Characteristics of Newly Isolated *Xanthobacter* Strains and Fatty Acid Compositions and Quinone Systems in Yellow-Pigmented Hydrogen-Oxidizing Bacteria

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Newly isolated *Xanthobacter* strains were characterized. In addition, the fatty acid compositions and quinone systems of gram-negative, yellow-pigmented, hydrogen-oxidizing bacteria belonging to the genera *Xanthobacter*, *Hydrogenophaga*, and *Variovorax* and related species were studied. *Xanthobacter* strains are nitrogen-fixing organisms that have a Q-10 ubiquinone system; the cellular fatty acids of these organisms include high levels of C_{18:1} acid, and their hydroxy fatty acids include high levels of 3-OH C_{16:0} acid. *Hydrogenophaga* strains are polarly flagellated organisms that have a Q-8 ubiquinone system. These bacteria can be divided into two groups on the basis of cellular fatty acid and hydroxy fatty acid compositions. *Variovorax* strains are peritrichously flagellated, non-nitrogen-fixing organisms that have a Q-8 ubiquinone system; the cellular fatty acids of these strains include high levels of C_{16:0}, C_{16:1} and C_{18:1} acids, and their hydroxy fatty acids include 3-OH C_{10:0} and 2-OH C_{14:0} acids. *Xanthobacter*, *Hydrogenophaga*, and *Variovorax* strains can be clearly distinguished from each other on the basis of their quinone systems and cellular fatty acid compositions.

Previously (28–31), we described a group of gram-negative methanol-utilizing bacteria on the basis of their morphological characteristics, utilization of carbon compounds, DNA base compositions, DNA-DNA hybridization data, cellular fatty acid compositions, ubiquinone systems, and enzyme electrophoretic properties. The group 5 bacteria that we described (29, 30) are nitrogen-fixing, hydrogen-oxidizing, non-spore-forming, gram-negative, rod-shaped, yellow-pigmented organisms that have a Q-10 ubiquinone system and cellular fatty acids that include high levels of C_{18:1}. *Xanthobacter* strains (22, 35, 38) are included in this group.

Corynebacterium autotrophicum (6) and “*Mycobacterium flavum*” (= “*Microbacterium flavum*”) (14, 23) were transferred to the new genus *Xanthobacter* as *Xanthobacter autotrophicus*

and *Xanthobacter flavus* by Wiegel et al. (38) and Malik and Claus (22), respectively. In 1987, *Xanthobacter agilis* (18) was described as a third *Xanthobacter* species, and this species could be clearly distinguished from the two other *Xanthobacter* species on the basis of pleomorphism, motility, and colony color (2). *X. autotrophicus* DSM 432^T (T = type strain), DSM 431, DSM 685, DSM 1393 (= JCM 7861), DSM 1618 (= JCM 7862), DSM 2009 (= JCM 7863), and DSM 597 (= JCM 7864), *X. flavus* NCIB 1007^T (= DSM 338^T), and all of our isolates (strains BY-1, BY-3 to BY-11, and BY-15) were gram-negative, non-spore-forming, rod-shaped, methanol-utilizing organisms whose cells were 0.5 to 0.9 by 1.0 to 3.0 μm and had rounded ends. Nonmucoid yellow colonies were produced on PYG medium, nutrient medium, or methanol-containing me-

TABLE 1. Quinone compositions of yellow colony-forming bacteria

Strain	% of total quinones													
	Ubiquinone homologs				Menaquinone homologs									
					MK-6		MK-7		MK-8		MK-9		MK-10	
	Q-7	Q-8	Q-9	Q-10	H ₀	H ₂	H ₀	H ₂	H ₀	H ₂	H ₀	H ₂	H ₀	H ₂
<i>Corynebacterium flavescens</i> NCIB 8707 ^T					1.6	0.9	9.3	11.3	14.7	58.4	0.4	3.5		
“ <i>Mycobacterium flavum</i> subsp. <i>methanicum</i> ” NCIB 9738							1.0	0.2	2.3	9.8	0.3	86.4		0.1
“ <i>Mycobacterium flavum</i> subsp. <i>methanicum</i> ” NCIB 9742							0.8		2.3	10.4		86.5		
<i>Hydrogenophaga flava</i> DSM 619 ^T	0.3	84.2	15.4	0.1										
<i>Hydrogenophaga pseudoflava</i> DSM 1034 ^T	1.3	94.2	4.5											
<i>Hydrogenophaga palleronii</i> DSM 63 ^T	1.4	96.6	1.9	0.1										
<i>Variovorax paradoxus</i> DSM 30034 ^T	0.9	97.9	1.2											

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TABLE 2. Cellular fatty acid compositions of yellow colony-forming bacteria

Strain	% of:												
	Straight-chain acids								Cyclo-propane acids		10-Methyl acids		3-Hydroxy acids
	C _{14:0}	C _{15:0}	C _{16:0}	C _{16:1}	C _{17:0}	C _{18:0}	C _{18:1}	C _{19:0}	C _{17:0}	C _{19:0}	t-C _{17:0}	t-C _{19:0}	2-OH C _{14:0}
<i>Corynebacterium flavescens</i> NCIB 8707 ^T			9.0	0.9		7.4	74.4				0.3	8.0	
" <i>Mycobacterium flavum</i> subsp. <i>methanicum</i> " NCIB 9738	0.1	7.2	25.5	6.7	0.7	4.5	45.3	0.2	0.5	2.8	2.9	3.6	
" <i>Mycobacterium flavum</i> subsp. <i>methanicum</i> " NCIB 9742	0.1	8.1	26.7	7.7	0.7	6.0	42.0	0.2		3.5	1.9	3.1	
<i>Hydrogenophaga flava</i> DSM 619 ^T	3.3	0.8	32.4	56.6	0.3	0.3	2.8		0.5				3.0
<i>Hydrogenophaga pseudoflava</i> DSM 1034 ^T	2.2	0.5	32.2	52.7	0.4	0.4	10.4		0.3				1.2
<i>Hydrogenophaga palleronii</i> DSM 63 ^T	0.2	0.1	31.5	45.2	1.0	0.2	21.4						0.1 0.2
<i>Variovorax paradoxus</i> DSM 30034 ^T	0.3	0.9	33.9	34.3	1.1	0.4	17.2		3.9				5.3

dia. The cells occurred singly or rarely in pairs and were non-motile. The organisms grew abundantly in nutrient broth and PYG broth. No water-soluble fluorescent pigment was produced on King B medium. Granules of poly-β-hydroxybutyric acid accumulated in the cells. The methyl red and the Voges-Proskauer tests in glucose phosphate broth were negative. Indole and hydrogen sulfide were not produced. Hydrolysis of gelatin and starch was not observed. Ammonia was produced. Denitrification was negative. Litmus milk was not changed. All of the strains utilized glycerol, succinic acid, citric acid, acetic acid, propionic acid, ethanol, *N,N*-dimethylformamide, and hydrogen, but did not grow at the expense of L-arabinose, galactose, maltose, lactose, trehalose, D-glucitol, D-mannitol, inositol, soluble starch, cellobiose, L-histidine, L-phenylalanine, tetramethylammonium hydroxide, or methane. All strains except *X. autotrophicus* DSM 431 utilized methanol; all strains except *X. autotrophicus* DSM 431 and DSM 597 utilized D-glucose; and all strains except *X. autotrophicus* DSM 431, DSM 1618, and DSM 2009 utilized malonic acid. Utilization of D-xylose, D-mannose, D-fructose, sucrose, D-ribose, monomethylamine, dimethylamine, and trimethylamine varied among the strains. None of the strains produced acid oxidatively from L-arabinose, D-xylose, D-glucose, D-mannose, galactose, maltose, lactose, trehalose, D-glucitol, D-mannitol, inositol, glycerol, and soluble starch. *X. autotrophicus* DSM 432^T, DSM 431, and DSM 685 produced acid weakly from D-fructose, and *X. autotrophicus* DSM 1393, DSM 1618, and DSM 2009 produced acid weakly from D-fructose and sucrose. However, other strains did not produce acid from D-fructose and sucrose. Acids were not produced fermentatively. *Xanthobacter* strains and

our isolates did not require amino acids for growth. The requirement for vitamins varied among strains. *X. autotrophicus* DSM 432^T, DSM 431, DSM 685, DSM 1393, DSM 1618, and DSM 2009 did not require vitamins for growth, but *X. flavus* NCIB 10071^T, *X. autotrophicus* DSM 597, and all of our isolates had an absolute requirement for biotin. On the basis of these physiological characteristics, all of our isolates were identified as *X. flavus* strains, and strain DSM 597 was reidentified as a member of *X. flavus*.

The yellow-pigmented bacteria *Corynebacterium flavescens* (= *Microbacterium flavum*) (5, 8, 14) and "*Mycobacterium flavum* subsp. *methanicum*" (20) were confused with *X. flavus* (= "*Mycobacterium flavum*" 301^T [= NCIB 1007^T]) until *X. flavus* and *C. flavescens* were described by Malik and Claus (22) and Barksdale et al. (5), respectively. *C. flavescens* (5) and "*Mycobacterium flavum* subsp. *methanicum*" strains are gram-positive bacteria and do not utilize hydrogen, methanol, monomethylamine, dimethylamine, trimethylamine, tetramethylammonium hydroxide, and *N,N*-dimethylformamide. Furthermore, these organisms have different menaquinone systems, as shown in Table 1. *C. flavescens* contains mycolic acid and a high level of C_{18:1} acid, whereas "*Mycobacterium flavum* subsp. *methanicum*" strains contain mycolic acid, a high level of C_{18:1} acid, and a relatively high level of C_{16:0} acid, as shown in Tables 2 and 3. Hydroxy fatty acids have not been detected in these strains.

The yellow-pigmented hydrogen-oxidizing bacteria (2) *Pseudomonas flava*, *Pseudomonas pseudoflava*, *Pseudomonas palleronii*, and *Pseudomonas taeniospiralis* were placed in the new genus *Hydrogenophaga* as *Hydrogenophaga flava*, *Hydro-*

TABLE 3. Hydroxy fatty acid compositions presence and carotenoid pigments of yellow colony-forming bacteria and the presence of mycolic acids in these bacteria

Strain	3-Hydroxy acid composition (%)			2-Hydroxy acid composition (% of 2-OH C _{14:0})	Presence of mycolic acids	Carotenoid pigment absorption maximum (nm)
	3-OH C _{10:0}	3-OH C _{15:0}	3-OH C _{16:0}			
<i>Corynebacterium flavescens</i> NCIB 8707 ^T					+	450
" <i>Mycobacterium flavum</i> subsp. <i>methanicum</i> " NCIB 9738					+	450
" <i>Mycobacterium flavum</i> subsp. <i>methanicum</i> " NCIB 9742					+	450
<i>Hydrogenophaga flava</i> DSM 619 ^T	100				—	450
<i>Hydrogenophaga pseudoflava</i> DSM 1034 ^T	100				—	450
<i>Hydrogenophaga palleronii</i> DSM 63 ^T		20.7	79.3		—	450
<i>Variovorax paradoxus</i> DSM 30034 ^T	100			100	—	420

TABLE 5. Characteristics which differentiate the genus *Xanthobacter* from related genera

Genus	Typical species	Color of colonies	Motility or position of flagella	Utilization of:		Quinone system	Major cellular fatty acid(s)	Major 3-hydroxy acid(s)	Major 2-hydroxy acid	Carotenoid pigment absorption maximum (nm)	G+C content (mol%) ^a	rRNA group ^b	16 rRNA sequence ^c
				H ₂	CH ₃ OH								
<i>Xanthobacter</i>	<i>Xanthobacter autotrophicus</i>	Yellow	— (+)	+	+	Q-10	C _{18:1}	C _{16:0}	ND ^d	450	66–69		
<i>Paracoccus</i>	<i>Paracoccus denitrificans</i> ^e	Colorless	—	+	+	Q-10	C _{18:1}	C _{10:0} (C _{14:0})	ND	ND	65–68	IV-3	α-3
<i>Spingomonas</i>	<i>Spingomonas paucimobilis</i> ^f	Yellow	Polar	—	—	Q-10	C _{18:1}	ND	C _{14:0}	450	64–66		
<i>Hydrogenophaga</i>	<i>Hydrogenophaga flava</i>	Yellow	Polar	+	—	Q-8	C _{16:1}	C _{10:0}	ND	450	66–69	III-1	
<i>Variovorax</i>	<i>Variovorax paradoxus</i>	Yellow	Peritrichous	+	—	Q-8	C _{16:0}	C _{14:0}	C _{14:0}	420	66–68	III-1	
<i>Alcaligenes</i>	<i>Alcaligenes faecalis</i> ^g	Colorless	Peritrichous	+	—	Q-8	C _{16:0}	C _{16:1}	C _{14:0}	ND	56–58	III-3	β-2
<i>Hydrogenobacter</i>	<i>Hydrogenobacter thermophilus</i> ^h	Colorless	—	+	—	Q-8	C _{18:0}	C _{20:1}	ND	ND	43–44		
<i>Comamonas</i>	<i>Comamonas acidovorans</i> ⁱ	Colorless	Polar	—	—	Q-8	C _{16:0}	C _{16:1}	C _{10:0}	ND	66–67	III-1	β-1
<i>Acidovorax</i>	<i>Acidovorax avenae</i> ^j	Colorless	Polar	—	—	Q-8	C _{16:0}	C _{16:1} (C _{18:1})	ND	ND	70–71	III-1	β-2
<i>Burkholderia</i>	<i>Burkholderia cepacia</i> ^k	Colorless	Polar	—	—	Q-8	C _{16:0}	C _{16:1}	C _{14:0} (C _{16:0})	ND	67–68	III-2	

^a Data from references 4, 5, 8, 9, 11, 31, and 39.^b Data from references 10 through 13, 21, 39, and 41.^c Data from reference 42.^d ND, not detected.^e Data from reference 32.^f Data from references 17, 26, 34, and 43.^g Data from references 1 and 21.^h Data from reference 19.ⁱ Data from reference 25.^j Data from reference 27.

Minimal characteristics for differentiating the genus *Xanthobacter* from related genera are shown in Table 5.

REFERENCES

- Akagawa, M., and K. Yamasato. 1989. Synonymy of *Alcaligenes aquamarinus*, *Alcaligenes faecalis* subsp. *homari*, and *Deleya aesta*: *Deleya aquamarina* comb. nov. as the type species of the genus *Deleya*. Int. J. Syst. Bacteriol. 39:462–466.
- Aragno, M., and H. G. Schlegel. 1991. The mesophilic, hydrogen-oxidizing (knallgas) bacteria, p. 344–384. In A. Balows, H. G. Truper, M. Dworkin, W. Harder, and K. H. Schleifer (ed.), The prokaryotes. A handbook on biology of bacteria, 2nd ed., vol. 1. Springer Verlag, New York.
- Auling, G., M. Dittbrenner, M. Maarzahl, T. Nokhal, and M. Reh. 1980. Deoxyribonucleic acid relationships among hydrogen-oxidizing strains of the genera *Pseudomonas*, *Alcaligenes*, and *Paracoccus*. Int. J. Syst. Bacteriol. 30:123–128.
- Auling, G., M. Reh, C. M. Lee, and H. G. Schlegel. 1978. *Pseudomonas pseudoflava*, a new species of hydrogen-oxidizing bacteria: its differentiation from *Pseudomonas flava* and other yellow-pigmented, gram-negative, hydrogen-oxidizing species. Int. J. Syst. Bacteriol. 28:82–95.
- Barksdale, L., M.-A. Lancelle, M. C. Pollice, J. Asselineau, M. Welby, and M. W. Norgard. 1979. Biological and chemical basis for the reclassification of *Microbacterium flavum* Orla-Jensen as *Corynebacterium flavescens* nom. nov. Int. J. Syst. Bacteriol. 29:222–233.
- Baumgarten, J., M. Reh, and H. G. Schlegel. 1974. Taxonomic studies on some gram-positive coryneform hydrogen bacteria. Arch. Microbiol. 100:207–217.
- Biswas, C. J., and O. W. Thiele. 1983. Ubiquinones (coenzyme Q) in hydrogen-oxidizing bacteria. Syst. Appl. Microbiol. 4:181–183.
- Collins-Thompson, D. L., T. Sorhaug, L. D. Witter, and Z. J. Ordal. 1972. Taxonomic consideration of *Microbacterium lacticum*, *Microbacterium flavum*, and *Microbacterium thermosphactum*. Int. J. Syst. Bacteriol. 22:65–72.
- Davis, D. H., R. Y. Stainer, and M. Doudoroff. 1970. Taxonomic studies on some gram negative polarly flagellated "hydrogen bacteria" and related species. Arch. Mikrobiol. 70:1–13.
- De Ley, J., P. Segers, K. Kersters, W. Mannheim, and A. Lievens. 1986. Intra- and intergeneric similarities of the *Bordetella* ribosomal ribonucleic acid cistrons: proposal for a new family, *Alcaligenaceae*. Int. J. Syst. Bacteriol. 36:405–414.
- De Vos, P., and J. De Ley. 1983. Intra- and intergeneric similarities of *Pseudomonas* and *Xanthomonas* ribosomal ribonucleic acid cistrons. Int. J. Syst. Bacteriol. 33:487–509.
- De Vos, P., K. Kersters, E. Falsen, B. Pot, M. Gillis, P. Segers, and J. De Ley. 1985. *Comamonas* Davis and Park 1962 gen. nov., nom. rev. emend., and *Comamonas terrigena* Hugh 1962 sp. nov., nom. rev. Int. J. Syst. Bacteriol. 35:443–453.
- De Vos, P., A. Van Landschoot, P. Segers, R. Tytgat, M. Gillis, M. Bauwens, R. Rossau, M. Goor, B. Pot, K. Kersters, P. Lizzaraga, and J. De Ley. 1989. Genotypic relationships and taxonomic localization of unclassified *Pseudomonas* and *Pseudomonas*-like strains by deoxyribonucleic acid-ribosomal ribonucleic acid hybridizations. Int. J. Syst. Bacteriol. 39:35–49.
- Doetsch, R. N., and M. J. Pelczar, Jr. 1948. The microbacteria. I. Morphological and physiological characteristics. J. Bacteriol. 56:37–49.
- Hertzberg, S., G. Borch, and S. Liaaen-Jensen. 1976. Bacterial carotenoids. L. Absolute configuration of zeaxanthin dirhamnoside. Arch. Microbiol. 110:95–99.
- Hollander, R., and G. Vobis. 1979. The association of *Mycobacterium flavum* 301 with gram-negative bacteria: ultrastructural and biochemical evidence. Antonie van Leeuwenhoek J. Microbiol. Serol. 45:605–611.
- Holmes, B., R. J. Owen, A. Evans, H. Malnick, and W. R. Willcox. 1977. *Pseudomonas paucimobilis*, a new species isolated from human clinical specimens, the hospital environment, and other sources. Int. J. Syst. Bacteriol. 27:133–146.
- Jenni, B., and M. Aragno. 1987. *Xanthobacter agilis* sp. nov., a motile, dinitrogen-fixing, hydrogen-oxidizing bacterium. Syst. Appl. Microbiol. 9:254–257.
- Kawasumi, T., Y. Igarashi, T. Kodama, and Y. Minoda. 1984. *Hydrogenobacter thermophilus* gen. nov., an extremely thermophilic, aerobic, hydrogen-oxidizing bacterium. Int. J. Syst. Bacteriol. 34:5–10.
- Kersten, D. K. 1964. Behavior of hydrocarbon-oxidizing mycobacteria toward various carbon sources. Mikrobiologiya 33:31–37.
- Kersters, K., and J. De Ley. 1984. Genus *Alcaligenes* Castellani and Chalmers 1919, 936^{AL}, p. 361–373. In N. R. Krieg and J. G. Holt (ed.), Bergey's manual of systematic bacteriology, vol. 1. The Williams & Wilkins Co., Baltimore.
- Malik, K. A., and D. Claus. 1979. *Xanthobacter flavus*, a new species of nitrogen-fixing hydrogen bacteria. Int. J. Syst. Bacteriol. 29:283–287.
- Orla-Jensen, S. 1919. The lactic acid bacteria. Host, Copenhagen.
- Reding, H. K., G. L. M. Croes, L. Dijkhuizen, and J. Wiegand. 1992. Emendation of *Xanthobacter flavus* as a motile species. Int. J. Syst. Bacteriol. 42:309–311.

25. Tamaoka, J., D. Ha, and K. Komagata. 1987. Reclassification of *Pseudomonas acidovorans* den Dooren de Jong 1926 and *Pseudomonas testosteroni* Marcus and Talalay 1959 as *Comamonas acidovorans* comb. nov. and *Comamonas testosteroni* comb. nov., with an emended description of the genus *Comamonas*. Int. J. Syst. Bacteriol. 37:52–59.
26. Urakami, T., H. Araki, H. Oyanagi, K. Suzuki, and K. Komagata. 1992. Transfer of *Pseudomonas aminovorans* (den Dooren de Jong 1926) to *Aminobacter* gen. nov. as *Aminobacter aganoensis* sp. nov. and *Aminobacter nigataensis* sp. nov. Int. J. Syst. Bacteriol. 42:84–92.
27. Urakami, T., C. Ito-Yoshida, H. Araki, T. Kijima, K. Suzuki, and K. Komagata. 1994. Transfer of *Pseudomonas plantarii* and *Pseudomonas glumae* to *Burkholderia* as *Burkholderia* spp. and description of *Burkholderia vandii* sp. nov. Int. J. Syst. Bacteriol. 44:235–245.
28. Urakami, T., and K. Komagata. 1981. Electrophoretic comparison of enzymes in gram negative methanol-utilizing bacteria. J. Gen. Appl. Microbiol. 27:381–403.
29. Urakami, T., and K. Komagata. 1986. Occurrence of isoprenoid compounds in gram-negative methanol-, methane-, and methylamine-utilizing bacteria. J. Gen. Appl. Microbiol. 32:317–341.
30. Urakami, T., and K. Komagata. 1987. Cellular fatty acid composition with special reference to the existence of hydroxy fatty acids in gram-negative methanol-, methane-, and methylamine-utilizing bacteria. J. Gen. Appl. Microbiol. 33:135–165.
31. Urakami, T., J. Tamaoka, and K. Komagata. 1985. DNA base composition and DNA-DNA homologies of methanol-utilizing bacteria. J. Gen. Appl. Microbiol. 31:243–253.
32. Urakami, T., J. Tamaoka, K. Suzuki, and K. Komagata. 1989. *Paracoccus alcaliphilus* sp. nov., an alkaliphilic and facultatively methylotrophic bacterium. Int. J. Syst. Bacteriol. 39:116–121.
33. Walther-Mauruschat, A., M. Aragno, F. Mayer, and H. G. Schlegel. 1977. Micromorphology of gram-negative hydrogen bacteria. II. Cell envelope, membranes, and cytoplasmic inclusions. Arch. Microbiol. 114:101–110.
34. Weeks, O. B. 1974. Genus *Flavobacterium* Bergey et al. 1923, 97, p. 357–364. In R. E. Buchanan and N. E. Gibbons (ed.), Bergey's manual of determinative bacteriology, 8th ed. The Williams & Wilkins Co., Baltimore.
35. Wiegel, J. 1991. The genus *Xanthobacter*, p. 2365–2383. In A. Balows, H. G. Truper, M. Dworkin, W. Harder, and K. H. Scheifer (ed.), The prokaryotes. A handbook on biology of bacteria, 2nd ed., vol. 3. Springer Verlag, New York.
36. Wiegel, J., and F. Mayer. 1978. Isolation of lipopolysaccharides and the effect of polymyxin B on the outer membrane of *Corynebacterium autotrophicum*. Arch. Microbiol. 118:67–69.
37. Wiegel, J., and H. S. Schlegel. 1984. Genus *Xanthobacter* Wiegel, Wilke, Baumgarten, Opitz and Schlegel 1978, 573^{AL}, p. 325–333. In N. R. Krieg and J. G. Holt (ed.), Bergey's manual of systematic bacteriology, vol. 1. The Williams & Wilkins Co., Baltimore.
38. Wiegel, J., D. Wilke, J. Baumgarten, R. Opitz, and H. S. Schlegel. 1978. Transfer of the nitrogen-fixing hydrogen bacterium *Corynebacterium autotrophicum* Baumgarten et al. to *Xanthobacter* gen. nov. Int. J. Syst. Bacteriol. 28:573–581.
39. Willems, A., J. Busse, M. Goor, B. Pot, E. Falsen, E. Jantzen, B. Hoste, M. Gillis, K. Kersters, G. Auling, and J. De Ley. 1989. *Hydrogenophaga*, a new genus of hydrogen-oxidizing bacteria that includes *Hydrogenophaga flava* comb. nov. (formerly *Pseudomonas flava*), *Hydrogenophaga palleronii* (formerly *Pseudomonas palleronii*), *Hydrogenophaga pseudoflava* (formerly *Pseudomonas pseudoflava* and “*Pseudomonas carboxydoflava*”), and *Hydrogenophaga taeniospiralis* (formerly *Pseudomonas taeniospiralis*). Int. J. Syst. Bacteriol. 39:319–333.
40. Willems, A., J. De Ley, M. Gillis, and K. Kersters. 1991. *Comamonadaceae*, a new family encompassing the acidovorans rRNA complex, including *Variovorax paradoxus* gen. nov., comb. nov., for *Alcaligenes paradoxus* (Davis 1969). Int. J. Syst. Bacteriol. 41:445–450.
41. Willems, A., M. Goor, S. Thielemans, M. Gillis, K. Kersters, and J. De Ley. 1992. Transfer of several phytopathogenic *Pseudomonas* species to *Acidovorax* as *Acidovorax avenae* subsp. *avenae* subsp. nov., comb. nov., *Acidovorax avenae* subsp. *citrulli*, *Acidovorax avenae* subsp. *cattleyae*, and *Acidovorax konjaci*. Int. J. Syst. Bacteriol. 42:107–119.
42. Woese, C. 1987. Bacterial evolution. Microbiol. Rev. 51:221–271.
43. Yabuuchi, E., I. Yano, H. Oyaizu, Y. Hashimoto, T. Ezaki, and H. Yamamoto. 1990. Proposals of *Sphingomonas paucimobilis* gen. nov. and comb. nov., *Sphingomonas parapaucimobilis* sp. nov., *Sphingomonas yanoikuyae* sp. nov., *Sphingomonas adhaesiva* sp. nov., *Sphingomonas capsulata* comb. nov., and two genospecies of the genus *Sphingomonas*. Microbiol. Immunol. 34:99–119.