Pseudomonas cedrina subsp. *fulgida* subsp. nov., a fluorescent bacterium isolated from the phyllosphere of grasses; emended description of *Pseudomonas cedrina* and description of *Pseudomonas cedrina* subsp. *cedrina* subsp. nov.

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The taxonomic position of a group of four strains, isolated from the phyllosphere of grasses, within the species *Pseudomonas cedrina* was investigated. The isolates formed a separate cluster through ribotyping and MALDI-TOF MS, which could be clearly differentiated from the type strain of *P. cedrina*. The differences found between the patterns of the type strain of *P. cedrina* and the novel isolates were more distinct than those between the type strain and recognized species of the genus *Pseudomonas*, which were phylogenetically related by 16S rRNA gene sequence analysis. Physiological characterization also revealed significant differences between the novel grass isolates and the type strain of *P. cedrina*. Siderotyping of the pyoverdines revealed identical pyoverdine-isoelectrofocusing patterns for the novel isolates and the type strain of *P. cedrina*. However, pyoverdine-mediated ⁵⁹Fe cross uptake studies indicated differences in the siderotype. In contrast, phylogenetic analysis based on 16S rRNA gene sequence analysis and DNA–DNA hybridization studies (reassociation value 76.4 %) supported the affiliation of the novel isolates to the species *P. cedrina*. As a consequence of these observations, the splitting of the species *P. cedrina* into two novel subspecies *Pseudomonas cedrina* subsp. *cedrina* subsp. nov. (type strain CFML 96-198^T=CIP 105541^T=DSM 17516^T) and *Pseudomonas cedrina* subsp. *fulgida* subsp. nov. (type strain P 515/12^T=DSM 14938^T=LMG 21467^T) is proposed.

The genus *Pseudomonas* is one of the genera harbouring the largest number of species and in which some taxonomic anomalies can be found. A multitude of genomovars and some species that should be considered synonymous have been described because the phenotypic characterizations did not reflect the results of the

phylogenetic analyses (Sutra *et al.*, 1997; Gardan *et al.*, 1999; Sikorski *et al.*, 2005). On the other hand, strains or species that should be affiliated to recognized species on the basis of DNA–DNA relatedness values have been investigated, but differences in the phenotypic and molecular data have led to the description of novel subspecies (Peix *et al.*, 2007) or, in some cases, have led to the proposal of separate species (Sikorski *et al.*, 2001).

In the context of studying the diversity of fluorescent pseudomonads associated with the phyllosphere of grasses, several genotypes determined by ribotyping were characterized (Behrendt *et al.*, 2003). One strain group, designated genotype E1 was found to be highly related to *Pseudomonas cedrina* on the basis of comparisons of the 16S rRNA gene sequence. DNA–DNA hybridization studies revealed a similarity value of 76.4 % (replicate value 78.3 %) indicating

Abbreviation: MALDI-TOF MS, matrix-assisted laser desorption ionization-time-of-flight mass spectrometry.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain P 515/12^T is AJ492830.

A supplementary table detailing the differential physiological characteristics of *P. cedrina* subsp. *cedrina* subsp. nov., *P. cedrina* subsp. *fulgida* subsp. nov. and related species and a supplementary figure showing the Riboprint patterns of *EcoRI*-restricted DNA from the novel isolates and related strains are available with the online version of this paper.

a clear affiliation to the species *P. cedrina* according to taxonomic rules (Wayne *et al.*, 1987). However, when compared to the strains of *P. cedrina* (originally published as *Pseudomonas cedrella* but corrected on validation) isolated from Lebanese spring water by Dabboussi *et al.* (1998, 1999), the isolates from grass showed differences in the phenotypic features that are normally used to distinguish species. For this reason, an extensive comparison of the novel grass isolates, strains P 515/12^T, P 515/10, P 517/04 and P 530/23, with the type strain of *P. cedrina* was performed to clarify their taxonomic position.

Analysis of 16S rRNA gene sequences of the novel grass isolate P 515/12^T and *P. cedrina* CFML 96-198^T revealed a close phylogenetic relationship with a sequence similarity value of 99.9% (Behrendt *et al.*, 2003). Ribotyping was performed in order to investigate the strains using a method that has potential for higher taxonomic resolution. As demonstrated by several studies (Gardan *et al.*, 1999; Sikorski *et al.*, 2001; Behrendt *et al.*, 2003; Clark *et al.*, 2006; Behrendt *et al.*, 2007), ribotyping is a highly discriminatory technique that is effective in differentiating strains inter- and intra-specifically within the genus *Pseudomonas* depending on the restriction enzymes used. The grass isolates and the type strains of related species that formed an internal cluster through the analysis of 16S rRNA gene sequences (Behrendt *et al.*, 2003) were studied by ribotyping with the restriction enzyme *EcoRI*. The analysis was performed with an automated RiboPrinter microbial characterization system (Qualicon Du Pont) as described by Behrendt *et al.* (2008). As already shown by Behrendt *et al.* (2003), the riboprint patterns of the novel grass isolates were highly similar to one another and formed a tight cluster (see Supplementary Fig. S1 in IJSEM online). They could be clearly differentiated from the pattern produced by the *P. cedrina* type strain, which was most similar to that of *Pseudomonas jessenii* DSM 17150^T. These clear differences obtained through the use of *EcoRI*, which is generally used to discriminate between *Pseudomonas* species, indicated that the grass isolates formed a separate group within the species *P. cedrina*.

Another powerful fingerprint technique that enables differentiation at the genus, species and sometimes, even strain level is matrix-assisted laser desorption/ionization-time-of-flight mass spectrometry (MALDI-TOF MS) (Conway *et al.*, 2001; Fenselau & Demirev, 2001; Stackebrandt *et al.*, 2005; Valentine *et al.*, 2005). MALDI-TOF MS analysis of the novel grass isolates and their close phylogenetic relatives as determined by 16S rRNA gene sequence analysis (Behrendt *et al.*, 2003) was performed according to the method of Tóth *et al.* (2008). As shown in Fig. 1, the grass isolates formed a cluster that was separated from the type strain of *P. cedrina* and related *Pseudomonas* species by clear differences in spectral patterns. Comparable to the ribotyping results, the spectra of the type strain of *P. cedrina* were closer to those of representative strains of other *Pseudomonas* species than to those of the group of novel grass isolates. These results supported the assumption that the novel strains formed a separate group within the species *P. cedrina*.

Characterization of pyoverdines by siderotyping has shown that these molecules are efficient taxonomical markers for the classification of fluorescent pseudomonads at the species level (Meyer *et al.*, 2002, 2007; Meyer & Geoffroy, 2004). The siderotypes of the grass isolates were compared with those of the *P. cedrina* type strain. Cultures for pyoverdine production and the electrophoretic characterization of the pyoverdine isoforms that accumulated in the growth media were performed according to Meyer *et al.* (1998), with the exception of the isoelectric pH (pI) values, which were determined using an internal standard made from a mixture of pyoverdines with defined pI values, as described by Fuchs *et al.* (2001). The purification of pyoverdines with the XAD chromatographic procedure and their use in pyoverdine-mediated ⁵⁹Fe uptake were performed as described previously (Meyer *et al.*, 1998). The novel strains displayed identical pyoverdine-isoelectrofocusing patterns with one isoform band at pI 7.3. In contrast, studies of pyoverdine-mediated iron cross uptake revealed differences in the siderotype (data not shown). While the type strain of *P. cedrina* was able to use the pyoverdines of the novel grass isolates at a similar efficiency to its own pyoverdine, the grass isolates were unable to uptake the pyoverdine from the type strain. These results indicated that the type strain formed another siderovar with a different pyoverdine from the novel grass isolates, but had a supplementary pyoverdine-Fe receptor that recognized the pyoverdine of the grass isolates. Thus, the results of siderotyping confirmed the grass isolates separate group position in the species *P. cedrina*.

An extensive investigation of the physiological characteristics of the novel isolates and the type strain of *P. cedrina* was carried out using API 20NE test strips (bioMérieux) and Biolog GN MicroPlates (Biolog Inc.) according to the manufacturer's instructions. Additional physiological and morphological features were determined by methods described previously (Behrendt *et al.*, 1999, 2008). Ice nucleation activity of the novel isolates was tested at -5 and -10 °C according to the method of Hildebrand *et al.* (1994). As shown in Table 1, the novel isolates displayed high conformity with each other as regards phenotypic features. Using Biolog GN MicroPlates, differences in the intensity of oxidation were noted for only a few carbohydrates. The utilization of L-ornithine differed between the strains. Whilst strain P 515/12^T did not use this substrate, the other novel isolates showed a weak reaction. In contrast, comparisons between the novel isolates and the type strain of *P. cedrina* revealed several differences in physiological characteristics (Table 1). Particularly, the different reaction for arginine dihydrolase was remarkable as this feature is generally species-specific and is an important component of the levan, oxidase, potato rot, arginine dihydrolase, tobacco hypersensitivity (LOPAT) test that is used for the primary differentiation of saprophytic and phytopathogenic species of fluorescent pseudomonads (Rudolph *et al.*, 1990). Furthermore, the differences in substrate utilization found between *P.*

Fig. 1. Dendrogram generated by BioTyper software (version 1.1, Bruker Daltonics) showing the similarity of MALDI-TOF mass spectra of cell extracts of the novel grass isolates, the type strain of *P. cedrina* and highly related species of the genus *Pseudomonas* [as determined by 16S rRNA gene sequence analysis (Behrendt *et al.*, 2003)].

Table 1. Physiological characteristics of *P. cedrina* CFML 96-198^T and the four novel isolates from grass

Strains: 1, *P. cedrina* CFML 96-198^T; 2, P 515/12^T; 3, P 515/10; 4, P 517/04; 5, P 530/23. Characteristics corresponding to all strains are given in the emended description of *P. cedrina*. + positive; –, negative; w, weakly positive.

Characteristic	1	2	3	4	5
Arginine dihydrolase	+	–	–	–	–
Formation of levan from sucrose	+	–	–	–	–
Reduction of nitrates to nitrites	+	–	–	–	–
Gelatin hydrolysis	+	–	–	–	–
Utilization on Biolog GN microplates:					
Adonitol	+	–	–	–	–
Alaninamide	–	+	+	+	+
i-Erythritol	+	–	–	–	–
DL- α -Glycerol phosphate	–	+	+	+	+
Glycyl L-glutamic acid	+	+	w	w	w
p-Hydroxyphenylacetic acid	+	–	–	–	–
myo-Inositol	–	+	+	+	+
α -Ketovaleric acid	+	+	w	w	w
L-Ornithine	–	–	w	w	w
Psicose	–	w	w	w	+
Putrescine	–	w	w	+	w
Quinic acid	–	+	w	w	w
L-Rhamnose	+	–	–	–	–
D-Serine	–	w	w	w	w
D-Sorbitol	+	–	–	–	–
Sucrose	+	–	–	–	–
D-Trehalose	+	–	–	–	–
Uridine	+	w	w	w	w
Xylitol	+	–	–	–	–

cedrina and the novel grass isolates with the Biolog GN MicroPlates were considerable and were more significant than the differences previously found between some recognized species of the genus (Behrendt *et al.*, 2007). Thus, the results of the phenotypic characterization performed in this study substantiated the conclusion by Behrendt *et al.* (2003) that the novel isolates form a separate phenotypic group in the species *P. cedrina*.

In summary, the novel isolates from grass could be clearly discriminated from the type strain of *P. cedrina* by ribotyping, MALDI-TOF MS analysis, siderotyping and physiological characterization, although the phylogenetic analysis of Behrendt *et al.* (2003) demonstrated an affiliation to the species *P. cedrina*. On this basis, the novel isolates merit a separate taxonomic status at the subspecies level and thus the name *Pseudomonas cedrina* subsp. *fulgida* subsp. nov. is proposed. According to Rule 40b of the Bacteriological Code (Lapage *et al.*, 1992), the description of a novel subspecies necessitates the proposal of the subspecies *Pseudomonas cedrina* subsp. *cedrina* subsp. nov. The description of *P. cedrina* (Dabboussi *et al.*, 1999) is therefore emended. As shown in Supplementary Table S1 (available in IJSEM online), both subspecies of *P. cedrina* can be differentiated from their phylogenetic neighbours by physiological characteristics despite the emendation of the species description.

Emended description of *Pseudomonas cedrina* corrig. Dabboussi *et al.* 2002

Possesses the following characteristics in addition to those described by Dabboussi *et al.* (1999). Cells are motile by

means of one or two polar flagella. All strains are positive for the utilization of *N*-acetyl-D-glucosamine, L-arabinose, D-arabitol, caprate, citrate, D-fructose, D-galactose, α -D-glucose, gluconate, D-mannitol, D-mannose, methyl pyruvate, monomethyl succinate, acetic acid, *cis*-aconitic acid, citric acid, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucosaminic acid, D-glucuronic acid, α -hydroxybutyric acid, β -hydroxybutyric acid, α -ketobutyric acid, α -ketoglutaric acid, DL-lactic acid, malate, malonic acid, propionic acid, D-saccharic acid, succinic acid, bromosuccinic acid, succinamic acid, glucuronamide, D-alanine, L-alanine, L-alanyl glycine, L-asparagine, L-aspartic acid, L-glutamic acid, L-histidine, hydroxy L-proline, L-leucine, L-proline, L-pyroglytamic acid, L-serine, L-threonine, γ -aminobutyric acid, urocanic acid, inosine, 2-aminoethanol and glycerol. None of the strains uses adipate, α -cyclodextrin, dextrin, glycogen, Tweens 40 or 80, *N*-acetyl-D-galactosamine, cellobiose, L-fucose, gentiobiose, α -lactose, α -D-lactose, lactulose, maltose, D-melibiose, methyl β -D-glucoside, phenylacetate, D-raffinose, turanose, γ -hydroxybutyric acid, itaconic acid, sebacic acid, glycyl L-aspartic acid, L-phenylalanine, DL-carnitine, thymidine, phenylethylamine, 2,3-butanediol, glucose 1-phosphate or glucose 6-phosphate. Oxidase and catalase reactions are positive whereas DNase, β -galactosidase and urease activities are negative. The strains do not produce indole from tryptophan. Hydrolysis of aesculin and tyrosine is negative. All strains are able to grow on cetrinide agar. β -Haemolysis of sheep blood does not occur.

Description of *Pseudomonas cedrina* subsp. *fulgida* subsp. nov.

Pseudomonas cedrina subsp. *fulgida* (ful'gi.da. L. fem. adj. *fulgida* flashing, glittering, shining, pertaining to the bright fluorescence).

Cells are Gram-negative, non-spore-forming rods of about 0.8 μ m in diameter and 2.5–4.2 μ m in length that occur singly. They are motile by one or two polar flagella. The white–yellowish colonies on King B medium are smooth with regular margins and they produce a pigment that gives off a light yellow–green fluorescence when irradiated with UV-light. Metabolism is aerobic. Does not hydrolyse starch or casein. Ice nucleation activity and formation of H₂S from sodium thiosulphate are negative. Optimal growth temperature is 21 °C. Growth can be observed at 4 °C, but none of the isolates are able to grow at 41 °C. Further physiological features are presented in Table 1.

The type strain, P 515/12^T (=DSM 14938^T=LMG 21467^T), was isolated from the phyllosphere of grasses in Paulinenaue (Germany).

Description of *Pseudomonas cedrina* subsp. *cedrina* subsp. nov.

Pseudomonas cedrina subsp. *cedrina* (ce'dri.na. L. fem. adj. *cedrina* of a cedar tree, the characteristic tree of Lebanon, the country from which isolates were taken).

The description is essentially as given by Dabboussi *et al.* (1999). Additional physiological features determined for the type strain are shown in Table 1.

The type strain, CFML 96-198^T (=CIP 105541^T=DSM 17516^T), was isolated from Lebanese spring waters.

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