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Isolation and characterization of a novel polychlorinated biphenyl-degrading bacterium, *Paenibacillus* sp. KBC101

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Abstract The biphenyl-utilizing bacterial strain KBC101 has been newly isolated from soil. Biphenyl-grown cells of KBC101 efficiently degraded di- to nonachlorobiphenyls. The isolate was identified as *Paenibacillus* sp. with respect to its 16S rDNA sequence and fatty acid profiles, as well as various biological and physiological characteristics. In the case of highly chlorinated biphenyl (polychlorinated biphenyl; PCB) congeners, the degradation activities of this strain were superior to those of the previously reported strong PCB degrader, *Rhodococcus* sp. RHA1. Recalcitrant coplanar PCBs, such as 3,4,3′,4′-CB, were also efficiently degraded by strain KBC101 cells. This is the first report of a representative of the genus *Paenibacillus* capable of degrading PCBs. In addition to growth on biphenyl, strain KBC101 could grow on dibenzofuran, xanthene, benzophenone, anthrone, phenanthrene, naphthalene, fluorene, fluoranthene, and chrysene as sole sources of carbon and energy. *Paenibacillus* sp. strain KBC101 presented heterogeneous degradation profiles toward various aromatic compounds.

Introduction

Polychlorinated biphenyls (PCBs) have been recognized as widespread environmental contaminants which are generally considered quite tolerant of biological degradation. Due to their hydrophobic nature, PCBs tend to be adsorbed strongly by organic matter, thus leading to their accumulation in soils and in the food chain (Safe 1994). Highly chlorinated PCBs can be detected in the environment and remain (soil, sediments, etc.) as contaminating pollutants.

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The microbial degradation of PCBs is regarded as one of the most effective procedures for removing them from the environment. Many PCB-degrading bacteria have been isolated, such as Gram-negative strains belonging to the genera *Pseudomonas*, *Alcaligenes*, *Achromobacter*, *Burkholderia*, *Acinetobacter*, *Comamonas*, *Sphingomonas*, and *Ralstonia*, and Gram-positive strains belonging to the genera *Arthrobacter*, *Corynebacterium*, *Rhodococcus*, and *Bacillus*.

Pseudomonas pseudoalcaligenes KF707 was isolated from soil near a biphenyl-producing factory in Japan (Furukawa and Miyazaki 1986). This strain could degrade a narrow range of PCB congeners, such as 4,4′-dichlorobiphenyl. *Burkholderia xenovorans* LB400T (Goris et al. 2004) was isolated from a PCB-contaminated site in New York (Bedard et al. 1987b; Bopp 1986), and was able to degrade a much greater range of PCB congeners than KF707. Among 19 PCB congeners tested, 17 were degraded by LB400, and only eight were oxidized by KF707 (Erickson and Mondello 1993; Gibson et al. 1993). *Rhodococcus* sp. strain RHA1 was isolated from γ-hexachlorocyclohexane contaminated soil in Japan. The strain RHA1 transformed 45 components of the 62 major peaks of PCB mixtures of Kanechlor 200, 300, and 400 within 3 days, which included tri-, tetra-, and pentachlorobiphenyls (Seto et al. 1995). *Bacillus* sp. JF8, which was isolated from compost, utilizes naphthalene and biphenyl as carbon sources at 60°C. Strain JF8 could degrade several PCB congeners including tetra- and pentachlorobiphenyl (Shimura et al. 1999). However, these bacteria are generally limited to congeners that have five or less chlorines, and showed very little ability to degrade the more highly chlorinated and coplanar PCBs.

Several bacteria have been also reported to degrade low-molecular weight polycyclic aromatic hydrocarbons (PAHs) and higher molecular weight PAHs, such as fluoranthene, pyrene, and benzo(*a*)pyrene (Cerniglia). These include members of the genera *Bacillus*, *Burkholderia*, *Cycloclasticus*, *Flavobacterium*, *Pseudomonas*, *Mycobacterium*, and *Strenotrophomonas* (Kanaly and Harayama 2000). However, the relationship between the genus of

a degrader and its substrate PAH has not yet been investigated.

The present work describes the isolation and characterization of highly chlorinated- and coplanar-PCB-degrading bacteria from soil, including the first identified representative of *Paenibacillus* able to degrade PCBs.

Materials and methods

Media

The S medium was composed of Na_2HPO_4 (1.6 g/l), KH_2PO_4 (10 g/l), $MgSO_4{\cdot}7H_2O$ (0.5 g/l), $NaNO_3$ (0.5 g/l), $(NH_4)_2SO_4$ (0.5 g/l), and $CaCl_2{\cdot}2H_2O$ (0.025 g/l) with the following trace elements: $FeCl_2{\cdot}4H_2O$ (1.5 g/l), $CoCl_2{\cdot}6H_2O$ (0.19 g/l), $MnCl_2{\cdot}4H_2O$ (0.1 g/l), $ZnCl_2$ (0.07 g/l), H_3BO_3 (0.062 g/l), $Na_2MoO_4{\cdot}2H_2O$ (0.036 g/l), $NiCl_2{\cdot}6H_2O$ (0.024 g/l), $CuCl_2{\cdot}2H_2O$ (0.017 g/l), and $AlK(SO_4)_2{\cdot}12H_2O$. The S agar plate contained 15 g agar/l.

Isolation of PCB-degrading bacteria

Soil samples contaminated with sediment from a waste water treatment facility in Japan were added to S liquid medium supplemented with biphenyl crystals, and incubated aerobically at 30°C on a reciprocal shaker at 200 r.p.m. Aliquots were transferred weekly to fresh medium and incubated under the same conditions; this process was repeated at least 3 times. Pure cultures were obtained by plating the enrichment culture on S agar plate and applying the substrate to the lids of inverted Petri dishes.

Genotypic analysis

For PCR amplification of 16S rRNA, genomic DNA was isolated using the InstaGene matrix (Bio-Rad, USA) which served as a template. The PCR product was purified and sequenced using a MicroSeq full 16S rDNA bacterial sequencing kit (Applied Biosystems, USA). The sequence was aligned by using CLUSTALW with all parameters set at their default values. Phylogenetic analyses were performed using the neighbour-joining method (Saitou and Nei 1987). Graphics for phylogenetic trees were produced by using the Treeview program (Page 1996).

Phenotypic characteristics

The cells morphological properties were examined by scanning electron microscopy (SEM), and included the shape of the cell, Gram-stain, the presence of spores, and colony morphology on nutrient agar. Biochemical reactions, catalase reaction, oxidase reaction, acid or gas production from carbohydrates and oxidation or fermentation from carbohydrates were determined by using the API system according to the manufacturer's instructions (BioMérieux, France).

Whole cell fatty acid analyses were performed by growing the cells at 30°C for 24 h on tripticase soy agar plates. Cellular fatty acids were saponified, methylated and extracted and then analysed by gas chromatography (GC) by following the procedures given for the Sherlock microbial identification system (MIDI). Identification and comparison were made using the Aerobe (TSBA version 5.0) database of the MIDI.

Analysis of PCB degradation competence

KBC101 uses biphenyl as a sole carbon source and cometabolize PCBs by biphenyl-metabolic enzymes. KBC101 cells grown on S-biphenyl medium and were transferred to fresh S medium at an optical density at 660 nm of 0.4. Ethylacetate solutions containing Kanechlor 200, 300, 400, and 500 or PCB congeners were added to the cell suspensions. The total PCB concentration was adjusted to 10 mg/l. Cells were incubated for 3 days at 30°C. Hydrochloric acid (100 μl) was added to 5 ml of the culture to stop whole cell growth. Background PCB-degradation activity was measured by using control cells which were inactivated by autoclaving at 121°C, for 15 min. *Pseudomonas* sp. strain DSM-10086 was isolated from a biphenyl-contaminated soil using biphenyl as a sole carbon source. *Rhodococcus* sp. strain ATCC55255 was isolated from an aquatic sediment sample using 4-chlorobiphenyl as a sole carbon source. These strains were used as references. A non-degradable PCB congener, 2,3′,4,4′,5-CB, was used as an internal standard.

GC analysis

Samples of PCB congeners were analysed using a GC (model G2800, Yanagimoto, Japan) equipped with a glass column (length, 2 m; inner diameter, 3.4 mm; outer diameter, 5 mm) packed with OV-1 (80/100 mesh) and an electron capture detector. The column, injection, and detector temperatures were 190, 250, and 230°C, respectively.

Growth characteristics of PAHs in liquid medium

KBC101 was analysed for its ability to utilize a variety of PAHs, as well as biphenyl, dibenzofuran, dibenzothiophene, xanthene, benzophenone, anthrone, naphthalene, dibenzo-*p*-dioxin, carbazole, fluorene, phenanthrene, pyrene, benzo[*a*]pyrene, fluoranthene, and chrysene. The cells were cultured in 5 ml of S medium with PAHs (dissolved in dimethyl formamide, f.c. 0.2 mM). The cell growth (30°C, 200 r.p.m.) was monitored by using a spectrophotometer (OD_{660}) for 1 week and are indicated as +/− in the results.

Chemicals

PCB congeners and Kanechlor 200, 300, 400, and 500 were purchased from GL Science. The other chemicals including PAHs were purchased from Wako Chemical., Tokyo.

Nucleotide sequence accession number

The nucleotide sequence described in this article is deposited in the EMBL/DDBJ/GenBank nucleotide sequence databases under the following accession no.: AB186915 (16S rDNA).

Results

Isolation of PCB-degrading bacteria

Strain KBC101 was isolated by enrichment culture with biphenyl as the sole carbon source from soil samples with sediment from the waste water treatment center and showed high degradation activity toward the PCB mixture (Fig. 1). The highly chlorinated PCBs, containing five to nine chlorines, were clearly degraded by KBC101 and the degradation profiles seemed to resemble those obtained with *Rhodococcus*. Compared with *Pseudomonas*, KBC101 was able to degrade highly chlorinated PCBs. These three microorganisms showed a high degree of degradation of less chlorinated PCBs.

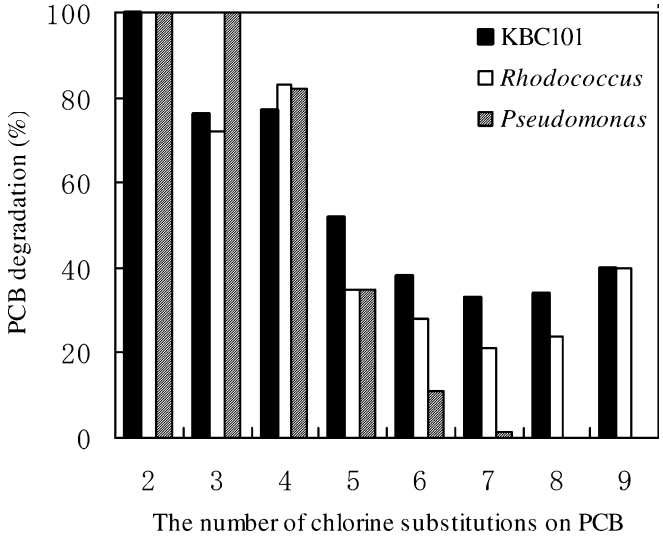

Fig. 1 Degradation of Kanechlor 200, 300, 400, 500 mixture by *Paenibacillus* sp. strain KBC101. Data are averages of duplicate experiments. Biphenyl-grown cells of each strain were incubated with S medium Kanechlor mixtures and biphenyl (final concentration of 10 p.p.m. and 130 mM, respectively) at 30°C for 3 days. The chlorinated compounds were analysed by gas chromatography

Identification of *Paenibacillus* sp. KBC101

Strain KBC101 is a Gram-positive, catalase-positive, oxidase-negative, rod-shaped coccus. Its spore-forming ability and the motility of its flagella have been confirmed by microscopic observation. Also, we examined the production of acid by strain KBC101 from carbohydrates (L-arabinose, D-xylose, glycerol, D-glucose, D-fructose, D-mannose, innositol, mannitol, and sorbitol) (Table 1). This strain grew with several of the carbohydrates as a sole carbon source with the exception of D-mannose and sorbitol. The profiles of enzymes produced from this strain and carbohydrate utilization were slightly different from those of the other species of *Paenibacillus*.

We determined the nucleotide sequence of the 16S rDNA of the strain KBC101 and constructed a phylogenetic tree by using corresponding regions (5–1,541 nt) of the 16S rDNA sequence (Fig. 2). KBC101 showed 16S rDNA sequence identity of 99% toward *P. validus*. The predominant fatty acids of the strain KBC101 were C15:0 anteiso (58.9%), C16:0 (7.36%), and C15:0 iso (6.81%). These fatty acid profiles differed from those of other species; in particular, C15:0 anteiso comprised >55% of the total fatty acid content (Table 2). The biochemical characteristics of the fatty acids of strain KBC101 were almost identical to those of the genus *Paenibacillus*, with the exception of C15:0 anteiso.

Effects of the position of chlorine substitution on PCB degradation

We examined the effects of the position of chlorine substitution on PCB degradation in KBC101. Seven pure PCB

Table 1 Phenotypic characteristics of *Paenibacillus* sp. strain KBC101. *NR* Not reported

Characteristic	KBC101	*P. validus*	*P. polymyxa*
Gram stain	Positive	NR	NR
Anaerobic growth	−	−	+
Optimal temperature (°C)	30	28–35	30
Catalase activity	+	+	+
Oxidase activity	−	−	−
Arginine dihydrolase activity	−	−	−
Citrate utilization	−	−	−
Urease activity	−	+	−
Indole production	−	−	−
Acid produced from			
L-Arabinose	−	−	+
D-Xylose	+	+	+
D-Glucose	+	+	+
Glycerol	+	+	+
D-Fructose	+	+	+
D-Mannose	−	+	+
Innositol	+	+	−
Mannitol	+	+	+
Sorbitol	−	−	+

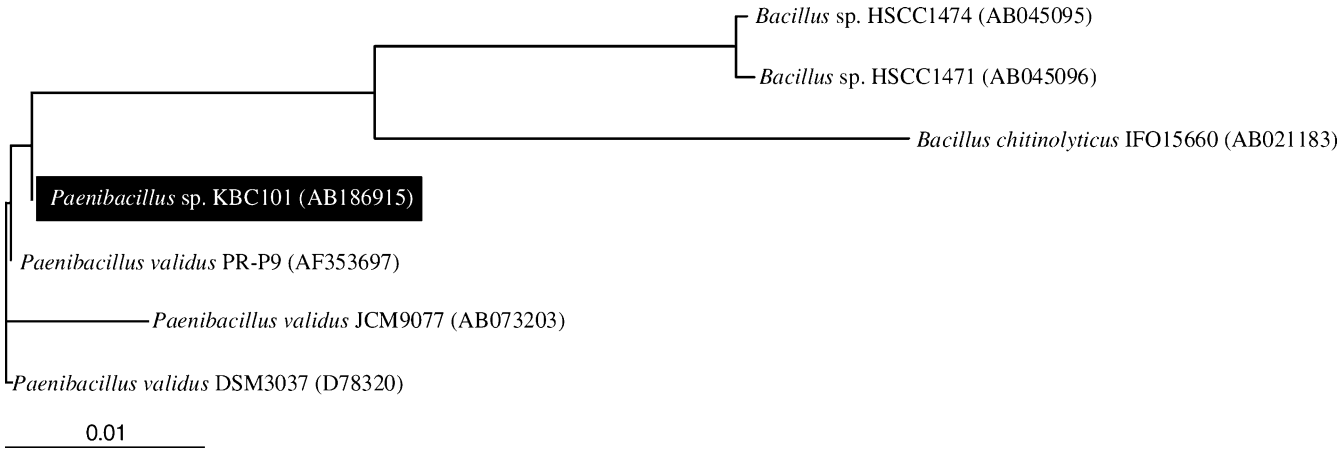

Fig. 2 Phylogenetic tree of *Paenibacillus* sp. KBC101. Strain KBC101 is highlighted against a dark background. GenBank nucleotide sequence accession numbers are indicated *in parentheses*

Table 2 Fatty acid profiles of *Paenibacillus* strains

Strains	15:0 iso	15:0 anteiso	16:00
KBC101	6.81	58.93	7.36
P. validus[a]	13.2	48	6.4
P. polymyxa[a]	6.8	48.6	15.9
P. pabuli[a]	10.9	48.6	13.2
P. alvei[a]	8.7	51.4	8.7
Paenibacillus spp	0.2–14.4	34.5–81.0	1.5–24.7

[a]Danne et al. (2002)

congeners including one of the coplanar PCBs, 3,4,3′,4′-CB, were used for this experiment. The results were compared with those reported for the PCB-degraders *Rhodococcus* sp. RHA1, *Burkholderia xenovorans* LB400T, and *P. pseudoalcaligenes* KF707 (Table 3). Strain RHA1 exhibited no degradation activity toward PCB congeners such as 3,4,3′,4′- and 2,4,5,2′,4′,5′-CB. Strain KF707 showed relatively low or no degradation activity toward all congeners. Strain LB400T showed low degradation activity toward PCB congeners such as 3,4,3′,4′-CB (coplanar PCB). On the other hand, strain KBC101 exhibited degradation activity toward all PCB congeners used in this experiment. In addition, KBC101 degraded even coplanar PCB which none of other strains were able to degrade. Strain KBC101 showed strong degradation activity toward *ortho*-chlorinated PCBs and moderate activity regarding *para*-chlorinated congeners.

Table 3 Phenotypic characteristics of *Paenibacillus* sp. strain KBC101. Experimental conditions the same as those used in Fig. 1 except that growing cells are used for KBC101, and resting cells for KF707 in the PCB degradation assay

PCB congener	Gram-positive bacteria		Gram-negative bacteria	
	KBC101[a]	RHA1[b]	KF707[c]	LB400T[c]
Ortho-chlorinated PCBs				
2,5,2′-CB	100 (%)	98	10	100
2,5,2′,5′-CB	72	76	9	100
2,4,5,2′,5′-CB	58	29	0	100
Para-chlorinated PCBs				
2,4,2′,4′-CB	33	83	0	81
2,4,3′,4′-CB	58	99	31	43
3,4,3′,4′-CB[d]	56	0	0	6
2,4,5,2′,4′,5′-CB	11	0	0	41

[a]Data are averages of duplicate experiments
[b]Result for *Rhodococcus* sp. RHA1 from Seto et al. (1995)
[c]Results for *Burkholderia xenovorans* LB400T and *Pseudomonas pseudoalcaligenes* KF707 reported by Gibson et al. (1993)
[d]Coplaner PCB 2,3′,4,4′,5-CB was used as the internal standard

Growth with PAHs

We determined the ability of KBC101 to grow using only PAHs as its source of carbon (Table 4). KBC101 grew on biphenyl, dibenzofuran, xanthene, benzophenone, an-

Table 4 Growth characteristics of *Paenibacillus* sp. KBC101 on various polycyclic aromatic hydrocarbons. + Weak growth, ++ moderate growth, +++ good growth, − no growth

Ring	Substrate	Growth
2	Dibenzofuran	+
	Dibenzothiophene	−
	Biphenyl	+++
	Benzophenone	+
	Anthrone	+++
	Naphthalene	+
	Dibenzo-*p*-dioxin	−
	Xanthene	+
	Carbazole	−
3	Phenanthrene	+
	Fluorene	++
4	Pyrene	−
	Fluoranthene	+
	Chrysene	+
5	Benzo[*a*]pyrene	−

throne, naphthalene, fluorene, fluoranthene, and chrysene. In addition to the PAHs, we also tested benzene, toluene, and phenol as a growth substrate, but KBC101 was not observed to grow using these compounds, as measured by turbidity of the culture.

Discussion

This is the first report of the degradation of PCBs by the genus *Paenibacillus*. The strain KBC101 was closely related to *P. validus* based on their 16S rDNA sequence similarity. Although the nucleotide sequence homology indicated that strain KBC101 was very close to *P. validus* strain PR-P9, the physiological and biological properties of these strains showed slight differences. For example, *P. validus* used a carbon source, e.g. D-xylose, D-glucose, glycerol, D-fructose, D-mannose, inositol, and mannitol, but not L-arabinose or sorbitol (Philipp et al. 2002). Strain KBC101 showed similar carbohydrate utilization except for D-mannose. The ratio of the C15:0 anteiso fatty acids (the most predominant cellular fatty acids for the genus *Paenibacillus*) in the strain KBC101 was quite different to those of several species of *Paenibacillus.* The C15:0 anteiso fatty acids in *P. validus*, *P. polymyxa* and *P. pabuli* were, on average, about 48% of the total (Danne et al. 2002). In contrast, the C15:0 anteiso fatty acids for KBC101 were about 59% of the total. These results strongly suggest that KBC101 belongs to the genus *Paenibacillus* and represents a novel *Paenibacillus* species.

However strains LB400T, RHA1, and KF707 hardly degraded the coplanar PCB (3,4,3′,4′-CB), and strain KBC101 degraded highly chlorinated PCB (11%) and the coplanar PCB (56%). Thus the ability of strain KBC101 to degrade PCBs seems to be superior to that of previously reported strong PCB degraders, such as *Rhodococcus* sp. RHA1 (Gram-positive bacteria). Compared with the substrate utilization of the other bacterial species, strain KBC101 seems to harbour specific enzymes that catalyze the oxidation of chlorinated compounds, having broad substrate specificity. According to the degradation profile of several PCB congeners, the dioxygenase of strain KBC101 seems to have different substrate specificity than the dioxygenase of Gram-negative bacteria (strains KF707 and LB400) and Gram-positive bacteria (strain RHA1). Recently, numerous biphenyl dioxygenase genes have been reported in some Gram-positive PCB degraders. For example *Rhodococcus* sp. RHA1 (Kitagawa et al. 2001) has five dioxygenase (A–E) genes. Although we cannot determine substrate specificities clearly by examining growth only, KBC101 grows with a variety of PAHs (those having two to four benzene rings), except for complex compounds such as pyrene and benzo[*a*]pyrene. So, it is supposed that strain KBC101 contains an enzyme that shows wide substrate specificity, or it contains several isozymes that are well-known in Gram-positive degraders.

It has been reported that *Bacillus* sp. strain JF8 also degraded a variety of PCB congeners and PAHs. It is relatively close at the genus level to strain KBC101. Thus, the dioxygenase of these two strains seems to have the same enzymatic character. However, strain JF8 is known to be a thermophilic bacteria which grows at 60°C (optimum). The enzymes from strain JF8 may have far more ionic pairs in their tertiary structure than those from strain KBC101, which allow them to retain a rigid form at high temperature. In general, substrate specificity tends to be broad at high temperature due to the molecular wobble of the enzyme and the substrate. Nevertheless, strain KBC101 is not a thermophile, it is able to degrade or grow on various PCBs and PAHs at moderate temperature. So, it is supposed that these dioxygenases from *Bacillus* sp. strain JF8 and *Paenibacillus* sp. strain KBC101 had broad substrate specificity due to a lack of molecular wobble.

Since the degradation profiles of strain KBC101 were slightly different from those of well-known PCB-degraders, the PCB-degrading enzymes from the genus *Paenibacillus* may provide new information regarding the evolution or origin of PCB dioxygenase. In order to confirm the above, the cloning and characterization of several dioxygenase genes of KBC101 are currently under way. Strain KBC101 is expected to be a promising microorganism for bioremediation, i.e. for the removal of various chlorinated compounds including coplanar PCBs and PAHs from contaminated sites.

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