Altererythrobacter indicus sp. nov., isolated from wild rice (*Porteresia coarctata* Tateoka)

N. Ramesh Kumar,¹ Sudha Nair,¹ Stefan Langer,² Hans-Jürgen Busse² and Peter Kämpfer³

Correspondence

Peter Kämpfer
peter.kaempfer@agr.uni-giessen.de

Sudha Nair
microbiology@mssrf.res.in

¹Microbiology Department, M. S. Swaminathan Research Foundation, 3rd Cross Street, Taramani Institutional Area, Chennai – 600 113, India

²Institut für Bakteriologie, Mykologie und Hygiene, Veterinärmedizinische Universität, A-1210 Wien, Austria

³Institut für Angewandte Mikrobiologie, Justus-Liebig-Universität Giessen, D-35392 Giessen, Germany

A Gram-negative, rod-shaped, non-spore-forming organism, strain MSSRF26^T, was isolated from mangrove-associated wild rice in India. On the basis of 16S rRNA gene sequence similarities, strain MSSRF26^T was shown to belong to the *Alphaproteobacteria*, most closely related to *Altererythrobacter luteolus* and *Altererythrobacter epoxidivorans* (96.1 and 95.9% similarity to the respective type strains). Chemotaxonomic data [major ubiquinones Q-10 (91%) and Q-9 (9%); major polyamine spermidine, with putrescine, cadaverine and spermine detected only in trace amounts; major polar lipids phosphatidylethanolamine, phosphatidylglycerol, diphosphatidylglycerol and sphingoglycolipid; major fatty acid C_{18:1ω7c} and C_{14:0} 2-OH as hydroxylated fatty acid] supported the affiliation of MSSRF26^T to the genus *Altererythrobacter*. Fatty acid data and physiological and biochemical tests allowed phenotypic differentiation of the isolate from described *Altererythrobacter* species. Strain MSSRF26^T therefore represents a novel species, for which the name *Altererythrobacter indicus* sp. nov. is proposed, with the type strain MSSRF26^T (=LMG 23789^T =DSM 18604^T).

The genus *Altererythrobacter* was proposed by Kwon *et al.* (2007) to accommodate the two species *Altererythrobacter epoxidivorans* and *A. luteolus*. *A. luteolus* was originally described as *Erythrobacter luteolus* (Yoon *et al.*, 2005b), but Kwon *et al.* (2007) showed that this species required separate generic status on the basis of both genotypic and phenotypic properties. The family *Erythrobacteraceae* (Lee *et al.*, 2005) now contains four genera, *Altererythrobacter*, *Erythrobacter*, *Erythromicrobium* and *Porphyrobacter*. All members of this family show an aerobic and chemo-organotrophic metabolism and some of them contain bacteriochlorophyll (BChl) *a* and carotenoids. However, certain species do not contain BChl *a*, such as *A. luteolus*, *A. epoxidivorans*, *Erythrobacter citreus* and *Erythrobacter flavus* (Denner *et al.*, 2002; Yoon *et al.*, 2003, 2005a, b; Lee *et al.*, 2005; Kwon *et al.*, 2007). Within the family, all members of the genus *Erythrobacter* were isolated from seawater environments, whereas *Erythromicrobium* species were isolated from freshwater environments and members of the genus *Porphyrobacter* from various aquatic

environments (Hiraishi *et al.*, 2002; Yoon *et al.*, 2004; Hiraishi & Imhoff, 2005; Shiba & Imhoff, 2005; Yurkov, 2005b).

Strain MSSRF26^T was isolated from mangrove-associated wild rice (*Porteresia coarctata* Tateoka) (Kumar & Nair, 2007). The rhizosphere soil samples were obtained by shaking the roots gently to remove loosely attached soil, and the adhering soil was rinsed in 10 ml sterile distilled water. The resulting rinse solution containing the rhizosphere bacteria was serially diluted and plated onto half-strength tryptone soy agar (TSA; HiMedia) supplemented with 2% NaCl and incubated at 28 °C.

The strain showed yellow-coloured colonies on nutrient agar (Oxoid) at 25–30 °C. Subcultivation was done on TSA at 28 °C for 48 h. Gram-staining was performed as described by Gerhardt *et al.* (1994). Cell morphology was observed under a Zeiss light microscope at ×1000, with cells grown for 3 days at 28 °C on TSA.

A set of physiological characteristics including catalase and oxidase tests, gas from glucose, nitrate reduction, utilization and acid production from various sugars, sodium citrate utilization, arginine dihydrolase, lysine decarboxylase and ornithine decarboxylase was assessed using

Abbreviation: BChl, bacteriochlorophyll.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain MSSRF26^T is DQ399262.

protocols described by Shieh *et al.* (2000). Indole production and casein and starch hydrolysis were examined using the methods of Smibert & Krieg (1994). Anaerobic growth was determined in tubes containing oxidative and fermentative test medium (OF basal medium; Difco) under mineral oil. A change in colour of the medium from yellow to orange to red was recorded as a positive reaction, and production of gas was identified by deep cracks in the medium. Results were noted after 7 days of incubation at 28 °C. Growth at different salt concentrations was monitored in tubes of tryptone soy broth (TSB; 1.7 % casein enzymic hydrolysate, 0.3 % papaic digest of soybean meal, 0.25 % dipotassium phosphate, 0.25 % glucose, pH 7.0) incubated for 7 days containing additional NaCl at concentrations ranging up to 12 %. Optimum growth was recorded at concentrations ranging from 0.5 to 2 % NaCl.

Growth at different temperatures was monitored in tubes of TSB with 2 % NaCl incubated for 7 days in water baths set at 25, 30, 37, 40, 42 and 45 °C. The presence or absence of BChl *a* was examined by registration of the *in vitro* absorption spectrum of a methanol extract of cells at 768–769 nm as described previously by Yoon *et al.* (2003). The DNA G + C content was determined by the Microbial Type

Culture Collection (MTCC), India, using the thermal denaturation method (Marmur & Doty, 1962), as already reported (Kumar & Nair, 2007).

The 16S rRNA gene was analysed as described by Kämpfer *et al.* (2003). Analysis of the sequence data was performed using the software package MEGA version 2.1 (Kumar *et al.*, 2001) after multiple alignment by CLUSTAL_X (Thompson *et al.*, 1997). The almost-complete 16S rRNA sequence of the strain was compared by sequence similarity calculations after a neighbour-joining analysis. Distances (distance options according to the Kimura-2 model) were determined and clustering with the neighbour-joining and maximum-parsimony methods was performed by using bootstrap values based on 1000 replications. The results of these calculations indicated that the closest relatives of the strain were *A. luteolus* and *A. epoxidivorans* (96.1 and 95.9 % similarity to the respective type strains). A tree is shown in Fig. 1.

Biomass for quinone, polar lipid and polyamine analyses was obtained from cells grown on PYE medium (0.3 % peptone from casein, 0.3 % yeast extract, pH 7.2). Respiratory quinones and polar lipids were determined according to Tindall (1990a, b) and Altenburger *et al.*

Fig. 1. Phylogenetic tree based on 16S rRNA gene sequences available from the EMBL database (accession numbers in parentheses) constructed after multiple alignment of data by CLUSTAL_X (Thompson *et al.*, 1997) as described in the text. Bootstrap values based on 1000 replications are listed as percentages at branching points. Bar, 0.01 substitutions per nucleotide position. Although the bootstrap values were not very high, the analysis clearly supported the allocation of strain MSSRF26^T to the genus *Altererythrobacter*.

(1996) and polyamines were analysed as described by Busse & Auling (1988) and Stolz *et al.* (2007).

Strain MSSRF26^T exhibited a quinone system consisting of ubiquinones Q-10 (91 %) and Q-9 (9 %). This trait is in accordance with the properties of its closest relatives, because *Altererythrobacter* and *Erythrobacter* species have also been reported to contain a quinone system with the predominant compound Q-10 (Denner *et al.*, 2002; Yoon *et al.*, 2003, 2004, 2005a, b; Kwon *et al.*, 2007). The polar lipid profile of strain MSSRF26^T consisted of the major compounds phosphatidylethanolamine, phosphatidylglycerol, diphosphatidylglycerol and sphingoglycolipid, moderate amounts of phosphatidyltrimethylethanolamine and phosphatidylcholine and minor amounts of phosphatidylmonomethylethanolamine, an unknown aminolipid, an unknown uncharacterized polar lipid and two unknown phospholipids (Fig. 2a). Additionally, trace amounts of three hydrophilic but not further characterized lipid spots could be detected (only lipid L2 is visible in Fig. 2a). A yellow pigment showing highly hydrophobic chromatographic behaviour was also detectable after staining for total lipids. It is worth mentioning here that, when biomass was grown on PYE medium supplemented with 3.0 % salts used for seawater aquaria, phosphatidylmonomethylethanolamine and one of the unknown phospholipids were not detected in the lipid profile of MSSRF26^T. This latter pigment also stained positive with α -naphthol, indicating that it contains a sugar moiety. A similar but distinguishable polar lipid profile in terms of major components was detected in *A. epoxidivorans* JCS350^T (Fig. 2b), of which biomass was grown in PYE medium supplemented with 3.0 % salts used for seawater aquaria. Its polar lipid profile did not exhibit the presence of phosphatidyltrimethylethanolamine, phosphatidylmonomethylethanolamine, the unknown aminolipid or the two unknown phospholipids, but it contained moderate to major amounts of phosphatidylcholine, another unknown aminolipid, an unknown glycolipid and another yellow pigment (yPig2) that stained positive with α -naphthol. Hence, the polar lipid profile of *A. epoxidivorans* JCS350^T shows striking characteristics that may be useful for differentiation at the species level. The polyamine patterns of MSSRF26^T and *A. epoxidivorans* JCS350^T exhibited the predominance of spermidine [17.0 and 11.2 $\mu\text{mol (g dry weight)}^{-1}$, respectively], whereas putrescine, cadaverine and spermine were either detected in trace amounts [$<1.0 \mu\text{mol (g dry weight)}^{-1}$] or not detectable. These polyamine patterns are in accordance with the characteristics of *Erythrobacter* species (Denner *et al.*, 2002; Hamana *et al.*, 2007).

The fatty acid profile (Kämpfer & Kroppenstedt, 1996) of strain MSSRF26^T is shown in Table 1. Cells of strains MSSRF26^T and *A. luteolus* CIP 108783^T were studied comparatively after growth on marine agar (Difco) for 48 h at 28 °C. This medium was also used by Kwon *et al.* (2007) for *A. epoxidivorans* JCS350^T. The major fatty acids of all three strains were C_{18:1} ω 7c and C_{16:0}. Both *Altererythrobacter* type strains and strain MSSRF26^T

Fig. 2. Polar lipid profiles of strain MSSRF26^T (a) and *A. epoxidivorans* JCS350^T (b) after two-dimensional TLC and detection with molybdatophosphoric acid. DPG, Diphosphatidylglycerol; PG, phosphatidylglycerol; PE, phosphatidylethanolamine; PC, phosphatidylcholine; SGL, sphingoglycolipid; AL1, unknown aminolipid; PL1–2, unknown phospholipids; GL1, unknown glycolipid; L1, unknown polar lipid; yPig1–2, yellow pigments that stain positive with α -naphthol.

contained C_{14:0} 2-OH as the major hydroxylated fatty acid. The fatty acids C_{16:0} 2-OH and 11-methyl C_{18:1} ω 7c were detected in *A. luteolus* CIP 108783^T and *A. epoxidivorans* JCM350^T, but not in strain MSSRF26^T. C_{17:1} ω 8c was found in strain MSSRF26^T and in only minor amounts for *A. epoxidivorans* JCM350^T. Also, the presence of very small amounts (1.0 %) of summed feature 3 (which can be considered to represent only C_{16:1} ω 7c and not C_{15:0})

Table 1. Fatty acid patterns (%) of strain MSSRF26^T and the type strains of the two other species of *Altererythrobacter*

All strains were grown on marine agar 2216 (Difco) for 48 h at 28 °C prior to analysis. —, Not detected/not reported.

Fatty acid	MSSRF26 ^T	<i>A. luteolus</i> CIP 108783 ^T		<i>A. epoxidivorans</i> JCS350 ^T	
		This study	Yoon <i>et al.</i> (2005b)	This study	Kwon <i>et al.</i> (2007)
Saturated fatty acids					
C _{16:0}	6.8	5.7	9.0	4.5	3.1
Cyclic fatty acids					
C _{17:0} cyclo	—	—	—	—	6.9
Unsaturated fatty acids					
C _{16:1} ω5c	—	2.3	3.3	1.4	2.2
C _{17:1} ω6c	5.2	3.7	5.1	12.1	—
C _{17:1} ω8c	1.0	—	—	0.8	—
C _{18:1} ω5c	2.0	1.8	3.4	0.8	—
C _{18:1} ω7c	76.7	52.8	47.7	43.7	46.9
11-Methyl C _{18:1} ω7c	—	6.1	7.1	7.8	—
Hydroxy fatty acids					
C _{15:0} 2-OH	—	—	—	1.2	—
iso-C _{16:0} 3-OH	—	—	—	1.7	—
C _{16:0} 2-OH	—	1.6	3.6	0.7	—
C _{16:1} 2-OH	—	0.8	0.8	—	—
C _{14:0} 2-OH	7.2	2.8	3.4	7.9	—
Summed feature 3*	1.0	22.4	13.9	16.1	32.9

*Summed features are groups of two or three fatty acids that cannot be separated by GLC with the MIDI system. Summed feature 3 contained one or more of the fatty acids C_{16:1}ω7c and C_{15:0} iso 2-OH.

iso 2-OH, because no other branched fatty acids were detected, suggesting the inability to synthesize this class of fatty acids) clearly distinguished MSSRF26^T from related species (Table 1).

Results of the physiological characterization are given in the species description and in Table 2 (differential characters), determined as described previously (Kämpfer *et al.*, 1991). Sequence comparisons based on almost-entire 16S rRNA gene sequences showed a clear affiliation of the strain to the genus *Altererythrobacter*. On the basis of unique phenotypic traits, we describe a novel *Altererythrobacter* species, for which we propose the name *Altererythrobacter indicus* sp. nov.

Description of *Altererythrobacter indicus* sp. nov.

Altererythrobacter indicus (in'di.cus. L. masc. adj. *indicus* pertaining to India, where the type strain was isolated).

Cells are Gram-negative, non-motile rods. Catalase test is positive and oxidase test is negative. Colonies produced on agar media are yellow and circular with an entire margin. BChl *a* is not detected. Metabolism is strictly aerobic. The quinone system is ubiquinone Q-10, with minor amounts of Q-9. In the polar lipid profile analysed from biomass grown on PYE medium, phosphatidylethanolamine, phosphatidylglycerol, diphosphatidylglycerol and sphingoglycolipid predominate. Phosphatidyl dimethylethanolamine and

phosphatidylcholine are present in moderate amounts and phosphatidylmonomethylethanolamine, an unknown aminolipid and two unknown phospholipids can be detected in minor amounts. The polyamine pattern exhibits spermidine as the characteristic feature. The fatty acid profile is composed largely of C_{18:1}ω7c (76.7%), C_{14:0} 2-OH (7.2%), C_{16:0} (6.8%) and C_{17:1}ω6c (5.2%). Indole is not produced and nitrate is not reduced. Optimal growth occurs at 25–30 °C, at pH 7 and in complex media containing about 2% NaCl. Growth occurs between 4 and 42 °C but not at 45 °C. Growth occurs at 0–12% NaCl. Gas is not produced from glucose and amylase, caseinase, citrate utilization, arginine dihydrolase and lysine and ornithine decarboxylase tests are negative. Grows in a mineral medium containing glucose and NH₄Cl. Acid is produced from D-glucose, sucrose, L-arabinose, cellobiose (delayed) and D-xylose (delayed). Glucose, L-arabinose, maltose, sucrose, L-alanine and L-proline can be utilized as sole carbon sources. Fructose, salicin, sorbitol, mannitol, trehalose and rhamnose are not utilized as sole carbon source. Carbon source utilization (including differentiating characters for all *Altererythrobacter* species) is indicated in Table 2. The DNA G + C content of the type strain is 66.8 mol%.

The type strain is strain MSSRF26^T (=LMG 23789^T = DSM 18604^T), isolated from the rhizosphere of mangrove-associated wild rice (*Porteresia coarctata* Tateoka).

Table 2. Phenotypic characteristics that differentiate strain MSSRF26^T from the type strains of the two other species of *Altererythrobacter* and closely related members of the family *Erythrobacteraceae*

Strains/genera: 1, MSSRF26^T, 2, *A. epoxidivorans* JCS350^T; 3, *A. luteolus* SW-109^T; 4, *Porphyrobacter*; 5, *Erythromicrobium ramosum* DSM 8510^T; 6, *Erythrobacter*; 7, '*Citromicrobium bathyomarinum*' JF-1. Data were taken from Hiraishi & Imhoff (2005), Shiba & Imhoff (2005), Yoon *et al.* (2004, 2005a, b, 2006), Yurkov (2005a, b), Yurkov *et al.* (1999) and this study. +, Positive; –, negative; w, weakly positive; v, variable reaction; v (+/–), variable, with the response of the majority of species in parentheses; ND, not determined/no data available; ND (–), negative for species for which data are available, but no data available for the majority. Data for *A. epoxidivorans* JCS350^T determined in this study are given in square brackets. All taxa are catalase-positive.

Characteristic	1	2	3	4*	5	6*	7
Cell shape	Rod	Ovoid–rod	Rod	Pleomorphic	Rod, branched	Rod	Pleomorphic
Oxidase	–	+	+	v (+)	+	+	+
Motility	–	–	–	v (+)	+	v (–)	+
Presence of BChl <i>a</i>	–	–	–	+	+	v (–)	+
pH range (optimum)	(7.0)	6–8.5 (6.5)	5.5–8.0 (7.0–8.0)	>5.0	(9.5)	5.5–8.0 (7.0–8.0)	5.5–10.0 (6–8)
Temperature range (optimum) (°C)	4–42 (25–30)	20–40 (35)	4–36 (30)	10– <60	25–30 (25)	10–40 (30–35)	4–45 (20–42)
Nitrate reduction	–	–	–	–	–	v (–)	–
Urease activity	ND	–	–	ND (–)	ND	v (–)	ND
Hydrolysis of:							
Aesculin	+	– [–]	+	v (+)	ND	+	ND
Gelatin	ND	–	–	v (–)	–	v (–)	–
Starch	–	ND	w	v (+)	–	v (–)	+
Tween 80	ND	+	+	v (+)	–	+	+
H ₂ S production	ND	–	–	ND (–)	ND	ND (–)	ND
Utilization of:							
Glucose	+	– [–]	+	+	+	v (+)	w
Fructose	–	– [–]	–	v (–)	+	v (–)	–
Acetate	w	– [–]	–	v (–)	+	+	w
Citrate	–	– [–]	–	–	+	v (–)	–
Formate	ND	–	–	ND	ND	v (–)	–
Pyruvate	–	– [–]	+	v (+)	+	v (+)	–
Glutamate	–	–	+	v	+	v (–)	+
Succinate	–	–	–	v	+	v (+)	–
Malate	+	– [–]	–	v (–)	+	v (–)	–
DNA G + C content (mol%)	66.8	54.5	60.3	63.8–66.8	64.2	60–67	67.5

*Data for all species in the genus.

Acknowledgements

We thank Dr S.-J. Kim for kindly providing the type strain of *A. epoxidivorans* and the manuscript describing it prior to publication. This work was carried out with financial support from the Department of Biotechnology, Government of India.

References

- Altenburger, P., Kämpfer, P., Makristathis, A., Lubitz, W. & Busse, H.-J. (1996). Classification of bacteria isolated from a medieval wall painting. *J Biotechnol* **47**, 39–52.
- Busse, H.-J. & Auling, G. (1988). Polyamine pattern as a chemotaxonomic marker within the *Proteobacteria*. *Syst Appl Microbiol* **11**, 1–8.

- Denner, E. B. M., Vybiral, D., Kobližek, M., Kämpfer, P., Busse, H.-J. & Velimirov, B. (2002). *Erythrobacter citreus* sp. nov., a yellow-pigmented bacterium that lacks bacteriochlorophyll *a*, isolated from the western Mediterranean Sea. *Int J Syst Evol Microbiol* **52**, 1655–1661.

- Gerhardt, P., Murray, R. G. E., Wood, W. A. & Krieg, N. R. (editors) (1994). *Methods for General and Molecular Bacteriology*. Washington, DC: American Society for Microbiology.

- Hamana, K., Sato, W., Gouma, K., Yu, J., Ino, Y., Umemura, Y., Mochizuki, C., Takatsuka, K., Kigure, Y. & other authors (2007). Cellular polyamine catalogues of the five classes of the phylum *Proteobacteria*: distributions of homospermidine within the class *Alphaproteobacteria*, hydroxyputrescine within the class *Betaproteobacteria*, norspermidine within the class *Gammaproteobacteria*, and spermidine within the classes *Deltaproteobacteria* and *Epsilonproteobacteria*. *Ann Gunma Health Sci* **27**, 1–16.

- Hiraishi, A. & Imhoff, J. F. (2005). Genus VII. *Porphyrobacter* Fuerst, Hawkins, Holms, Sly, Moore and Stackebrandt 1993, 132^{VP}. In *Bergey's Manual of Systematic Bacteriology*, 2nd edn, vol. 2, part C, pp. 275–279. Edited by D. J. Brenner, N. R. Krieg, J. T. Staley & G. M. Garrity. New York: Springer.
- Hiraishi, A., Yonemitsu, Y., Matsushita, M., Shin, Y. K., Kuraishi, H. & Kawahara, K. (2002). Characterization of *Porphyrobacter sanguineus* sp. nov., an aerobic bacteriochlorophyll-containing bacterium capable of degrading biphenyl and dibenzofuran. *Arch Microbiol* **178**, 45–52.
- Kämpfer, P. & Kroppenstedt, R. M. (1996). Numerical analysis of fatty acid patterns of coryneform bacteria and related taxa. *Can J Microbiol* **42**, 989–1005.
- Kämpfer, P., Steiof, M. & Dott, W. (1991). Microbiological characterization of a fuel-oil contaminated site including numerical identification of heterotrophic water and soil bacteria. *Microb Ecol* **21**, 227–251.
- Kämpfer, P., Dreyer, U., Neef, A., Dott, W. & Busse, H.-J. (2003). *Chryseobacterium defluvii* sp. nov., isolated from wastewater. *Int J Syst Evol Microbiol* **53**, 93–97.
- Kumar, N. R. & Nair, S. (2007). *Vibrio rhizosphaerae* sp. nov., a red-pigmented bacterium that antagonizes phytopathogenic bacteria. *Int J Syst Evol Microbiol* **57**, 2241–2246.
- Kumar, S., Tamura, K., Jakobsen, I.-B. & Nei, M. (2001). MEGA2: molecular evolutionary genetics analysis software. *Bioinformatics* **17**, 1244–1245.
- Kwon, K. K., Woo, J.-H., Yang, S.-H., Kang, J.-H., Kang, S. G., Kim, S.-J., Sato, T. & Kato, C. (2007). *Altererythrobacter epoxidivorans* gen. nov., sp. nov., an epoxide hydrolase-active, mesophilic marine bacterium isolated from cold-seep sediment, and reclassification of *Erythrobacter luteolus* Yoon et al. 2005 as *Altererythrobacter luteolus* comb. nov. *Int J Syst Evol Microbiol* **57**, 2207–2211.
- Lee, K.-B., Liu, C.-T., Anzai, Y., Kim, H., Aono, T. & Oyaizu, H. (2005). The hierarchical system of the 'Alphaproteobacteria': description of *Hyphomonadaceae* fam. nov., *Xanthobacteraceae* fam. nov. and *Erythrobacteraceae* fam. nov. *Int J Syst Evol Microbiol* **55**, 1907–1919.
- Marmur, J. & Doty, P. (1962). Determination of the base composition of deoxyribonucleic acid from its thermal denaturation temperature. *J Mol Biol* **5**, 109–118.
- Shiba, T. & Imhoff, J. F. (2005). Genus IV. *Erythrobacter* Shiba and Shimidu 1982, 215^{VP}. In *Bergey's Manual of Systematic Bacteriology*, 2nd edn, vol. 2, part C, pp. 267–268. Edited by D. J. Brenner, N. R. Krieg, J. T. Staley & G. M. Garrity. New York: Springer.
- Shieh, W. Y., Chen, A.-L. & Chiu, H.-H. (2000). *Vibrio aerogenes* sp. nov., a facultatively anaerobic marine bacterium that ferments glucose with gas production. *Int J Syst Evol Microbiol* **50**, 321–329.
- Smibert, R. M. & Krieg, N. R. (1994). Phenotypic characterization. In *Methods for General and Molecular Bacteriology*, pp. 607–654. Edited by P. Gerhardt, R. G. E. Murray, W. A. Wood & N. R. Krieg. Washington, DC: American Society for Microbiology.
- Stolz, A., Busse, H.-J. & Kämpfer, P. (2007). *Pseudomonas knackmussii* sp. nov. *Int J Syst Evol Microbiol* **57**, 572–576.
- Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F. & Higgins, D. G. (1997). The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Res* **25**, 4876–4882.
- Tindall, B. J. (1990a). Lipid composition of *Halobacterium lacusprofundi*. *FEMS Microbiol Lett* **66**, 199–202.
- Tindall, B. J. (1990b). A comparative study of the lipid composition of *Halobacterium saccharovorum* from various sources. *Syst Appl Microbiol* **13**, 128–130.
- Yoon, J.-H., Kim, H., Kim, I.-G., Kang, K. H. & Park, Y.-H. (2003). *Erythrobacter flavus* sp. nov., a slight halophile from the East Sea in Korea. *Int J Syst Evol Microbiol* **53**, 1169–1174.
- Yoon, J.-H., Kang, K. H., Oh, T.-K. & Park, Y.-H. (2004). *Erythrobacter aquimaris* sp. nov., isolated from sea water of a tidal flat of the Yellow Sea in Korea. *Int J Syst Evol Microbiol* **54**, 1981–1985.
- Yoon, J.-H., Oh, T.-K. & Park, Y.-H. (2005a). *Erythrobacter seohaensis* sp. nov. and *Erythrobacter gaetbuli* sp. nov., isolated from a tidal flat of the Yellow Sea in Korea. *Int J Syst Evol Microbiol* **55**, 71–75.
- Yoon, J.-H., Kang, K. H., Yeo, S.-H. & Oh, T.-K. (2005b). *Erythrobacter luteolus* sp. nov., isolated from a tidal flat of the Yellow Sea in Korea. *Int J Syst Evol Microbiol* **55**, 1167–1170.
- Yoon, J.-H., Kang, S.-J., Lee, M.-H., Oh, H. W. & Oh, T.-K. (2006). *Porphyrobacter dokdonensis* sp. nov., isolated from sea water. *Int J Syst Evol Microbiol* **56**, 1079–1083.
- Yurkov, V. V. (2005a). Genus III. "Citromicrobium" Yurkov, Krieger, Stackebrandt and Beatty 1999, 4523. In *Bergey's Manual of Systematic Bacteriology*, 2nd edn, vol. 2, part C, pp. 263–266. Edited by D. J. Brenner, N. R. Krieg, J. T. Staley & G. M. Garrity. New York: Springer.
- Yurkov, V. V. (2005b). Genus V. *Erythromicrobium* Yurkov, Stackebrandt, Holmes, Fuerst, Hugenholtz, Golecki, Gad'on, Gorlenko, Kompantseva and Drevs 1994c, 432^{VP}. In *Bergey's Manual of Systematic Bacteriology*, 2nd edn, vol. 2, part C, pp. 268–273. Edited by D. J. Brenner, N. R. Krieg, J. T. Staley & G. M. Garrity. New York: Springer.
- Yurkov, V. V., Krieger, S., Stackebrandt, E. & Beatty, J. T. (1999). *Citromicrobium bathyomarinum*, a novel aerobic bacterium isolated from deep-sea hydrothermal vent plume waters that contains photosynthetic pigment-protein complexes. *J Bacteriol* **181**, 4517–4525.