INTERNATIONAL JOURNAL OF SYSTEMATIC BACTERIOLOGY, Jan. 1996, p. 16–22 Vol. 46, No. 1
0020-7713/96/$04.00+0

Transfer of "*Pseudomonas riboflavina*" (Foster 1944), a Gram-Negative, Motile Rod with Long-Chain 3-Hydroxy Fatty Acids, to *Devosia riboflavina* gen. nov., sp. nov., nom. rev.

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The taxonomic position of "*Pseudomonas riboflavina*" was studied by 16S rRNA gene sequencing and chemotaxonomic methods. This organism is a gram-negative, strictly aerobic rod and has a DNA guanine-plus-cytosine content of 61.4 mol%; the major isoprenoid quinone is ubiquinone 10, and the unusual cellular fatty acids 3-hydroxytetracosenoic acid (3-OH 24:1) and 3-hydroxyhexacosenoic acid (3-OH 26:1) are the major 3-hydroxy cellular fatty acids. A phylogenetic analysis based on 16S rRNA sequences revealed that "*P. riboflavina*" IFO 13584^T (T = type strain) occupies an independent position in the α subclass of the *Proteobacteria*. On the basis of our data, we propose that "*P. riboflavina*" IFO 13584^T should be transferred to the genus *Devosia* gen. nov. as *Devosia riboflavina* sp. nov., nom. rev.

The original description of the genus *Pseudomonas* Migula 1894 was so vague that an extremely wide variety of aerobic, gram-negative, rod-like bacteria were included in the genus. 16S rRNA cataloging (34) and DNA-rRNA hybridization (2–4) revealed that members of the genus *Pseudomonas* belonged to the α, β, and γ subclasses of the *Proteobacteria*. The level of heterogeneity in the genus *Pseudomonas* has been reduced by transferring various pseudomonads belonging to Palleroni's rRNA groups (19) other than group I to other existing genera or new genera (24, 26, 32, 33, 35, 36). However, there are still several misnamed pseudomonads.

Foster (7) described "*Pseudomonas riboflavina*" as a soil bacterium which oxidized riboflavin to lumichrome. In *Bergey's Manual of Determinative Bacteriology*, 8th ed. (5), "*P. riboflavina*" was treated as a species incertae sedis because it was not motile motility even though the original description indicated that it was motile. DNA-rRNA hybridization studies (4, 24) showed that "*P. riboflavina*" belongs to rRNA superfamily IV (α subclass), but its precise position in the α subclass has not been determined. We investigated a strain assigned to "*P. riboflavina*" by phenotypic, chemotaxonomic, and phylogenetic methods. The results of a 16S rRNA gene sequence analysis placed "*P. riboflavina*" IFO 13584^T (T = type strain) in an independent position in the α subclass. In view of the results of our molecular and chemotaxonomic analyses, we propose that "*P. riboflavina*" IFO 13584^T should be classified in the new genus *Devosia* as *Devosia riboflavina* sp. nov., nom. rev.

MATERIALS AND METHODS

Bacterial strains and cultivation. The strain which we examined was *D. riboflavina* IFO 13584^T (= ATCC 9526^T = Foster strain 4R3337 [7]). Only one strain of this species is available in culture collections. The organism was cultivated aerobically at 28°C in medium containing (per liter) 10.0 g of peptone (Difco Laboratories, Detroit, Mich.), 2.0 g of yeast extract (Difco), 1.0 g of $MgSO_4 \cdot 7H_2O$, and 15 g of agar (if needed) (pH 7.0). Cells were harvested by centrifugation at the stationary phase for PCR and chemotaxonomic experiments.

Morphological and physiological tests. Cells in the early exponential growth phase grown on solid media were used for morphological and physiological tests. The size, shape, and motility of cells were determined with a phase-contrast microscope. Flagellation was examined with a model JEM-1200EX transmission electron microscope (JEOL, Akishima, Japan) after shadowing with platinum-palladium.

Catalase activity was determined by bubble production in a 3% hydrogen peroxide solution. Oxidase activity was determined by oxidation of 1% tetramethyl-*p*-phenylenediamine on filter paper. Other conventional tests were performed with API 20 NE strips (BioMérieux S.A., Marcy-l'Etoile, France).

DNA base composition analysis. DNA was extracted by the methods of Marmur (15) and Saito and Miura (21), with some modifications, including deproteinization with phenol-chloroform (1:1, vol/vol) and solubilization of DNA in TMK buffer (10 mM $MgSO_4 \cdot 7H_2O$, 25 mM KCl, 50 mM Tris-HCl; pH 7.6). The guanine-plus-cytosine (G+C) content of the DNA was determined by the method of Mesbah et al. (16).

Respiratory quinone analysis. Isoprenoid quinones were extracted from 200 mg of freeze-dried cells with chloroform-methanol (2:1, vol/vol) and were purified by thin-layer chromatography by using *n*-hexane–diethyl ether (85:15, vol/vol) as the solvent. The ubiquinone fraction was extracted with acetone, dried under a nitrogen gas stream, and then analyzed by high-performance liquid chromatography (HPLC) (model LC-5A apparatus; Shimadzu, Kyoto, Japan) with a Zorbax octyldecyl silane column (4.6 by 150 mm).

Cellular fatty acid analysis. The procedures used to prepare cellular fatty acid methyl esters were the procedures described by Suzuki and Komagata (25). The fatty acid methyl ester composition was determined by the method of Sakane and Yokota (23). 3-Hydroxy (3-OH) fatty acids were identified by gas chromatography-mass spectrometry as their *O*-trimethylsilyl methyl ester derivatives (36).

LPS analysis. Lipopolysaccharides (LPS) were isolated from dried cells by using the phenol-chloroform-petroleum ether extraction method (9). The analytical methods used were essentially the methods described previously in detail (39, 41). Total fatty acids were determined as methyl ester derivatives by using an OV-1 packed glass column (2.6 mm [inside diameter] by 2 m). Reducing sugar contents were determined by HPLC by using a Shimadzu model LC-5A pumping system, a Shim-pack ISA-07/S2504 column (4.0 by 250 mm), and the method described by Mikami and Ishida (17). The fluorescence intensities of the effluent were determined with a Shimadzu model RF-530 spectrophotometer and a Chromatopack model C-R5A (Shimadzu). Polyacrylamide gel electrophoresis of LPS was performed by the method of Komuro and Galanos (13).

PCR amplification, cloning, and sequencing of 16S ribosomal DNA. The 16S rRNA gene was amplified by a PCR (20) by using TaKaRa *Taq* (Takara Shuzo, Kyoto, Japan) and primers 9F (5′-GAGTTTGATCCTGGCTCAG) and 1541R (5′-AAGGAGGTGATCCAACC). The conditions used for thermal cycling were as follows: denaturation of the target DNA at 94°C for 2 min, followed by 40 cycles consisting of denaturation at 94°C for 1 min, primer annealing at 55°C for 1 min, and primer extension at 72°C for 2 min. After the last cycle, the reaction mixture was kept at 72°C for 5 min and then cooled to 4°C. The 1.5-kb amplified 16S ribosomal DNA fragment was separated by agarose gel electrophoresis and purified by using a Prep-A-Gene DNA purification kit (Bio-Rad Laboratories, Hercules, Calif.).

The purified fragment was made blunt ended with T4 DNA polymerase by using a DNA blunting kit (Takara Shuzo), and the 5′ end was phosphorylated with T4 polynucleotide kinase (Takara Shuzo) by following the manufacturer's instructions. The DNA was ligated into the dephosphorylated *Hin*cII site of

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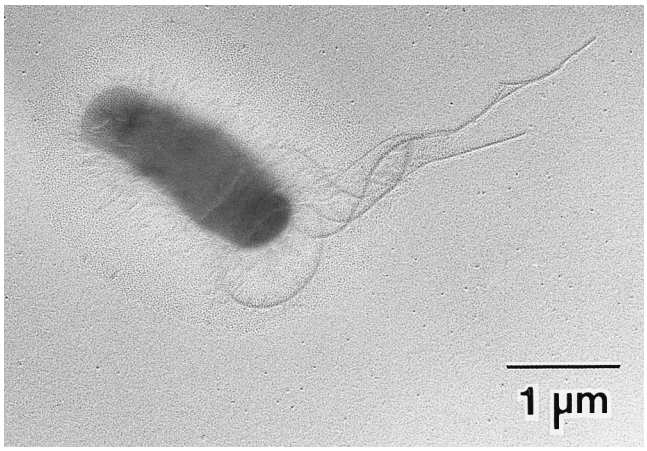

FIG. 1. Transmission electron micrograph of a motile cell of *D. riboflavina* IFO 13584^T.

phagemid vector pUC118 (Takara Shuzo). *Escherichia coli* JM109 (37) was used as the host. The single-stranded DNA used as a sequencing template was obtained after infection with bacteriophage M13KO7 (31). The plasmid was prepared by using a Miniprep protocol (14).

The single-stranded DNA and cloned plasmid material were sequenced by using an AutoRead sequencing kit (Pharmacia, Uppsala, Sweden) and were analyzed with a Pharmacia A.L.F. DNA Sequencer II instrument. The 5′-fluorescein-labeled oligonucleotide primers used were M13 Universal and Reverse Primer (Pharmacia) and primer 1111R (5′-TTGCGCTCGTTGCGGGACT).

Phylogenetic analysis. The 16S rRNA sequences of the strains examined and sequences of reference organisms obtained from databases were aligned with the *E. coli* sequence (1). The CLUSTAL V software package (10) was used to generate evolutionary distances (K_{nuc} values [12]) and similarity values, and a phylogenetic tree was constructed by using the neighbor-joining method (22) and the K_{nuc} values. Positions at which secondary structures varied between strains (positions 66 to 103, 179 to 220, 447 to 487, 841 to 845, 1004 to 1036, 1134 to 1140, 1247 to 1290, and 1446 to 1456) and positions at which sequences were not determined in some reference organisms (positions 1457 to 1524; *E. coli* numbering system) were not included in the analysis. The total number of nucleotides compared was 1,147 after we eliminated all sites at which sequences were not determined in any sequences. The topology of the phylogenetic tree was evaluated by the bootstrap resampling method of Felsenstein (6) with 1,000 replicates.

Nucleotide sequence accession number. The sequence data were deposited in the DDBJ database and appear in the DDBJ, EMBL, GSDB, and NCBI nucleotide sequence databases under accession number D49423.

TABLE 1. Phenotypic characteristics of *D. riboflavina* IFO 13584^T

Characteristic	Strain IFO 13584^T
Color of colonies	Cream
Morphology of cells	Rods
Gram stain reaction	−
Motility	+
Spore formation	−
Oxidase activity	+
Catalase activity	+
Urease activity	+
Nitrate reduction	w+
Hydrolysis of:	
Gelatin	−
Starch	−
Acid production from:	
D-Arabinose	+
D-Galactose	−
D-Glucose	−
Inositol	−
Lactose	−
D-Fructose	−
Maltose	−
Mannitol	−
Sucrose	−
D-Xylose	−
Decarboxylation of:	
L-Alanine	−
L-Lysine	−
L-Ornithine	−
Oxidation of riboflavin	−

RESULTS AND DISCUSSION

Morphological and physiological characteristics. Strain IFO 13584^T was a gram-negative, rod-shaped organism whose cells were 0.4 to 0.8 μm wide and 2.0 to 8.0 μm long. Motile cells were observed in the early growth phase, and these cells had several polar flagella (Fig. 1).

Strain IFO 13584^T had oxidase and catalase activities and grew vigorously on nutrient agar (Difco) at 28°C. Some of the phenotypic characteristics of this organism are summarized in Table 1.

TABLE 2. Comparison of the genus *Devosia* with morphologically similar genera belonging to the α subclass of the *Proteobacteria* and the genus *Pseudomonas*[a]

Genus	Flagella	Oxidase activity[b]	Catalase activity[b]	Major hydroxy fatty acids[c]		Quinone[d]	G+C content (mol%)
				2-OH	3-OH		
Devosia	Polar	+	+		24:1, 26:1	Q-10	61.4
Acetobacter	Lateral, peritrichous	−	+	16:0	16:0	Q-10	51-65
Acidiphilium	Lateral, polar	− or w	ND	(16:0)	14:0 (18:0)	Q-10	62-70
Acidomonas	Peritrichous	+	+	14:0, 16:0	14:0, 16:0	Q-10	63-65
Agrobacterium	Peritrichous	+ or −	+		14:0	Q-10	55-63
Bradyrhizobium	Polar	ND	ND		12:0, 14:0	Q-10	61-65
Brevundimonas	Polar	+	+		12:0	Q-10	65-68
Gluconobacter	Polar	−	ND	14:0	16:0 (Δ19:0)	Q-10	56-64
Methylobacterium	Lateral, polar	+ or w	+		14:0	Q-10	60-70
Mycoplana	Peritrichous	+	ND		12:0 (14:0)	Q-10	63-68
Rhizomonas	Lateral, polar	+	+	14:0		Q-10	58-65
Rhizobium	Peritrichous, polar	ND	ND		14:0 (i13:0)	Q-10	59-64
Sphingomonas	Polar	ND	+	14:0		Q-10	59-68
Pseudomonas	Polar	+ or −	+	12:0	10:0, 12:0	Q-9	59-68

[a] Data from this study and references 10a, 13a, 18, 27 through 30, 36, 38, and 40.
[b] +, positive; w, weakly positive; −, negative; ND, not determined.
[c] Parentheses indicate major hydroxy fatty acids that occur in some species. i, iso branched; Δ, cyclo.
[d] Q-10, ubiquinone 10; Q-9, ubiquinone 9.

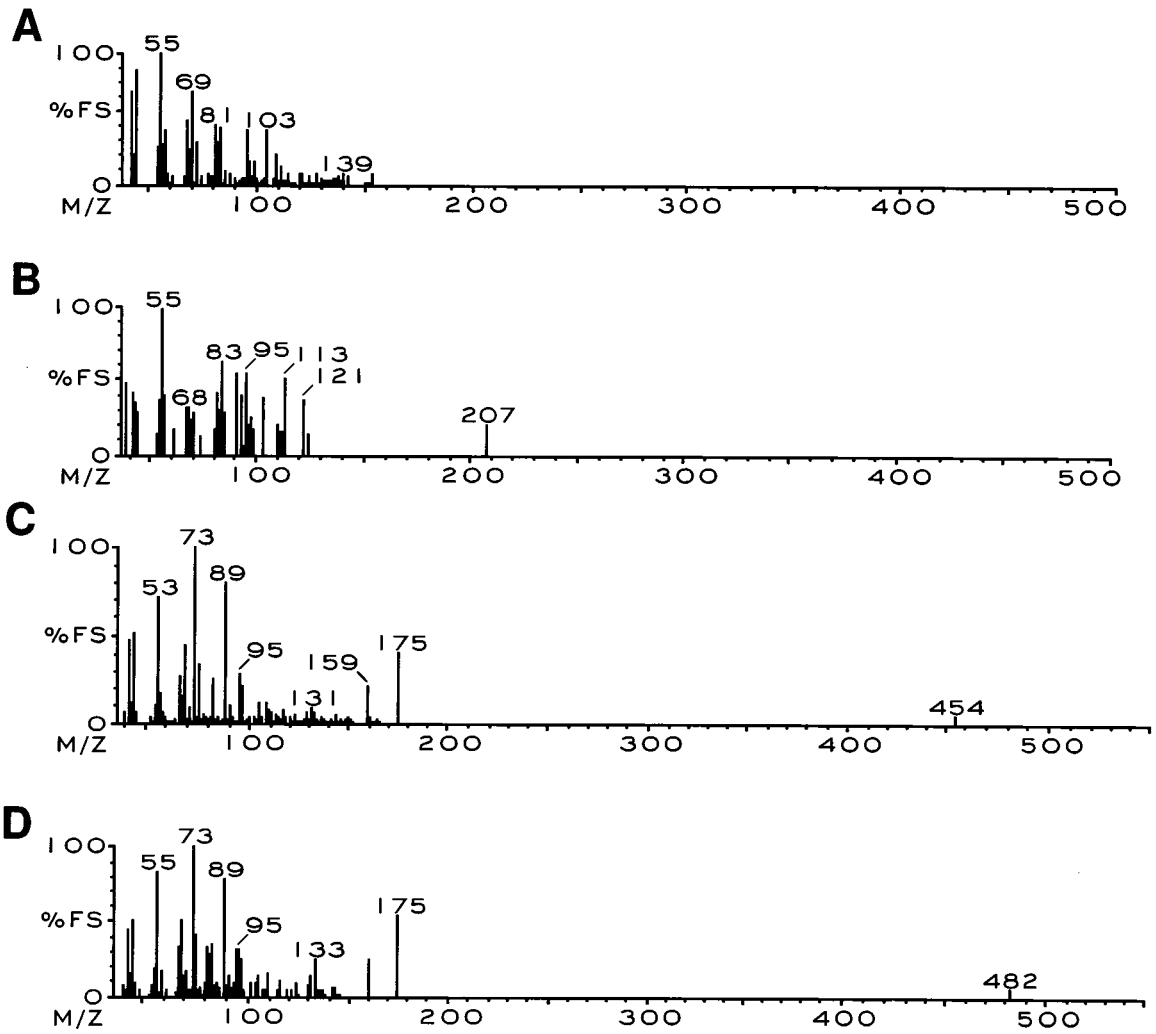

FIG. 2. Electron impact mass spectra of 3-OH 24:1 methyl ester (A), 3-OH 26:1 methyl ester (B), 3-*O*-trimethylsilyl 24:1 methyl ester (C), and 3-*O*-trimethylsilyl 26:1 methyl ester (D) from *D. riboflavina* IFO 13584^T.

Chemotaxonomic characteristics. Some chemotaxonomic characteristics of *D. riboflavina* IFO 13584^T are shown in Table 2. The major quinone of this strain was ubiquinone 10, which suggested that it belongs to the α subclass of the *Proteobacteria*. The G+C content of the DNA was 61.4 mol%.

2-Hydroxy (2-OH) fatty acids were not detected by a thin-layer chromatography analysis of strain IFO 13584^T. In the gas-liquid chromatographic analysis performed with the 2-m OV-1 column, 3-hydroxytetracosenoic acid (3-OH 24:1) methyl ester and 3-hydroxyhexacosenoic acid (3-OH 26:1) methyl ester had relative retention times of 5.93 and 11.94, respectively, with respect to 3-hydroxyoctadecanoic acid (3-OH 18:0) methyl ester, which was used as an internal standard. The gas chromatography-mass spectrometry data for methyl esters and trimethyl esters of 3-OH 24:1 and 3-OH 26:1 are shown in Fig. 2. The electron impact mass spectra of the methyl esters were characterized by the presence of *m/z* 103, which indicated that the hydroxyl group in the long-chain fatty acid was located at the *n*-3 position. No molecular ion peak was observed. The electron impact mass spectra of trimethylsilyl methyl ester derivatives revealed the presence of 3-OH 24:1 and 3-OH 26:1, which were characterized by peaks at *m/z* 454 (M-15) for the 3-*O*-trimethylsilyl 24:1 methyl ester and *m/z* 482

TABLE 3. Cellular fatty acid composition of *D. riboflavina* IFO 13584^T

Fatty acid	% of total fatty acids[a]
Nonpolar acids	
14:0	1.0
14:1	14.2
16:0	18.2
16:1	3.5
17:0	0.7
18:0	3.4
18:1	58.9
3-OH acids	
3-OH 18:0	4.6
3-OH 20:0	1.8
3-OH 20:1	1.8
3-OH 22:0	6.1
3-OH 22:1	8.0
3-OH 24:1	41.0
3-OH 26:1	36.9

[a] The percentage of an acid relative to the total nonpolar and 3-OH acids, respectively.

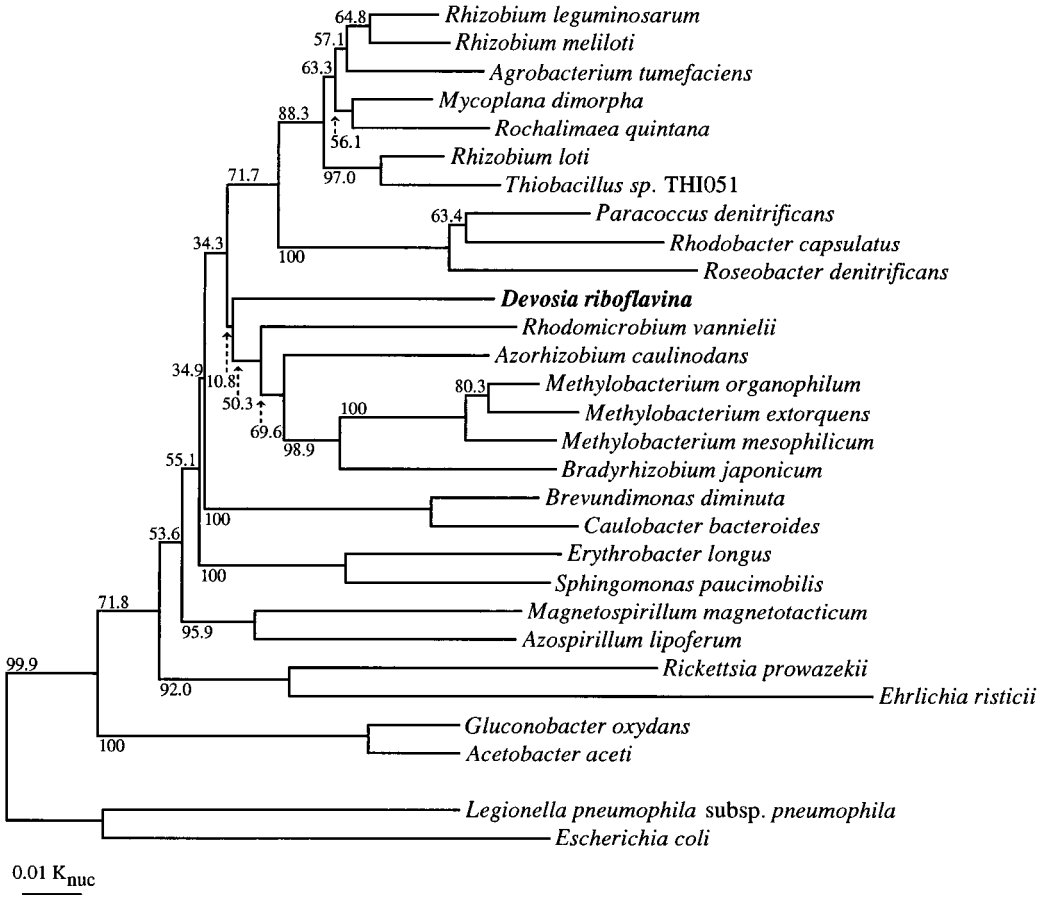

FIG. 3. Phylogenetic tree derived from 16S rRNA sequence data for members of α subclass of the *Proteobacteria*. *E. coli* was used as the root organism. Bar = 0.01 K_{nuc} in nucleotide sequences. The lengths of the vertical lines are not significant. The numbers on the branches are confidence limits (expressed as percentages) estimated from the bootstrap analysis performed with 1,000 replicates.

(M-15) for the 3-*O*-trimethylsilyl 26:1 methyl ester. Thus, IFO 13584^T contained 3-OH 24:1 and 3-OH 26:1 as its major 3-OH fatty acids and 3-OH 18:0, 3-hydroxycosanoic acid (3-OH 20:0), 3-hydroxycosenoic acid (3-OH 20:1), 3-hydroxydocosanoic acid (3-OH 22:0), and 3-hydroxydocosenoic acid (3-OH 22:1) as minor components (Table 3). 3-OH fatty acids which were shorter than 3-OH 18:0 were not detected in any analysis.

The analysis of LPS purified from cells by extraction with phenol-chloroform-petroleum ether (9) revealed the presence of the long-chain acids 3-OH 24:1, 3-OH 26:1, and 3-OH 22:1, as well as octadecanoic acid (18:0), octadecenoic acid (18:1), and hexadecanoic acid (16:0) as fatty acid components and glucose, galactose, mannose, and glucosamine as sugar components. Thus, the long-chain 3-OH fatty acids were components of the LPS molecule, which is an important outer membrane component. No other bacteria that contain 3-OH 24:1

TABLE 4. 16S rRNA sequence signatures that distinguish the genus *Devosia* from other taxa in the *Proteobacteria*

Position of base or base pair[a]	Base(s) in:								
	Devosia	*Rhizobiaceae*	*Erythrobacter-Sphingobacterium* group	*Azospirillum-Magnetospirillum* group	*Bradyrhizobium-Methylobacterium* group	*Brevundimonas-Caulobacter* group	*Paracoccus-Rhodobacter-Roseobacter* group	*Ehrlichia-Rickettsia* group	*Acetobacter-Gluconobacter* group
155:166	G:C	C:G	G/C:C/G	U:G	C:G	C:G	C/U:G/A	U/A:A/U	C/U:G
240:286	A:U	U:A	U:A	C:G	C:G	C:G	U:A	C/U:G/A	U:A
445:489	A:U	G:C	G:C	A/G:U/C	G:C	G:C	G:C	G:C/U	G:C
681:709	U:A	G:C	G:C	G/C:C/G	G:C	G:C	G/A:C/U	U:A	C:G
694	G	A	A	A	A	A	A	A	A
1419:1481	A:U	G:C	G:C	G:C	G:C	G:C	G/A:C/U	G:C/U	G:C

[a] *E. coli* numbering.

TABLE 5. Similarity matrix for 16S rRNA sequences of *D. riboflavina* and related organisms

Organism	% Similarity																
	Devosia riboflavina IFO 13584^T	*Rhizobium meliloti* IAM 12611^T	*Rhizobium loti* ATCC 33669^T	*Rhizobium leguminosarum* IAM 12609^T	*Agrobacterium tumefaciens* DSM 30150^T	*Mycoplana dimorphia* IAM 13154^T	*Thiobacillus* sp. strain THI051	*Rochalimaea quintana*[a]	*Azorhizobium caulinodans* ORS571^T	*Rhodomicrobium vannielii* EY33^T	*Methylobacterium organophilum* JCM 2833^T	*Sphingomonas paucimobilis* GIFU 2395^T	*Magnetospirillum magnetotacticum* MS1^T	*Brevundimonas diminuta* ATCC 11568^T	*Paracoccus denitrificans* LMG 4218^T	*Acetobacter aceti* NCIMB 8621^T	*Rickettsia prowazekii* Breinl
Rhizobium meliloti IAM 12611^T	93.1																
Rhizobium loti ATCC 33669^T	93.0	96.4															
Rhizobium leguminosarum IAM 12609^T	92.6	97.4	95.4														
Agrobacterium tumefaciens DSM 30150^T	92.5	96.0	94.7	96.0													
Mycoplana dimorpha IAM 13154^T	92.5	96.8	96.3	96.7	95.9												
Thiobacillus sp. strain THI051	92.1	95.7	96.9	94.3	93.2	95.6											
Rochalimaea quintana[a]	91.9	96.0	95.3	95.3	94.5	96.3	94.5										
Azorhizobium caulinodans ORS571^T	91.6	91.7	91.7	92.5	91.8	92.4	92.0	91.5									
Rhodomicrobium vannielii EY33^T	91.2	91.8	92.0	92.4	91.2	92.1	91.2	91.1	92.0								
Methylobacterium organophilum JCM 2833^T	90.5	90.7	90.2	91.5	90.4	92.2	89.5	90.7	92.3	91.3							
Sphingomonas paucimobilis GIFU 2395^T	89.8	89.5	89.7	89.6	89.5	89.9	88.9	88.9	89.7	88.9	88.9						
Magnetospirillum magnetotacticum MS1^T	89.7	89.1	89.5	89.6	89.1	89.7	88.6	89.7	90.2	88.9	89.0	88.8					
Brevundimonas diminuta ATCC 11568^T	89.4	89.8	90.2	91.0	90.2	89.8	89.0	89.6	91.2	88.8	89.2	89.2	88.1				
Paracoccus denitrificans LMG 4218^T	88.8	92.2	92.2	92.5	90.5	91.9	91.3	90.2	89.9	89.7	89.2	88.3	87.3	88.9			
Acetobacter aceti NCIMB 8621^T	87.5	87.4	88.6	88.0	88.0	88.0	87.5	87.5	88.5	88.1	87.6	86.3	87.9	87.4	85.9		
Rickettsia prowazekii Breinl	87.5	86.9	87.6	86.9	86.1	87.1	86.1	86.8	84.7	87.3	85.8	86.1	86.7	85.0	86.3	84.1	
Escherichia coli[a]	84.0	84.0	84.3	84.2	83.9	84.4	82.8	83.7	83.5	84.5	82.0	83.5	84.4	83.9	82.5	84.2	81.3

[a] Strain not known.

and 3-OH 26:1 as major components have been described. A sodium deoxycholate-polyacrylamide gel electrophoresis analysis revealed the S-type character (data not shown).

Phylogenetic position. Our sequencing experiments generated a continuous stretch of sequence from position 29 to position 1524. The phylogenetic tree constructed by using the neighbor-joining method and K_{nuc} values shows that IFO 13584^T is phylogenetically related to members of the α subclass of the *Proteobacteria* (Fig. 3). De Vos et al. (4) and Segers et al. (24) reported that "*P. riboflavina*" ATCC 9526^T (= IFO 13584^T) was a member of the α subclass as determined by DNA-rRNA hybridization, but its precise position in the α subclass was not known. The results of a phylogenetic analysis based on 16S rRNA sequence data showed that IFO 13584^T occupies a distinct position in the α subclass (Fig. 3). The phylogenetic independence of this organism was also reflected by the signature sequences (Table 4). The phylogenetic neighbors of strain IFO 13584^T are members of the *Rhizobiaceae*, with which it exhibited 16S rRNA similarity values ranging from 91.9 to 93.1% (Table 5). The levels of 16S rRNA similarity between IFO 13584^T and *Azorhizobium caulinodans*, *Rhodomicrobium vannielli*, and *Methylobacterium organophilum* are 91.6, 91.2, and 90.5%, respectively. We do not know to which group in the α subclass strain IFO 13584^T belongs. IFO 13584^T branched off after the *Azospirillum-Magnetospirillum* cluster (cluster α-1), the *Erythrobacter-Sphingomonas* cluster (cluster α-4), and the *Brevundimonas-Caulobacter* cluster (cluster α-2) and before the *Rhizobiaceae* cluster (cluster α-2) and the *Paracoccus-Roseobacter* cluster (cluster α-3). The bootstrap analysis resulted in relatively low levels of confidence (34.3 to 71.8%) for the separation of clusters α-2, α-3, and α-4, so the branching order in this region is not definite. The genus *Legionella*, which comprises bacteria that are known to contain long-chain 3-OH cellular fatty acids (11), was included in the γ subclass of the *Proteobacteria* (8).

"*P. riboflavina*" IFO 13584^T is phylogenetically independent. This organism can be differentiated from other members of the α subclass of the *Proteobacteria* on the basis of many taxonomic characteristics (Table 2) and 16S rRNA sequence signatures (Table 4). Above all, the absence of 3-OH fatty acids which are shorter than 3-OH 18:0 and the presence of 3-OH 24:1 and 3-OH 26:1 in cells as the major 3-OH fatty acids are the key characteristics used for discrimination. On the basis of the findings described above, we propose that "*P. riboflavina*" IFO 13584^T should be placed in the new genus *Devosia*. Descriptions of the new genus and species are given below. Unfortunately, only one strain is available. Other strains belonging to the genus should be isolated and investigated in the future.

Description of *Devosia* gen. nov. *Devosia* (De.vos′i.a. M.L. dim. ending *-ia*; M.L. fem. n. *Devosia*, honoring Paul De Vos, a Belgian microbiologist, for his basic contributions to the taxonomy of pseudomonads). Cells are rod shaped, 0.4 to 0.8 μm wide, and 2.0 to 8.0 μm long. Motile by means of several polar flagella. Endospores are not formed. Gram negative. Obligately aerobic. Oxidase and catalase positive.

The major respiratory quinone is ubiquinone 10. The major cellular hydroxy fatty acids are 3-OH 24:1 and 3-OH 26:1. 3-OH fatty acids which are shorter than 3-OH 18:0 are absent. The G+C content of the DNA of the type strain of the type species is 61.4 mol% (as determined by HPLC). Phylogenetically related to members of the α subclass of the *Proteobacteria.*

The type species is *Devosia riboflavina.*

Description of *Devosia riboflavina* sp. nov., nom. rev. *Devosia riboflavina* (ri.bo.fla′vi.na. M. L. fem. adj. *riboflavina*, oxidating

riboflavin). The description of *D. riboflavina* below is based on the original description of Foster (7) and our data. Gram-negative, non-spore-forming rods that are 0.4 to 0.8 by 2.0 to 8.0 μm. Motile cells have several polar flagella. Colonies are circular with entire or slightly undulate margins and cream colored. Obligately aerobic. Oxidase, catalase, and urease positive. Riboflavin is oxidized to lumichrome. Organic nitrogenous substances, such as amino acids, are required for growth. Glycine, urea, and NH_4Cl cannot be substituted for organic material as nitrogen sources in media containing riboflavin as the sole energy source. Acid is produced from D-arabinose. Acid and gas are not produced from D-galactose, D-glucose, inositol, lactose, D-fructose, maltose, mannitol, sucrose, D-xylose, and ethanol. Esculin is hydrolyzed. Gelatin and starch are not hydrolyzed. Nitrate is slightly reduced to nitrite. Indole is not produced. Vigorous growth occurs on nutrient agar at 28°C. As determined by API 20 NE tests, the following substrates are assimilated by the type strain: L-arabinose, glucose, maltose, D-mannitol, D-mannose, and *N*-acetyl-D-glucosamine. The following substrates are not assimilated by the type strain as determined by API 20 NE tests: adipic acid, *n*-capric acid, DL-malic acid, phenyl acetate, potassium gluconate, and sodium citrate. β-Galactosidase and β-glucosidase activities are present in the type strain, as determined by API 20 NE tests. Arginine dehydrolase activity is not present in the type strain, as determined by a API 20 NE test.

The major respiratory quinone is ubiquinone 10. The major cellular fatty acids are 18:1 (nonpolar acid) and 3-OH 24:1 and 3-OH 26:1 (hydroxy acids). No 2-OH hydroxy acid is present. The G+C content of the DNA of the type strain is 61.4 mol%, as determined by HPLC.

The type strain is strain IFO 13584 (= ATCC 9526).

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