First publ. in: The Prokaryotes; Vol. 7 / Martin Dworkin (ed.-in-chief) ... New York : Springer, 2006, pp. 5-11

The Genus *Pelobacter*

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The genus *Pelobacter* was proposed as a taxonomic entity consisting of strictly anaerobic, Gram-negative, nonspore-forming, rod-shaped bacteria that use only a very limited number of substrates. The members of the genus are all unable to ferment sugars and therefore cannot be grouped with any other genus in the family Bacteroidaceae (Krieg and Holt, 1984). The genus comprises five different species, *P. acidigallici* (Schink and Pfennig, 1982), *P. venetianus* (Schink and Stieb, 1983), *P. carbinolicus* (Schink, 1984), *P. propionicus* (Schink, 1984), and *P. acetylenicus* (Schink, 1985), which all are based on 3–5 described strains.

Comparisons of the various *Pelobacter* species by DNA-DNA hybridization experiments revealed that the genus is rather inhomogenous; therefore, a reorganization may perhaps be necessary in the future (J. P. Touzel and B. Schink, unpublished observations). Whereas the species *P. venetianus*, *P. carbinolicus*, and *P. acetylenicus* form a homogenous cluster, *P. acidigallici* and *P. propionicus* appear to be only distantly related to the others. These findings are consistent to some extent with the fermentation patterns of these species (see below). Comparison of three *Pelobacter* species with other anaerobes on the basis of 16S rRNA structure analysis supports this view. Whereas *P. venetianus* and *P. carbinolicus* exhibit a rather high similarity, with an S_{AB} of 0.70, *P. acidigallici* is related to both at an S_{AB} of only 0.53 (Stackebrandt et al., 1989). It is interesting to note that these three Pelobacter strains did not show any resemblance to other fermenting Gram-negative strict anaerobes; instead, they appeared to be highly related to several strains of sulfur-reducing anaerobes, namely, *Desulfuromonas succinoxidans*, *D. acetexigens*, and *D. acetoxidans*, to which they are even more closely related than *P. acidigallici* is to the other two *Pelobacter* species. Since *Pelobacter* species and the obligately sulfur-respiring bacteria are quite diverse metabolically and the latter are supposed to have derived directly from phototrophic ancestors, it has been suggested that the genus *Pelobacter* represents a group of fermenting bacteria that developed a fermentative metabolism as a "secondary" evolutionary event and that they are separate from the first fermentative bacteria (Stackebrandt et al., 1989).

Habitat

All *Pelobacter* strains have been isolated so far from marine or freshwater sediments. The name *Pelobacter* was based on this origin (Greek *pelos* meaning mud, sediment). Enrichments from sewage sludges led to similar isolates as well. Viable counts using the characteristic substrates gallic acid, acetoin, polyethylene glycol, and acetylene showed that there were approximately 100 cells/ml of each of the *Pelobacter* species in sediment and up to 2,500 cells/ml in sewage sludge. Since their substrate ranges are comparably small, their ecological niche in such sediments can be understood rather well in most cases. *P. acidigallici* is restricted to the utilization of trihydroxybenzenoids, which are probably its only energy source in its natural habitat. *P. venetianus*, *P. carbinolicus*, *P. propionicus*, and *P. acetylenicus* were enriched and isolated with polyethylene glycol, 2,3-butanediol, and acetylene, respectively, but the ecological importance of these substrates in the respective environments is questionable. Since all these species can also ferment ethanol, either in syntrophic cooperation with hydrogen scavengers or in pure culture, it appears more probable that degradation of this important fermentation intermediate is their predominant function in these environments. *P. carbinolicus* has been identified as the dominant ethanol-degrading bacterium in digesting industrial sewage sludge (Dubourguier et al., 1986), and high numbers (10^6–10^7 cells/ml) of syntrophically ethanol-oxidizing anaerobes were detected also in other sewage sludges (Schink et al., 1985) and in freshwater creek sediments (Eichler and Schink, 1985). *Pelobacter* has to compete for ethanol with certain homoacetogenic bacteria, e.g., *Clostridium aceticum* (Wieringa, 1940) or *Acetobacterium carbinolicum* (Eichler and Schink, 1984), which appear to be at least as successful in freshwater sediments (Schink et al., 1985), especially if the sediment is slightly acidic (Schink et al., 1985) or the temperature is low (Conrad et al., 1989). The ecological importance of ethanol fermentation to propionate by *P. propionicus* has been elucidated by enumerations and by tracer experiments (Schink et al., 1985). These studies revealed that up to 20% of the total ethanol turnover can go through propionate and that bacteria forming propionate from ethanol contribute significantly to the total ethanol-metabolizing microbial community.

It has to be concluded that bacteria of the metabolic types represented by the various *Pelo-*

This chapter was taken unchanged from the second edition.

bacter species make up a significant part of the anaerobic microbial population in sediments and sewage sludge. No *Pelobacter*-like bacteria have so far been isolated from the rumen. The numerically predominant, syntrophically ethanol-oxidizing *Pelobacter* species represent new isolates of the metabolic type of the S-strain in the mixed culture "*Methanobacillus omelianskii*" (Bryant et al., 1967). These *Pelobocter* species have become accessible to pure culture growth in our laboratory by the use of unusual substrates that all can be converted easily into acetaldehyde, the key intermediate in the energy metabolism of these bacteria (see next section).

Isolation

Growth Media

All *Pelobacter* strains have been enriched and isolated in a carbonate-buffered, sulfide-reduced mineral medium that contained only one organic energy and carbon source. Since they grow with substrates that yield 2-carbon intermediates exclusively, they have to form pyruvate and sugars via reductive carboxylation of acetyl coenzyme A and need carbon dioxide for this reaction. Use of a bicarbonate-buffered medium is therefore recommended for enrichment, isolation, and maintenance. Three different versions of this medium are described below for the isolation of *Pelobacter* from freshwater, estuarine, and marine sediment, respectively (after Widdel and Pfennig, 1981; Schink and Pfennig, 1982):

Pelobacter Growth Media

Dissolve in 1 liter of distilled water:

Autoclave the complete mineral medium in a vessel equipped with 1) a filter inlet to allow flushing of the headspace with sterile oxygen-free gas; 2) screw-cap inlets for addition of thermally unstable additives after autoclaving; 3) a silicon tubing connection from the bottom of the vessel out to a dispensing tap (if possible with a protecting bell) for sterile dispensing of the medium (do not use latex tubing; it releases compounds which are highly toxic to many anaerobes); and 4) a stirring bar.

After autoclaving, connect the vessel with the still-hot medium to a line of oxygen-free nitrogen/carbon dioxide mixture (90%: 10%) at low pressure (<100 mbar), flush the headspace and cool it under this atmosphere to room temperature, perhaps with the help of a cooling water bath.

The mineral medium is amended with the following additions from stock solutions that have been sterilized separately (amounts/l of medium): a) 30 ml of 1 M $NaHCO_3$ solution (autoclaved in a *tightly closed* screw-cap bottle with about 30% headspace; the bottle should be autoclaved inside another protective vessel, e.g., a polypropylene beaker, to avoid spills of carbonates if the bottle breaks in the autoclave); b) 2 ml of 0.5 M $Na_2S9{\cdot}H_2O$ solution (autoclaved separately under oxygen-free gas atmosphere as above); c) 1 ml of trace element solution, e.g., SL 10 (Widdel et al., 1983); d) 0.5 ml of 10-fold concentrated, filter-sterilized vitamin solution (Pfennig, 1978); and e) adequate amounts of sterile 1 M HC1 or 1 M $Na_2\ CO_3$ to adjust the pH to 7.1–7.3.

The complete medium is dispensed into either screw-cap bottles or screw-cap tubes which are filled completely to the top, leaving a lentil-sized air bubble for pressure equilibration. Enrichment cultures usually produce gas in the first enrichment stages and are better cultivated in half-filled serum bottles (50–100 ml volume) under a headspace of nitrogen: carbon dioxide mixture (90%:10%).

This mineral medium is amended with the respective organic substrates for enrichment and cultivation of pure cultures. The vitamin mixture is not really needed by all strains.

Selective Enrichment

All enrichment cultures were set up in our laboratory at 27–30°C in 50-ml fluid cultures inoculated with about 5 ml of sediment or sludge. Smaller inocula may also lead to isolation of the same bacteria, but this has not been evaluated in our lab. *P. acidigallici* can be selectively enriched with either one of its growth substrates (see Table 1) at 5–10 mM concentration. For enrichment of *P. venetianus*, either polyethylene glycol (mol wt 106–20,000; 0.1% w/v) or methoxyethanol (10 mM; Tanaka and Pfennig, 1988) is recommended. In this medium, 10 mM 2,3-butanediol enriches for *P. carbinolicus* from marine sediments and for *P. propionicus* from freshwater sediments. *P. acetylenicus* is successfully enriched with mineral medium under the above-mentioned nitrogen: carbon dioxide atmosphere containing 5–10% acetylene in addition.

Isolation

After 3–4 transfers in liquid medium, a homogeneous microbial population should have become established in liquid enrichment cultures. Purification of *Pelobacter* species is most easily done by serial dilution in agar deep cultures ("agar shakes"; Pfennig, 1978). Roll tubes have not been used and are not necessary since these bacteria neither consume nor produce insoluble gaseous compounds. *P. acetylenicus* can be easily purified with 10 mM acetoin as substrate. Other procedures (streaking on agar plates in an anoxic glove box or on agar surfaces in flat agar bottles) have not been tried yet, but there is no reason why such methods would not be successful as well, if the solid media are incubated under a nitrogen/carbon dioxide atmosphere.

Preservation

Liquid cultures were maintained in our laboratory in 50-ml bottles at 4°C for 4–12 weeks

Table 1. Properties of the five *Pelobacter* species.

	P. acidigallici	*P. venetianus*	*P. carbinolicus*	*P. acetylenicus*	*P. propionicus*
Width (μm)	0.5–0.8	0.5–1.0	0.5–0.7	0.6–0.8	0.5–0.7
Length (μm)	1.5–3.5	2.5	1.2–3.0	1.5–4.0	1.2–6.0
GC content (mol%)	51.8	52.2	52.3	57.1	57.4
Substrate metabolized					
Gallic acid	+	–	–	–	–
Pyrogallol	+	–	–	–	–
Phloroglucinol	+	–	–	–	–
Phloroglucinolcarboxylate	+	–	–	–	–
Acetoin	–	+	+	+	+
2,3-Butanediol	–	+	+	+	+
Ethylene glycol	–	+[a]	+	–	–
Polyethylene glycols	–	+	–	–	–
Ethanol	–	+[b]	+[b]	+[b]	+
n-Propanol	–	+[b, c]	+[b, c]	+[b, c]	+[c]
n-Butanol	–	+[b, c]	+[b, c]	+[b, c]	+[c]
1,2-Propanediol	–	+[c]	–	+[c]	–
Acetylene	–	–	–	+	–
Lactate	–	–	–	–	+
Pyruvate	–	–	–	–	+
Glycerol	–	+[c]	–	+[c]	–
Typical Products	Acetate (CO_2)	Acetate, ethanol	Acetate, ethanol	Acetate, ethanol	Acetate, propionate

[a]Growth is possible only at very low concentration (<1 mM) or in continuous culture.
[b]Growth is possible only in the presence of a hydrogen-scavenging anaerobe, e.g., a methanogenic bacterium.
[c]Growth is possible only in the presence of small amounts of acetate for cell carbon synthesis.
Symbols: +, growth; –, no growth.

between transfers. Longer storage intervals may be possible as well. Long-term preservation is easily accomplished by storage of dense cell suspensions in glass capillaries kept in liquid nitrogen.

Identification

Morphological and Cytological Properties

Cells of all *Pelobacter* species are Gram-negative, short rods that do not form spores (Fig. 1). The cell ends are usually rounded; however, *P. acetylenicus* cells can be slightly pointed (Fig. 1e). The cell sizes vary from 0.5 to 1.0 μm in width and from 1.2 to 6.0 μm in length. More exact cell sizes of the different type strains are listed in Table 1. The temperature optima for growth are in the range of 28–35°C; the pH optima are 6.5–7.5. On the basis of the GC content of the DNA, two clusters can be defined; the one (*P. acidigallici*, *P. venetianus*, *P. carbinolicus)* has a GC value at 50–53 mol%, the other one *(P. acetylenicus*, *P. propionicus)* at 57–58 mol%. It should be noted that this clustering does not agree with the subgroupings based on DNA and RNA homologies (see "Introduction," this chapter) or with physiological similarities.

Cytochromes have been found only in *P. propionicus*. A *b*-type cytochrome was detected at a very low level (Schink et al., 1987), but there is no evidence that this cytochrome plays any role in ATP-generating electron transport (see below).

Physiological Properties and Biochemistry

Table 1 presents a listing of all substrates used by the various *Pelobacter* species described so far. It is obvious from this table that *Pelobacter acidigallici* differs in its substrate spectrum from all other *Pelobacter* species. It utilizes only trihydroxybenzenoids for growth, and it ferments them to acetate as sole fermentation product. With this, it resembles *Eubacterium oxidoreducens* (Krumholz and Bryant, 1986) to some extent, but does not depend on formate as an external co-substrate for degradation of these compounds. Growth experiments with increased substrate concentrations have revealed that the pathway of gallic acid fermentation leads via pyrogallol and phloroglucinol (Samain et al., 1986) and has nothing in common with the pathway of anaerobic benzoate degradation (Evans, 1977). Obviously, three hydroxyl groups in alternating position at the ring polarize the π-electron system sufficiently to permit selective reduction to dihydrophloroglucinol and ring opening by a thiolytic or hydrolytic mechanism. The isomerization of pyrogallol to phloroglucinol has recently been characterized as a unique transhydroxylase reaction involving a tetrahydroxybenzene as co-substrate (Brune and Schink, 1990). The third trihydroxybenzene isomer, hydroxyhy-

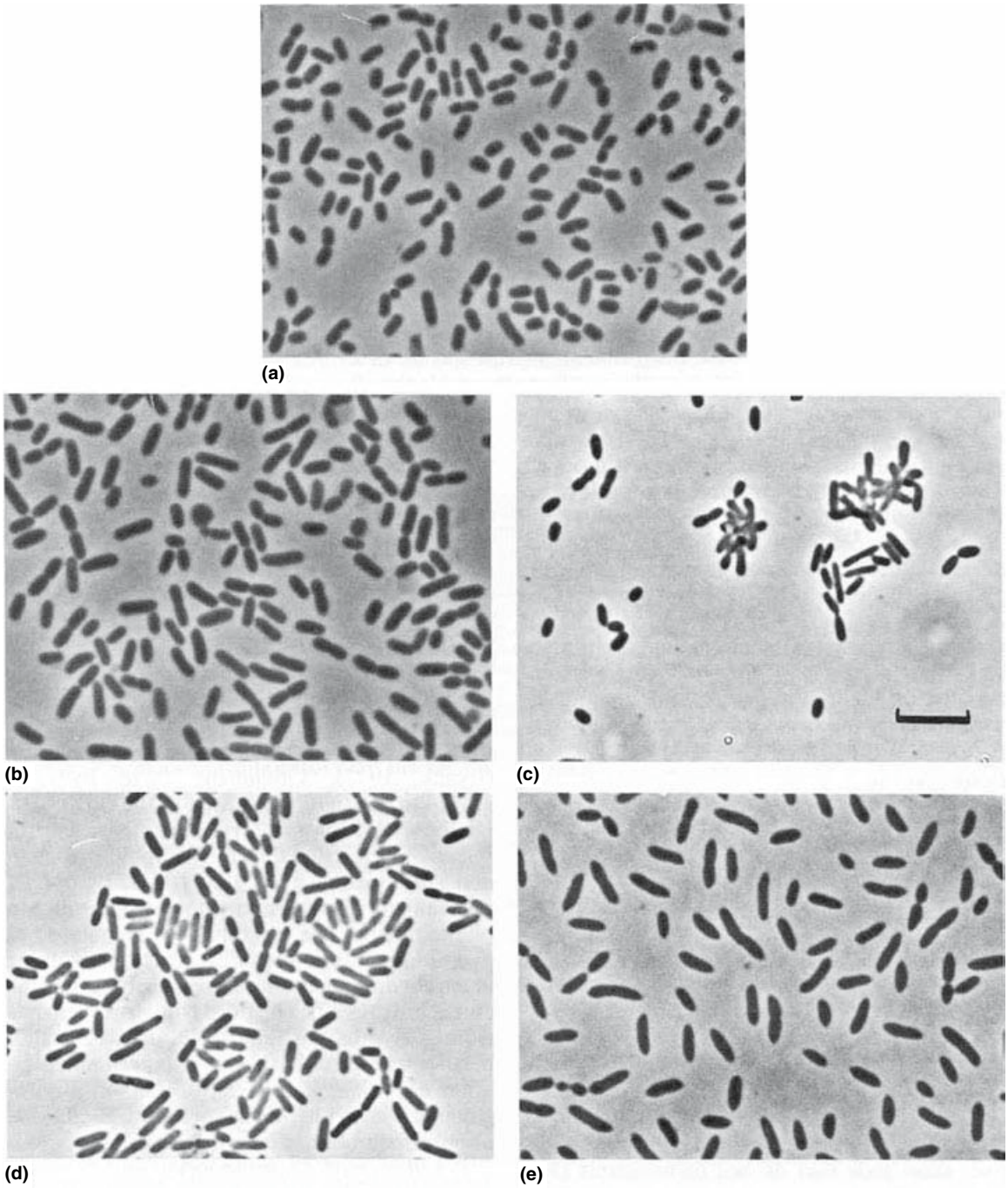

Fig. 1. Phase contrast photomicrographs of cells of *Pelobacter* species. Bar = 5 μm for all figures. (a) *P. acidigallici*; (b) *P. venetianus*; (c) *P. carbinolicus*; (d) *P. acetylenicus*; (e) *P. propionicus*.

droquinone, is not metabolized by these bacteria, but it is fermented by other new anaerobic bacteria, also via phloroglucinol (A. Brune, S. Schnell and B. Schink, unpublished observations).

P. venetianus, *P. carbinolicus*, and *P. acetylenicus* have been enriched and isolated with polyethylene glycol, 2,3-butanediol, or acetylene, respectively. They can all grow with acetoin, some also with ethylene glycol or ethanolamine. All these substrates are converted to acetaldehyde, which is further dismutated to acetate and ethanol as final products. ATP is formed exclusively by substrate level phosphorylation via the acetate kinase reaction. The higher homologs of

ethylene glycol, 1,2-propanediol and 1,2-butanediol, are dismutated to propanol and propionate or butanol and butyrate, respectively, provided that the medium contains some acetate (2–3 mM) for synthesis of cell material. Glycerol undergoes a similar dismutation to 3-hydroxypropionate and 1,3-propanediol. It is interesting to note that glycerol fermentation also requires the presence of acetate and that this substrate cannot itself be assimilated.

In the presence of hydrogen-scavenging anaerobes, e.g., homoacetogens or methanogens, *Pelobacter* oxidizes primary aliphatic alcohols to the corresponding acids; with propanol and butanol, acetate is again required for cell matter synthesis. This syntrophic oxidation of ethanol via "interspecies hydrogen transfer" was first observed with the S-strain isolated from the syntrophic mixed culture "*Methanobacillus omelianskii*" (Bryant et al., 1967), which was lost many years ago. *Pelobacter* strains are the only representatives of this type of metabolism that are available today in pure cultures. Pure and mixed culture experiments have been carried out recently to understand the energetics and kinetics of interspecies hydrogen transfer in model cultures of *P. acetylenicus* and hydrogen-scavenging homoacetogenic and methanogenic partners (Seitz et al., 1988; Seitz et al., in preparation).

The biochemistry of polyethylene glycol degradation is not yet understood, neither in *P. venetianus* nor in other polyethylene glycol-degrading anaerobes (Dwyer and Tiedje, 1986; Wagener and Schink, 1988). *P. venetianus* degrades all polymers from the dimer up to a molecular weight of 40,000. Growth experiments in batch and continuous culture have shown that ethylene glycol can also support growth if it is provided at limiting amounts and that acetaldehyde is the first free intermediate in both polymer and monomer degradation (Strass and Schink, 1986). Perhaps the polymer is attacked by a diol dehydratase-like reaction that transforms the terminal ether linkage into an unstable half-acetal linkage yielding acetaldehyde as product. Unfortunately, the cleavage reaction is very difficult to demonstrate in cell-free extracts, and a B_{12} compound of atypical structure appears to be involved (E. Schramm and B. Schink, unpublished observations). This cleavage reaction occurs inside the cells, and it is not clear how high-molecular-weight polyethylene glycols are able to cross the cytoplasmic membrane at sufficiently high transport rates.

Anaerobic degradation of polyethylene glycols is of major ecological concern because many industrially produced nonionic surfactants contain polyethylene glycols as hydrophilic moieties that may be subject to anaerobic degradation in anoxic sediments and sludge (Wagener and Schink, 1987, 1988).

P. carbinolicus is related to *P. venetianus* and has basically the same biochemistry and physiology. It degrades ethylene glycol rather than polyethylene glycols, and it was originally enriched and isolated with acetoin or 2,3-butanediol as substrate. 2,3-Butanediol is oxidized to acetoin, which undergoes oxidative cleavage to acetyl CoA and acetaldehyde by a dichlorophenol indophenol-dependent enzyme analogous to pyruvate dehydrogenase (Oppermann et al., 1988). The physiological electron acceptor of this enzyme is not yet known. Acetaldehyde is either oxidized by a benzyl viologen-dependent enzyme to acetyl CoA or, depending on the electron balance, reduced to ethanol.

P. acetylenicus is the first strict anaerobe known to ferment an unsaturated hydrocarbon in pure culture. Again, the first intermediate of acetylene fermentation is acetaldehyde, which is further dismutated to acetate and ethanol. The enzyme that hydrates acetylene to acetaldehyde could not be demonstrated in a cell-free assay system; perhaps unusual cofactors are also involved in this reaction. A report on an acetylene-hydratase enzyme in cell-free extracts of an aerobic *Rhodococcus* species (deBont and Peck, 1980) could not be reproduced in our hands either. The function of such an acetylene-hydrating enzyme in an anoxic environment is hard to understand since acetylene is probably not an important substrate in such environments. Perhaps its main role is hydration of other possibly toxic compounds, such as nitriles or cyanides, but there is no experimental evidence so far for such activities.

P. propionicus differs from the other *Pelobacter* species by producing propionate as one of its main fermentation products. Degradation of acetoin, 2,3-butanediol, and ethanol probably follows the same routes via acetaldehyde and acetyl CoA, as outlined above for the other species. The biochemistry of propionate formation from these C-2 compounds has been studied in detail (Schink et al., 1987). The key reaction is catalyzed by pyruvate synthase (pyruvate ferredoxin oxidoreductase), which operates here in the opposite direction to that predicted by its chemical equilibrium. The equilibrium is shifted by the exergonic propionate-forming reaction chain via methylmalonyl CoA; this chain is not coupled to ATP-yielding electron transport phosphorylation in these bacteria. This reaction in *P. propionicus* and other bacteria with similar biochemical capacities (Stams et al., 1984; Samain et al., 1982) is probably responsible for the formation of C-3 compounds from C-2 compounds in significant amounts in anoxic sediments and sludges (Goldberg and Cooney, 1981; Schink et al., 1985).

Applications

All *Pelobacter* strains discussed in this chapter may act as important syntrophic oxidants of primary aliphatic alcohols in sediments and sludges, where they have been found to be predominant (Dubourgier et al., 1986). Of technological interest may be the capacity of *P. venetianus* and similar isolates to degrade polyethylene glycols and to attack nonionic surfactants based on these compounds. These surfactants are of growing interest in the industrial manufacture of detergents, soaps, emulsifiers, etc. Aerobic degradation of polyethylene glycol-containing surfactant wastes creates enormous problems of foam formation in conventional activated-sludge sewage treatment and in natural waters. Anaerobic degradation of most of these compounds to methane can easily be achieved in packed column reactors, in which *P. venetianus*-like anaerobes ferment the polyethylene glycol moieties to substrates for the methanogenic microbial community (Wagener and Schink, 1987).

P. propionicus produces acetate and propionate from the substrates listed in Table 1. Propanol is fermented together with acetate exclusively to propionate. This fermentation may be of interest for biological production of propionate at high purity.

Acknowledgments. The author wishes to thank N. Pfennig and H. G. Trüper for their help on all questions concerning bacterial taxonomy and in the establishment of this new genus. The assistance of Martin Bomar in compiling the phase contrast photomicrographs shown in Fig. 1 is highly appreciated.

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