***Burkholderia cocovenenans* (van Damme et al. 1960) Gillis et al. 1995 and *Burkholderia vandii* Urakami et al. 1994 are junior synonyms of *Burkholderia gladioli* (Severini 1913) Yabuuchi et al. 1993 and *Burkholderia plantarii* (Azegami et al. 1987) Urakami et al. 1994, respectively**

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Reference strains of *Burkholderia cocovenenans* and *Burkholderia vandii* were compared with strains of other *Burkholderia* species using SDS-PAGE of whole-cell proteins, DNA–DNA hybridization and extensive biochemical characterization. *Burkholderia gladioli* and *B. cocovenenans* were indistinguishable in the chemotaxonomic and biochemical analyses. *Burkholderia plantarii* and *B. vandii* had indistinguishable whole-cell protein patterns but the *B. vandii* type strain differed from *B. plantarii* strains in several biochemical tests. The DNA–DNA binding levels (higher than 70%) indicated that (i) *B. gladioli* and *B. cocovenenans*, and (ii) *B. plantarii* and *B. vandii* each represent a single species. It is concluded that *B. cocovenenans* and *B. vandii* are junior synonyms of *B. gladioli* and *B. plantarii*, respectively.

Keywords: *Burkholderia vandii*, *Burkholderia cocovenenans*, *Burkholderia plantarii*, *Burkholderia gladioli*, taxonomy

INTRODUCTION

The genus *Burkholderia* is expanding rapidly and presently comprises 14 named species and three unnamed genomovars as described by Vandamme et al. (1997). In the same study, considerable similarity between (i) *Burkholderia cocovenenans* and *Burkholderia gladioli* and (ii) *Burkholderia plantarii* and *Burkholderia vandii* was reported (Vandamme et al., 1997).

The organism presently known as *B. cocovenenans* was first described by van Damme et al. (1960) as *Pseudomonas cocovenenans*, an organism responsible for the production of toxoflavin and bongkrekic acid. Later, it was shown that '*Pseudomonas farinofervens*' strains, isolated from cases of food poisoning caused by the consumption of fermented corn flour, also belonged to *P. cocovenenans* (Zhao et al., 1990). Gillis et al. (1995) showed that *P. cocovenenans* belongs to the *Burkholderia* rRNA branch, and transferred it to the genus as *B. cocovenenans*. This transfer was later supported by partial 16S rRNA sequence analysis (Zhao et al., 1995). In a polyphasic taxonomic study of *Burkholderia* strains isolated from cystic fibrosis

patients, a striking similarity was observed between the protein patterns from reference strains of *B. gladioli* and *B. cocovenenans* (Vandamme et al., 1997). *B. gladioli* strains are traditionally isolated from *Gladiolus* spp. and *Iris* spp., for which *B. gladioli* is reported to be pathogenic (Palleroni, 1984). *B. gladioli* has also been cultured from respiratory secretions of cystic fibrosis patients (Christenson et al., 1989).

The name *B. vandii* was proposed by Urakami et al. (1994) for a single plant-associated antibiotic-producing strain. Although the results indicated a close relationship with two other plant-pathogenic species, *Burkholderia glumae* and *B. plantarii*, *B. vandii* could be distinguished from other members of the genus *Burkholderia* on the basis of physiological characteristics and DNA–DNA hybridizations.

In the present study, additional strains of *B. gladioli* and *B. cocovenenans* were included in the protein electrophoretic analyses, and quantitative DNA–DNA hybridizations were performed between the type strains of the different species involved. We also investigated the biochemical characteristics of several representative strains of the different species.

Table 1. List of *Burkholderia* strains studied

ATCC, American Type Culture Collection, Rockville, MD, USA; CCUG, Culture Collection, University of Göteborg, Department of Clinical Bacteriology, Göteborg, Sweden; JCM, Japanese Collection of Microorganisms, Institute of Physical and Chemical Research, Saitama, Japan; LMD, Laboratorium voor Microbiologie, Technische Universiteit, Delft, The Netherlands; LMG, BCCM/LMG Culture Collection Laboratorium voor Microbiologie Gent, Universiteit Gent, Belgium; NCIMB, National Collection of Industrial and Marine Bacteria, Aberdeen, UK; NCPPB, National Collection of Plant-Pathogenic Bacteria, Harpenden Laboratory, Hertfordshire, UK; NCTC, National Collection of Type Cultures, London, UK; PDDCC, Plant Diseases Division Culture Collection, DSIR Mount Albert Research Centre, Auckland, New Zealand.

Species	Strain designation	Other strain designation	Source
<i>B. andropogonis</i>	LMG 2129 ^T	NCPPB 934 ^T	<i>Trifolium repens</i> , leaf spot (USA, 1954)
<i>B. caryophylli</i>	LMG 2155 ^T	NCPPB 2151 ^T	<i>Dianthus caryophyllus</i> (USA, 1951)
<i>B. cepacia</i> genomovar I	LMG 1222 ^T	NCTC 10743 ^T	<i>Allium cepa</i>
	LMG 6988	CCUG 1603	Leg wound (Sweden, 1972)
	LMG 6992	CCUG 2857	Soil (Trinidad, 1960)
	LMG 13053		Cystic fibrosis patient (Belgium, 1987)
<i>B. cepacia</i> genomovar III	LMG 14274		Cystic fibrosis patient (Belgium, 1993)
	LMG 16661		Cystic fibrosis patient (UK)
	LMG 14294	NCTC 13011	Cystic fibrosis patient (Belgium, 1993)
<i>B. cepacia</i> genomovar IV	LMG 14295		Cystic fibrosis patient (Belgium, 1993)
	LMG 15949		Cystic fibrosis patient (Belgium, 1993)
	LMG 11626 ^T	LMD 38.13 ^T	Poisoned bongkreik (Java)
<i>B. cocovenenans</i>	LMG 18113	NCIMB 12451	
	LMG 2216 ^T	ATCC 10248 ^T	<i>Gladiolus</i> sp. (USA)
	LMG 6881	NCPPB 1051	<i>Gladiolus</i> sp. (Zimbabwe)
	LMG 6882	NCPPB 1887	<i>Gladiolus</i> sp. (USA)
<i>B. gladioli</i>	LMG 18157	CC40	Cystic fibrosis patient (USA)*
	LMG 18158	L1	Cystic fibrosis patient (USA)*
	LMG 18159	OCMH1	Cystic fibrosis patient (USA)*
	LMG 18160	OCMH2	Cystic fibrosis patient (USA)*
	LMG 14190 ^T	ATCC 29195 ^T	Soil (Germany)
	LMG 14932	ATCC 29198	Soil (Germany)
<i>B. glumae</i>	LMG 1277	NCPPB 2391	<i>Oryza sativa</i> (Japan)
	LMG 2196 ^T	NCPPB 2981 ^T	<i>Oryza sativa</i> (Japan)
	LMG 6952	PDDCC 3728	<i>Oryza sativa</i> (Japan)
<i>B. multivorans</i>	LMG 13010 ^T	NCTC 13007 ^T	Cystic fibrosis patient (Belgium, 1992)
	LMG 14275		Cystic fibrosis patient (Belgium, 1993)
	LMG 14293		Cystic fibrosis patient (Belgium, 1993)
<i>B. plantarii</i>	LMG 9035 ^T	ICMP 9424 ^T	<i>Oryza sativa</i> (Japan)
	LMG 10907	ICMP 9425	Soil (Japan)
	LMG 10908	ICMP 9427	<i>Oryza sativa</i> (Japan)
<i>B. pyrrocinia</i>	LMG 14191 ^T	ATCC 15958 ^T	Soil
<i>B. vandii</i>	LMG 16020 ^T	JCM 7957 ^T	<i>Vanda</i> sp. (Japan)
<i>B. vietnamiensis</i>	LMG 6998	CCUG 7246	Blood (Sweden, 1978)
	LMG 10929 ^T	TVV 75 ^T	Rice rhizosphere (Vietnam)
	LMG 16232	CCUG 31370	Human bronchial alveolar lavage (Sweden)

* See Christenson *et al.* (1989).

METHODS

Strains and culture conditions. The strains used in this study are listed in Table 1. All the strains were routinely grown on Trypticase soy agar (BBL, Becton Dickinson Microbiology Systems) and were incubated in air at 28 °C or 37 °C.

SDS-PAGE of whole-cell proteins. Strains were grown on buffered nutrient agar (pH 6.8), containing 0.1% (w/v) beef extract, 0.2% (w/v) yeast extract, 0.5% (w/v) NaCl, 0.5%

(w/v) peptone, 0.04% (w/v) KH₂PO₄, 0.24% Na₂HPO₄ · 12H₂O and 2.0% (w/v) agar, for 48 h at 28 °C. Preparation of whole-cell proteins and SDS-PAGE was performed as described before (Pot *et al.*, 1994). Densitometric analysis, normalization and interpolation of the protein profiles, and numerical analysis were performed using the GelCompar 4.0 software package (Applied Maths). The correlation coefficient is expressed as percentage similarity for convenience.

Preparation of high-molecular-weight DNA and DNA-DNA hybridization experiments. Preparation of high-molecular-weight DNA for DNA-DNA hybridization experiments and the determination of the degree of DNA-DNA binding by the initial renaturation rate method was performed as described previously (Vandamme *et al.*, 1992; De Ley *et al.*, 1970). Each value given is the mean of at least two hybridization experiments. The total DNA concentration was $65 \mu\text{g ml}^{-1}$, and the optimal renaturation temperature in $2 \times \text{SSC}$ ($1 \times \text{SSC}$ is 0.15 M NaCl , plus 0.015 M sodium citrate, pH 7.0) was 80.7°C .

Biochemical characterization. Biochemical tests were carried out as described previously (Holmes *et al.*, 1975).

RESULTS

SDS-PAGE of whole-cell proteins and DNA-DNA hybridization experiments

The reproducibility of the SDS-PAGE technique was checked by preparing protein extracts in duplicate. The correlation level between the patterns obtained with different extracts of the same strain was more

than 93 % (data not shown). After numerical analysis and visual comparison of the profiles, 10 clusters could be delineated, while several strains each occupied a separate position in the dendrogram (Fig. 1). Fig. 2 shows the whole-cell protein profiles of a selection of *B. gladioli*, *B. cocovenenans*, *B. glumae*, *B. plantarii* and *B. vandii* strains. The results of the DNA-DNA hybridization experiments are shown in Table 2.

Biochemical characteristics

Biochemical tests were performed on *B. cocovenenans* (strains LMG 11626^T and LMG 18113), *B. plantarii* (strains LMG 9035^T, LMG 10907 and LMG 10908), *B. vandii* (strain LMG 16020^T) and *B. glumae* (strains LMG 1277, LMG 2196^T and LMG 6952). Data on the biochemical characteristics of *B. gladioli* strains are available from a previous study (Vandamme *et al.*, 1997). All strains tested were positive for the following characteristics: motility and growth at room temperature; growth on MacConkey's agar and on β -hydroxybutyrate; catalase and lecithinase activity; alkali production on Christensen's citrate and growth on Simmons' citrate agar; acid production from ammonium-salt medium with glucose, L-arabinose,

Fig. 1. Dendrogram derived from the unweighted pair group mean linkage of correlation coefficients between the protein patterns of the strains studied. The correlation coefficient is expressed as percentage similarity for convenience.

Fig. 2. Electrophoretic protein patterns of a selection of strains investigated. The molecular-mass markers used (left-hand lane) were (from top to bottom) β -galactosidase, bovine albumin, egg albumin, glyceraldehyde-3-phosphate dehydrogenase, trypsinogen, trypsin inhibitor and lysozyme.

Table 2. DNA–DNA binding values of all strains examined

Strain	% DNA–DNA binding value with strain						
	LMG 11626 ^T	LMG 2216 ^T	LMG 2196 ^T	LMG 9035 ^T	LMG 16020 ^T	LMG 1222 ^T	LMG 10929 ^T
<i>B. cocovenenans</i> LMG 11626 ^T	100						
<i>B. gladioli</i> LMG 2216 ^T	73	100					
<i>B. glumae</i> LMG 2196 ^T	23	0	100				
<i>B. plantarii</i> LMG 9035 ^T	13	27	59	100			
<i>B. vandii</i> LMG 16020 ^T				77	100		
<i>B. cepacia</i> LMG 1222 ^T	13	11	38	4	21	100	
<i>B. vietnamiensis</i> LMG 10929 ^T	31				30	36	100

Table 3. Biochemical tests yielding strain- or taxon-dependent results

Values given are the number of strains showing the character.

Character	<i>B. gladioli</i> (n = 12)	<i>B. cocovenenans</i> (n = 2)	<i>B. glumae</i> (n = 3)	<i>B. vandii</i> (n = 1)	<i>B. plantarii</i> (n = 3)
Growth at 37 °C	12	2	3	0	0
Growth at 42 °C	0	2	3	0	0
Growth on cetrinide	2	2	3	1	3
Pigment production	1	0	0	0	0
Pigment production on tyrosine	1	0	0	0	0
Oxidase activity	12	1	1	1	3
Oxidative reaction	11	2	3	1	3
Nitrate reduction	5	2	3	1	3
Urease activity	9	2	3	0	3
Gelatinase production	10	0	1	1	3
Malonate utilization	0	2	1	1	1
β -Galactosidase activity	3	2	3	1	0
Acid production from peptone water and glucose	0	0	0	0	3
Acid production from:					
Glucose (10 %, w/v)	10	2	3	1	3
Lactose (10 %, w/v)	1	0	0	1	3
Acid production in ammonium-salt medium from:					
Adonitol	12	1	3	0	0
Cellobiose	7	2	3	1	3
Glycerol	11	2	3	1	0
Raffinose	0	0	3	0	0
Rhamnose	0	0	0	0	3
Salicin	0	1	1	1	0
Casein digestion	11	1	0	1	3

dulcitol, inositol, mannitol, sorbitol, trehalose, D-xylitol and fructose; hydrolysis of Tween 20, Tween 80 and tyrosine; and presence of poly- β -hydroxybutyrate inclusion granules. All strains tested were negative for the following characteristics: motility at 37 °C; tolerance to KCN; hydrogen sulphide and indole production; gluconate oxidation; phenylpyruvic acid production; arginine, lysine and ornithine decarboxylase

activity; gas production from peptone water and glucose; acid production from ammonium-salt medium with lactose and sucrose; growth in the presence of 0.4 % selenite; nitrite reduction; aesculin and starch hydrolysis; fluorescence on King's B medium; growth at 5 °C; and arginine desiminase and DNase activity. Tests in which there were differences among strains are shown in Table 3.

DISCUSSION

Relationship between *B. cocovenenans* and *B. gladioli*

Zhao *et al.* (1990) allocated the name *Pseudomonas cocovenenans* for a group of strains isolated from fermented corn flour and reported a DNA–DNA binding value of 96% between strains NCIB 9450^T (LMG 11626^T) and NCIMB 12451 (LMG 18113). A mean DNA–DNA binding level of about 58% was reported towards a *B. cepacia* reference strain; other *Burkholderia* species were not included in the hybridization assays. *B. cocovenenans* was reported to differ biochemically from other *Burkholderia* species, including *B. gladioli*, and both species were subsequently transferred to the genus *Burkholderia* (Yabuuchi *et al.*, 1992; Gillis *et al.*, 1995), which was proposed by Yabuuchi *et al.* (1992) for the rRNA group II pseudomonads. However, the surprisingly high similarity in whole-cell protein patterns between *B. gladioli* and the type strain of *B. cocovenenans* (Vandamme *et al.*, 1997) prompted us to perform DNA–DNA hybridizations between the type strains of both species and to investigate the biochemical characteristics of other reference strains of both species. The whole-cell protein patterns of the additional *B. cocovenenans* and *B. gladioli* reference strains were highly similar (Fig. 2). However, when subjected to numerical analysis, two separate clusters, each comprising both *B. cocovenenans* and *B. gladioli* strains, were formed. The reason for this is a high-density protein band in the region between 35 and 43 kDa, which is present in some strains but absent in others (Fig. 2). When this region was omitted from the numerical analysis, all strains formed a single homogeneous cluster (data not shown) as expected from the high DNA–DNA binding values between the *B. cocovenenans* strains LMG 11626^T and LMG 18113 (cluster I and III, respectively) (Zhao *et al.*, 1995) and between the *B. gladioli* and *B. cocovenenans* type strains (both cluster I) (Table 2). Zhao *et al.* (1995) reported that *B. cocovenenans* could be distinguished from *B. gladioli* by differences in the utilization of leucine (absent in *B. cocovenenans* strains and present in *B. gladioli* strains) and nicotinate (present in *B. cocovenenans* strains and absent in *B. gladioli* strains). However, the data for the utilization for nicotinate were erroneously cited from Palleroni & Holmes (1981), where *B. gladioli* was reported to be positive for the utilization of nicotinate. Biochemical tests performed in the present study (Table 3) show that the *B. gladioli* and *B. cocovenenans* strains differ in the utilization of malonate and the capability of growth at 42 °C. In summary, the DNA–DNA binding level and whole-cell protein pattern similarity indicate that both taxa represent a single species. Differences in the utilization of malonate and leucine, and growth at 42 °C represent intraspecies variability like several other tests shown in Table 3. We conclude that *B. gladioli* and *B. cocovenenans* represent the same taxon, with *B. cocovenenans* a junior synonym of *B. gladioli*.

Relationship between *B. vandii* and *B. plantarii*

The name *B. vandii* was proposed by Urakami *et al.* (1994) for a single strain isolated from *Vanda* sp. They reported a DNA–DNA binding value of 57% between *B. vandii* LMG 16020^T and the type strain of *B. plantarii*. This value is at the borderline for species separation. In our analyses, we found a DNA–DNA binding value of 77% between the type strains of the two species, whereas in general our DNA–DNA binding values tend to be lower than those reported by Urakami *et al.* (1994). We previously reported a high similarity in the whole-cell protein patterns and fatty acid composition of *B. vandii* and *B. plantarii* strains (Vandamme *et al.*, 1997). Biochemically, the *B. vandii* strain differed in several characteristics from the *B. plantarii* strains examined, as shown in Table 3. However, the high level of DNA–DNA hybridization, which is in agreement with the protein electrophoretic similarity, in our opinion, outweighs these biochemical differences. These differences reveal the presence of biochemical sub-groups within this species and may warrant the creation of different biotypes or even subspecies within *B. plantarii*. However, we feel that such taxonomic modification should only be proposed when additional strains substantiate the results obtained with strain LMG 16020^T. We therefore conclude that *B. vandii* and *B. plantarii* represent the same species, and that *B. vandii* should be considered a junior synonym of *B. plantarii*. We do not propose a separate status for strain LMG 16020 within this species until similar isolates become available and can be characterized.

Differentiation of *B. glumae*, *B. gladioli* (including *B. cocovenenans*) and *B. plantarii* (including *B. vandii*)

Although the protein patterns of *B. gladioli* and *B. glumae* are similar (Fig. 2), the DNA–DNA binding level between *B. glumae* LMG 2196^T and reference strains of *B. gladioli* was not significant (below 25%). *B. glumae* can be distinguished from *B. gladioli* by the production of acid from raffinose in ammonium-salt medium (Table 3). Several other biochemical differences have been described by Azegami *et al.* (1987). Surprisingly, we found a rather high level of DNA–DNA binding between the *B. glumae* and *B. plantarii* type strains (59%). Both taxa have clearly different whole-cell protein patterns (Figs 1 and 2) and can also be distinguished by biochemical characteristics (Zhao *et al.*, 1995). Furthermore, Stead (1992) and Vandamme *et al.* (1997) reported that both species can be differentiated by cellular fatty acid analyses.

ACKNOWLEDGEMENTS

T.C. acknowledges the support received from the Vlaams Instituut voor Bevordering van Wetenschappelijk-technologisch onderzoek in de Industrie (Belgium) in the form of a bursary for advanced study. P.V. and K.K. are indebted to the Fund for Scientific Research-Flanders (Belgium) for a

position as a postdoctoral fellow, and for research and personnel grants, respectively. We acknowledge the financial support received from the Cystic Fibrosis Trust (UK) (grant RS15) and wish to thank Renata Coopman for excellent technical assistance.

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