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TAXONOMIC DESCRIPTION
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Altererythrobacter halimionae sp. nov. and *Altererythrobacter endophyticus* sp. nov., two endophytes from the salt marsh plant *Halimione portulacoides*

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Abstract

Two Gram-negative, rod-shaped, motile bacterial strains, named CPA5^T and BR75^T, were isolated from the halophyte *Halimione portulacoides*. Both presented optimum growth at 30 °C, pH 7.0–7.5 and 1–2 % NaCl (w/v) for strain CPA5^T, and pH 7.5–8.0 and 2 % NaCl (w/v) for strain BR75^T. Phylogenetic analyses based on 16S rRNA gene sequences affiliated both strains to the genus *Altererythrobacter*. CPA5^T presented highest 16S rRNA gene sequence similarity with *Altererythrobacter aestuarii* KYW147^T (96.5 %), followed by *Altererythrobacter namhicola* KYW48^T (95.9 %), *Novosphingobium indicum* H25^T (95.6 %) and *Altererythrobacter oceanensis* Y2^T (95.5 %). BR75^T displayed highest similarity with *Altererythrobacter marensis* MSW-14^T (96.5 %), followed by *Altererythrobacter xinjiangensis* S3-63^T, *Altererythrobacter luteolus* SW-109^T and *Altererythrobacter indicus* MSSRF26^T (96.1 %). Neither strain contained Bacteriochlorophyll *a*. The main fatty acids observed for CPA5^T were $C_{17:1}\omega6c$ and summed features 3 ($C_{16:1}\omega7c$ and/or iso-$C_{15:0}$ 2-OH) and 8 ($C_{18:1}\omega7c$ and/or $C_{18:1}\omega6c$). The latter summed feature was the dominant fatty acid observed for strain BR75^T as well. The major polar lipids were phosphatidylethanolamine, unidentified phospholipids and unidentified glycolipids for both strains. The predominant ubiquinone was Q-10 for both strains, and the DNA G+C contents were 63.4 mol% and 58.3 mol% for CPA5^T and BR75^T, respectively. Based on phenotypic and genotypic results, both strains represent novel species belonging to the genus *Altererythrobacter* for which the names *Altererythrobacter halimionae* sp. nov. (type strain CPA5^T=CECT 9130^T=LMG 29519^T) and *Altererythrobacter endophyticus* sp. nov (type strain BR75^T=CECT 9129^T=LMG 29518^T) are proposed.

The genus *Altererythrobacter* was described in 2007 [1], emended in 2012 [2] and 2016 [3], and belongs to the family *Erythrobacteraceae* [4]. At the time of writing, the genus contains 22 validly published species, several of which frequently isolated from marine and estuarine environments (e.g. [5–8]). Its occurrence in association with plants is rare and there is only one species that has been isolated from the rhizosphere of wild rice [9].

The genus *Altererythrobacter* comprises Gram-negative bacteria that do not produce H_2S. Cells cannot grow in anaerobic conditions and nitrate is not reduced. Cell suspensions and colonies are yellow, and the methanol-soluble pigment indicates the absence of Bacteriochlorophyll *a* (BChl *a*). The main quinone is Q-10 [1] and the major polar lipids are phosphatidylethanolamine, phosphatidylglycerol, diphosphatidylglycerol and sphingoglycolipid [2]. The DNA G+C content range is 54.5–67.5 mol%, and the catalase reaction can be positive or negative [3]. The major fatty acids include $C_{18:1}\omega7c$ [1], $C_{16:1}\omega7c$ and $C_{17:1}\omega6c$.

The diversity of the endophytic community of the halophyte *Halimione portulacoides* was assessed in a salt marsh in Aveiro, Portugal. Briefly, healthy specimens of the halophyte were collected, aboveground and belowground tissues from these specimens were separated, surface-sterilized, macerated in phosphate buffer solution and studied for their bacterial diversity [10]. This study focuses on two strains obtained in those isolation efforts: strain CPA5^T, isolated from the aboveground tissues; and BR75^T, isolated from the belowground tissues of the halophyte. Strains CPA5^T and

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Abbreviations: BChl *a*, Bacteriochlorophyll *a*; GL, unidentified glycolipid; IAA, indole-3-acetic acid; Knuc, substitution rate; MA, marine agar; ML, maximum-likelihood; NJ, neighbour joining; PE, phosphatidylethanolamine; PL, unidentified phospholipid.
The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequences of strains CPA5^T and BR75^T are KY310593 and KY310591, respectively.
Two supplementary figures are available with the online Supplementary Material.

BR75^T were originally isolated from and routinely cultured on marine agar (MA, Difco Laboratories, France) culture medium, at 28 °C, under aerobic conditions.

Genomic DNA was extracted, subjected to PCR amplification for the 16S rRNA gene, and sequenced as described elsewhere [10]. Primers 27F [11] and 704F [12] were used for sequencing the 16S rRNA gene. The nearly full-length sequences obtained for CPA5^T (1412 nt) and BR75^T (1406 nt) were used for similarity analyses using the Identify tool included in the EzTaxon platform [13]. For strain CPA5^T, the closest matches were observed with type strains *Altererythrobacter aestuarii* KYW147^T (96.5 % similarity of the 16S rRNA gene sequence), followed by *Altererythrobacter namhicola* KYW48^T (95.9 %), *Novosphingobium indicum* H25^T (95.6 %), and *Altererythrobacter oceanensis* Y2^T (95.5 %). For strain BR75^T, the most closely related type strains were *Altererythrobacter marensis* MSW-14^T (96.5 %), followed by *Altererythrobacter xinjiangensis* S3-63^T and *Altererythrobacter luteolus* SW-109^T (96.1 %) and *Altererythrobacter indicus* MSSRF26^T (96.1 %). 16S rRNA gene sequence similarity percentages to other type strains were below 95.5 and 96.0 % for CPA5^T and BR75^T, respectively.

The 16S rRNA gene sequences of strains CPA5^T and BR75^T were aligned with the sequences of related type strains retrieved from the EzTaxon database [13]. The sequences were then aligned using CLUSTAL Omega [14] and edited using BioEdit version 7.2.5 [15]. MEGA version 6.0 [16] was used to cluster the sequences by applying the neighbour-joining (NJ, [17]) and maximum-likelihood (ML, [18]) methods. The Kimura two-parameter model [19] was used

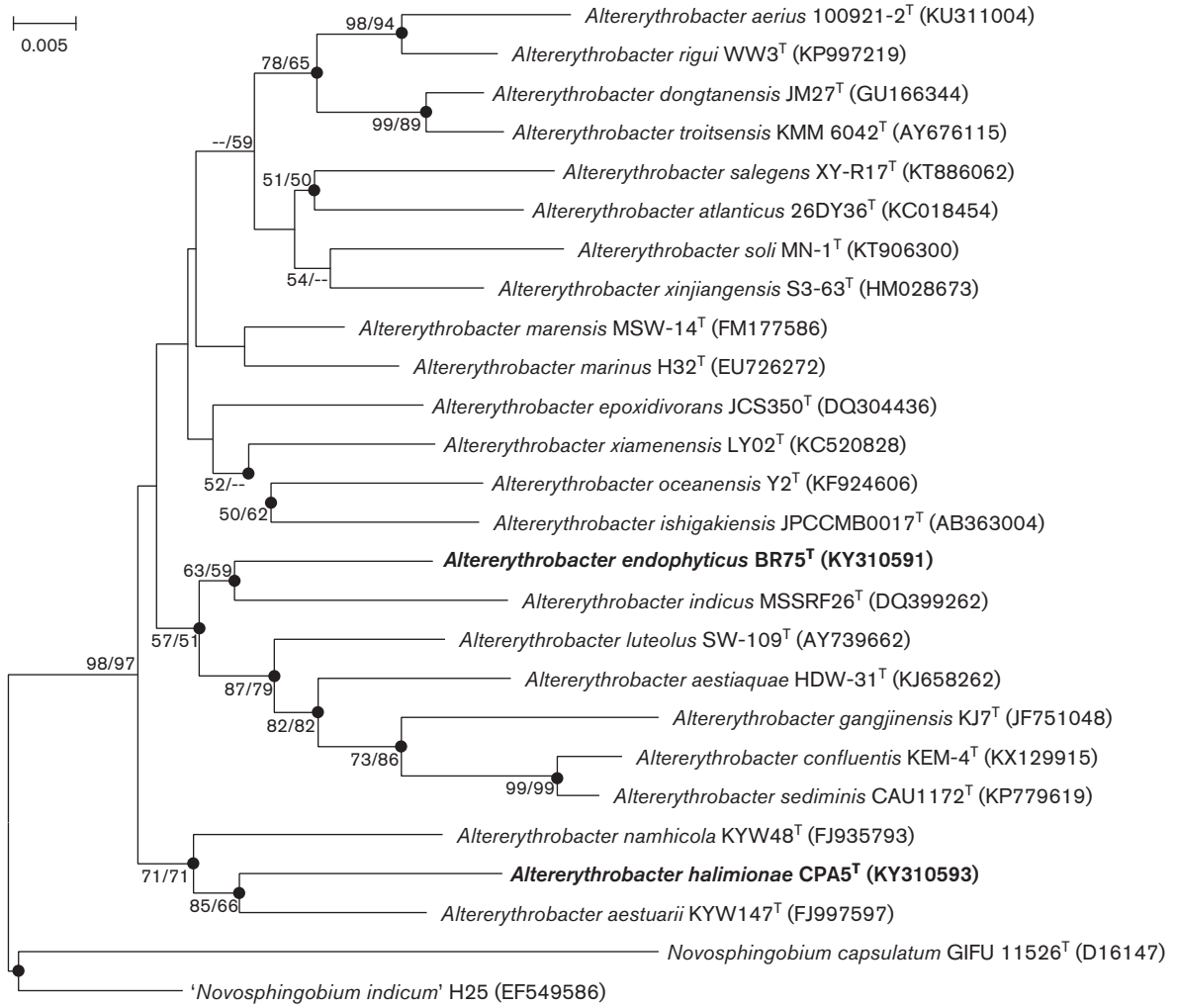

Fig. 1. Neighbour-joining (NJ) tree showing the phylogenetic positions of strains CPA5^T and BR75^T and representatives of other related taxa based on 16S rRNA gene sequences. Full circles denote nodes that were also recovered in the maximum-likelihood (ML) tree, based on the same sequences. Bootstrap values (expressed as percentages of 1000 replications) which are ≥50 % are shown at branch points, following the order: NJ/ML. Accession numbers for the type strains are shown in parentheses. Bar, 0.005 nt substitution rate (K_{nuc}) units.

Table 1. Differential characteristics of CPA5^T, BR75^T and related type strains

Strains: 1, CPA5^T; 2, BR75^T; 3, *A. aestuarii* KCTC 22735^T (data from this study, unless otherwise stated); 4, *A. marensis* KCTC 22370^T (data from this study, unless otherwise stated). +, Positive; w, weakly positive; —, negative.

Characteristic	1	2	3	4
Motility	+	+	—*	+†
Catalase activity	+	+	+*	w†
Hydrolysis of casein	—	+	—*	—†
NaCl (w/v) range	0–5 %	0–5 %	0–6 %*	0–9 %†
pH range	5–11.5	5–11.5	5–11*	6.1–11.1†
Temperature range	18–37 °C	18–37 °C	10–40 °C*	4–42 °C†
API 20NE results:				
Reduction of nitrates to nitrites	—	—	+‡	—
β-galactosidase (para-nytrophenyl-β-D-galactopyranose)	—	+	—	—
Assimilation of malic acid	—	+	—	+
API ZYM results:				
Esterase (C4), esterase lipase (C8), α-chymotrypsin	+	+	+‡	+
Lipase (C14)	+	w	—	—
Valine arylamidase	+	+	w‡	+
Cystine arylamidase	w	—	—	w§
Trypsin	w	—	+	w§
Acid phosphatase	+	+	—	—§
Naphthol-AS-BI-phosphohydrolase	+	+	w‡	w§
β-Galactosidase	—	w	—	—
β-Glucuronidase	—	+	—	—
α-Glucosidase	—	—	+‡	—
β-Glucosidase	—	+	+	—
API 50CH results (acid production):				
Aesculin ferric citrate	—	+	—‡	+
Salicin	—	—	—	+
DNA G+C content (mol%)	63.4	58.3	67.2*	63.1†

*Data from [6].

†Data from [7].

‡Result differed from that published in [6].

§Result differed from that published in [7].

in clustering, and bootstrap values based on 1000 replications were obtained in these phylogenetic analyses. The obtained phylogenetic trees clearly placed both strains in independent clusters in the genus *Altererythrobacter* (Fig. 1). An extended overview of the placement of strains CPA5^T and BR75^T in the context of the family *Erythrobacteraceae* is represented in Fig. S1 (available in the online Supplementary Material).

The optimal conditions for growth were tested using a base of MA medium. The range and optimum conditions were first tested at varying temperatures, then pH and finally NaCl concentrations. Tests were performed by incubating strains at 4, 18, 26, 30, 37, 42.5 and 50 °C, pH from 4 to 12 in 0.5 intervals, and NaCl tolerance was tested using concentrations of 0, 0.5, 1, 2, 3, 5, 10, 15 and 20 % NaCl (w/v) in a medium composed of 5 g l^{-1} yeast extract (Alfa Aesar, MA) and 10 g l^{-1} tryptone casein peptone (Amresco, Texas, USA). Optimum temperature for growth was observed at 30 °C for both strains. Optimum growth for CPA5^T was observed at pH 7–7.5 and 1–2 % NaCl (w/v), and for strain BR75^T at pH 7.5–8 and 2 % NaCl (w/v).

Biochemical and phenotypic tests were performed with cells grown on MA medium for 48 h, at 30 °C. The Gram-staining reaction was performed with a kit, and manufacturer's instructions (Merck, Germany) were followed. Catalase and oxidase activities were assessed using H_2O_2-reagent and oxidase strips, respectively (both from Liofilchem, Italy). Light microscopy was used for determination of cell size, morphology and motility. Additionally, cells grown in half-strength MA for 72 h were placed on cavity slides and gliding motility was assessed by using the hang-drop method [20]. Oxygen metabolism was assessed by observing growth on thioglycollate medium (Merck, Germany) for 7 days. The ability to produce H_2S was assessed using Kligler's iron agar (Merck, Germany). Ability to hydrolyse starch, Tween 20, xylan, casein and cellulose, and to produce indole-3-acetic acid (IAA) were assessed as described in [10]. To assess presence of Bacteriochlorophyll *a* and absorbance peaks of the pigments, cells were grown on MB, washed once with distilled water, vigorously resuspended in 90 % (v/v) acetone and centrifuged. The supernatant was then removed and kept at 4 °C in the dark overnight. Absorption peaks were assessed from 300 to 800 nm using the Thermo Spectroscopy Genesys 6. Additional biochemical tests were performed for strains CPA5^T and BR75^T as well as type strains *A. marensis* KCTC 22370^T and *A. aestuarii* KCTC 22735^T, using API 20NE, API ZYM and API 50CH strips (bioMérieux, France) following the manufacturer's instructions, except for using 0.9 % (w/v) NaCl to prepare inocula. The results for biochemical and phenotypic tests are detailed in the description of the new species, and differentiating characteristics are stated in Table 1.

The assessment of respiratory quinones, polar lipids and fatty acids was conducted as described in [21] and performed with strains CPA5^T, *A. aestuarii* KCTC 22735^T, BR75^T and *A. marensis* KCTC 22370^T simultaneously. Cells were grown in MB at 30 °C for 48 h to obtain biomass for quinone and polar lipids assays. The main quinone detected for all strains was Q-10, and Q-9 and Q-8 were detected in minor amounts. The main fatty acids observed for CPA5^T were $C_{17:1}\omega6c$ (13.8 %) and summed features 3 ($C_{16:1}\omega7c$ and/or iso-$C_{15:0}$ 2-OH; 21.4 %) and 8 ($C_{18:1}\omega7c$ and/or $C_{18:1}\omega6c$; 32.6 %), comprising over 67 % of total fatty acids. For strain BR75^T the main fatty acids were comprised in summed feature 8, representing 76.3 % of total fatty acids. The results were in accordance to what is observed in other *Altererythrobacter* species; the characteristic fatty acid of the genus ($C_{18:1}\omega7c$) was present in the summed feature 8

Table 2. Fatty acid composition of strains CPA5^T, BR75^T and related type strains

Strains: 1, CPA5^T; 2, BR75^T; 3, *A. aestuarii* KCTC 22735^T (data from this study); 4, *A. aestuarii* KYW147^T (data from [6]); 5, *A. marensis* KCTC 22370^T (data from this study); 6, *A. marensis* MSW-14^T (data from [7]). Values represent percentage of total fatty acids. —, Not detected; TR, trace amount (<1 %).

Fatty acid	1	2	3	4	5	6
Saturated						
$C_{15:0}$	1.6	—	TR	3.2	—	1.6
$C_{16:0}$	7.1	5.8	9.0	5.8	4.9	13
$C_{17:0}$	4.7	—	TR	—	—	—
$C_{18:0}$	TR	1.1	TR	—	TR	3.7
Unsaturated						
$C_{16:1}\omega5c$	TR	—	1.5	—	1.4	1.9
$C_{17:1}\omega6c$	13.8	3.1	6.3	19.9	3.4	6.8
$C_{17:1}\omega8c$	1.5	TR	1.1	2.1	—	—
$C_{18:1}\omega5c$	1.3	TR	1.4	—	2.1	2.2
$C_{18:1}\omega7c$	—	—	—	35.2	—	—
$C_{18:1}\omega7c$ 11-methyl	9.4	—	13.3	—	24.0	—
Hydroxyl						
$C_{14:0}$ 2-OH	2.3	8.1	1.0	7.5	2.3	1.3
$C_{15:0}$ 2-OH	TR	TR	TR	3.5	—	—
$C_{16:0}$ 2-OH	—	TR	3.1	—	1.5	1.4
Summed feature*						
3	21.4	2.6	19.4	22.7	8.7	8.8
7	—	—	—	—	—	52.8
8	32.6	76.3	41.1	—	50.4	—

*Summed feature 3 contains $C_{16:1}\omega7c$ and/or iso-$C_{15:0}$ 2-OH; summed feature 7 contains $C_{18:1}\omega9c$ and/or $C_{18:1}\omega12t$ and/or $C_{18:1}\omega7c$; summed feature 8 contains $C_{18:1}\omega7c$ and/or $C_{18:1}\omega6c$.

in our analysis. The complete fatty acid composition for all tested strains is presented in Table 2. The polar lipid profiles obtained are depicted in Fig. S2, available in the online Supplementary Material. For strain CPA5^T, the polar lipids detected in major amounts included phosphatidylethanolamine (PE), an unidentified glycolipid (GL2) and three unidentified phospholipids (PL2, PL3 and PL5). The profile for the phylogenetically close relative *A. aestuarii* KCTC 22735^T was similar to that obtained for strain CPA5^T, albeit presenting small differences in regards to the minor polar lipids. For strain BR75^T, the major polar lipids were PE, an unidentified glycolipid (GL2) and four unidentified phospholipids (PL2, PL3, PL4 and PL5). The profile was highly similar to that of *A. marensis* KCTC 22370^T and only minor discrepancies in polar lipids amounts were observed. These results further indicate that strains CPA5^T and BR75^T belong to the genus *Altererythrobacter* but present slight differences with the most closely related strains.

Determination of G+C content was performed by high-performance liquid chromatography [22]. The results obtained (63.4 mol% for CPA5^T and 58.3 mol% BR75^T) are in agreement with what has been previously observed in the genus (54.5–67.5 mol%; [3]).

Detailed results for each strain are given in the respective species description section. Considering the phylogenetic and 16S rRNA gene sequencing data and the similarities in physiological and biochemical traits, it is clear that CPA5^T and BR75^T belong to the genus *Altererythrobacter*. Given that the 16S rRNA sequence similarities did not surpass the threshold for genomic delimitation of a new species (97 % sequence similarity; [23, 24]), there was no need to perform DNA–DNA relatedness tests. Strains CPA5^T and BR75^T are, nevertheless, distinguishable from validly published species of the genus, as they present differences in certain traits (Table 1). Differences between the novel species BR75^T and the closely related reference strain of *A. marensis* include the ability to hydrolyse casein, to assimilate malic acid, to produce acid from salicin, and activity of β-galactosidase, β-glucosidase and β-glucuronidase. Differences between CPA5^T and *A. aestuarii* include motility and activity of lipase, acid phosphatase and β-glucosidase. Accordingly, strains CPA5^T and BR75^T represent novel species of the genus *Altererythrobacter*, for which the names *Altererythrobacter halimionae* sp. nov. and *Altererythrobacter endophyticus* sp. nov, respectively, are proposed.

DESCRIPTION OF *ALTERERYTHROBACTER HALIMIONAE* SP. NOV.

Altererythrobacter halimionae (ha.li.mi.o'nae. N.L. gen. n. *halimionae* of the marsh plant *Halimione portulacoides*).

Cells are Gram-negative rods (1.59–3.56 µm in length, 0.5–0.96 µm in width), aerobic, motile but not by gliding. Colony on MA after incubation at 30 °C for 48 h is yellow, opaque, with smooth edges and a diameter of 0.5–1 mm. Growth is observed from 18 to 37 °C (optimum 30 °C), at pH 5.0 to 11.5 (optimum 7.0–7.5) and in the presence of 0.5 to 5.0 % (w/v) NaCl [optimum 1–2 % (w/v) NaCl], being slightly halophilic. Positive for catalase, oxidase, hydrolysis of Tween 20 and xylan and production of IAA (45.5 µg ml^{-1}). Does not hydrolyse casein, starch, cellulose, and does not produce H_2S. Bacteriochlorophyll *a* is absent and acetone-soluble peaks are observed at 454 and 482 nm. In API 20NE strips, it is positive for hydrolysis of aesculin (β-glucosidase), and negative for reduction of nitrates, indole production, fermentation of D-glucose, arginine dihydrolase, urease, hydrolysis of gelatin (protease), para-Nytrophenyl-βD-galactopyranose (β-galactosidase), assimilation of D-glucose, L-arabinose, D-mannose, D-mannitol, *N*-acetyl-glucosamine, maltose, potassium gluconate, capric acid, adipic acid, malic acid, trisodium citrate, phenylacetic acid. In an API ZYM strip, it is positive for alkaline phosphatase, esterase (C4), esterase lipase (C8), lipase (C14), leucine arylamidase, valine arylamidase, α-chymotrypsin, acid phosphatase and Naphthol-AS-BI-phosphohydrolase; weakly positive for cysteine arylamidase and trypsin. In this strip, it is negative for α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, *N*-acetyl-β-glucosaminidase, α-mannosidase and α-fucosidase. In API 50CH it is negative for acid production from glycerol,

erythritol, D-arabinose, L-arabinose, D-ribose, D-xylose, L-xylose, D-adonitol, methyl-βD-xylopyranoside, D-galactose, D-glucose, D-fructose, D-mannose, L-sorbose, L-rhamnose, dulcitol, inositol, D-mannitol, D-sorbitol, methyl-αD-mannopyranoside, methyl-αD-glucopyranoside, *N*-acetylglucosamine, amygdalin, arbutin, aesculin ferric citrate, salicin, cellobiose, maltose, lactose (bovine), melibiose, D-sucrose, trehalose, inulin, melezitose, raffinose, starch, glycogen, xylitol, gentiobiose, turanose, D-lyxose, D-tagatose, D-fucose, L-fucose, D-arabitol, L-arabitol, potassium gluconate, potassium 2-ketogluconate, potassium 5-ketogluconate. The main quinone is Q-10 and the main fatty acids are $C_{17:1}$ $\omega6c$ and summed features 3 ($C_{16:1}\omega7c$ and/or iso-$C_{15:0}$ 2-OH) and 8 ($C_{18:1}\omega7c$ and/or $C_{18:1}\omega6c$). The major polar lipids comprise phosphatidylethanolamine and unidentified polar lipids.

The type strain CPA5^T (=CECT 9130^T=LMG 29519^T) was isolated from the surface-sterilized aboveground tissues of the halophyte *Halimione portulacoides*. The G+C content of the DNA of the type strain is 63.4 mol%.

DESCRIPTION OF *ALTERERYTHROBACTER ENDOPHYTICUS* SP. NOV.

Altererythrobacter endophyticus (*en.do.phy'ti.cus.* Gr. pref. *endo* within; Gr. n. *phyton* plant; L. neut. suff. -icus adjectival suffix used with the sense of belonging to; N.L. masc. adj. *endophyticus* within plant, endophytic).

Cells are Gram-negative aerobic rods (1.46–3.95 µm in length, 0.59–1.41 µm in width), motile but not by gliding. After incubation at 30 °C for 48 h on MA, colony is yellow, opaque, with smooth edges and 0.5–1.2 mm in diameter. Growth occurs from 18 to 37 °C (optimum 30 °C), at pH 5.0–11.5 (optimum 7.5–8.0) and in the presence of 0.5 to 5.0 % (w/v) NaCl [optimum 2 % (w/v) NaCl], being slightly halophilic. Bacteriochlorophyll *a* is absent, and acetone-soluble peaks are observed at 454–455 and 482–483 nm. Cells are catalase and oxidase positive, and hydrolyse casein, Tween 20 and xylan, and produce IAA (90.8 µg ml^{-1}). H_2S is not produced, and starch and cellulose are not hydrolysed. In an API 20NE strip, it is positive for hydrolysis of aesculin (β-glucosidase), para-Nytrophenyl-βD-galactopyranose (β-galactosidase) and assimilation of malic acid. It is negative for reduction of nitrates, indole production, fermentation of D-glucose, arginine dihydrolase, urease, hydrolysis of gelatin (protease), assimilation of D-glucose, L-arabinose, D-mannose, D-mannitol, *N*-acetyl-glucosamine, maltose, potassium gluconate, capric acid, adipic acid, trisodium citrate and phenylacetic acid. In the API ZYM strip, it is positive for alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, α-chymotrypsin, acid phosphatase, Naphthol-AS-BI-phosphohydrolase, β-glucuronidase, and β-glucosidase, and weakly positive for lipase (C14) and β-galactosidase. It is negative for cystine arylamidase, trypsin, α-galactosidase, *N*-acetyl-β-glucosaminidase, α-mannosidase and α-fucosidase. In API 50CH it is positive for acid production from aesculin ferric citrate, and negative for glycerol, erythritol, D-arabinose, L-arabinose, D-ribose, D-xylose, L-xylose, D-adonitol, methyl-βD-xylopyranoside, D-galactose, D-glucose, D-fructose, D-mannose, L-sorbose, L-rhamnose, dulcitol, inositol, D-mannitol, D-sorbitol, methyl-αD-mannopyranoside, methyl-αD-glucopyranoside, *N*-acetylglucosamine, amygdalin, arbutin, salicin, cellobiose, maltose, lactose (bovine), melibiose, D-sucrose, trehalose, inulin, melezitose, raffinose, starch, glycogen, xylitol, gentiobiose, turanose, D-lyxose, D-tagatose, D-fucose, L-fucose, D-arabitol, L-arabitol, potassium gluconate, potassium 2-ketogluconate, potassium 5-ketogluconate. The predominant fatty acids are those contained in summed feature 8 ($C_{18:1}\omega7c$ and/or $C_{18:1}\omega6c$), and the principal respiratory quinone is Q-10. The major polar lipids comprise phosphatidylethanolamine and unidentified polar lipids.

The type strain BR75^T (=CECT 9129^T=LMG 29518^T) was isolated from the surface-sterilized belowground tissues of the halophyte *Halimione portulacoides*. The G+C content of the DNA of the type strain is 58.3 mol%.

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Conflicts of interest
The authors declare that there are no conflicts of interest.

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