Paenibacillus wynnii sp. nov., a novel species harbouring the *nifH* gene, isolated from Alexander Island, Antarctica

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Soil taken from 12 different locations at Mars Oasis on Alexander Island, Antarctica, yielded unidentified isolates of endospore-forming bacteria. Soil from four of the locations contained Gram-negative, facultatively anaerobic, motile rods that were able to grow at 4 °C and which formed ellipsoidal spores that lay paracentrally or subterminally in swollen or slightly swollen sporangia. All of the strains harboured the nitrogenase gene *nifH*. Phenotypic tests, amplified rDNA restriction analysis (ARDRA), fatty acid analysis and SDS-PAGE analysis suggested that the isolates represented a novel taxon of *Paenibacillus*. 16S rRNA gene sequence comparison supported the proposal of a novel species, *Paenibacillus wynnii* sp. nov. (type strain, LMG 22176^T = CIP 108306^T).

Alexander Island, west Antarctica, was discovered by Admiral von Bellingshausen in January 1821. Bellingshausen named it as the Alexander Coast, honouring the expedition's patron Czar Alexander I of Russia, since it was initially believed to be part of the Antarctic mainland. Later, it was found to be an island joined to the mainland only by the sea ice of King George VI sound. On the east coast of the island and overlooking the sound, at the foot of Two Step Cliffs near the junction of the Mars and Saturn Glaciers, is a lithosol desert called Mars Oasis (71° 53' S 68° 15' W; Wynn-Williams, 1996) (Supplementary Fig. S1 available in IJSEM Online). From the austral summer of 1993/94 onwards, Mars Oasis was developed as a research site by the late Dr David Wynn-Williams to study 'survival and colonization at biological limits'. Dr Wynn-Williams described the site as remarkable

due to the presence of two pools which have abundant algal and cyanobacterial communities. These communities are also present in fine soils. Green moss is locally abundant, rather than the blackened form prevalent on exposed ridges (Wynn-Williams, 1993).

Aerobic endospore-forming bacteria have been isolated from Antarctic soils in the past. Most of the recently described species from these habitats are thermoacidophiles belonging to the genus *Alicyclobacillus* (Nicolaus *et al.*, 1998) or to the genus *Bacillus* (Hudson *et al.*, 1989; Llarch *et al.*, 1997; Logan *et al.*, 2000; Nicolaus *et al.*, 1996). Other isolates belong to established neutrophilic species of *Bacillus* or remain unidentified (Forsyth & Logan, 2000; Hudson & Daniel, 1988; Hudson *et al.*, 1988; Logan *et al.*, 2002, 2004a; Ramana *et al.*, 2000; Van Trappen *et al.*, 2002; Xiao *et al.*, 1994). Four species of *Paenibacillus* have been reported from Antarctic soils, all from maritime Antarctica (location map available as Supplementary Fig. S1 in IJSEM Online). *Paenibacillus macquariensis* (Marshall & Ohye, 1966; transferred to *Paenibacillus* by Ash *et al.*, 1993) was isolated from Macquarie Island. *Paenibacillus cineris* and *Paenibacillus cookii* (Logan *et al.*, 2004b) were both isolated from soil samples from Candlemas Island. *Paenibacillus antarcticus* (Montes *et al.*, 2004) was isolated from the sediment of a lake on Livingston Island. Bacterial isolations from ice samples of the Dyer Plateau, near Alexander Island,

Abbreviation: ARDRA, amplified rDNA restriction analysis.

The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA and *nifH* gene sequences of *Paenibacillus wynnii* LMG 22176^T are AJ633647 and AJ867247, respectively.

A map showing the location of Alexander Island, an additional phylogenetic tree based on *nifH* gene sequences, two tables detailing fatty acid content and a similarity matrix of *nifH* gene sequences of *Paenibacillus* species are available as supplementary material in IJSEM Online.

did not yield any endospore-forming bacteria (Christner *et al.*, 2000).

For the present study, 12 samples of soil collected from Mars Oasis in December 1999 were examined for the presence of endospore-forming bacteria as described by Logan *et al.* (2000). Endospore-forming isolates were purified and maintained on slopes of nutrient agar (NA; Oxoid) containing 5 mg MnSO₄ l⁻¹. Eleven out of the 12 soil samples yielded aerobic endospore-formers giving a total of 25 isolates. These isolates were subjected to a phenotypic analysis using the API 20E and API 50CH kits in conjunction with 50CHB/E medium (bioMérieux). Data were subjected to numerical analysis using Gower's general similarity coefficient (S_G) as described by Logan *et al.* (2000). Three strains were identified as *Bacillus cereus*, *Bacillus licheniformis* and *Bacillus megaterium* (data not shown). Thirteen isolates that produced spherical endospores were morphologically similar to *Bacillus sphaericus*, but they were not identifiable as members of this species and await further study. Five of the soil samples yielded nine strains that showed similar microscopic appearances and biochemical profiles. Although plate cultures of these strains grew more slowly when incubated at 20 °C rather than at 30 °C, they produced larger numbers of colonies. Strains R-16774 and R-16897 were isolated from a soil sample taken from under a moss bank by a pond. R-16781 was from a silty moraine soil that had no moss cover and R-16780 was from soil lying beneath a moss mat in a pond. LMG 22176^T, R-16777, R-16778 and R-16779 were repeated isolations from a sample of gypsum-encrusted soil. R-22540 was isolated from a sample of exposed polygon soil by a pond heavily colonized by cyanobacteria. Polygon soils are so named because of their surface patterning owing to the action of frost. The strains were characterized by phenotypic tests, amplified rDNA restriction analysis (ARDRA; using five restriction enzymes *Hae*III, *Dpn*II, *Rsa*I, *Bfa*I and *Tru*9I), SDS-PAGE analysis [with cells grown on NA supplemented with glucose (NAG) for 48 h and on trypticase soy agar (TSA; Oxoid) for 24 h] and gas chromatography of fatty acid methyl esters (FAME), as described by Logan *et al.* (2002). The 16S rRNA gene sequence and DNA base composition of strain LMG 22176^T were determined as described by Logan *et al.* (2000).

As the levels of nitrogen in Antarctic soils are considered to be low (Holdgate *et al.*, 1967; Lewis Smith, 1988; Wynn-Williams, 1996), we searched for the presence of the nitrogenase reductase structural gene, *nifH*, in our isolates. Strains belonging to *Paenibacillus durus* (LMG 4659), *Paenibacillus borealis* (LMG 21603^T) and *Rhizobium leguminosarum* bv. *viciae* (patent strain CECT 4585) were included as positive controls and two strains of *P. cookii* (LMG 18419^T and R-11600) and the type strain of *P. cineris* (LMG 18439^T; Logan *et al.*, 2004b) were also screened for the presence of the *nifH* gene. Universal degenerate primers PolF and PolR (Poly *et al.*, 2001) were synthesized by Sigma-Genosys and used to amplify a 360 bp fragment from the

nifH gene. The PCR amplification was performed from fresh colonies grown at room temperature for 2 days on NA as described by Pozo *et al.* (2002). The thermal cycling profile used was that of Poly *et al.* (2001), except that the initial denaturation step was extended to 7 min at 94 °C, as the *Taq* Gold polymerase used for this work (Applied Biosystems) requires a hot-start step, according to the manufacturer. Strains R-16780 and R-16781 did not yield any PCR products until the annealing temperature and time were set to 52 °C and 1.5 min, respectively. The *nifH* fragments obtained for strains LMG 22176^T, R-16774, R-16780, R-16781, R-16897 and R-22540 were sequenced by the dideoxy chain terminator method, using the ABI-PRISM Big Dye Terminator Cycle Sequencing Ready Reaction kit and an automated sequencer (ABI 377; Applied Biosystems). The Mars Oasis *Paenibacillus* strains and the *P. cineris* and *P. cookii* type strains were also tested for nitrogenase activity by the acetylene-reduction method (Hardy *et al.*, 1968). All strains were inoculated in screw-capped tubes with 5 ml semisolid (0.2 % agar) Burk's medium (Wilson & Knight, 1952) supplemented with 1 % glucose and 0.01 % yeast extract. Strains were stab-inoculated from fresh colonies grown on tryptone-yeast extract plates (Beringer, 1974) and incubated for 15 h at 28 °C. After incubation, the caps were replaced by silicone stoppers and 10 % of the inner atmosphere of the tubes was replaced by acetylene, generated from calcium carbide (Sigma) in distilled water. Tubes were incubated at 28 °C for 2 h after which 500 µl samples were removed from the tubes and analysed by gas chromatography as described by Rodelas *et al.* (1998).

The Mars Oasis isolates were found to be Gram-negative, facultatively anaerobic, motile rods which formed ellipsoidal or oval spores, lying subterminally and paracentrally in swollen and unswollen sporangia; swelling sometimes occurred at the opposite pole of the sporangium to the spore (Fig. 1). This sporangial morphology and a characteristic pattern of medium to strong acid production reactions from

Fig. 1. Photomicrograph of sporangia and vegetative cells of *P. wynnii* sp. nov. LMG 22176^T viewed by phase-contrast microscopy. Ellipsoidal spores lie subterminally and paracentrally in sporangia that are usually swollen. Bar, 2 µm.

Table 1. Characteristics that differentiate *P. wynnii* sp. nov. from selected *Paenibacillus* species

Species: 1, *P. wynnii* sp. nov. (eight strains tested); 2, *P. borealis* (one strain tested); 3, *P. macquariensis* (three strains tested); 4, *P. cineris* (four strains tested); 5, *P. cookii* (eight strains tested); 6, *P. polymyxa* (data from Logan & Berkeley, 1984); 7, *P. macerans* (Logan & Berkeley, 1984; Priest *et al.*, 1988); 8, *P. graminis* (Berge *et al.*, 2002); 9, *P. antarcticus* (Montes *et al.*, 2004); 10, *P. odorifer* (Berge *et al.*, 2002). Characteristics were determined using API 20E and 50 CHB kits, except for casein and starch hydrolysis, salt tolerance, oxidase reaction and growth at 50 °C. +, 85–100 % positive; v, variable (26–74 % positive); –, 0–15 % positive; w, weakly positive; NA, no data available.

Characteristic	1	2	3	4	5	6	7	8	9	10
Growth at 50 °C	–	–	–	+	+	–	+	–	–	–
Casein hydrolysis	–	–	v	w	w	+	–	NA	–	NA
Starch hydrolysis	+	–	w	–	+	+	+	NA	+	NA
Growth on 3 % NaCl	–	w	+	+	+	+	NA	NA	+	NA
Oxidase	–	–	–	+	+	–	+	–	+	–
ONPG	v	–	–	+	+	+	+	NA	–	NA
Production of H ₂ S	–	–	–	–	–	–	–	NA	–	NA
Voges–Proskauer	–	–	–	v	v	+	v	NA	–	NA
Gelatin hydrolysis	–	–	–	–	v	+	v	NA	–	NA
Nitrate reduction	+	–	–	+	+	+	v	+	–	+
Gas from carbohydrates	–	–	–	–	–	+	–	+	–	–
Acid from carbohydrates:										
Arbutin	v	+	v	+	+	+	+	+	–	+
D-Arabinose	–	–	–	w	–	–	+	–	–	–
D-Arabitol	–	+	–	–	–	–	+	–	–	–
D-Mannose	+	+	–	v	w	+	+	+	+	v
D-Turanose	+	+	–	+	+	+	+	+	+	+
Glycerol	v	–	–	–	w	+	+	+	–	+
Inulin	v	+	–	v	–	v	+	v	–	+
L-Fucose	–	w	–	–	w	v	+	–	–	v
myo-Inositol	–	–	–	+	–	–	v	–	–	–
Sorbitol	+	+	–	w	–	–	v	–	–	–
Sucrose	+	+	–	+	+	+	+	+	+	+
Fatty acid content:*										
iso-C _{15:0}	6.9	13.2	13.8	6	6.5	10.9	6.4	11.3	11.0	14.4
anteiso-C _{15:0}	34.0	37.0	59.3	46	36	54.5	44.9	40.8	40.0	49.3
C _{16:0}	30.9	12.5	8.6	18	11	8.7	21.9	8	8	14.7

*Values are percentages of total fatty acid content obtained for the type strains of the species.

a wide range of carbohydrates in the API 50CHB gallery suggested that this group of strains might represent a species of the genus *Paenibacillus*. However, the reaction profiles in the API 20E strip and API 50CHB gallery and their microscopic morphologies did not allow the strains to be identified confidently with an established species of this genus (Table 1). Strains R-16774, R-16777, R-16778 and R-22540 clustered together at 90 % S_G, R-16897 joined this cluster at 85 % S_G and all merged with LMG 22176^T, R-16781 and R-16779 at 80 % S_G. Strain R-16780 showed a slightly narrower range of reactions and clustered with the other isolates at only 75 % S_G. Notwithstanding this, the overall profile of the Mars Oasis isolates separated them from other *Paenibacillus* species in a cluster analysis based upon these phenotypic data. In the ARDRA study (data not shown), all of the Mars Oasis isolates showed identical

profiles, which indicated that their 16S rRNA gene sequences are very similar. Comparison of ARDRA profiles of the strains with a database of over 1000 authentic strains of species of aerobic endospore-forming bacteria (including *P. macquariensis* and *P. odorifer*) did not yield any positive identification. The closest ARDRA pattern was that of *P. macquariensis*, with 80.9 % similarity. The 16S rRNA gene sequence of LMG 22176^T, according to a FASTA search (Pearson & Lipman, 1988), showed highest similarity to the established species *P. odorifer* (96.1 %; Berge *et al.*, 2002), *P. borealis* (95.2 %; Elo *et al.*, 2001), *P. macquariensis* (95.2 %; Marshall & Ohye, 1966) and *P. antarcticus* (95.2 %; Montes *et al.*, 2004). In a phylogenetic cluster (Fig. 2) based on the neighbour-joining algorithm (Saitou & Nei, 1987), LMG 22176^T grouped with *P. macquariensis* and *P. antarcticus* (bootstrap value of 92 %). As the 16S rRNA gene sequence

Fig. 2. Phylogenetic position based on neighbour-joining of the 16S rRNA gene sequence of *P. wynnii* sp. nov. among related *Paenibacillus* species. Bootstrap values (expressed as percentages of 1000 replications) greater than 60% are shown at branch points. Strain and accession numbers are given in parentheses. The tree is rooted using *Paenibacillus polymyxa* as an outgroup (not shown). Bar, 3% sequence divergence.

similarity of LMG 22176^T with all established *Paenibacillus* species was well below 97%, the Mars Oasis isolates can be considered as a novel genomospecies according to the current guidelines for the definition of a bacterial species (Stackebrandt *et al.*, 2002). In the SDS-PAGE analysis of cultures grown on NAG, the medium on which the laboratory database is based, reproducible profiles were obtained for seven of the nine isolates, but R-16674 and R-22540 grew poorly on this medium. Strains LMG 22176^T, R-16777, R-16778, R-16779, R-16781 and R-16897 clustered at 95% similarity, while R-16780 joined this cluster at 89%. These results reflect limited intraspecies variation (Fig. 3) and are consistent with these strains being representatives of the same species. R-16780 was the least typical member of the group in the phenotypic analysis based upon API tests. Cluster analysis of the SDS-PAGE profiles of the isolates together with those of the type strains of *P. odorifer* and *P. macquariensis* (also grown on NAG; data not shown) revealed that the Mars Oasis isolates could be readily separated from these species, showing similarities of 68 and 49%, respectively. As strains R-16674 and R-22540 grew poorly on NAG, SDS-PAGE profiles were also determined for cells of all isolates grown on TSA; the profiles obtained in

this way clearly clustered in two distinct groups (Fig. 3). One of these groups contained profiles that were quite similar to those derived from cells grown on NAG (84–91% similarity), while the other group was clearly distinct (72% similarity). These groupings of TSA-grown cells were not seen in the analyses of API characters or of fatty acid profiles (see below). Strain R-16774 showed 97% similarity to R-16781 in the TSA-based analysis, while the latter strain showed 96% similarity to R-16777, R-16778 and LMG 22176^T in the NAG-based analysis, which implies that R-16774 and R-16781 probably belong to the same species. Less clear is the position of R-22540, which shows only 86% similarity to R-16897; however, as the latter grouped with the five other isolates at 95% similarity in the NAG-based analysis and showed a typical profile for the group in the API analysis, we may be confident that R-22540 also belongs to the species represented by the core strains LMG 22176^T, R-16777, R-16778, R-16779, R-16780, R-16781 and R-16897. The variability of the SDS-PAGE profiles derived from cells grown on TSA might be explained solely by the composition of the medium, particularly the larger amounts of amino acids it contains. Another possible explanation is that better growth on TSA resulted in a shift, for some strains, of the growth phase at which cell extracts were prepared. The metabolism of spore-formers changes when spore formation starts and the Mars Oasis isolates would not sporulate on TSA.

The fatty acid profiles of the Mars Oasis strains were compared with those of closely related species as identified by 16S rRNA gene sequence analysis (see above). In a clustering based on UPGMA of Euclidean distance coefficients (data not shown), the seven core isolates clustered together at a Euclidean distance above 95% and were clearly grouped separately from the *Paenibacillus* close relatives. The fatty acid compositions of all nine Mars Oasis isolates (Supplementary Table S1, available in IJSEM Online) showed a dominance of the fatty acid anteiso-C_{15:0} (33.7%, SD 2.7) and C_{16:0} (32.2%, SD 7.15). The proportion of the latter fatty acid varies appreciably among the isolates, but is high in comparison with closely related *Paenibacillus* species and other Antarctic *Paenibacillus*

Fig. 3. Normalized computer profiles from SDS-PAGE analyses of whole-cell proteins of *P. wynnii* strains on NAG (48 h) and TSA (24 h). The dendrogram is based on UPGMA clustering of the correlation coefficient (*r*) of the total protein profiles. The zone used for clustering is marked by a shaded bar on top.

species (Supplementary Table S2, available in IJSEM Online).

When the Mars Oasis *Paenibacillus* isolates were screened for the *nifH* gene, all strains showed a band of the same molecular mass as described for the *nifH* fragment by Poly *et al.* (2001), while strains of *P. cookii* and *P. cineris* did not show any bands. Comparison of the *nifH* gene partial sequences of isolates LMG 22176^T, R-16774, R-16780, R-16781, R-16897 and R-22540 with the EMBL database revealed that none of the fragments was identical to a previously known sequence. The closest *nifH* sequence (identity of 84.51 % for R-16781, to 86.78 % for LMG 22176^T) was the one from 'uncultured nitrogen fixing clone C5' (GenBank accession no. AF099797; Widmer *et al.*, 1999). Closest matches (81–76 %) of *nifH* sequences for species with validly published names were with *P. graminis* (GenBank accession no. AJ229394), *P. macerans* (AJ223993) and *P. odorifer* (AJ223992). Comparison of translated *nifH* sequences to NifH proteins from databases (not shown) gave in all cases the highest similarity to sequence AAD17884 ('uncultured nitrogen-fixing bacterium C5'; Widmer *et al.*, 1999). Several strains showed a typical aerotactic pattern of growth as described for microaerophilic nitrogen-fixing organisms (Döbereiner & Pedrosa, 1987). Acetylene-reduction was positive for *P. cineris* and *P. cookii* type strains and for Mars Oasis strains LMG 22176^T, R-16774, R-16775, R-16778, R-16779, R-16781, R-16897 and R-22540. Mars Oasis strains R-16777 and R-16780 released little or no ethylene from acetylene. Results for acetylene reduction were, however, highly variable between different inoculations. The *P. cineris* and *P. cookii* type strains also grew in the other media tested (Döbereiner & Day, 1976; Mollica *et al.*, 1985, supplemented with 0.01 % yeast extract and 0.2 % agar), while the Mars Oasis isolates failed to grow in either of them. Although considerable variability of the band strengths was found when screening for the *nifH* gene in the Mars Oasis *Paenibacillus* strains and no bands were found for *P. cineris* and *P. cookii*, all the strains tested were positive for acetylene reduction. These apparently contradictory observations are reminiscent of the experience of Achouak *et al.* (1999), who reported weak acetylene reduction reactions for different *Paenibacillus* *amylolyticus*, *P. larvae*, *P. macquariensis* and *P. peoriae* strains, although no *nifH* gene amplicon could be detected in their genomes. The sequences of the *nifH* gene obtained for strains R-16774 and R-22540 clustered with the sequences obtained for the other four Mars Oasis *Paenibacillus* isolates (*nifH* sequence similarity tree, Supplementary Fig. S2 and similarity matrix, Supplementary Table S3, available in IJSEM Online). It is interesting to note that the *nifH* gene sequence for an uncultivated organism from an Oregon forest site (Widmer *et al.*, 1999) clusters together with those of the Mars Oasis isolates. Hamelin *et al.* (2002) commented that *nifH* gene sequences are well conserved and may be as effective taxonomic tools as 16S rRNA gene sequences. The high similarity of the *nifH* sequences of strains R-16774 and

R-22540 to the *nifH* sequence of the representative strain of the Mars Oasis *Paenibacillus* isolates represents further confirmation that these strains belong to the same species.

Our failure to identify the Mars Oasis *Paenibacillus* isolates by the phenotypic and genotypic methods described and the high similarities of the strains to each other in these analyses support the proposal of a novel species, *Paenibacillus wynnii* sp. nov.

Description of *Paenibacillus wynnii* sp. nov.

Paenibacillus wynnii (wynn' i. i. N. L. gen. n. *wynnii* of Wynn, in honour of the late Dr. David Wynn-Williams, the Antarctic microbiologist who developed Mars Oasis as a research site).

Facultatively anaerobic, Gram-negative, motile, curved rods that occur singly or in pairs and have slightly tapered ends. Endospores are ellipsoidal or oval and lie paracentrally and subterminally in sporangia that may be swollen. Occasionally, the swelling may be at the opposite pole of the sporangium to the spore (Fig. 1). Cell diameter is 0.5–0.7 µm and cell lengths range from 3–5 µm. After 3 days incubation on nutrient agar at 20 °C, the maximum colony diameter is 2 mm. Colonies are circular, convex and glossy with entire margins. Smaller colonies are transparent and whitish, while larger colonies are pale yellow–orange with whitish margins and darker centres. They bear a watery biomass, but may be mucoid. Older colonies are firmly attached to the agar. The optimum temperature for growth is 20 °C. Some strains grow at 37 °C, but none grow at 40 °C. Growth in broth at 4 °C appears within 7 days. Minimum pH for growth lies between 6.0 and 6.5, optimum pH is 7.0–8.0 and the maximum pH lies between 9.5 and 10.0. Catalase-positive and oxidase-negative. Does not tolerate the presence of 3 % NaCl. Growth on skimmed milk agar plates is scarce and casein is not hydrolysed. Starch is hydrolysed. The species fixes nitrogen as demonstrated by the presence of the *nifH* gene in all strains and acetylene reduction in most of them. In the API 20E strip, *o*-nitrophenyl β-D-galactopyranoside hydrolysis is variable and nitrate is reduced. Arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase, citrate utilization, hydrogen sulphide production, urease, tryptophan deaminase, indole production, Voges–Proskauer reaction and gelatin hydrolysis reactions are negative. In the API 50CH gallery using the CHB suspension medium, hydrolysis of aesculin is positive. Acid without gas is produced from the following carbohydrates: amygdalin, D-cellobiose, D-fructose, galactose, D-gentiobiose, D-glucose, glycogen, lactose, maltose, mannitol, D-mannose, D-melibiose, *N*-acetylglucosamine, D-raffinose, salicin, starch, sucrose, D-trehalose, D-turanose and D-xylose. Acid production is variable for L-arabinose, arbutin, gluconate, glycerol, inulin, D-melezitose, methyl-xyloside, rhamnose, ribose, sorbitol and xylitol. Acid is not produced from: adonitol, D-arabinose, D- and L-arabitol, dulcitol, erythritol, D- and L-fucose, 2-keto- and 5-keto-D-gluconate, D-lyxose, *myo*-inositol, methyl

D-glucoside, methyl D-mannoside, L-sorbose, D-tagatose and L-xylose. The main cellular fatty acids are anteiso-C_{15:0} and C_{16:0}, each present at about 33 %. The following fatty acids are present in smaller, decreasing amounts (between about 7 and 1 %) C_{16:1}ω11c, C_{14:0}, iso-C_{15:0}, iso-C_{14:0}, iso-C_{16:0}, C_{18:0} and iso-C_{17:0} (detailed FAME data are given in Supplementary Tables S1 and S2 available in IJSEM Online). The DNA G+C composition of LMG 22176^T is 44.6 mol%. In the variable reactions listed above, the type strain is positive or weakly positive for: *o*-nitrophenyl β-D-galactopyranoside hydrolysis and acid production from gluconate, glycerol, inulin, D-melezitose, rhamnose, sorbitol and xylitol.

The type strain, LMG 22176^T (= CIP 108306^T), was isolated from a soil sample collected from the Mars Oasis, Antarctica.

Acknowledgements

We are most grateful to N. J. Russell for collecting soil samples from Mars Oasis and to H. G. Trüper for advice on nomenclatural etymology. We are most grateful to bioMérieux Inc. for providing API materials and for supporting M.R.-D. P.D.V. is indebted to the National Fund for Scientific Research, Flanders (FWO, Vlaanderen) for personnel and research grant G.0156.02. J.H. is most grateful to the BOF (UGent) for a personal grant. B.R. is indebted to the Spanish Ministry of Science and Technology (MCYT), Programa Ramón y Cajal for a personal grant.

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