Characteristics of a New Obligate Methanol-Oxidizing Bacterium

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A new obligate methylotrophic bacterium which utilizes methanol as a sole source of carbon and energy was isolated from soil. It was Gram-negative, nonmotile, nonspore-forming rod, and strictly aerobic bacterium. Catalase and oxidase activities were present. Nitrate was reduced to nitrite. Vitamins and other growth factors were not required. Generation time was 1.6 hr under the optimal condition. The isolate assimilated methanol via the ribulose mono-phosphate pathway (Entner-Doudoroff varient) and did not have α-ketoglutarate dehydrogenase. It assimilated ammonia through glutamate dehydrogenase. The guanine plus cytosine content of the DNA was 61.0 mol%. The cellular fatty acid composition was primarily straight-chain saturated $C_{16:0}$ acids (palmitic acids) and unsaturated $C_{16:1}$ acids (palmitoleic acids), and the isolate also contained two unidentified C_{17} branched fatty acids. The major ubiquinone was Q-8, and Q-6 and Q-7 were present as minor components. Phosphatidylethanolamine and phosphatidylglycerol were predominantly present, and diphosphatidylglycerol was also detected. Based on the physiological and biochemical properties, the isolate was assigned to a novel species of the genus *Methylobacillus*, *Methylobacillus methanolovorus* sp. nov.

KEY WORDS □ **obligate methylotrophic bacterium; ribulose monophosphate pathway; *Methylobacillus methanolovorus***

At present, methylotrophic bacteria are divided into the obligate, the restricted facultative, and the facultative bacteria, respectively, on the basis of the range of carbon compounds utilized, as sole carbon and energy source (8, 10, 11). Obligate methylotrophs are defined as organisms that have the ability to utilize compounds that are more reduced than carbon dioxide and contain no carbon-carbon bonds. Facultative methylotrophs, on the other hand, are organisms that can utilize such C_1 compounds but are also capable of growth on multicarbon compounds. In addition, restricted facultative methylotrophic bacteria, which are a small group of intermediate organisms, can only utilize a relatively narrow range of multicarbon compounds as well as C_1 compounds.

Methylotrophic bacteria are a good source for the production of single cell proteins from methanol (3, 16, 17) and can convert C_1-com pounds into commercially important compounds such as amino acids, organic acids, biopolymers, coenzymes, vitamins, and cytochrome *c* (1, 16, 20, 24). These facts lead the bacteria to receive a great deal of attention as valuable microorganisms having commercial and biotechnological potentials. In spite of the importance of the practical applications, the systematics of this group remained rather undeveloped so far (6). Therefore, it is necessary to have some representative strains of methylotrophic bacteria studied in detail (6, 14).

In this study, we have isolated and characterized a new strain of methanol-oxidizing bacterium which grows fast on methanol in order to assist the establishment of the systematics of methylotrophic bacteria and also to use it for commercial and biotechnological purposes.

MATERIALS AND METHODS

Isolation of bacteria

A new strain was isolated from soil sample from Kwangju, Korea. The selection medium was composed of liquid mineral salt medium(MSM) of Kim *et al.* (12) containing 1.0% (v/v) methanol. Cells were grown in a 500 m*l* flask and agitated at 150 rpm for 2 days at 30°C. An aliquot of 0.5 m*l* of the turbid suspension was then transferred to a fresh medium supplemented with 1.0% (v/v) methanol and incubated as before. After serial transfer, small amounts of suspension were spread on a solid methanol (1.0%, v/v)-MSM plates and the plates were incubated at 30°C for 2 days. From the plates, the fast-growing colonies were

transferred to fresh methanol-MSM plates. After several selection steps, a few fast-growing strains were isolated.

Nutritional and biochemical properties

The isolates were tested for their ability to utilize the following one-carbon compounds by using the liquid MSM medium (w/v): monomethylamine, 0.2%; dimethylamine, 0.2%; trimethylamine, 0.2%; formaldehyde, 0.001 to 0.04%; sodium formate, 0.01 to 0.2%. Methane gas was supplied as a gas mixture of 30% methane-70% air. The isolates were also tested for their ability to grow on the following multi-carbon compounds (each 0.2%, w/v): glucose, D-fructose, D-lactose, D-rhamnose, DL-sucrose, D-melibiose, D-arabinose, mannitol, inositol, sorbitol, ethanol, propanol, butanol, citrate, succinate, propionate, acetate, L-asparagine, L-arginine, L-tyrosine, L-cysteine, L-aspartic acid, L-glutamic acid, L-methionine, L-glycine, L-lysine, L-tryptophan. From these tests, a strain which grows fast only on methanol was isolated and studied in detail. General biochemical tests were performed by the method of Gerhardt *et al.*(5). For the test of antibiotic sensitivity, various antibiotic discs (BBL) were used.

Enzyme assay

3-Hexulose phosphate synthase, the key enzyme of the ribulose monophosphate pathway, activity was assayed by the method of Ferenci *et al.* (4). Glucose 6-phosphate dehydrogenase (22), 6-phosphogluconate dehydrogenase (22), and 2-keto-3-deoxy-6-phosphogluconate aldolase (21) activities were also assayed. Methanol dehydrogenase was assayed by the method of Anthony and Zatman (2). Proteins were determined by the method of Lowry *et al.* (18).

Determination of DNA base composition

DNA was extracted by the method of Marmur (19), and the guanine-plus-cytosine content was determined by the method of Tamaoka and Komagata (23) using the reversed phase high performance liquid chromatograph (Hitachi) equipped with L-3000 photo diode array detector and D-2000 chromato-integrator. Cosmosil packed column RP-18 (4.6×150 mm, Nacalai tesque) was also used. Standard DNAs were purchased from Yamasa (code No. 7160) as a kit.

Ubiquinone system

Quinone system was determined by the thin layer chromatography as described by Yamada *et al.* (29) using the reverse phase high performance thin layer chromatograph (HPTLC, 10×10 cm, Merck). The mixture of acetone and water (80:20) was used as a developing solution.

Cellular fatty acid composition

Cells grown at the late exponential phase were used for the cellular fatty acid analysis. Fatty acid composition was determined by the method of Ikemoto *et al.* (9) using a gas chromatograph (Shimadzu GC-14A) equipped with a coated fused silica capillary column (DURA bond-1, 0.25 mm ×30 m). Temperatures for column, injector, and detector were 180°C, 250°C, and 250°C, respectively. Elongation coefficient A_{16} was calculated as the ratio between concentrations of *cis*-vaccenic and palmitoleic acids.

Phospholipid composition

Phospholipid composition was analyzed by the method of Komagata and Suzuki (13) using the thin layer chromatography. Phospholipid was extracted and applied to the reverse phase HPTLC (10×10 cm, Merck). Solvent systems employed for chromatography were chloroform-methanol-water (65:25:4, v/v) for the first development, and chloroform-acetic acid-methanol-water (80:18:12:5) for the second development.

RESULTS

Morphology

The obligate methanol-oxidizing bacterium was Gram-negative, nonmotile, nonspore-forming, and rod-shape with dimensions of 0.2×1.0-1.2 μm (Fig. 1). No internal complex membrane and capsules were observed. Colonies have whitish-yellow, raised, and smooth surface with undulate margin. The colony sizes were variable (1~5 mm in diameter) (Table 1).

Physiological and biochemical characteristics

Of the C_1 compounds tested, the isolate was able to grow only on methanol, not on other C_1 compounds as well as multicarbon compounds tested.

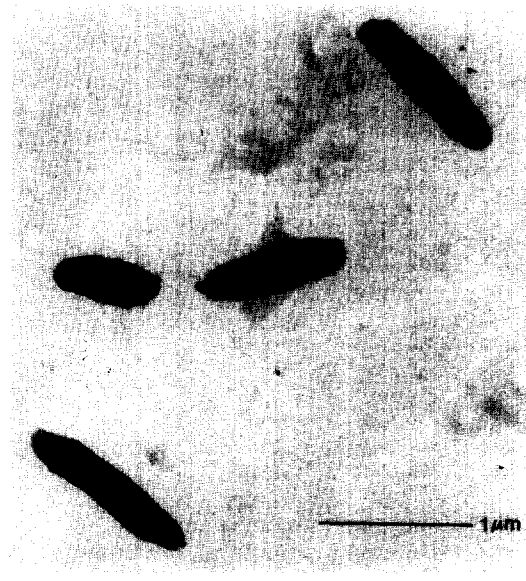

Fig. 1. *Electron micrograph of Methylobacillus methanolovorus.*

Table 1. *Morphological and biochemical characteristics of Methylobacillus methanolovorus.*

Characteristics	*Methylobacillus methanolovorus*
Gram reaction	negative
Cell morphology	rod
size	0.2×1.0−1.2 μm
Colony shape	raised, undulate, and smooth surface
diameter	1.0~5.0 mm
color	whitish-yellow
Flagella	absent
Motility	absent
G+C mol%	61.0%
Oxidase	Positive
Catalase	Positive
Gelatin hydrolysis	negative
H_2S production	negative
Reduction of nitrate to nitrite	positive
Indole production	negative
Citrate utilization	negative
Plasmid	present
Oxygen relation	Obligate
Generation time	1.6 hours
Carbon assimilation pathway	Ribulose monophosphate pathway (Entner-Doudoroff varient)
Ammonium assimilation	Glutamate dehydrogenase

Cell aggregation and pigmentation were not observed in MSM medium. Catalase and oxidase were present in the isolate. Acid was not produced from D-glucose. Gelatin and starch were not hydrolyzed. Nitrate was reduced to nitrite (Table 1). Vitamins and other growth factors were not essential for growth. The isolate did not grow in the presence of 3% sodium chloride. The isolate grew well in the pH and temperature range of pH 6.0~8.0 and 28°C~42°C, respectively, but no growth occured at 45°C. Good nitrogen source was ammonium oxalate. The optimum methanol concentration was 0.5%. The generation time was found to be 1.6 hr. Growth was sensitive to gentamicin (10 mcg), amikacin (30 mcg), minocycline (30 mcg), and tobramycin (10 mcg), but was resistant to chloramphenicol (30 mcg), vancomycin (39 mcg), carbenicillin (100 mcg), and cefazolin (30 mcg), and ampicillin (10 mcg).

Enzymological studies revealed the presence of the key enzyme of the RuMP pathway, 3-hexulose-6-phosphate synthase. It was also found that glucose-6-phosphate dehydrogenase was active with NAD and 6-phosphogluconate dehydrogenase was active with both NAD and NADP.

Table 2. *Enzyme activities in cell-free extracts of Methylobacillus methanolovorus.*

Enzyme	Enzyme activity (nmol/mg protein/min)
3-Hexulose-6-phosphate synthase	2150
Glucose-6-phosphate dehydrogenase	
(NAD-dependent)	1200
(NADP-dependent)	1750
2-Keto-3-deoxy-phosphogluconate aldolase	
(NADH-dependent)	85
6-Phosphogluconate dehydrogenase	
(NAD-dependent)	110
(NADP-dependent)	245
α-Ketoglutarate dehydrogenase	
(NAD-dependent)	0
Glutamate dehydrogenase	
(NADH-dependent)	0
(NADPH-dependent)	280
Methanol dehydrogenase (PMS)[a]	216

[a] Phenazine methosulfate

2-Keto-3-deoxy-6-phosphogluconate aldolase activity was also found. It indicated that decomposition of hexosephosphates is accomplished through the Entner-Doudoroff pathway. α-Ketoglutarate dehydrogenase was not found. Ammonium was assimilated by means of glutamate dehydrogenase. The cell-free extract contained a phenazine methosulfate-linked methanol dehydrogenase which requires ammonium ion as an activator (Table 2).

DNA base composition

The guanine-plus-cytosine content of the DNA of the isolate was estimated to be 61.0%.

Cellular fatty acid composition

Straight-chain saturated $C_{16:0}$ acids (palmitic acids) and unsaturated $C_{16:1}$ acids (palmitoleic acids) were predominated. However, small amounts of unsaturated $C_{18:1}$ acids (vaccenic acids) and unidentified C_{17} branched fatty acids (X1 and X2) were also detected. The elongation coefficient was 0.17 (Table 3).

Quinone system

The isolate contained Q-8 as major component and Q-6 and Q-7 as minor components.

Phospholipid

The major phospholipid were found to be phosphatidylethanolamine and phosphatidylglycerol. And diphosphatidylglycerol (cardiolipin) was also present.

DISCUSSION

On the basis of the range of carbon compounds utilized, methylotrophic bacteria are classified

Table 3. *Cellular fatty acid compositions of Methylobacillus methanolovorus.*

Fatty acid composition	% fatty acids
3-OH $C_{10:0}$ hydroxy acid	9.82
$C_{12:0}$	0.19
$C_{14:0}$	0.91
$C_{16:1}$	35.43
$C_{16:0}$	36.78
$C_{18:1}$	5.94
X1[a]	7.35
X2[b]	3.48
Elongation coefficient (A_{16})	0.17

[a,b] unidentified C_{17} branched fatty acids.

into the obligate, the restricted facultative, and the facultative bacteria, respectively (8, 10, 11, 26, 27, 28, 30). The obligate methylotrophic bacteria can use only single-carbon compounds such as methanol, methylamine, and formate, and the facultative bacteria are able to use not only such C_1 compounds but also various multicarbon compounds. In addition, the restricted facultative bacteria also grow on a limited range of more complex organic compounds. The type strains of the obligate and the restricted facultative bacteria are *Methylobacillus* (26, 30) and *Methylophilus* (10), respectively. Very recently, Govorukhina and Trotsenko (7) proposed a new genus, *Methylovorus*, occupying an intermediate taxonomic position between the genera *Methylobacillus* and *Methylophilus*. So far, it is difficult to find out some distinguishing traits for their classification, since they are similar in morphological, physiological and biochemical properties. They assimilate methanol or methylamine through the RuMP pathway. In addition, some strains can utilize glucose or D-fructose.

The strain, isolated from soil in Kwangju, was similar to the genus *Methylobacillus* in morphophysiological and biochemical properties. It was gram-negative, catalase-, oxidase-positive, nonmotile and employed the Entner-Doudoroff varient of the RuMP pathway. As shown in Table 4, although the genera *Methylophilus* and *Methylobacillus* are known to assimilate methanol by the RuMP pathway, they clearly differ from ammonium assimilation pathways. *Methylophilus* empolys the glutamate cycle, while *Methylobacillus* uses glutamate dehydrogenase (25). The isolate employs glutamate dehydrogenase. And it also contained phosphatidylethanolamine and phosphatidylglycerol as the major phospholipids and possessed diphosphatidylglycerol as minor component. Interestingly, diphosphatidylglycerol was not present in *Methylophilus* (7). And it had a relatively high content of cis-vaccenic acid in the fatty acid composition (A_{16}=0.17) and could grow well at 30°C but grow even at the 42°C. These properties were similar to those of *Methylobacillus* (26). So it was belonged to the genus *Methylobacillus*. The isolate, however, was different from the type strains, *Methylobacillus glycogenes* ATCC 29475 (26) or *Methylobacillus flagellatus* nov. sp. (6), in the following aspects. The guanine-plus-cytosine content of DNA in the isolate was relatively higher than those of the type strains, and unidentified branched C_{17} fatty acids were present in the strain. In *Methylobacillus glycogenes*, major ubiquinone was Q-8, and Q-7 and Q-9 were present as minor component. However, the isolate contained Q-8 as major, but Q-6 and Q-7 as minor component. *Methylobacillus flagellatus* had flagella located polarly (from one to four), but

Table 4. *Main characteristics that differentiate the obligate and the restricted facultative methylotrophic bacteria.*

Characteristics	*Methylophilus*[a]	*Methylovorus*[b]	*Methylobacillus*[c]	*Methylobacillus methanolovorus*
Growth temperature (°C)	28~35	35~42	28~42	28~42
6-Phosphogluconate dehydrogenase (NADP-dependent)	+	−	+	+
Ammonium assimilation	GS/GOGAT system	GS/GOGAT system	Glutamate dehydrogenase	Glutamate dehydrogenase
G+C mol%	50~53	56~57	50~56	61.0
Fatty acid elongation coefficient (A_{16})	0.01~0.02	0.04~0.06	0.14~0.16	0.17
Branched C_{17} fatty acids	+	−	−	+
Diphosphatidyl glycerol	−	+	+	+

[a] Data from Jenkins *et al.* (10).
[b] Data from Govorukhina and Trotsenko (7).
[c] Data from Urakami and Komagata (26), and Yordy and Weaver (30).

the isolate had no flagellum. And the total protein profiles in denaturing polyacrylamide gel electrophoresis were also found to be different (data not shown). It is worthwhile noting that the isolate grew only on methanol, not on other one-carbon compounds such as methane or methylamine, and it could not utilize any multicarbon compounds like glucose or D-fructose. Therefore, we concluded that the isolate was a new bacterium and assigned to *Methylobacillus methanolovorus* sp. nov. (from Latin, *vorus* means consuming).

In a commercial and biotechnological aspects, the isolate have some valuable properties. Generally, the methylotrophs used for the production of single cell protein should have several common properties such as high growth rate, high growth yield, and high optimal growth temperature. Especially, they employ RuMP pathway for carbon assimilation and glutamate dehydrogenase for ammonia assimilation due to the efficiency of energy consumption (15). Fortunately, the isolate have all of the above properties and, therefore, it may be possible to apply the strain to the commercial and biotechnological purposes.

ACKNOWLEDGEMENT

This work was supported by a research grant from Chosun University on the year of 1991. And we thank to Dr. Trotsenko (Institute of Biochemistry and Physiology of Microorganisms, Russia Academy of Sciences, Pushchino) for enzyme assays.

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(Received May 25, 1993)
(Accepted June 27, 1993)

초 록: 새로운 절대 메탄올 산화세균의 분리 및 특성

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유일한 탄소 및 에너지원으로 메탄올만을 이용하여 성장하는 새로운 절대 메탄올 자화세균을 토양으로 부터 분리하였다. 분리균주는 그람음성의 운동성이 없고 포자를 형성하지 않는 간균으로 절대호기성 세균이었다. 이 균주는 catalase 활성과 oxidase 활성을 가지고 있으며 nitrate를 nitrite로 환원시킬 수 있고 성장시 vitamin이나 특이한 생육인자를 요구하지 않았다. 세대시간은 1.6시간으로 메탄올 동화경로는 ribulose monophosphate pathway(Entner-Doudoroff 변형경로)를 이용하나 α-ketoglutarate dehydrogenase 활성은 없었다. Ammonium ion은 glutamate dehydrogenase를 이용하여 동화하였다. DNA의 guanine plus cytosine 함량은 61.0 mol%이고 세포내 지방산으로는 주로 straight-chain saturated $C_{16:0}$ acids(palmitic acids)와 unsaturated $C_{16:1}$ acids(palmitoleic acids)를 가지고 있으나 이외에도 두 종류의 unidentified C_{17} branched fatty acid도 포함하고 있었다. Major ubiquinone은 Q-8이나 Q-6와 Q-7을 특이하게 소량 가지고 있었다. Phosphatidylethanolamine과 phosphatidylglycerol이 주요한 phospholipid의 구성물질이나 diphosphatidylglycerol도 소량 포함하고 있었다. 위와같은 생리적, 생화학적 자료로 부터 분리균주를 새로운 종 즉, *Methylobacillus methanolovorus* sp. nov.로 명명하였다.