Syst. Appl. Microbiol.*, 1986, vol. 8, pp. 181–184.
35. Virunanon, C., Chantaroopamai, S., Denduangbaripant, J., and Chulalaksananukul, W., Solventogenic-cellulolytic clostridia from 4-step-screening process in agricultural waste and cow intestinal tract, *Anaerobe*, 2008, vol. 14, pp. 109–117.
36. Sasaki, D., Hori, T., Haruta, S., Ueno, Y., Ishii, M., and Igarashi, Y., Methanogenic pathway and community structure in a thermophilic anaerobic digestion process of organic solid waste, *J. Biosci. Bioeng.*, 2011, vol. 111, no. 1, pp. 41–46.
37. Sleat, R. and Mah, R.A., *Clostridium populeti* sp. nov., a cellulolytic species from a woody-biomass digestor, *Int. J. Syst. Bacteriol.*, 1985, vol. 35, pp. 160–163.
38. Kongjan, P., O-Thong, S., and Angelidaki, I., Performance and microbial community analysis of two-stage process with extreme thermophilic hydrogen and thermophilic methane production from hydrolysate in UASB reactors, *Biores. Technol.*, 2011, vol. 102, pp. 4028–4035.
39. Nishiyama, T., Ueki, A., Kaku, N., and Ueki, K., *Clostridium sufflavum* sp. nov., isolated from a methanogenic reactor treating cattle waste, *Int. J. Syst. Evol. Microbiol.*, 2009, vol. 59, pp. 981–986.
40. Tang, Y-Q., Ji, P., Hayashi, J., Koike, Y., Wu, X.L., and Kida, K., Characteristic microbial community of a dry thermophilic methanogenic digester: its long-term stability and change with feeding, *Appl. Microbiol. Biotechnol.*, 2011, vol. 91, no. 5, pp. 1447–1461.
41. Parshina, S.N., Kleerebezem, R., Sanz, J.L., Lettinga, G., Nozhevnikova, A.N., Kostrikina, N.A., Lysenko, A.M., and Stams, A.J.M., *Soehngenia saccharolytica* gen. nov., sp. nov. and *Clostridium amygdalinum* sp. nov., two novel anaerobic, benzaldehyde-converting bacteria, *Int. J. Syst. Evol. Microbiol.*, 2003, vol. 53, pp. 1791–1799.
42. *Bergey's Manual of Systematic Bacteriology, 2nd ed.*, Whitman, W.B., Ed., Dordrecht: Springer, 2009.
43. He, Y.L., Ding, Y.F., and Long, Y.Q., Two cellulolytic *Clostridium* species: *Clostridium cellulosi* sp. nov. and *Clostridium cellulofermentans* sp. nov., *Int. J. Syst. Bacteriol.*, 1991, vol. 41, no. 2, pp. 306–309.
44. Ueno, Y., Haruta, S., Ishii, M., and Igarashi, Y., Microbial community in anaerobic hydrogen-producing microflora enriched from sludge compost, *Appl. Microbiol. Biotechnol.*, 2001, vol. 57, pp. 555–562.
45. Nissila, M.E., Tahti, H.P., Rintala, J.A., and Puhakka, J.A., Effects of heat treatment on hydrogen production potential and microbial community of thermophilic compost enrichment cultures, *Biores. Technol.*, 2011, vol. 102, pp. 4501–4506.

46. Shiratori, H., Sasaya, K., Ohiwa, H., Ikeno, H., Ayame, S., Kataoka, N., Miya, A., Beppu, T., and Ueda, K., *Clostridium clariflavum* sp. nov. and *Clostridium caenicola* sp. nov., moderately thermophilic, cellulose-/cellobiose-digesting bacteria isolated from methanogenic sludge, *Int. J. Syst. Evol. Microbiol.*, 2009, vol. 59, pp. 1764–1770.

47. Kato, S., Haruta, S., Cui, Z.J., Ishii, M., Yokota, A., and Igarashi, Y., *Clostridium straminisolvens* sp. nov., a moderately bacterium isolated from a cellulose-degrading bacterial community, *Int. J. Syst. Evol. Microbiol.*, 2004, vol. 54, pp. 2043–2047.

48. Viljoen, J.A., Fred, E.B., and Peterson, W.H., The fermentation of cellulose by thermophilic bacteria, *J. Agricult. Sci.,* 1926, vol. 16, pp. 1–17.

49. Liu, H., Zhang, T., and Fang, H.H.P., Thermophilic H_2 production from a cellulose-containing wastewater, *Biotech. Lett.*, 2003, vol. 25, pp. 365–369.

50. Hernon, F., Forbes, C., and Colleran, E., Identification of mesophilic and thermophilic fermentative species in anaerobic granular sludge, *Wat. Sci. Technol.*, 2006, vol. 54, pp. 19–24.

51. O-Thong, S., Prasertsan, P., and Birkeland, N.-K., Evaluation of methods for preparing hydrogen-producing seed inocula under thermophilic condition by process performance and microbial community analysis, *Bioresource Technol.*, 2009, vol. 100, pp. 909–918.

52. Yokoyama, H., Moriya, N., Ohmori, H., Waki, M., Ogino, A., and Tanaka, Y., Community analysis of hydrogen-producing extreme thermophilic anaerobic microflora enriched from cow manure with five substrates, *Appl. Microbiol. Biotechnol.*, 2007, vol. 77, pp. 213–222.

53. Cann, I.K.O., Stroot, P.G., Mackie, K.R., White, B.A., and Mackie, R.I., Characterization of two novel saccharolytic, anaerobic thermophiles, *Thermoanaerobacterium polysaccharolyticum* sp. nov. and *Thermoanaerobacterium zeae* sp. nov., and emendation of the genus *Thermoanaerobacterium, Int. J. Syst. Evol. Microbiol.*, 2001, vol. 51, pp. 293–302.

54. Attwood, G.T., Reilly, K., and Patel, B.K., *Clostridium proteoclasticum* sp. nov., a novel proteolytic bacterium from the bovine rumen, *Int. J. Syst. Bacteriol.*, 1996, vol. 46, pp. 753–758.

55. Rezgui, R., Maaroufi, A., Fardeau,, M.L., Ben Ali Gam, Z., Cayol, J.L., Ben Hamed, S., and Labat, M., *Anaerosalibacter bizertensis* gen. nov., sp. nov., a new halotolerant bacterium isolated from sludge, *Int. J. Syst. Evol. Microbiol.*, 2012, vol. 62, pp. 2469–2474.

56. Tarlera, S., Muxi, L., Soubes, M., and Stams, A.J.M., *Caloramator proteoclasticus* sp. nov., a new moderately thermophilic anaerobic proteolytic bacterium, *Int. J. Syst. Bacteriol.*, 1997, vol. 47, no. 3, pp. 651–656.

57. Etchebehere, C., Pavan, M.E., Zorzopulos, J., Soubes, M., and Muxi, L., *Coprothermobacter platensis* sp. nov., a new anaerobic proteolytic thermophilic bacterium isolated from an anaerobic mesophilic sludge, *Int. J. Syst. Bacteriol.*, 1998, vol. 48, pp. 1297–1304.

58. Ollivier, B.M., Mah, R.A., Ferguson, T.J., Boone, D.R., Garcia, J.L., and Robinson, R., Emendation of the genus *Thermobacteroides: Thermobacteroides proteolyticus* sp. nov. a proteolytic acetogen from a methanogenic enrichment, *Int. J. Syst. Bacteriol.*, 1985, vol. 35, no. 4, pp. 425–428.

59. Sasaki, K., Morita, M., Sasaki, D., Nagaoka, J., Matsumoto, N., Ohmura, N., and Shinozaki, H., Syntrophic degradation of proteinaceous materials by the thermophilic strains *Coprothermobacter proteolyticus* and *Methanothermobacter thermautotrophicus, J. Biosci. Bioeng.*, 2011, vol. 112, no. 5, pp. 469–472.

60. Dighe, A.S., Shouche, Y.S., and Ranade, D.R., *Selenomonas lipolytica* sp. nov., an obligately anaerobic bacterium possessing lipolytic activity, *Int. J. Syst. Bacteriol.*, 1998, vol. 48, pp. 783–791.

61. Chen, S. and Dong, X., *Acetanaerobacterium elongatum* gen. nov., sp. nov., from paper mill waste water, *Int. J. Syst. Evol. Microbiol.*, 2004, vol. 54, pp. 2257–2262.

62. Tanaka, K., Nakamura, K., and Mikami, E., Fermentation of cinnamate by a mesophilic strict anaerobe, *Acetivibrio multivorans* sp. nov, *Arch. Microbiol.*, 1991, vol. 155, no. 2, pp. 120–124.

63. Zellner, G., Stackebrandt, E., Nagel, D., Messner, P., Weiss, N., and Winter, J., *Anaerofilum pentosovorans* gen. nov., sp. nov., and *Anaerofilum agile* sp. nov., two new, strictly anaerobic, mesophilic, acidogenic bacteria from anaerobic bioreactors, *Int. J. Syst. Bacteriol.*, 1996, vol. 46, pp. 871–875.

64. Xing, D., Ren, N., Li, Q., Lin, M., Wang, A., and Zhao, L., *Ethanoligenens harbinense* gen. nov., sp. nov., isolated from molasses waste water, *Int. J. Syst. Evol. Microbiol.*, 2006, vol. 56, pp. 755–760.

65. Chen, S., Niu, L., and Zhang, Y., *Saccharofermentans acetigenes* gen. nov., sp. nov., an anaerobic bacterium isolated from sludge treating brewery wastewater, *Int. J. Syst. Evol. Microbiol.*, 2010, vol. 60, pp. 2735–2738.

66. Ueki, A., Abe, K., Ohtaki, Y., Kaku, N., Watanabe, K., and Ueki, K., *Bacteroides paurosaccharolyticus* sp. nov., isolated from a methanogenic reactor treating waste from cattle farms, *Int. J. Syst. Evol. Microbiol.,* 2011, vol. 61, pp. 448–453.

67. Dong, X., Xin, Y., Jian, W., Liu, X., and Ling, D., *Bifidobacterium thermacidophilum* sp. nov., isolated from an anaerobic digester, *Int. J. Syst. Evol. Microbiol.*, 2000, vol. 50, pp. 119–25.

68. Fang, H.H.P., Liu, H., and Zhang, T., Characterization of a hydrogen-producing granular sludge, *Biotech. Bioeng.*, 2002, vol. 78, pp. 44–52.

69. Weiss, A., Jérôme, V., Freitag, R., and Mayer, H.K., Diversity of the resident microbiota in a thermophilic municipal biogas plant, *Appl. Microbiol. Biotechnol.*, 2008, vol. 81, no. 1, pp. 163–73.

70. Menes, R.J. and Muxi, L., *Anaerobaculum mobile* sp. nov., a novel anaerobic, moderately thermophilic, peptide-fermenting bacterium that uses crotonate as an electron acceptor, and emended description of the genus *Anaerobaculum, Int. J. Syst. Evol. Microbiol.*, 2002, vol. 52, pp. 157–164.

71. Hernandez-Eugenio, G., Fardeau, M-L., Cayol, J.-L., Patel, B.K.C., Thomas, P., Macarie, H., Garcia, J.-L., and Ollivier, B., *Sporanaerobacter acetigenes* gen. nov., sp. nov., a novel acetogenic, facultatively sulfurreducing bacterium, *Int. J. Syst. Evol. Microbiol.*, 2002, vol. 52, pp. 1217–1223.

72. Cirne, D.G., Bond, P., Pratt, S., Lant, P., and Batstone, D.J., Microbial community analysis during continuous fermentation of thermally hydrolysed waste activated sludge, *Water Sci. Technol.*, 2012, vol. 65, no. 1, pp. 7–14.

73. Slobodkin, A.I. and Nozhevnikova, A.N., Effect of *Methanothrix thermoacetophila* on ethanol degradation by a methanogenic microbial association, *Prikl. Biokhim. Mikrobiol.*, 1990, vol. 26, no. 2, pp. 825–831.

74. Lettinga, G., Anaerobic digestion and wastewater treatment systems, *Antonie van Leeuwenhoek*, 1995, vol. 67, pp. 3–28.

75. Stams, A.J.M., Sousa, D.Z., Kleerebezem, R., and Plugge, C.M., Role of syntrophic microbial communities in high-rate methanogenic bioreactors, *Wat. Sci. Technol.*, 2012, vol. 66, no. 2, pp. 352–362.

76. McInerney, M.J., Bryant, M.P., Hespell, R.B., and Costerton, J.W., *Syntrophomonas wolfei* gen. nov. sp. nov., an anaerobic, syntrophic, fatty acid-oxidizing bacterium, *Appl. Environ. Microbiol.,* 1981, vol. 41, no. 4, pp. 1029–1039.

77. Roy, F., Samain, E., Dubourguier, H.C., and Albagnac, G., *Synthrophomonas sapovorans* sp. nov., a new obligately proton-reducing anaerobe oxidizing saturated and unsaturated long chain fatty acids, *Arch. Microbiol.*, 1986, vol. 145, pp. 142–147.

78. Lorowitz, W.H., Zhao, H.X., and Bryant, M.P., *Syntrophomonas wolfei* subsp. *saponavida* subsp. nov., a long-chain fatty-acid-degrading, anaerobic, syntrophic bacterium; *Syntrophomonas wolfei* subsp. *wolfei* subsp. nov.; and emended descriptions of the genus and species, *Int. J. Syst. Bacteriol.*, 1989, vol. 39, pp. 122–126.

79. Zhang, C., Liu, X., and Dong, X., *Syntrophomonas curvata* sp. nov., an anaerobe that degrades fatty acids in co-culture with methanogens, *Int. J. Syst. Evol. Microbiol.*, 2004, vol. 54, pp. 969–973.

80. Zhang, C., Liu, X., and Dong, X., *Syntrophomonas erecta* sp. nov., a novel anaerobe that syntrophically degrades short-chain fatty acids, *Int. J. Syst. Evol. Microbiol.*, 2005, vol. 55, pp. 799–803.

81. Hatamoto, M., Imachi, H., Fukayo, S., Ohashi, A., and Harada, H., *Syntrophomonas palmitatica* sp. nov., an anaerobic, syntrophic, long-chain fatty-acid-oxidizing bacterium isolated from methanogenic sludge, *Int. J. Syst. Evol. Microbiol.*, 2007, vol. 57, pp. 2137–2142.

82. Sousa, D.Z., Smidt, H., Alves, M.M., and Stams, A.J.M., *Syntrophomonas zehnderi* sp. nov., an anaerobe that degrades long-chain fatty acids in co-culture with *Methanobacterium formicicum, Int. J. Syst. Evol. Microbiol.*, 2007, vol. 57, pp. 609–615.

83. Ariesyady, H.D., Ito, T., and Okabe, S., Functional bacterial and archaeal community structures of major trophic groups in a full-scale anaerobic sludge digester, *Wat. Res*, 2007, vol. 41, pp. 1554–1568.

84. Sekiguchi, Y., Kamagata, Y., Nakamura, K., Ohashi, A., and Harada, H., *Syntrophothermus lipocalidus* gen. nov., sp. nov., a novel thermophilic, syntrophic, fatty-acid-oxidizing anaerobe which utilizes isobutyrate, *Int. J. Syst. Evol. Microbiol.*, 2000, vol. 50, pp. 771–779.

85. Jackson, B.E., Bhupathiraju, V.K., Tanner, R.S., Woese, C.R., and McInerney, M.J., *Syntrophus aciditrophicus* sp. nov., a new anaerobic bacterium that degrades fatty acids and benzoate in syntrophic association with hydrogen-using microorganisms, *Arch. Microbiol.*, 1999, vol. 171, pp. 107–114.

86. Mountfort, D.O., Brulla, W.J., Krumholz, L.R., and Bryant, M.P., *Syntrophus buswellii* gen. nov. sp. nov.: a benzoate catabolizer from methanogenic ecosystems, *Int. J. Syst. Bacteriol.,* 1984, vol. 34, no. 2, pp. 216–217.

87. Boone, D.R. and Bryant, M.P., Propionate-degrading bacterium, *Syntrophobacter wolinii* sp. nov. gen. nov., from methanogenic ecosystems, *Appl. Environ. Microbiol.,* 1980, vol. 40, pp. 626–632.

88. Kovacik, W.P., Scholten, J.C.M., Culley, D., Hickey, R., Zhang, W., and Brockman, F.J., Microbial dynamics in upflow anaerobic sludge blanket (UASB) bioreactor granules in response to short-term changes in substrate feed, *Microbiology*, 2010, vol. 156, pp. 2418–2427.

89. Wallrabenstein, C., Hauschild, E., and Schink, B., *Syntrophobacter pfennigii* sp. nov., new syntrophically propionate-oxidizing anaerobe growing in pure culture with propionate and sulfate, *Arch. Microbiol.*, 1995, vol. 164, no. 5, pp. 346–352.

90. Harmsen, H.J.M., Van Kuijk, B.L.M., Plugge, C.M., Akkermans, A.D.L., De Vos, W.M., and Stams, A.J.M., *Syntrophobacter fumaroxidans* sp. nov., a syntrophic propionate-degrading sulfatereducing bacterium, *Int. J. Syst. Bacteriol.*, 1998, vol. 48, pp. 1383–1387.

91. Chen, S., Liu, X., and Dong, X., *Syntrophobacter sulfatireducens* sp. nov., a novel syntrophic, propionate-oxidizing bacterium isolated from UASB reactors, *Int. J. Syst. Evol. Microbiol.*, 2005, vol. 55, pp. 1319–1324.

92. McMahon, K.D., Zheng, D., Stams, A.J.M., Mackie, R.I., and Raskin, L., Microbial population dynamics during start-up and overload conditions of anaerobic digesters treating municipal solid waste and sewage sludge, *Biotechnol. Bioeng.*, 2004, vol. 87, pp. 823–834.

93. Roest, K., Heilig, H.G., Smidt, H., de Vos, W.M., Stams, A.J., and Akkermans, A.D., Community analysis of a full-scale anaerobic bioreactor treating paper mill wastewater, *Syst. Appl. Microbiol.*, 2005, vol. 28, pp. 175–185.

94. Plugge, C.M., Balk, M., and Stams, A.J.M., *Desulfotomaculum thermobenzoicum* subsp. *thermosyntrophicum* subsp. nov., a thermophilic, syntrophic, propionate-oxidizing, spore-forming bacterium, *Int. J. Syst. Evol. Microbiol.*, 2002, vol. 52, pp. 391–399.

95. de Bok, F.A.M., Harmsen, H.J.M., Plugge, C.M., de Vries, M.C., Akkermans, A.D.L., de Vos, W.M., and Stams, A.J.M., The first true obligately syntrophic propionate-oxidizing bacterium, *Pelotomaculum schinkii* sp. nov., co-cultured with *Methanospirillum hungatei*, and emended description of the genus *Pelotomaculum, Int. J. Syst. Evol. Microbiol.*, 2005, vol. 55, pp. 1697–1703.

96. Imachi, H., Sekiguchi, Y., Kamagata, Y., Hanada, S., Ohashi, A., and Harada, H., *Pelotomaculum thermopropionicum* gen. nov., sp. nov., an anaerobic, thermo-

philic, syntrophic propionate-oxidizing bacterium, *Int. J. Syst. Evol. Microbiol.*, 2002, vol. 52, pp. 1729–1735.

97. Imachi, H., Sakai, S., Ohashi, A., Harada, H., Hanada, S., Kamagata, Y., and Sekiguchi, Y., *Pelotomaculum propionicicum* sp. nov., an anaerobic, mesophilic, obligately syntrophic, propionate-oxidizing bacterium, *Int. J. Syst. Evol. Microbiol.*, 2007, vol. 57, pp. 1487–1492.
98. Qiu, Y.-L., Sekiguchi, Y., Hanada, S., Imachi, H., Tseng, I.-C., Cheng, S.-S., Ohashi, A., Harada, H., and Kamagata, Y., *Pelotomaculum terephthalicum* sp. nov. and *Pelotomaculum isophthalicum* sp. nov.: two anaerobic bacteria that degrade phthalate isomers in syntrophic association with hydrogenotrophic methanogens, *Arch. Microbiol.*, 2006, vol. 185, pp. 172–182.
99. Qiu, Y-L., Sekiguchi, Y., Imachi, H., Kamagata, Y., Tseng, I.-C., Cheng, S-S., Ohashi, A., and Harada, H., *Sporotomaculum syntrophicum* sp. nov., a novel anaerobic, syntrophic benzoate-degrading bacterium isolated from methanogenic sludge treating wastewater from terephthalate manufacturing, *Arch. Microbiol.*, 2003, vol. 179, pp. 242–249.
100. Liu, Y., Balkwill, D.L., Aldrich, H.C., Drake, G.R., and Boone, D.R., Characterization of the anaerobic propionate degrading syntrophs *Smithella propionica* gen. nov., sp. nov. and *Syntrophobacter wolinii, Int. J. Syst. Bacteriol.*, 1999, vol. 49, pp. 545–556.
101. Schnurer, A., Schink, B., and Svensson, B.H., *Clostridium ultunense* sp. nov., a mesophilic bacterium oxidizing acetate in syntrophic association with a hydrogenotrophic methanogenic bacterium, *Int. J. Syst. Bacteriol.,* 1996, vol. 46, no. 4, pp. 1145–1152.
102. Westerholm, M., Dolfing, J., Sherry, A., Gray, N.D., Head, I.A., and Schnurer, A., Quantification of syntrophic acetate-oxidizing microbial communities in biogas processes, *Environ. Microbiol. Rep.*, 2011, vol. 3, pp. 500–505.
103. Hattori, S., Kamagata, Y., Hanada, S., and Shoun, H., *Thermacetogenium phaeum* gen. nov., sp. nov., a strictly anaerobic, thermophilic, syntrophic acetate-oxidizing bacterium, *Int. J. Syst. Evol. Microbiol.*, 2000, vol. 50, pp. 1601–1609.
104. Tang, Y-Q., Fujimura, Y., Shigematsu, T., Morimura, S., and Kida, K., Anaerobic treatment performance and microbial population of thermophilic upflow anaerobic filter reactor treating Awamori distillery wastewater, *J. Biosci. Bioeng.*, 2007, vol. 104, no. 4, pp. 281–287.
105. Sekiguchi, Y., Imachi, H., Susilorukmi, A., Muramatsu, M., Ohashi, A., Harada, H., Hanada, S., and Kamagata, Y., *Tepidanaerobacter syntrophicus* gen. nov., sp. nov., an anaerobic, moderately thermophilic, syntrophic alcohol- and lactate-degrading bacterium isolated from thermophilic digested sludges, *Int. J. Syst. Evol. Microbiol.,* 2006, vol. 56, pp. 1621–1629.
106. Balk, M., Weijma, J., and Stams, A.J.M., *Thermotoga lettingae* sp. nov., a novel thermophilic, methanol-degrading bacterium isolated from a thermophilic anaerobic reactor, *Int. J. Syst. Evol. Microbiol.*, 2002, vol. 52, pp. 1361–1368.
107. Krumholz, L.R. and Bryant, M.P., *Syntrophococcus sucromutans* sp. nov. gen. nov. uses carbohydrates as electron donors and formate, methoxymonobenzenoids or *Methanobrevibacter* as electron acceptor systems, *Arch. Microbiol.*, 1986, vol. 143, pp. 313–318.
108. Gujer, W. and Zehnder, A.J.B., Conversion processes in anaerobic digestion, *Wat. Sci. Technol.*, 1983, vol. 15, nos. 8–9, pp. 127–167.
109. Nozhevnikova, A.N., Nekrasova, V., Ammann, A., Zehnder, A.J.B., Wehrli, B., and Holliger, C., Influence of temperature and high acetate concentrations on methanogenensis in lake sediment slurries, *FEMS Microbiol. Ecol.*, 2007, vol. 62, pp. 336–344.
110. Jetten, M.S.M., Stams, A.J.M., and Zehnder, A.J.B., Methanogenesis from acetate: a comparison of the acetate metabolism in *Methanothrix soehngenii* and *Methanosarcina* spp, *FEMS Microbiol. Rev.*, 1992, vol. 88, pp. 181–198.
111. Montero, B., Garcia-Morales, J.L., Sales, D., and Solera, R., Evolution of microorganisms in thermophilic-dry anaerobic digestion, *Biores. Technol.*, 2008, vol. 99, pp. 3233–3243.
112. Uz, I., Rasche, M.E., Townsend, T., Ogram, A.V., and Lindner, A.S., Characterization of methanogenic and methanotrophic assemblages in landfill samples, *The Royal Soc. Biol. Lett.*, 2003, vol. 270, pp. 202–205.
113. Nayak, B.S., Levine, A.D., Cardoso, A., and Harwood, V.J., Microbial population dynamics in laboratory-scale solid waste bioreactors in the presence or absence of biosolids, *J. Appl. Microbiol.*, 2009, vol. 107, pp. 1330–1339.
114. Huser, B.A., Wuhrmann, K., and Zehnder, A.J.B., *Methanotrix soehngenii* gen. nov. sp. nov., a new acetotrophic non-hydrogen-oxidizing methane bacterium, *Arch. Microbiol.*, 1982, vol. 132, pp. 1–9.
115. Nozhevnikova, A.N., Zhilina, T.N., and Sokolova, T.G., Species composition of methane bacteria in fermented cattle manure, *Prikl. Biokhim. Mikrobiol.*, 1988, vol. 24, pp. 555–560.
116. Grotenhuis, J.T., Smit, M., Plugge, C.M., Xu, Y.S., van Lammeren, A.A., Stams, A.J., and Zehnder, A.J., Bacteriological composition and structure of granular sludge adapted to different substrates, *Appl. Environ. Microbiol.*, 1991, vol. 57, pp. 1942–1949.
117. Kobayashi, H.A., Conway de Macario, E., Williams, R.S., and Macario, A.J., Direct characterization of methanogens in two high-rate anaerobic biological reactors, *Appl. Environ. Microbiol.*, 1988, vol. 54, pp. 693–698.
118. Visser, F.A., van Lier, J.B., Macario, A.J., and Conway de Macario, E., Diversity and population dynamics of methanogenic bacteria in a granular consortium, *Appl. Environ. Microbiol.*, 1991, vol. 57, pp. 1728–1734.
119. Ike, M., Inoue, D., Miyano, T., Liu, T.T., Sei, K., Soda, S., and Kadoshin, S., Microbial population dynamics during startup of a full-scale anaerobic digester treating industrial food waste in Kyoto eco-energy project, *Biores. Technol.*, 2010, vol. 101, pp. 3952–3957.
120. McHugh, S., Carton, M., Collins, G., and O'Flaherty, V., Reactor performance and microbial community dynamics during anaerobic biological treatment of wastewaters at 16–37°C, *FEMS Microbiol. Ecol.*, 2004, vol. 48, pp. 369–378.

121. Pender, S., Toomey, M., Carton, M., Eardly, D., Patching, J.W., Colleran, E., and O'Flaherty, V., Long-term effects of operating temperature and sulphate addition on the methanogenic community structure of anaerobic hybrid reactors, *Water Res.*, 2004, vol. 38, pp. 619–630.

122. Laloui-Carpentier, W., Li, T., Vigneron, V., Mazeas, L., and Bouchez, T., Methanogenic diversity and activity in municipal solid waste landfill leachates, *Antonie van Leeuwenhoek,* 2006, vol. 89, pp. 423–434.

123. Lerm, S., Kleybocker, A., Miethling-Graff, R., Alawi, M., Kasina, M., Liebrich, M., and Wurdemann, H., Archaeal community composition affects the function of anaerobic co-digesters in response to organic overload, *Waste Manage*, 2012, vol. 32, pp. 389–399.

124. Fielding, E.R., Archer, D.B., Conway de Macario, E., and Macario, A.J., Isolation and characterization of methanogenic bacteria from landfills, *Appl. Environ. Microbiol.*, 1988, vol. 54, pp. 835–836.

125. Macario, A., J, Conway de Macario, E., Ney, U., Schoberth, S.M., and Sahm, H., Shifts in methanogenic subpopulations measured with antibody probes in a fixed-bed loop anaerobic bioreactor treating sulfite evaporator condensate, *Appl. Environ. Microbiol.*, 1989, vol. 55, pp. 1996–2001.

126. Sponza, D.T. and Cigal, C., Relationships between anaerobic consortia and removal efficiencies in an UASB reactor degrading 2,4-dichlorophenol (DCP), *J. Environ. Manage,* 2008, vol. 87, pp. 177–192.

127. Ma, K., Liu, X., and Dong, X., *Methanobacterium beijingense* sp. nov., a novel methanogen isolated from anaerobic digesters, *Int. J. Syst. Evol. Microbiol.*, 2005, vol. 55, pp. 325–329.

128. Cuzin, N., Ouattara, A.S., Labat, M., and Garcia, J.L., *Methanobacterium congolense* sp. nov., from a methanogenic fermentation of cassava peel, *Int. J. Syst. Evol. Microbiol.*, 2001, vol. 51, pp. 489–493.

129. Patel, G.B., Sprott, G.D., and Fein, J.E., Isolation and characterization of *Methanobacterium espanolae* sp. nov., a mesophilic, moderately acidiphilic methanogen, *Int. J. Syst. Bacteriol.,* 1990, vol. 40, pp. 12–18.

130. Chen, A.C., Ueda, K., Sekiguchi, Y., Ohashi, A., and Harada, H., Molecular detection and direct enumeration of methanogenic archaea and methanotrophic bacteria in domestic solid waste landfill soils, *Biotech. Lett*, 2003, vol. 25, pp. 1563–1569.

131. Zellner, G., Stackebrandt, E., Messner, P., Tindall, B.J., Conway de Macario, E., Kneifel, H., Sleytr, U.B., and Winter, J., *Methanocorpusculaceae* fam. nov., represented by *Methanocorpusculum parvum, Methanocorpusculum sinense* spec. nov. and *Methanocorpusculum bavaricum* spec. nov, *Arch. Microbiol.*, 1989, vol. 151, pp. 381–390.

132. Zellner, G., Alten, C., Stackebrandt, E., Conway de Macario, E., and Winter, J., Isolation and characterization of *Methanocorpusculum parvum* gen. nov., spec. nov., a new tungsten requiring, coccoid methanogen, *Arch. Microbiol.*, 1987, vol. 147, pp. 13–20.

133. Simankova, M.V., Kotsyurbenko, O.R., Lueders, T., Nozhevnikova, A.N., Wagner, B., Conrad, R., and Friedrich, M.W., Isolation and characterization of new strains of methanogens from cold terrestrial habitats, *Syst. Appl. Microbiol.*, 2003, vol. 26, pp. 312–318.

134. Ollivier, B.M., Mah, R.A., Garcia, J.L., and Boone, D.R., Isolation and characterization of *Methanogenium bourgense* sp. nov, *Int. J. Syst. Bacteriol.*, 1986, vol. 36, pp. 297–301.

135. Zellner, G., Messner, P.P., Winter, J., and Stackebrandt, E., *Methanoculleus palmolei* sp. nov., an irregularly coccoid methanogen from an anaerobic digester treating wastewater of a palm oil plant in North-Sumatra, Indonesia, *Int. J. Syst. Bacteriol.,* 1998, vol. 48, pp. 1111–1117.

136. Zellner, G., Sleytr, U.B., Messner, P., Kneifel, H., and Winter, J., *Methanogenium liminatans* spec. nov., a new coccoid, mesophilic methanogen able to oxidize secondary alcohols, *Arch. Microbiol.*, 1990, vol. 153, pp. 287–293.

137. Ferry, J.G., Smith, P.H., and Wolfe, R.S., *Methanospirillum*, a new genus of methanogenic bacteria, and characterization of *Methanospirillum hungatii* sp. nov, *Int. J. Syst. Bacteriol.*, 1974, vol. 24, pp. 465–469.

138. Meesap, K., Boonapatcharoen, N., Techkarnjanaruk, S., and Chaiprasert, P., Microbial communities and their performances in anaerobic hybrid sludge bed-fixed film reactor for treatment of palm oil mill effluent under various organic pollutant concentrations, *J. Biomed. Biotechnol.*, 2012, vol. 2012. Article ID 902707. 11 p. doi: 10.1155/2012/902707

139. Parshina, S.N., Ermakova, A.V., Bomberg, M., and Detkova, E.N., *Methanospirillum stamsii* sp. nov., a psychrotolerant, hydrogenotrophic, methanogenic archaeon isolated from an anaerobic expanded granular sludge bed bioreactor operated at low temperature, *Int. J. Syst. Evol. Microbiol.*, 2014, vol. 64, pp. 180–186.

140. Bryant, M.P. and Boone, D.R., Emended description of strain MST (DSM 800T), the type strain of *Methanosarcina barkeri, Int. J. Syst. Bacteriol.*, 1987, vol. 37, pp. 169–170.

141. Mah, R.A. and Kuhn, D.A., Transfer of the type species of the genus *Methanococcus* to the genus *Methanosarcina*, naming it *Methanosarcina mazei* (Barker 1936) comb. nov. et emend. and conservation of the genus *Methanococcus* (approved lists 1980) with *Methanococcus vannielii* (approved lists 1980) as the type species request for an opinion, *Int. J. Syst. Bacteriol.,* 1984, vol. 34, pp. 263–265.

142. Zhilina, T.N. and Zavarzin, G.A., *Methanosarcina vacuolata* sp. nov. a vacuolated methanosarcina, *Int. J. Syst. Bacteriol.*, 1987, vol. 37, pp. 281–283.

143. Roest, K., Altinbas, M., Paulo, P.L., Heilig, H.G.H.J., Akkermans, A.D.L., Smidt, H., de Vos, W.M., and Stams, A.J.M., Enrichment and detection of microorganisms involved in direct and indirect methanogenesis from methanol in an anaerobic thermophilic bioreactor, *Microbial Ecol.*, 2005, vol. 50, pp. 440–446.

144. Nozhevnikova, A.N. and Yagodina, T.G., A thermophilic acetate methanogenic bacterium, *Mikrobiologiya*, 1982, vol. 51, pp. 642–649.

145. Kamagata, Y. and Mikami, E., Isolation and characterization of a novel thermophilic *Methanosaeta* strain, *Int. J. Syst. Bacteriol.*, 1991, vol. 41, pp. 191–196.

146. Imachi, H., Sakai, S., Sekiguchi, Y., Hanada, S., Kamagata, Y., Ohashi, A., and Harada, H., *Methanolinea tarda* gen. nov., sp. nov., a methane-producing archaeon isolated from a methanogenic digester sludge, *Int. J. Syst. Evol. Microbiol.*, 2008, vol. 58, pp. 294–301.

147. Kotelnikova, S.V., Obraztsova, A.Ya., Gongadze, G.M., and Laurinavichius, K.S., *Methanobacterium thermoflexum* sp. nov. and *Methanobacterium defluvii* sp. nov., thermophilic rod-shaped methanogens isolated from anaerobic digestor sludge, *Syst. Appl. Microbiol.*, 1993, vol. 16, pp. 427–435.

148. Wasserfallen, A., Nolling, J., Pfister, P., and Reeve, J., and Conway de Macario, E., Phylogenetic analysis of 18 thermophilic *Methanobacterium* isolates supports the proposals to create a new genus, *Methanothermobacter* gen. nov., and to reclassify several isolates in three species, *Methanothermobacter thermautotrophicus* comb. nov., *Methanothermobacter wolfeii* comb. nov., and *Methanothermobacter marburgensis* sp. nov., *Int. J. Syst. Evol. Microbiol.*, 2000, vol. 50, pp. 43–53.

149. Zeikus, J.G. and Wolfe, R.S., *Methanobacterium thermoautotrophicus* sp. n., an anaerobic, autotrophic, extreme thermophile, *J. Bacteriol.*, 1972, vol. 109, pp. 707–715.

150. Zhilina, T.N. and Ilarionov, S.A., Characterization of formate-utilizing methane bacteria and description of *Methanobacterium thermoformicicum* sp. nov., *Mikrobiologiya*, 1984, vol. 53, pp. 785–790.

151. Laurinavichyus, K.S., Kotel'nikova, S.V., and Obraztsova, A.Ya., *Methanobacterium thermophilum*, a new species of thermophilic methanogenic bacteria, *Mikrobiologiya*, 1988, vol. 57, pp. 1035–1041.

152. Winter, J., Lerp, C., Zabel, H.-P., Wildenauer, F.X., König, H., and Schindler, F., *Methanobacterium wolfei*, sp. nov., a new tungsten-requiring, thermophilic, autotrophic methanogen, *Syst. Appl. Microbiol.*, 1984, vol. 5, pp. 457–466.

153. Cheon, J., Hong, F., Hidaka, T., Koshikawa, H., and Tsuno, H., Microbial population dynamics in a thermophilic methane digester fed with garbage, *Water Sci Technol.*, 2007, vol. 55, pp. 175–182.

154. Jiang, B., Parshina, S.N., van Doesburg, W., Lomans, B.P., and Stams, A.J.M., *Methanomethylovorans thermophila* sp. nov., a thermophilic, methylotrophic methanogen from an anaerobic reactor fed with methanol, *Int. J. Syst. Evol. Microbiol.*, 2005, vol. 55, pp. 2465–2470.

155. Zinder, S.H., Sowers, K.R., and Ferry, J.G., *Methanosarcina thermophila* sp. nov. a thermophilic, acetotrophic, methane-producing bacterium, *Int. J. Syst. Bacteriol.*, 1985, vol. 35, pp. 522–523.

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