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ORIGINAL ARTICLE

Chryseobacterium rhizoplanae sp. nov., isolated from the rhizoplane environment

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Abstract A slightly yellow pigmented strain (JM-534^T) isolated from the rhizoplane of a field-grown *Zea mays* plant was investigated using a polyphasic approach for its taxonomic allocation. Cells of the isolate were observed to be rod-shaped and to stain Gram-negative. Comparative 16S rRNA gene sequence analysis showed that the isolate had the highest sequence similarities to *Chryseobacterium lactis* (98.9 %), *Chryseobacterium joostei* and *Chryseobacterium indologenes* (both 98.7 %), and *Chryseobacterium viscerum* (98.6 %). Sequence similarities to all other *Chryseobacterium* species were 98.5 % or below. The fatty acid analysis of the strain resulted in a *Chryseobacterium* typical pattern consisting mainly of the fatty acids $C_{15:0}$ iso, $C_{15:0}$ iso 2-OH, $C_{17:1}$ iso ω*9c*, and $C_{17:0}$ iso 3-OH. DNA–DNA hybridizations with the type strains of *C. lactis*, *C. joostei, C. viscerum* and *C. indologenes* resulted in values below 70 %. Genomic fingerprinting showed that the isolate was very different to the type strains of these species. Differentiating biochemical and chemotaxonomic properties showed that the isolate JM-534^T represents a novel species, for which the name *Chryseobacterium rhizoplanae* sp. nov. (type strain JM-534^T = LMG 28481^T = CCM 8544^T = CIP 110828^T) is proposed.

Keywords *Chryseobacterium* · *Rhizoplanae* · Taxonomy

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The genus *Chryseobacterium* described by Vandamme et al. (1994) now harbours a large number of species, some of which have been isolated from plant material including the rhizosphere/rhizoplane environment. *Chryseobacterium formosense* was isolated from the rhizosphere of *Lactuca sativa* L. (garden lettuce) in Taiwan (Young et al. 2005), *Chryseobacterium soldanellicola* and *Chryseobacterium taeanense* from roots of sand-dune plants (Park et al. 2006), *Chryseobacterium luteum* from the phyllosphere of grasses (Behrendt et al. 2007), *Chryseobacterium gregarium* from decaying plant material (Behrendt et al. 2008), *Chryseobacterium elymi*, *Chryseobacterium hagamense*, *Chryseobacterium lathyri*, and *Chryseobacterium rhizosphaerae* from the rhizosphere of coastal sand dune plants (Cho et al. 2010), *Chryseobacterium ginsengisoli* from the rhizosphere of ginseng (Nguyen et al. 2013), *Chryseobacterium kwangjuense* from pepper (*Capsicum annuum* L.)

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roots (Sang et al. 2013), and *Chryseobacterium zeae, Chryseobacterium arachidis* and *Chryseobacterium geocarposphaerae* from rhizospheres of different plants (Kämpfer et al. 2014). Another *Chryseobacterium* species, *Chryseobacterium hispalense*, was found to produce plant-growth promoting activities (Montero-Calasanz et al. 2013).

Strain JM-534^T, was isolated from the rhizoplane of 1 week old sweet corn (*Zea mays* L.) grown at the E.V. Smith Research Station in Tallassee (Tallapoosa county), Alabama (USA). The strain was initially isolated on tryptic soy agar (TSA, Oxoid) at 30 °C and also further maintained and subcultivated on this agar at 30 °C for 48 h. Analyses of the 16S rRNA gene sequence, the fatty acid methyl ester composition of whole cell hydrolysates, and further biochemical and physiological features were conducted to characterize the strain. In addition, DNA–DNA hybridizations and comparative nucleic acid fingerprinting analysis were performed with type strains of those species most closely related on the basis of 16S rRNA gene sequence similarities, among them *Chryseobacterium lactis* LMG 12278^T, *Chryseobacterium joostei* CIP 105533^T, *Chryseobacterium indologenes* CCUG 14556^T, and *Chryseobacterium viscerum* 687B-08^T. *C. lactis* LMG 12278^T, *C. joostei* CIP 105533^T, *C. indologenes* CCUG 14556^T and *C. viscerum* 687B-08^T were obtained from LMG, CCUG, CIP and Dr. Fernández-Garáyzabal, Madrid, Spain, respectively, and cultured under the same conditions for comparative testing.

The cultural and morphological characteristics were recorded from cultures grown on TSA. Gram staining was performed according to Gerhardt et al. (1994) and the motility test was done under a light microscope with cells grown for 3 days in tryptic soy broth (TSB; Oxoid) at 30 °C. Temperature-dependent growth was tested at 4, 11, 30, 36, 40 and 45 °C on nutrient agar (Oxoid). NaCl tolerance was investigated at different concentrations of NaCl [0.5–8.0 % (w/v)] in TSB. pH dependent growth was tested in TSB adjusted with HCl and NaOH to pH values between 4.0 and 12.0.

Strain JM-534^T was observed to show Gram-negative staining behavior and to form visible (diameter about 2 mm) yellowish colonies within 48 h at 28 °C. Colonies were observed to have a translucent glistening appearance with entire edges. Strain JM-534^T did not grow below 4 °C or above 37 °C. All strains tested grew very slowly at 36 °C and at a NaCl concentration of 1–3 % (w/v).

A yellow pigment of the flexirubin type (identified by the KOH method according to Reichenbach 1989) was found to be produced on nutrient agar. Oxidase activity tested positive using the oxidase reagent (bioMérieux) according to the instructions of the manufacturer. Cells of strain JM-534^T were observed to be non-motile rods (approximately 1 µm wide and 2 µm long). No spores were observed. Strain JM-534^T and the reference strains grew well on nutrient agar, brain heart infusion agar, R2A agar and TSA, but not on MacConkey agar (Oxoid).

Strain JM-534^T was physiologically/biochemically characterized using the 96-well plate test system (Kämpfer et al. 1991) and by some additional biochemical tests: production of hydrogen sulphide using the lead acetate paper and triple-sugar-iron methods, indole reaction with Ehrlich's and Kovacs' reagents, activity of arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase, DNase (Oxoid CM321; supplemented with 0.01 % toluidine blue), β-galactosidase (ONPG), and urease on Christensen's urea agar (Kämpfer 1990); hydrolysis of casein, gelatin (plate method), starch, and tyrosine (Smibert and Krieg 1994). Similar to many other *Chryseobacterium* species, the strain was found to be able to utilise very few carbon sources, but was able to hydrolyze some chromogenic substrates. The biochemical/physiological data are given in Table 1 and in the species description.

For fatty acid extraction the strains were cultured on TSA at 28 °C for 48 h.

The analysis of the cellular fatty acid profiles was performed as described elsewhere (Kämpfer and Kroppenstedt 1996) using a HP gas chromatograph HP 6890 with a Sherlock MIDI software version 2.11 and the TSBA peak naming table version 4.1. The results showed a *Chryseobacterium*-typical profile for JM-534^T with the following identified as the most abundant fatty acids: $C_{15:0}$ iso, $C_{17:0}$ iso 3-OH, $C_{17:1}$ iso ω*9c* and $C_{15:0}$ iso 2-OH. The latter was detected as summed feature as defined by MIDI ($C_{15:0}$ iso 2-OH/$C_{16:1}$ ω*7c*) but has been clearly identified as characteristic of *Chryseobacterium* species in previous studies (Vandamme et al. 1994; Montero-Calasanz et al. 2013). Slight differences were found in comparison of the fatty acid profile with those of the type strains of the most closely related *Chryseobacterium* species (Table 2).

Table 1 Comparison of the characteristics of strain JM-534^T with closely related *Chryseobacterium* species

Characteristic	1	2	3	4	5
Acid production from					
Sucrose	−	−[a]	−[b]	−	+
Arabinose	+	−[a]	−[b]	−	−
Salicin	+	−[a]	−[b]	−	−
Trehalose	+	(+)[a]	+[b]	+[b]	+
Growth at 36–37 °C	+	+[a]	−[b]	+[b]	+
Growth on MacConkey agar	−	+[a]	+[b]	−	+

Strains/species 1, *Chrsyeobacterium* sp. JM-534^T; 2, *Chryseobacterium lactis* LMG 12278^T; 3, *Chryseobacterium joostei* CIP 105533^T; 4, *Chryseobacterium indologenes* CCUG 14556^T; 5, *Chryseobacterium viscerum* 687B-08^T. All data are from this study. +, positive; (+), weakly positive; −, negative. All strains produced acid from D-glucose and maltose and not from D-ribose and D-xylose. All strains were positive for digestion of casein and esculin hydrolysis

[a] Results in agreement with those reported by Holmes et al. (2013)

[b] Results in agreement with those reported by Hugo et al. (2003)

Table 2 Fatty acid composition of strain JM-534^T and closest related *Chryseobacterium* species

Fatty acid	1	2	3	4	5
$C_{13:0}$ iso		1.2	2.0		
Unknown 13.565	5.5	6.9	6.4	13.1	7.5
Unknown 13.566[a]					
$C_{15:0}$ iso	38.6	39.4	44.8	28.4	34.3
$C_{15:1}$ iso F		1.8	1.2	3.4	2.1
$C_{15:0}$ iso 3-OH	2.8	2.7	2.4	2.1	3.4
$C_{15:0}$ anteiso		0.6			
$C_{16:0}$	1.4	1.6	1.7	1.2	1.0
$C_{16:0}$ 3-OH	1.3	1.2	1.0	0.8	1.8
$C_{16:0}$ iso 3-OH			1.3	0.8	1.6
Unknown 16.580[a]					
Unknown 16.582	1.4	1.2	1.4	1.3	1.3
$C_{17:0}$ 2-OH					
$C_{17:0}$ iso	1.9	1.9	2.2	1.1	0.9
$C_{17:0}$ iso 3-OH	20.4	15.6	14.2	14.3	20.2
$C_{17:1}$ iso ω*9c*	17.9	19.2	15.6	23.4	14.5
$C_{18:1}$ ω*5c*			0.4		
Summed feature 4[b]	8.7	6.5	5.4	9.8	11.2
Summed feature 5[b]					

Taxa are listed as 1, *Chryseobacterium* sp. JM-534^T; 2, *C. lactis* LMG 12278^T; 3, *C. joostei* CIP 105533^T; 4, *C. indologenes* CCUG 14556^T; 5, *C. viscerum* 687B-08^T. All data are from this study

[a] Unknown fatty acid; numbers indicate equivalent chain length

[b] Fatty acids that could not be separated by GC using the Microbial Identification System (Microbial ID) software were considered summed features. Summed feature four contains $C_{15:0}$ iso 2-OH and/or $C_{16:1}$ ω7*t*. As shown in several studies, summed feature: $C_{15:0}$ iso 2-OH/$C_{16:1}$ ω*7c*, could be clearly identified as $C_{15:0}$ iso 2-OH (Vandamme et al. 1994; Montero-Calasanz et al. 2013). Summed feature five contains $C_{17:1}$ iso I and/or $C_{17:1}$ anteiso B

Phylogenetic analysis was carried out based on nearly full-length 16S rRNA gene sequences. The 16S rRNA gene fragment of strain JM-534^T obtained by sequence analysis (GenBank/EMBL/DDBJ accession number KP033261) is a continuous stretch of 1,429 nucleotides spanning gene positions 43 to 1,475 (according to *E. coli* numbering published by Brosius et al. 1978). Pairwise sequence similarities to the closest related type strains were obtained using the EzTaxon type strain database (Kim et al. 2012). Phylogenetic trees were constructed using ARB release 5.2 (Ludwig et al. 2004) and the "All-Species Living Tree" Project (LTP; Yarza et al. 2008) database release LTPs115 (March 2014). Several phylogenetic trees were calculated including 78 type strains of *Chryseobacterium* species and the type strains of *Elizabethkingia* species as outgroup. The trees were based on gene sequence positions 82–1,394 (numbered according to the *E. coli* numbering published by Brosius et al. 1978) which were covered by the sequenced 16S rRNA gene fragments of all included type strains. Phylogenetic trees were constructed with the maximum-likelihood method using RAxML v7.04 (Stamatakis 2006) with GTR-GAMMA and rapid bootstrap analysis (100 resamplings) and the maximum-parsimony method using DNAPARS version 3.6 (Felsenstein 2005). Trees based on 100 resamplings (bootstrap analysis, Felsenstein 1985). To reduce the size of the final tree shown here, type strains not directly clustering with JM-534^T were removed from the tree without changing the overall tree topology (Fig. 1). Strain JM-534^T shared more than 98.5 % 16S rRNA gene sequence similarity with the type strains of four *Chryseobacterium* species: *C. lactis* (98.9 %), *C. joostei* (98.7 %), *C. indologenes* (98.7 %) and *C. viscerum* (98.6 %) and formed a cluster with those type strains and the type strain of *C. ginsengisoli*, which however shares less than 98.5 % 16S rRNA gene

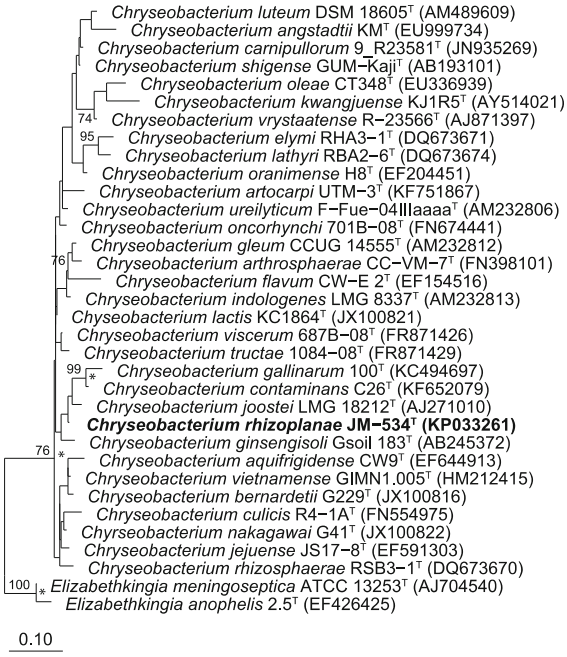

Fig. 1 Maximum-likelihood tree based on nearly full-length 16S rRNA gene sequences showing the phylogenetic affiliation of strain JM-534^T to the closest related type strains of the genus *Chryseobacterium*. The tree was calculated in ARB using RAxML (GTR-GAMMA and rapid bootstrap analysis) and based on 16S rRNA gene sequence positions 82–1,394 (according to *E. coli* numbering, Brosius et al. 1978). Numbers at nodes represent bootstrap values >70 %. All type strains of the genus *Chryseobacterium* were included in the analysis. Less related type strains were removed after tree construction without changing the overall tree topology. *Asterisk* mark nodes that showed also a high bootstrap support in the Maximum-parsimony analysis. *Elizabethkingia* type strains were used as outgroups. *Bar* 0.1 substitutions per sequence position

sequence similarity with JM-534^T. Clustering was not supported by high bootstrap values independently of the applied treeing method.

For further genotypic analysis high molecular weight genomic DNA was extracted as described by Pitcher and Saunders (1989). DNA–DNA hybridisation (DDH) experiments were performed with strain JM-534^{T}and the type strains of the four most closely related *Chryseobacterium* species according to the method of Ziemke et al. (1998) except that for nick translation 2 µg of DNA were labelled during 3 h of incubation at 15 °C. Strain JM-534^T showed a moderate DNA–DNA similarity to *C. joostei* CIP 105533^T (62 %, reciprocal 64 %), and low DNA–DNA similarities to *C. lactis* LMG 12278^T (49 %, reciprocal 18 %), *C. viscerum* 687B-08^T (49 %, reciprocal 43 %) and *C. indologenes* CCUG 14556^T (43 %, reciprocal 49 %).

The five strains were furthermore compared at the genomic level using genomic fingerprint patterns generated with three different RAPD-PCRs and a rep-PCR method, the $(GTG)_5$-PCR. RAPD-PCR analysis was performed with primers A, B, and C (Ziemke et al. 1997) and $(GTG)_5$-PCR with primer $(GTG)_5$ (Versalovic et al. 1994), respectively, as described in detail by Glaeser et al. (2013). A cluster analysis of the nucleic acid fingerprinting pattern was performed in Gel Compare II version 4.5 (Applied Maths) using the UPGMA clustering method and the Pearson correlations considering the presence and absence of DNA bands as well as DNA band intensities. The analysis of all five fingerprint profiles clearly showed the distinction between the five strains (Fig. 2). Depending on the applied fingerprinting method strain JM-534^T clustered differently to the different type strains.

On the basis of the results of this polyphasic study, it is concluded that strain JM-534^T represents a novel species, for which the name *Chryseobacterium rhizoplanae* sp. nov. is proposed.

Description of *Chryseobacterium rhizoplanae* sp. nov.

Chryseobacterium rhizoplanae (rhi.zo.plánae. Gr. n. rhiza a root; L. neut. n. *planum*, flat ground, surface; N.L. fem. n. *rhizoplana* the rhizoplane; N.L. gen. n. *rhizoplanae*, of the rhizoplane, the region of the root epidermis of a plant where soil particles and bacteria adhere).

Cells are Gram-stain negative. They are non-motile, non-spore forming rods, approximately 1 µm in width and 2 µm in length. Aerobic, oxidase positive, catalase positive. Good growth occurs after 48 h on nutrient agar, brain heart infusion agar, TSA and R2A agar at 4–36 °C. No growth occurs on MacConkey agar (Oxoid) at 28 °C. Unable to grow below 4 °C and above 40 °C. Grows in the presence of 1.0–3.0 % NaCl as additional ingredient of nutrient agar. Colonies on nutrient agar produce a yellowish colour and appear circular, translucent and glistening with entire edges. The yellow pigment is of the flexirubin type, non-diffusible and non-fluorescent. Acid is produced from D-glucose, L-arabinose, maltose, D-trehalose and salicin. No acid is produced from

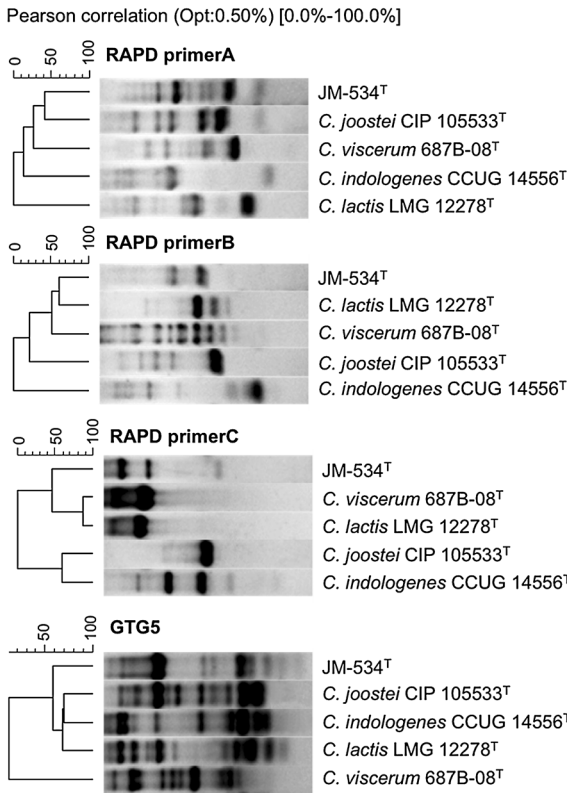

Fig. 2 Cluster analysis of genomic fingerprint pattern obtained for strain JM-534^T and the type strains of the four closest related *Chryseobacterium* species. Four different genomic fingerprint methods were applied, three RAPD-PCRs generated with primers A, B, and C and a rep-PCR, the $(GTG)_5$-PCR. Genomic fingerprint patterns were obtained by 1.5 % agarose gel electrophoresis and staining with ethidium bromide. Cluster analyses were performed in GelCompare II (Applied Math) using the UPGMA clustering method based in the Pearson correlation

sucrose, adonitol, D-arabitol, dulcitol, erythritol, *i*-inositol, lactose, D-mannitol, D-melibiose, α-methyl-D-glucoside, raffinose, L-rhamnose, D-sorbitol and D-xylose. Urease activity and hydrolysis of casein, gelatin, starch, DNA and tyrosine are positive, while indole production, hydrogen-sulphide production, activity of arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase, and β-galactosidase are negative. A very weak β-galactosidase activity is recorded after 72 h of incubation.

The following compounds are weakly utilized as a sole source of carbon: D-glucose, L-arabinose, maltose and salicin. The following compounds are not utilized as a sole source of carbon: acetate, propionate, *N*-acetylgalactosamine, *N*-acetylglucosamine, D-cellobiose, D-galactose, gluconate, D-mannose, D-fructose, and glycerol, D-mannitol, maltitol, α-D-melibiose, D-rhamnose, D-ribose, D-sucrose, D-xylose, adonitol, *i*-inositol, D-sorbitol, putrescine, *cis*-aconitate, *trans*-aconitate, 4-aminobutyrate, adipate, azelate, fumarate, glutarate, DL-3-hydroxybutyrate, itaconate, DL-lactate, 2-oxoglutarate, pyruvate, suberate, citrate, mesaconate, L-alanine, β-alanine, L-ornithine, L-phenylalanine, L-serine, L-aspartate, L-histidine, L-leucine, L-proline, L-tryptophan, 3-hydroxybenzoate, 4-hydroxybenzoate and phenylacetate. The chromogenic substrates *p*-nitrophenyl-α-D-glucopyranoside, *p*-nitrophenyl-β-D-glucopyranoside (weak), *p*-nitrophenyl-β-D-galactopyranoside, *p*-nitrophenyl-β-D-xylopyranoside, bis-*p*-nitrophenyl-phosphate, bis-*p*-nitrophenyl-phenyl-phosphonate, bis-*p*-nitrophenyl-phosphoryl-choline, 2-deoxythymidine-2′-*p*-nitrophenyl-phosphate, L-alanine-*p*-nitroanilide, γ-L-glutamate-*p*-nitroanilide, and L-proline-*p*-nitroanilide are hydrolysed. *p*-Nitrophenyl-β-D-glucuronide is not hydrolysed. The major cellular fatty acids are $C_{15:0}$ iso, $C_{15:0}$ iso 2-OH, and $C_{17:0}$ iso 3-OH.

The type strain, JM-534^T (= LMG 28481^T = CCM 8544^T = CIP 110828^T), was isolated from the surface of field-grown sweet corn (*Z. mays* L.) roots in Tallassee, Alabama USA. The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain JM-534^T is KP033261.

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References

Behrendt U, Ulrich A, Spröer C, Schumann P (2007) *Chryseobacterium luteum* sp. nov., associated with the phyllosphere of grasses. Int J Syst Evol Microbiol 57:1881–1885

Behrendt U, Ulrich A, Schumann P (2008) *Chryseobacterium gregarium* sp. nov., isolated from decaying plant material. Int J Syst Evol Microbiol 58:1069–1074

Brosius J, Palmer ML, Kennedy PJ, Noller HF (1978) Complete nucleotide-sequence of a 16S ribosomal-RNA gene from *Escherichia coli*. Proc Natl Acad Sci USA 75:4801–4805

Cho SH, Lee KS, Shin DS, Han JH, Park KS, Lee CH, Park KH, Kim SB (2010) Four new species of *Chryseobacterium* from the rhizosphere of coastal sand dune plants, *Chryseobacterium elymi* sp. nov., *Chryseobacterium hagamense* sp. nov., *Chryseobacterium lathyri* sp. nov. and

Chryseobacterium rhizosphaerae sp. nov. Syst Appl Microbiol 33:122–127

Felsenstein J (1985) Confidence limits of phylogenies: an approach using the bootstrap. Evolution 39:783–791

Felsenstein J (2005) PHYLIP (phylogeny inference package) version 3.6. Distributed by the author. Department of Genome Sciences, University of Washington, Seattle

Gerhardt P, Murray RGE, Wood WA, Krieg NR (1994) Methods for general and molecular bacteriology. American Society for Microbiology, Washington, DC

Glaeser SP, Galatis H, Martin K, Kämpfer P (2013) *Niabella hirudinis* and *Niabella drilacis* sp. nov., isolated from the medicinal leech *Hirudo verbana*. Int J Syst Evol Microbiol 63:3487–3493

Holmes B, Steigerwalt AG, Nicholson AC (2013) DNA–DNA hybridization study of strains of *Chryseobacterium*, *Elizabethkingia* and *Empedobacter* and of other usually indole-producing non-fermenters of CDC groups IIc, IIe, IIh and IIi, mostly from human clinical sources, and proposals of *Chryseobacterium bernardetii* sp. nov., *Chryseobacterium carnis* sp. nov., *Chryseobacterium lactis* sp. nov., *Chryseobacterium nakagawai* sp. nov. and *Chryseobacterium taklimakanense* comb. nov. Int J Syst Evol Microbiol 63:4639–4662

Hugo CJ, Segers P, Hoste B, Vancanneyt M, Kersters K (2003) *Chryseobacterium joostei* sp. nov., isolated from the dairy environment. Int J Syst Evol Microbiol 53:771–777

Kämpfer P (1990) Evaluation of the titertek-enterobac-automated system (TTE-AS) for identification of members of the family Enterobacteriaceae. Zentralbl Bakteriol 273:164–172

Kämpfer P, Kroppenstedt RM (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 characterisation of a fuel–oil contaminated site including numerical identification of heterotrophic water and soil bacteria. Microb Ecol 21:227–251

Kämpfer P, McInroy JA, Glaeser SP (2014) *Chryseobacterium zeae* sp. nov., *Chryseobacterium arachidis* sp. nov., and *Chryseobacterium geocarposphaerae* sp. nov. isolated from the rhizosphere environment. Antonie Van Leeuwenhoek 105:491–500

Kim OS, Cho YJ, Lee K, Yoon SH, Kim M, Na H, Park SC, Jeon YS, Lee JH, Yi H, Won S, Chun J (2012) Introducing EzTaxon-e: a prokaryotic 16S rRNA gene sequence database with phylotypes that represent uncultured species. Int J Syst Evol Microbiol 62:716–721

Ludwig W, Strunk O, Westram R, Richter L, Meier H, Yadhukumar, Buchner A, Lai T, Steppi S, Jobb G, Forster W, Brettske I, Gerber S, Ginhart AW, Gross O, Grumann S, Hermann S, Jost R, Konig A, Liss T, Lussmann R, May M, Nonhoff B, Reichel B, Strehlow R, Stamatakis A, Stuckmann N, Vilbig A, Lenke M, Ludwig T, Bode A, Schleifer KH (2004) ARB: a software environment for sequence data. Nucleic Acid Res 32:1363–1371

Montero-Calasanz MD, Göker M, Rohde M, Spröer C, Schumann P, Busse H-J, Schmid M, Tindall BJ, Klenk HP, Camacho M (2013) *Chryseobacterium hispalense* sp. nov., a plant growth-promoting bacterium isolated from a rainwater pond in an olive plant nursery and emendation of the species *Chryseobacterium defluvii, Chryseobacterium indologenes, Chryseobacterium wanjuense* and *Chryseobacterium gregarium*. Int J Syst Evol Microbiol 63:4386–4395

Nguyen NL, Kim YJ, Hoarig VA, Yang DC (2013) *Chryseobacterium ginsengisoli* sp. nov., isolated from the rhizosphere of ginseng and emended description of *Chryseobacterium gleum*. Int J Syst Evol Microbiol 63:2975–2980

Park MS, Jung SR, Lee KH, Lee M-S, Do JO, Kim SB, Bae KS (2006) *Chryseobacterium soldanellicola* sp. nov. and *Chryseobacterium taeanense* sp. nov., isolated from roots of sand-dune plants. Int J Syst Evol Microbiol 56:433–438

Pitcher DG, Saunders NA (1989) Rapid extraction of bacterial genomic DNA with guanidium thiocyanate. Lett Appl Microbiol 8:151–156

Reichenbach H (1989) The order Cytophagales Leadbetter 1974, 99^{AL}. In: Staley JT, Bryant MP, Pfennig N, Holt JC (eds) Bergey's manual of systematic bacteriology, vol 3. Williams & Wilkins, Baltimore, pp 2011–2073

Sang MK, Kim HS, Myung IS, Ryu CM, Kim BS, Kim KD (2013) *Chryseobacterium kwangjuense* sp. nov., isolated from pepper (*Capsicum annuum* L.) root. Int J Syst Evol Microbiol 63:2835–2840

Smibert RM, Krieg NR (1994) Phenotypic characterization. In: Gerhardt P, Murray RGE, Wood WA, Krieg NR (eds) Methods for general and molecular bacteriology. American Society for Microbiology, Washington, DC, pp 607–654

Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22:2688–2690

Vandamme P, Bernardet J-F, Segers P, Kersters K, Holmes B (1994) New perspectives in the classification of the flavobacteria: description of *Chryseobacterium* gen. nov., *Bergeyella* gen. nov., and *Empedobacter* nom. rev. Int J Syst Bacteriol 44:827–831

Versalovic J, Schneider M, de Bruijn FJ, Lupski JR (1994) Genomic fingerprinting of bacteria using repetitive sequence-based polymerase chain reaction. Methods Mol Cell Biol 5:25–40

Yarza P, Richter M, Peplies J, Euzéby J, Amann R, Schleifer KH et al (2008) The all-species living tree project: a 16S rRNA-based phylogenetic tree of all sequenced type strains. Syst Appl Microbiol 31:241–250

Young CC, Kämpfer P, Shen FT, Lai WA, Arun AB (2005) *Chryseobacterium formosense* sp. nov., isolated from the rhizosphere of *Lactuca sativa* L. (garden lettuce). Int J Syst Evol Microbiol 55:432–436

Ziemke F, Brettar I, Höfle MG (1997) Stability and diversity of the genetic structure of a *Shewanella putrefaciens* population in the water column of the central Baltic. Aquat Microb Ecol 13:63–74

Ziemke F, Höfle MG, Lalucat J, Rosselló-Mora R (1998) Reclassification of *Shewanella putrefaciens* Owen's genomic group II as *Shewanella baltica* sp. nov. Int J Syst Bacteriol 48:179–186