Paenibacillus siamensis sp. nov., *Paenibacillus septentrionalis* sp. nov. and *Paenibacillus montaniterrae* sp. nov., xylanase-producing bacteria from Thai soils

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Three strains of xylanase-producing bacteria, S5-3^T, X13-1^T and MXC2-2^T, isolated from soils in Thailand, were characterized taxonomically based on their phenotypic and chemotaxonomic characteristics and 16S rRNA gene sequence comparisons. They were Gram-positive, facultatively anaerobic, spore-forming, rod-shaped bacteria. They contained meso-diaminopimelic acid in the cell-wall peptidoglycan. The DNA G+C contents were respectively 45.8, 47.3 and 48.8 mol%. The predominant isoprenoid quinone was MK-7, and anteiso-C_{15:0} and C_{16:0} were the dominant cellular fatty acids. Phylogenetic analyses based on 16S rRNA gene sequence comparison showed that they were affiliated to the genus *Paenibacillus*. Strains S5-3^T, X13-1^T and MXC2-2^T were closely related to *Paenibacillus granivorans* A30^T and *Paenibacillus agaridevorans* DSM 1355^T (94.7–98.6% 16S rRNA gene sequence similarity). The similarity between the three novel strains ranged from 96.3 to 98.4%. DNA–DNA relatedness, DNA G+C contents and some phenotypic characteristics could clearly distinguish the strains from each other and from related *Paenibacillus* species. Therefore, strains S5-3^T, X13-1^T and MXC2-2^T represent novel species of the genus *Paenibacillus*, for which the names *Paenibacillus siamensis* sp. nov. (type strain S5-3^T = KCTC 13038^T = PCU 279^T = TISTR 1831^T), *Paenibacillus septentrionalis* sp. nov. (type strain X13-1^T = KCTC 13039^T = PCU 280^T = TISTR 1830^T) and *Paenibacillus montaniterrae* sp. nov. (type strain MXC2-2^T = KCTC 13036^T = PCU 281^T = TISTR 1836^T) are proposed.

Representatives of the genus *Bacillus* were first described as a group of micro-organisms that were characterized by endospore formation; the genus has subsequently been divided into a number of genera that belong to several families. This was the case for the genus *Paenibacillus*, which was proposed by Ash *et al.* (1993, 1994) and belongs to the family 'Paenibacillaceae'. Some of these bacteria excrete diverse assortments of extracellular polysaccharide-

hydrolysing enzymes, including xylanases (Zamost *et al.*, 1991; Morales *et al.*, 1995; Hespell, 1996; Aý *et al.*, 1998; Nielsen & Sorensen, 1997; Lee *et al.*, 2000). Strains of *Paenibacillus barcinonensis*, *P. favisporus*, *P. phyllosphaerae*, *P. xylanilyticus*, *P. cellulosityticus*, *P. panacisoli* and *P. soli* have been reported to degrade xylan (Rivas *et al.*, 2005a, b, 2006; Sánchez *et al.*, 2005; Velázquez *et al.*, 2004; Ten *et al.*, 2006; Park *et al.*, 2007). In this paper, we describe novel xylanase-producing bacteria isolated from Thai soils based on their phenotypic and chemotaxonomic characteristics and 16S rRNA gene sequence comparisons.

Three strains of xylanase-producing bacteria were isolated from soil samples collected from Muang and Viengsa districts in Nan province, in the northern part of Thailand, by the spread plate method on XC agar medium and

Abbreviations: DAP, diaminopimelic acid; NJ, neighbour-joining.

The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequences of strains S5-3^T, MXC2-2^T and X13-1^T are AB295645–AB295647, respectively.

Extended 16S rRNA gene sequence-based neighbour-joining and maximum-parsimony trees are available as supplementary material with the online version of this paper.

incubation at 40 °C for 2 days. The XC medium contained 10 g oat-spelt xylan (Sigma), 5 g peptone (Difco), 1 g yeast extract (Difco), 4 g K₂HPO₄, 1 g MgSO₄ · 7H₂O, 0.2 g KCl, 0.02 g FeSO₄ · 7H₂O and 1000 ml distilled water and was adjusted to pH 7.0. The capacity of the cultures to produce xylanase was detected as described by Teather & Wood (1982). Colonies grown on C agar medium, i.e. XC medium with the oat-spelt xylan omitted, were examined for their cell shape and colonial appearance, spore formation and pigmentation after incubation at 37 °C for 2 days. Motility was observed by phase-contrast microscopy. Catalase and oxidase activities, hydrolysis of L-arginine, aesculin, casein, gelatin, starch and tyrosine, methyl red and Voges–Proskauer reactions, DNase activity, indole production, nitrate reduction, Simmons' citrate test, growth on triple-sugar iron (TSI) agar, dihydroxyacetone production from glycerol, urease activity and acid production from carbohydrates were determined as described by Barrow & Feltham (1993). Additional biochemical characteristics were recorded after 2 days incubation in API 50 CHB strips. Growth under anaerobic conditions on agar plates was investigated using a Gaspak (BBL) anaerobic jar. Growth at pH 5, 6, 7, 8 and 9, in 3 and 5 % NaCl and at 10, 15, 20, 30, 37, 45, 50, 55 and 60 °C was tested by using C agar medium. All other tests were carried out by using C medium as a basal component and by incubating the cultures at 37 °C. Diaminopimelic acid in the cell wall and isoprenoid quinone were determined as described by Komagata & Suzuki (1987).

DNA was prepared by the method of Saito & Miura (1963). DNA base composition was determined by reversed-phase HPLC (Tamaoka & Komagata, 1984). The 16S rRNA genes of the strains were amplified and PCR products were purified and sequenced as described previously (Tanasupawat *et al.*, 2004). The sequences determined (1464–1504 bases) were aligned with selected sequences obtained from the GenBank/EMBL/DDBJ databases by employing CLUSTAL_X version 1.83 (Thompson *et al.*, 1997). Phylogenetic trees were reconstructed by using the neighbour-joining (NJ) method (Saitou & Nei, 1987) and the maximum-parsimony method in the MEGA 4 software version 4 (Tamura *et al.*, 2007). Confidence values of branches of the phylogenetic trees were determined using bootstrap analyses (Felsenstein, 1985) based on 1000 resamplings.

Strain S5-3^T, X13-1^T and MXC2-2^T are Gram-positive, facultatively anaerobic, motile, rod-shaped bacteria. Central or subterminal ellipsoidal endospores are observed in swollen sporangia. Colonies of strain S5-3^T are white, circular or oval, flat, undulate and opaque (0.05–2.5 mm in diameter), whereas colonies of strains X13-1^T and MXC2-2^T are white, circular, convex, entire and translucent (0.02–1.0 mm in diameter) on C agar plates. The strains were characterized based on their morphological, cultural, physiological and biochemical properties including chemotaxonomic characteristics. Results are listed in the species descriptions and Tables 1 and 2. In the 16S rRNA gene sequence-based phylogenetic tree reconstructed

Table 1. Differential characteristics of the novel strains and *P. agaridevorans* KCTC 3849^T

Strains: 1, S5-3^T; 2, X13-1^T; 3, MXC2-2^T; 4, *P. agaridevorans* KCTC 3849^T (data from this study and from Uetanabaro *et al.*, 2003). +, Positive; w, weakly positive; –, negative.

Characteristic	1	2	3	4
Catalase	+	+	–	+
Oxidase	+	–	–	–
Nitrate reduction	–	–	–	+
Voges–Proskauer reaction	+	+	+	–
Growth in 5 % NaCl	+	+	+	–
Growth at 50 °C	+	–	+	–
Acid from:				
Amygdalin, salicin	+	–	+	+
L-Arabinose, L-rhamnose, D-xylose	+	–	+	–
D-Fructose, D-mannose	–	–	w	–
D-Galactose, D-lactose	+	–	+	+
Glycerol	–	–	w	–
Glycogen, starch	+	+	+	–
Inulin	–	–	+	–
D-Mannitol	+	–	+	–
Melezitose	–	–	–	+
Cellobiose, gentiobiose, maltose, melibiose, raffinose, sucrose, trehalose, turanose	+	–	+	+
Methyl α-D-glucoside	+	–	–	+
Methyl β-xyloside	+	–	+	+
D-Ribose	+	–	w	–
DNA G + C content (mol%)	45.8	47.3	48.8	51

Table 2. Cellular fatty acid profiles of the novel strains and *P. agaridevorans* KCTC 3849^T

Strains: 1, S5-3^T; 2, X13-1^T; 3, MXC2-2^T; 4, *P. agaridevorans* KCTC 3849^T. Data were determined in this study. Values are percentages of total fatty acids; ND, not detected.

Fatty acid	1	2	3	4
Saturated fatty acids				
C _{12:0}	ND	0.1	0.1	0.1
C _{14:0}	1.2	1.6	2.1	0.9
C _{15:0}	3.3	0.7	2.1	1.2
C _{16:0}	15.6	19.3	19.8	13.1
C _{16:0} N-alcohol	ND	ND	0.2	ND
C _{16:0} ω7c alcohol	ND	ND	0.8	0.1
C _{17:0}	1.4	0.3	0.9	0.5
C _{18:0}	0.4	0.3	0.6	1.7
Unsaturated fatty acids				
C _{14:1} ω5	ND	ND	0.1	0.1
C _{16:1} ω11c	1.6	1.7	5.6	0.2
C _{18:1} ω9c	ND	ND	0.2	0.6
C _{18:3} ω6c (6,9,12)	ND	ND	0.1	ND
Branched fatty acids				
anteiso-C _{11:0}	ND	0.1	0.1	ND
iso-C _{14:0}	1.8	1.8	2.2	2.7
iso-C _{15:0}	2.8	3.9	3.8	5.4
anteiso-C _{15:0}	41.3	36.2	34.7	42.4
iso-C _{16:0}	10.9	10.1	12.1	17.7
iso-C _{17:0}	6.4	9.0	5.7	5.6
anteiso-C _{17:0}	12.9	14.4	7.3	6.5
iso-C _{17:1} ω10c	ND	ND	0.5	ND
iso-C _{18:0}	0.4	0.3	0.3	0.2

according to the NJ method, strains S5-3^T, X13-1^T and MXC2-2^T were grouped in a monophyletic cluster within the genus *Paenibacillus* (Fig. 1). Trees constructed by the NJ and maximum-parsimony methods including strains S5-3^T, X13-1^T and MXC2-2^T and representatives of all *Paenibacillus* species are shown as Supplementary Figs S1 and S2, available in IJSEM Online. Strains S5-3^T, X13-1^T and MXC2-2^T were closely related to each other (96.3–98.4% 16S rRNA gene sequence similarity) and to *Paenibacillus granivorans* A30^T (97.5, 96.9 and 98.6% similarity, respectively) and *Paenibacillus agaridevorans* DSM 1355^T (94.7, 95.6 and 96.0%). In addition, they were related to *Paenibacillus agarexedens* DSM 1327^T, *P. alkaliterrae* KSL-134^T, *P. curdlanolyticus* DSM 10247^T and *P. xinjiangensis* B538^T with 92.9–95.4% sequence similarity.

The three strains contained *meso*-diaminopimelic acid (*meso*-DAP) as the diagnostic diamino acid in the cell-wall peptidoglycan and MK-7 as the major isoprenoid quinone. The three strains showed similar fatty acid profiles, but there were significant quantitative differences. Anteiso-C_{15:0} (34.7–41.3%) and C_{16:0} (15.6–19.8%) were the dominant cellular fatty acids. The percentages of the other fatty acids are listed in Table 2. Anteiso-C_{15:0}, C_{16:1}ω11c and anteiso-C_{17:0} were detected in S5-3^T in significantly different amounts from MXC2-2^T. In addition, C_{14:1}ω5, C_{16:0}

Fig. 1. NJ tree of 16S rRNA gene sequences showing the phylogenetic relationships between strains S5-3^T, X13-1^T and MXC2-2^T and some *Paenibacillus* species. Bootstrap percentages above 51% based on 1000 replications are shown. Bar, 0.01 substitutions per nucleotide position. Extended NJ and maximum-parsimony trees including representatives of all *Paenibacillus* species are available as Supplementary Figs S1 and S2.

N-alcohol, C_{16:0}ω7c alcohol, iso-C_{17:1}ω10c, C_{18:1}ω9c and C_{18:3}ω6c (6,9,12), detected in strain MXC2-2^T, were not detectable in S5-3^T or X13-1^T (Table 2).

The three novel strains could be differentiated from each other and from *P. granivorans* A30^T and *P. agaridevorans* KCTC 3849^T by their catalase and oxidase production, nitrate reduction, Voges–Proskauer reaction, growth in 5% NaCl and at 50 °C, acid production from carbohydrates and DNA G+C contents, as shown in Table 1 and reported by Van der Maarel *et al.* (2000). DNA–DNA relatedness values among strains S5-3^T, X13-1^T and MXC2-2^T and *P. agaridevorans* KCTC 3849^T were 2.2–18.5%. We were unable to determine DNA–DNA hybridization results between *P. granivorans* A30^T and our strains in this study because *P. granivorans* A30^T was deposited in the CBS as a patent strain and was not available (Euzéby, 2008). Based on these results, these strains represent three novel species of the genus *Paenibacillus* (Shida *et al.*, 1997; Van der Maarel *et al.*, 2000; Uetanabaro *et al.*, 2003; Yoon *et al.*, 2005), for which the names *Paenibacillus siamensis* sp. nov., *Paenibacillus septentrionalis* sp. nov. and *Paenibacillus montaniterrae* sp. nov. are proposed.

Description of *Paenibacillus siamensis* sp. nov.

Paenibacillus siamensis (si.am.en'sis. N.L. masc. adj. *siamensis* pertaining to Siam, the old name of Thailand, where the type strain was isolated).

Cells are Gram-positive rods, 0.5–0.8 × 3.0–12.0 μm. Central or subterminal ellipsoidal endospores are observed

in swollen sporangia. Facultatively anaerobic. Grows at pH 7–9, at 15–50 °C, in 3 and 5 % NaCl and under anaerobic conditions; does not grow at pH 5–6, 10 °C or 55–60 °C. Positive for catalase, oxidase, the Voges–Proskauer reaction, urease and hydrolysis of aesculin, starch and Tween 80; negative for the methyl red test, DNase, indole production, growth on Simmons' citrate and TSI agar, nitrate reduction, dihydroxyacetone production and hydrolysis of L-arginine, casein, gelatin and L-tyrosine. Acid is produced from amygdalin, aesculin, L-arabinose, cellobiose, D-galactose, gentiobiose, methyl α -D-glucoside, glycogen, D-lactose, maltose, D-mannitol, melibiose, raffinose, L-rhamnose, D-ribose, salicin, starch, sucrose, trehalose, turanose, methyl β -xyloside and D-xylose. No acid production from D-arabinose, D- or L-arabitol, D-adonitol, N-acetylglucosamine, arbutin, dulcitol, erythritol, D-fructose, D- or L-fucose, gluconate, 2- or 5-ketogluconate, D-glucose, glycerol, inositol, inulin, D-lyxose, D-mannose, methyl α -D-mannoside, melezitose, D-tagatose, L-sorbose, D-sorbitol, xylitol or L-xylose. The cell-wall diamino acid is *meso*-DAP. The major menaquinone is MK-7. The DNA G + C content of the type strain is 45.8 mol%. The predominant cellular fatty acids are anteiso-C_{15:0} and C_{16:0}.

The type strain is S5-3^T (=KCTC 13038^T =PCU 279^T =TISTR 1831^T).

Description of *Paenibacillus septentrionalis* sp. nov.

Paenibacillus septentrionalis (sep.ten'tri.o.na'lis. L. masc. adj. *septentrionalis* northern, referring to the isolation of the type strain from the northern province, Nan, Thailand).

Cells are Gram-positive rods, 0.5–0.8 × 2.0–12 µm. Central or subterminal ellipsoidal endospores are observed in swollen sporangia. Facultatively anaerobic. Grows at pH 7–9, at 15–45 °C, in 3 and 5 % NaCl and under anaerobic conditions; does not grow at pH 5–6, 10 °C or 50–60 °C. Positive for catalase, the Voges–Proskauer reaction, urease and hydrolysis of aesculin, starch and Tween 80; negative for oxidase, the methyl red test, DNase, indole production, growth on Simmons' citrate and TSI agar, nitrate reduction, dihydroxyacetone production and hydrolysis of L-arginine, casein, gelatin and L-tyrosine. Acid production from aesculin, D-glucose, glycogen and starch. No acid production from adonitol, amygdalin, D- or L-arabinose, D- or L-arabitol, arbutin, cellobiose, dulcitol, erythritol, D-fructose, D- or L-fucose, D-galactose, gentiobiose, gluconate, 2- or 5-ketogluconate, glycerol, methyl α -D-glucoside, N-acetylglucosamine, inositol, inulin, D-lactose, maltose, D-mannose, methyl α -D-mannoside, D-mannitol, melezitose, melibiose, raffinose, L-rhamnose, D-ribose, D- or L-xylose, methyl β -D-xyloside, salicin, L-sorbose, D-sorbitol, sucrose, trehalose, xylitol, turanose, D-lyxose or D-tagatose. The cell-wall diamino acid is *meso*-DAP. The major menaquinone is MK-7. The DNA G + C content of the

type strain is 47.3 mol%. The predominant cellular fatty acids are anteiso-C_{15:0} and C_{16:0}.

The type strain is X13-1^T (=KCTC 13039^T =PCU 280^T =TISTR 1830^T).

Description of *Paenibacillus montaniterrae* sp. nov.

Paenibacillus montaniterrae (mon.ta'ni.ter'rae. L. adj. *montanus* of a mountain, L. n. *terra* soil; N.L. gen. n. *montaniterrae* of mountain soil, where the type strain was isolated).

Cells are Gram-positive rods, 0.5–0.8 × 2–11 µm. Central or subterminal ellipsoidal endospores are observed in swollen sporangia. Facultatively anaerobic. Grows in 3 and 5 % NaCl, at pH 7–9 and at 15–50 °C and under anaerobic conditions; does not grow at pH 5–6, 10 °C or 55–60 °C. Positive for the Voges–Proskauer reaction, urease and hydrolysis of aesculin, starch and Tween 80; negative for catalase, oxidase, the methyl red test, DNase, indole production, growth on Simmons' citrate and TSI agar, nitrate reduction, dihydroxyacetone production and hydrolysis of L-arginine, casein, gelatin and L-tyrosine. Acid production from amygdalin, aesculin, L-arabinose, cellobiose, D-fructose, D-galactose, D-glucose, glycerol, glycogen, gentiobiose, inulin, D-lactose, maltose, D-mannitol, D-mannose, melibiose, methyl β -xyloside, raffinose, L-rhamnose, D-ribose, salicin, starch, sucrose, trehalose, turanose and D-xylose. No acid production from N-acetylglucosamine, D-adonitol, arbutin, D-arabinose, D- or L-arabitol, erythritol, dulcitol, D- or L-fucose, gluconate, 2- or 5-ketogluconate, inositol, melezitose, methyl α -D-mannoside, D-lyxose, methyl α -D-glucoside, D- or L-sorbitol, L-xylose, xylitol or D-tagatose. The cell-wall diamino acid is *meso*-DAP. The major menaquinone is MK-7. The DNA G + C content of the type strain is 48.8 mol%. The predominant cellular fatty acids are anteiso-C_{15:0} and C_{16:0}.

The type strain is MXC2-2^T (=KCTC 13036^T =PCU 281^T =TISTR 1836^T).

Acknowledgements

This study was supported in part by a Government Research Grant, Chulalongkorn University (2005–2007), and a grant from the KRIBB Research Initiative Program.

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