Erythrobacter seohaensis sp. nov. and *Erythrobacter gaetbuli* sp. nov., isolated from a tidal flat of the Yellow Sea in Korea

Jung-Hoon Yoon, Tae-Kwang Oh and Yong-Ha Park

Correspondence

Jung-Hoon Yoon
jhyoon@kribb.re.kr

Korea Research Institute of Bioscience and Biotechnology (KRIIB), PO Box 115, Yusong, Taejeon, Korea

Two Gram-negative, non-spore-forming, slightly halophilic strains, SW-135^T and SW-161^T, which were isolated from a tidal flat of the Yellow Sea in Korea, were subjected to a polyphasic taxonomic study. The two isolates lacked bacteriochlorophyll *a* and contained ubiquinone-10 (Q-10) as the predominant respiratory lipoquinone and C_{18:1}ω7c and C_{17:1}ω6c as the major fatty acids. The DNA G+C contents of strains SW-135^T and SW-161^T were 62.2 and 64.5 mol%, respectively. Phylogenetic analyses based on 16S rRNA gene sequences showed that the two strains fall within the radiation of the cluster comprising *Erythrobacter* species. Strains SW-135^T and SW-161^T exhibited a 16S rRNA gene sequence similarity value of 96.9% and a mean DNA–DNA relatedness level of 12.3%. Sequence similarities between strains SW-135^T and SW-161^T and the type strains of recognized *Erythrobacter* species ranged from 96.7 to 98.5%. Levels of DNA–DNA relatedness were low enough to indicate that strains SW-135^T and SW-161^T represent members of two species separate from all recognized *Erythrobacter* species. On the basis of polyphasic taxonomic data, strains SW-135^T (=KCTC 12228^T=DSM 16221^T) and SW-161^T (=KCTC 12227^T=DSM 16225^T) were classified as two novel *Erythrobacter* species, for which the names *Erythrobacter seohaensis* sp. nov. and *Erythrobacter gaetbuli* sp. nov. are proposed, respectively.

The genus *Erythrobacter* was proposed by Shiba & Simidu (1982) and at the time of writing comprised five recognized species, *Erythrobacter longus* (Shiba & Simidu, 1982), *Erythrobacter litoralis* (Yurkov *et al.*, 1994), *Erythrobacter citreus* (Denner *et al.*, 2002), *Erythrobacter flavus* (Yoon *et al.*, 2003a) and *Erythrobacter aquimaris* (Yoon *et al.*, 2004b). Phylogenetic analysis based on 16S rRNA gene sequences revealed that the genus *Erythrobacter* belongs to the α -Proteobacteria (Anzai *et al.*, 2000; Denner *et al.*, 2002; Yoon *et al.*, 2003a). Some *Erythrobacter* species contain bacteriochlorophyll (Bchl) *a* and carotenoids (Shiba & Simidu, 1982; Yurkov *et al.*, 1994). Here we describe two slightly halophilic orange–yellow pigmented *Erythrobacter*-like strains, SW-135^T and SW-161^T, which were isolated from a tidal flat of the Yellow Sea in Korea. Tidal flat (Korean name, gaetbul) environments have recently provided several novel micro-organisms (Yi *et al.*, 2003, 2004; Yoon *et al.*, 2003b, c, 2004a). Accordingly, the aim of the

present work was to elucidate the taxonomic positions of strains SW-135^T and SW-161^T using a polyphasic taxonomic approach that combined phenotypic, genetic and chemotaxonomic analyses.

Intertidal sediment provided the source for isolation of the bacterial strains. A standard dilution plating technique was used to isolate strains SW-135^T and SW-161^T on marine agar 2216 (MA; Difco) at 30 °C. *E. longus* DSM 6997^T, *E. litoralis* DSM 8509^T and *E. citreus* DSM 14432^T were obtained from DSMZ, Germany. *E. flavus* KCCM 41642^T and *E. aquimaris* KCCM 41818^T were obtained from previous studies (Yoon *et al.*, 2003a, 2004b). Cell morphology was examined by light microscopy (Nikon E600) and transmission electron microscopy (TEM). For TEM observation, cells were negatively stained with 1% (w/v) phosphotungstic acid and, after air drying, grids were examined under a model CM-20 transmission electron microscope (Philips). Presence of flagella was examined by TEM using cells from exponentially growing cultures. Growth under anaerobic conditions was determined after incubation in a Forma anaerobic chamber on MA and MA supplemented with nitrate that had been prepared anaerobically using nitrogen gas. Growth in the absence of NaCl was investigated in trypticase soy broth without NaCl. Growth at various NaCl concentrations was investigated in

Published online ahead of print on 23 July 2004 as DOI 10.1099/ij.s.0.63233-0.

Abbreviation: Bchl, bacteriochlorophyll.

The GenBank/EMBL/DBJ accession numbers for the 16S rRNA gene sequences of strains SW-135^T and SW-161^T are AY562219 and AY562220, respectively.

marine broth 2216 (MB; Difco) or trypticase soy broth (Difco). Growth at various temperatures (4–45 °C) was measured on MA. Catalase and oxidase activities and hydrolysis of casein, starch and Tweens 20, 40, 60 and 80 were determined as described by Cowan & Steel (1965). Hydrolysis of hypoxanthine, tyrosine and xanthine was tested on MA using the substrate concentrations described by Cowan & Steel (1965). Hydrolysis of aesculin, gelatin and urea, and nitrate reduction were studied as described by Lanyi (1987) with a modification that artificial sea water was used for preparation of media. The artificial sea water contained (per litre distilled water) 23.6 g NaCl, 0.64 g KCl, 4.53 g MgCl₂·6H₂O, 5.94 g MgSO₄·7H₂O and 1.3 g CaCl₂·2H₂O (Levring, 1946). H₂S production was tested as described by Bruns *et al.* (2001). For *in vivo* pigment-absorption spectrum analysis, the strains were cultivated aerobically in the dark at 30 °C in MB, peptone/yeast extract/glucose/vitamin (PYGV) medium (Fuerst *et al.*, 1993; DSMZ medium no. 621) and *Erythromicrobium/Roseococcus* medium (Yurkov *et al.*, 1994; DSMZ medium no. 767). *E. longus* DSM 6997^T and *E. litoralis* DSM 8509^T were used as positive controls for spectrum analysis. The cultures were

washed twice by centrifugation using a MOPS buffer (0.01 M MOPS/NaOH, 0.1 M KCl, 0.001 M MgCl₂, pH 7.5) and disrupted by sonication with a Branson Sonifier 450. After removal of cell debris by centrifugation, the absorption spectrum of the supernatant was examined on a Beckman Coulter DU800 spectrophotometer. Susceptibility to antibiotics was detected on MA plates by using antibiotic discs (concentrations are given in Table 1). Acid production from carbohydrates was determined as described by Leifson (1963), and utilization of various substrates for growth was determined as described by Yurkov *et al.* (1994).

Strains SW-135^T and SW-161^T were cultivated for 3 days in MB at 30 °C to obtain the cell mass required for respiratory lipoquinone analysis and DNA extraction. Respiratory lipoquinones were analysed as described by Komagata & Suzuki (1987) using reversed-phase HPLC. Chromosomal DNA was isolated and purified according to the method described by Yoon *et al.* (1996) with the exception that ribonuclease T1 was used together with ribonuclease A. For fatty acid methyl ester (FAME) analysis,

Table 1. Differential phenotypic characteristics of *Erythrobacter* species

Taxa: 1, *E. seohaensis* sp. nov.; 2, *E. gaetbuli* sp. nov.; 3, *E. longus* (data for type strain from Shiba & Simidu, 1982; Yurkov *et al.*, 1994); 4, *E. litoralis* (Yurkov *et al.*, 1994); 5, *E. citreus* (Denner *et al.*, 2002; Vybiral *et al.*, 1999); 6, *E. flavus* (Yoon *et al.*, 2003a); 7, *E. aquimaris* (Yoon *et al.*, 2004b). +, Positive; –, negative; w+, weakly positive; ND, not determined; v, variable. Data in parentheses are for the type strain. All species are rod-shaped, positive for catalase and oxidase, susceptible to chloramphenicol (100 µg per disc; 30 µg per disc for *E. citreus*) and utilization of acetate. All species are Gram-negative, non-sporulating and resistant to polymyxin B (100 U per disc; 300 U per disc for *E. citreus*).

Characteristic	1 (n=1)	2 (n=1)	3 (n=1)	4 (n=1)	5 (n=2)	6 (n=2)	7 (n=3)
Colour of colonies	Orange–yellow	Orange–yellow	Orange	Red or orange	Yellow	Yellow	Orange
Motility	–	–	+	+	–	+	–
Presence of BChl <i>a</i>	–	–	+	+	–	–	–
Nitrate reduction	–	–	+	–	+	–	–
Hydrolysis of:							
Gelatin	–	–	+	–	ND	–	–
Starch	–	–	–	–	(–)	+	v (+)
Utilization of:							
Glucose	+	+	+	+	v (w+)	–	+
Fructose	–	–	ND	+	(–)	–	–
Citrate	–	–	–	–	v (w+)	–	–
Pyruvate	+	+	+	+	–	+	+
Glutamate	–	–	+	+	ND	–	–
Succinate	+	+	–	+	ND	–	+
Lactate	–	–	–	+	–	v (+)	–
Malate	–	+	–	–	–	–	+
Susceptibility to:							
Penicillin (20 U; 10 U for <i>E. citreus</i>)	–	–	–	–	v (–)	–	–
Streptomycin (50 µg; 10 µg for <i>E. citreus</i>)	–	–	–	–	v (–)	–	–
Optimum growth temperature (°C)	30–35	30–37	25–30	25–30	ND	30–37	30–37
DNA G+C content (mol%)	62.2	64.5	60.7	67	62.0–62.4 (62.0)	64.0–64.1 (64.0)	62.2–62.9 (62.2)

cell mass of strains SW-135^T and SW-161^T was harvested after cultivation for 5 days at 30 °C on MA. FAMES were extracted and prepared according to the standard protocol of the MIDI/Hewlett Packard Microbial Identification System (Sasser, 1990). The DNA G+C content was determined by the method of Tamaoka & Komagata (1984) with a modification that DNA was hydrolysed and the resultant nucleotides were analysed by reversed-phase HPLC. The 16S rRNA gene was amplified by PCR using two universal primers as described by Yoon *et al.* (1998). Sequencing of the amplified 16S rRNA gene and phylogenetic analysis were performed as described by Yoon *et al.* (2003a). DNA–DNA hybridization was performed fluorometrically by the method of Ezaki *et al.* (1989) using photobiotin-labelled DNA probes and microdilution wells. Hybridization was performed with five replications for each sample. From the values obtained, the highest and lowest values in each sample were excluded. DNA–DNA relatedness values are the mean of the remaining three values.

Strains SW-135^T and SW-161^T showed similar phenotypic characteristics except for the following. Maximum growth temperatures of strains SW-135^T and SW-161^T were 40 and 43 °C, respectively. Strain SW-135^T grew at 10 °C, whereas strain SW-161^T grew at 15 °C but not at 10 °C. Malate was utilized by strain SW-161^T but not by strain SW-135^T. Strain SW-135^T produced acid from sucrose but strain SW-161^T did not. Acid was produced from D-glucose and maltose by strain SW-161^T but not by strain SW-135^T. Morphological, cultural, physiological and biochemical characteristics of the two isolates are summarized in Table 1 or are given in the formal species descriptions below. Phenotypic characteristics that differentiate strains SW-135^T and SW-161^T from *Erythrobacter* species are summarized in Table 1. The predominant respiratory lipoquinone detected in strains SW-135^T and SW-161^T was ubiquinone-10 (Q-10), at peak area ratios of approximately 91–95 %. The fatty acid profiles of the two strains were characterized by high levels of unsaturated fatty acids C_{18:1}ω7c and C_{17:1}ω6c and significant amounts of straight-chain fatty acid C_{16:0} (Table 2). Hydroxy fatty acids were present, but branched fatty acids were not detected in the two strains. These fatty acid profiles were similar to those of the type strains of recognized *Erythrobacter* species, particularly *E. aquimaris* (Table 2). However, strains SW-135^T and SW-161^T differed from each other and from other recognized *Erythrobacter* species in the relative abundance of shared components (Table 2). The DNA G+C contents of strains SW-135^T and SW-161^T were 62.2 and 64.5 mol%, respectively.

The 16S rRNA gene sequences of strains SW-135^T and SW-161^T determined in this study comprised 1444 and 1441 nt, respectively, representing approximately 96 % of the *Escherichia coli* 16S rRNA gene sequence. Similarity between the 16S rRNA gene sequences of strains SW-135^T and SW-161^T was 96.9 %. Comparative 16S rRNA gene sequence analysis showed that the two strains are phylogenetically related to *Erythrobacter* species (Fig. 1).

Table 2. Percentage cellular fatty acid compositions of strains SW-135^T and SW-161^T and reference type strains of *Erythrobacter* species

Strains: 1, *E. seohaensis* sp. nov. SW-135^T; 2, *E. gaetbuli* sp. nov. SW-161^T; 3, *E. longus* DSM 6997^T (data from Yoon *et al.*, 2003a); 4, *E. litoralis* DSM 8509^T (Yoon *et al.*, 2003a); 5, *E. flavus* KCCM 41642^T (Yoon *et al.*, 2003a); 6, *E. citreus* RE35F/1^T (Denner *et al.*, 2002); 7, *E. aquimaris* KCCM 41818^T (Yoon *et al.*, 2004b). —, Not detected. Fatty acids representing less than 0.5 % in all strains were omitted.

Fatty acid	1	2	3	4	5	6	7
Straight-chain							
C _{15:0}	2.7	1.6	2.8	0.5	3.0	0.3	2.7
C _{16:0}	11.7	8.3	11.4	2.7	6.4	8.2	10.3
C _{17:0}	1.5	0.7	10.1	—	7.3	—	3.2
C _{18:0}	—	—	1.0	—	0.5	—	0.4
Branched							
Anteiso-C _{15:0}	—	—	—	—	—	0.6	—
Anteiso-C _{16:0}	—	—	—	—	—	0.7	—
Anteiso-C _{17:0}	—	—	—	—	—	1.2	—
Unsaturated							
C _{16:1} ω5c	1.9	2.2	—	0.7	—	3.6	1.3
C _{17:1} ω6c	18.5	17.8	3.9	28.5	6.2	5.6	27.6
C _{17:1} ω8c	1.7	2.2	4.8	4.3	8.1	0.7	2.5
C _{18:1} ω5c	1.1	1.5	—	2.2	—	4.2	1.5
C _{18:1} ω7c	31.7	40.0	50.9	46.9	46.2	49.3	26.8
11-Methyl-C _{18:1} ω7c	5.4	4.2	—	3.7	5.5	4.4	4.4
Hydroxy							
C _{14:0} 2-OH	6.9	6.2	5.0	2.9	0.9	0.9	3.9
C _{15:0} 2-OH	5.3	3.6	8.6	2.6	9.5	—	7.4
C _{16:0} 2-OH	2.3	1.4	1.5	1.5	1.4	—	2.2
C _{18:1} 2-OH	—	0.7	—	—	0.3	2.0	0.5
iso-C _{16:0} 3-OH	—	0.8	—	1.1	—	1.0	—
Summed feature 3*	8.6	8.3	—	2.3	4.6	14.9	4.6

*Summed features represent groups of two or more fatty acids that could not be separated by GLC with the MIDI system; summed feature 3 contained iso-C_{15:0} 2-OH and/or C_{16:1}ω7c.

Similarity values between strain SW-135^T and the type strains of recognized *Erythrobacter* species ranged from 98.5 % (with *E. citreus*) to 96.9 % (with *E. flavus*, *E. longus* and *E. litoralis*). Similarities between the 16S rRNA gene sequence of strain SW-161^T and those of the type strains of recognized *Erythrobacter* species ranged from 98.1 % (with *E. flavus*) to 96.7 % (with *E. longus*). Sequence similarities to all other species of the family *Sphingomonadaceae* included in the phylogenetic analysis were lower than 97.2 % (Fig. 1). DNA–DNA relatedness observed between strains SW-135^T and SW-161^T was 12.3 %, suggesting that the two strains represent members of different genomic species (Wayne *et al.*, 1987). Strains SW-135^T and SW-161^T exhibited DNA–DNA relatedness levels of 9.7–20.2 % and 8.5–18.9 %, respectively, to the type strains of recognized species of the genus *Erythrobacter*. This genomic evidence

Fig. 1. Neighbour-joining tree based on 16S rRNA gene sequences showing the phylogenetic positions of strains SW-135^T and SW-161^T within the family *Sphingomonadaceae*. Bootstrap values (1000 replications) are shown as percentages at each node only if they are 50% or greater. Bar, 0.01 substitutions per nucleotide position. *Rhodospirillum rubrum* ATCC 11170^T was used as outgroup.

demonstrated that strains SW-135^T and SW-161^T represent two separate species within the genus *Erythrobacter* (Wayne *et al.*, 1987).

A neighbour-joining tree showing estimated phylogenetic relationships, inferred from comparisons of 16S rRNA gene sequences, showed that strains SW-135^T and SW-161^T fall within a phyletic radiation comprising all recognized *Erythrobacter* species (Fig. 1). The relationship between the cluster comprising the two isolates and recognized *Erythrobacter* species and the cluster comprising the genera *Porphyrobacter* and *Erythromicrobium* was supported by a bootstrap confidence value of 100% (Fig. 1). The respiratory lipoquinone and fatty acid profiles support the result of the monothetic classification based on 16S rRNA gene sequence analysis, although no clear-cut chemotaxonomic differentiation may exist between the genus *Erythrobacter* and the two phylogenetically related genera *Porphyrobacter* and *Erythromicrobium* (Fuerst *et al.*, 1993; Rainey *et al.*, 2003; Yurkov *et al.*, 1994). Strains SW-135^T and SW-161^T were isolated from the same region and were similar in most morphological and phenotypic characteristics except for thermotolerance and acid production from certain substrates (Table 1). However, the two strains were phylogenetically and genetically different. There were also phenotypic, phylogenetic and genetic differences between strains SW-135^T and SW-161^T and other recognized *Erythrobacter* species (Table 1, Fig. 1). Therefore, on the basis of the data presented, strains SW-135^T and SW-161^T should be placed in the genus *Erythrobacter* as two distinct novel species, for which the names *Erythrobacter seohaensis* sp. nov. and *Erythrobacter gaetbuli* sp. nov. are proposed, respectively.

Description of *Erythrobacter seohaensis* sp. nov.

Erythrobacter seohaensis (seo.ha.en'sis. N.L. masc. adj. *seohaensis* of Seohae, the Korean name of the Yellow Sea in Korea, from where the type strain was isolated).

Cells are rod-shaped (0.6–0.8 × 1.5–4.0 µm) and non-spore-forming. Colonies on MA (5 days, 30 °C) are smooth, glistening, circular, convex, orange–yellow in colour and 1.0–2.0 mm in diameter. Growth occurs at 10 and 40 °C, but not at 4 °C or above 41 °C. Optimal pH for growth is 7.0–8.0; growth is observed at pH 5.5 but not at pH 5.0. Optimal growth occurs in the presence of 2–3% (w/v) NaCl; growth does not occur without NaCl or in the presence of >9% NaCl. Anaerobic growth does not occur on MA or MA supplemented with nitrate. Urease-negative. Aesculin, Tweens 20, 40, 60 and 80 and tyrosine are hydrolysed. Casein, hypoxanthine and xanthine are not hydrolysed. H₂S is not produced. Acid is produced from D-cellobiose, D-melezitose and sucrose. Acid is not produced from adonitol, L-arabinose, D-fructose, D-galactose, D-glucose, *myo*-inositol, lactose, maltose, D-mannitol, D-mannose, melibiose, D-raffinose, L-rhamnose, D-ribose, D-sorbitol, D-trehalose or D-xylose. Butyrate is utilized, but formate, methanol, ethanol and benzoate are not utilized. The predominant respiratory lipoquinone is Q-10. The fatty acid profile is shown in Table 2. The DNA G+C content is 62.2 mol% (determined by HPLC). Other phenotypic characteristics are given in Table 1.

The type strain, SW-135^T (=KCTC 12228^T=DSM 16221^T), was isolated from a tidal flat of the Yellow Sea in Korea.

Description of *Erythrobacter gaetbuli* sp. nov.

Erythrobacter gaetbuli (gaet.bu'li. N.L. gen. n. *gaetbuli* of gaetbul, the Korean name for a tidal flat).

Cells are rod-shaped (0.6–0.8 × 2.0–4.0 µm) and non-spore-forming. Colonies on MA (5 days, 30 °C) are smooth, glistening, circular, convex, orange–yellow in colour and 1.0–2.0 mm in diameter. Growth occurs at 15 and 43 °C, but not at 10 °C or above 44 °C. Optimal pH for growth is 7.0–8.0; growth is observed at pH 5.5 but not at pH 5.0. Optimal growth occurs in the presence of 2–3% (w/v) NaCl; growth does not occur without NaCl or in the

presence of >9% NaCl. Anaerobic growth does not occur on MA or MA supplemented with nitrate. Urease-negative. Aesculin, Tweens 20, 40, 60 and 80 and tyrosine are hydrolysed. Casein, hypoxanthine and xanthine are not hydrolysed. H₂S is not produced. Acid is produced from D-cellobiose, D-glucose, maltose and D-melezitose. Acid is not produced from adonitol, L-arabinose, D-fructose, D-galactose, *myo*-inositol, lactose, D-mannitol, D-mannose, melibiose, D-raffinose, L-rhamnose, D-ribose, D-sorbitol, sucrose, D-trehalose or D-xylose. Butyrate is utilized, but formate, methanol, ethanol and benzoate are not utilized. The predominant respiratory lipoquinone is Q-10. The fatty acid profile is shown in Table 2. The DNA G+C content is 64.5 mol% (determined by HPLC). Other phenotypic characteristics are given in Table 1.

The type strain, SW-161^T (=KCTC 12227^T=DSM 16225^T), was isolated from a tidal flat of the Yellow Sea in Korea.

Acknowledgements

This work was supported by the 21C Frontier programme of Microbial Genomics and Applications (grant MG02-0401-001-1-0-0) from the Ministry of Science and Technology (MOST) of the Republic of Korea and a grant from the KRIIBB Research Initiative Program.

References

- Anzai, Y., Kim, H., Park, J.-Y., Wakabayashi, H. & Oyaizu, H. (2000). Phylogenetic affiliation of the pseudomonads based on 16S rRNA sequence. *Int J Syst Evol Microbiol* **50**, 1563–1589.
- Bruns, A., Rohde, M. & Berthe-Corti, L. (2001). *Muricauda ruestringensis* gen. nov., sp. nov., a facultatively anaerobic, appendaged bacterium from German North Sea intertidal sediment. *Int J Syst Evol Microbiol* **51**, 1997–2006.
- Cowan, S. T. & Steel, K. J. (1965). *Manual for the Identification of Medical Bacteria*. London: Cambridge University Press.
- 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.
- Ezaki, T., Hashimoto, Y. & Yabuuchi, E. (1989). Fluorometric deoxyribonucleic acid-deoxyribonucleic acid hybridization in micro-dilution wells as an alternative to membrane filter hybridization in which radioisotopes are used to determine genetic relatedness among bacterial strains. *Int J Syst Bacteriol* **39**, 224–229.
- Fuerst, J. A., Hawkins, J. A., Holmes, A., Sly, L. I., Moore, C. J. & Stackebrandt, E. (1993). *Porphyrobacter neustonensis* gen. nov., sp. nov., an aerobic bacteriochlorophyll-synthesizing budding bacterium from fresh water. *Int J Syst Bacteriol* **43**, 125–134.
- Komagata, K. & Suzuki, K. (1987). Lipids and cell-wall analysis in bacterial systematics. *Methods Microbiol* **19**, 161–203.
- Lanyi, B. (1987). Classical and rapid identification methods for medically important bacteria. *Methods Microbiol* **19**, 1–67.
- Leifson, E. (1963). Determination of carbohydrate metabolism of marine bacteria. *J Bacteriol* **85**, 1183–1184.
- Levring, T. (1946). Some culture experiments with *Ulva* and artificial seawater. *K Fysiogr Sällsk Lund Förh* **16**, 45–56.
- Rainey, F. A., Silva, J., Nobre, M. F., Silva, M. T. & da Costa, M. S. (2003). *Porphyrobacter cryptus* sp. nov., a novel slightly thermophilic, aerobic, bacteriochlorophyll *a*-containing species. *Int J Syst Evol Microbiol* **53**, 35–41.
- Sasser, M. (1990). *Identification of Bacteria by Gas Chromatography of Cellular Fatty Acids*. Newark, DE: MIDI Inc.
- Shiba, T. & Simidu, U. (1982). *Erythrobacter longus* gen. nov., sp. nov., an aerobic bacterium which contains bacteriochlorophyll *a*. *Int J Syst Bacteriol* **32**, 211–217.
- Tamaoka, J. & Komagata, K. (1984). Determination of DNA base composition by reverse-phase high-performance liquid chromatography. *FEMS Microbiol Lett* **25**, 125–128.
- Vybiral, D., Denner, E. B. M., Haller, C. M., Busse, H.-J., Witte, A., Höfle, M. G. & Velimirov, B. (1999). Polyphasic classification of 0.2 µm filterable bacteria from the Western Mediterranean Sea. *Syst Appl Microbiol* **22**, 635–646.
- Wayne, L. G., Brenner, D. J., Colwell, R. R. & 9 other authors (1987). Report of the ad hoc committee on reconciliation of approaches to bacterial systematics. *Int J Syst Bacteriol* **37**, 463–464.
- Yi, H., Chang, Y.-H., Oh, H. W., Bae, K. S. & Chun, J. (2003). *Zooshikella ganghwensis* gen. nov., sp. nov., isolated from tidal flat sediments. *Int J Syst Evol Microbiol* **53**, 1013–1018.
- Yi, H., Bae, K. S. & Chun, J. (2004). *Thalassomonas ganghwensis* gen. nov., sp. nov., isolated from tidal flat sediment. *Int J Syst Evol Microbiol* **54**, 377–380.
- Yoon, J.-H., Kim, H., Kim, S.-B., Kim, H.-J., Kim, W. Y., Lee, S. T., Goodfellow, M. & Park, Y.-H. (1996). Identification of *Saccharomonospora* strains by the use of genomic DNA fragments and rRNA gene probes. *Int J Syst Bacteriol* **46**, 502–505.
- Yoon, J.-H., Lee, S. T. & Park, Y.-H. (1998). Inter- and intraspecific phylogenetic analysis of the genus *Nocardioide*s and related taxa based on 16S rDNA sequences. *Int J Syst Bacteriol* **48**, 187–194.
- Yoon, J.-H., Kim, H., Kim, I.-G., Kang, K. H. & Park, Y.-H. (2003a). *Erythrobacter flavus* sp. nov., a slight halophile from the East Sea in Korea. *Int J Syst Evol Microbiol* **53**, 1169–1174.
- Yoon, J.-H., Kim, I.-G., Kang, K. H., Oh, T.-K. & Park, Y.-H. (2003b). *Bacillus marisflavi* sp. nov. and *Bacillus aquimaris* sp. nov., isolated from sea water of a tidal flat of the Yellow Sea in Korea. *Int J Syst Evol Microbiol* **53**, 1297–1303.
- Yoon, J.-H., Weiss, N., Kang, K. H., Oh, T.-K. & Park, Y.-H. (2003c). *Planococcus maritimus* sp. nov., isolated from sea water of a tidal flat in Korea. *Int J Syst Evol Microbiol* **53**, 2013–2017.
- Yoon, J.-H., Kang, K. H., Oh, T.-K. & Park, Y.-H. (2004a). *Shewanella gaetbuli* sp. nov., a slight halophile isolated from a tidal flat in Korea. *Int J Syst Evol Microbiol* **54**, 487–491.
- Yoon, J.-H., Kang, K. H., Oh, T.-K. & Park, Y.-H. (2004b). *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.
- Yurkov, V., Stackebrandt, E., Holmes, A. & 7 other authors (1994). Phylogenetic positions of novel aerobic, bacteriochlorophyll *a*-containing bacteria and description of *Roseococcus thiosulfatophilus* gen. nov., sp. nov., *Erythromicrobium ramosum* gen. nov., sp. nov., and *Erythrobacter litoralis* sp. nov. *Int J Syst Bacteriol* **44**, 427–434.