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TAXONOMIC DESCRIPTION

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Arthrobacter ulcerisalmonis sp. nov., isolated from an ulcer of a farmed Atlantic salmon (*Salmo salar*), and emended description of the genus *Arthrobacter sensu lato*

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Abstract

A Gram-stain positive, pleomorphic, oxidase-negative, non-motile isolate from the ulcer of a farmed Atlantic salmon (*Salmo salar*), designated strain T11b^T, was subjected to a comprehensive taxonomic investigation. A comparative analysis of the 16S rRNA gene sequence showed highest similarities to the type strains of *Pseudarthrobacter siccitolerans* (98.1%) and *Arthrobacter methylotrophus* and *Pseudarthrobacter phenanthrenivorans* (both 98.0%). The highest ANI value observed between the assembled genome of T11b^T and the publicly available *Pseudarthrobacter* and *Arthrobacter* type strain genomes were 81.15 and 80.99%, respectively. The major respiratory quinone was menaquinone MK-9(H_2). The polyamine pattern contained predominantly spermidine. The polar lipid profile consisted of the major lipids diphosphatidylglycerol, phosphatidylglycerol, monogalactosyl-diacylglycerol and dimannosylglyceride. Minor amouts of trimannosyldiacylglycerol and phosphatidylinositol were also detected. The peptidoglycan was of the type A3α L-Lys–L-Ser–L-Thr–L-Ala (A11.23). In the fatty acid profile, anteiso and iso branched fatty acids predominated (anteiso $C_{15:0}$, iso $C_{16:0}$, anteiso $C_{17:0}$). Moderate to low DNA–DNA similarities, physiological traits as well as unique traits in the fatty acid pattern distinguished strain T11b^T from the next related species. All these data point to the fact that strain T11b^T represents a novel species of the genus *Arthrobacter* for which we propose the name *Arthrobacter ulcerisalmonis* sp. nov. The type strain is T11b^T (=CIP 111621^T=CCM 8854^T=LMG 30632^T=DSM 107127^T).

Arthrobacter species comprise mostly soil bacteria and these were frequently referred as such, based only on cell morphology alone, but bacteria of this genus present irregular morphology forms depending on the media employed and phase of growth. Dependence on morphology and habitat of *Arthrobacter* species has led to great confusion in the classification of new species into this genus creating considerable problems in their identification [1]. Based on studies on phylogenetic grouping, 16S rRNA gene sequence similarities and cell components as peptidoglycans, quinones systems, polar lipid profiles of *Arthrobacter*, selected species were reclassified into several genera [2]. The genus *Arthrobacter sensu lato* was proposed to harbour *Arthrobacter* species which could not be reclassified into new genera due to the lack of stable diagnostic traits at the time being [2]. While the genus *Arthrobacter sensu stricto* is restricted to the four species of the '*Arthrobacter globiformis* group', *Arthrobacter sensu lato* comprises the '*Arthrobacter agilis* group', the '*Arthrobacter citreus* group', the '*Arthrobacter psychrolactophilus*' group, the '*Arthrobacter pigmenti*' group as well as *Arthrobacter rhombi*, *Arthrobacter halodurans* and *Arthrobacter woluwensis* [2].

Strain T11b^T was obtained from an ulcer of Atlantic salmon collected in southern Chile in November 2013 (S 35° 45′ 0″ W 71° 0′ 0″), in the course of searching for *Flavobacterium psychrophilum* causing ulcers on salmonids in the freshwater life cycle stage [3]. The strain was isolated on TYES agar plates (tryptone yeast extract [4]) and was obtained in

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The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain T11b^T is MK211245. The Whole Genome Shotgun project has been deposited at DDBJ/ENA/GenBank under the accession UXAU00000000. The version described in this paper is version UXAU0100000.
Two supplementary figures are available with the online version of this article.

mixed cultures. From this sample, two other morphotypes were observed, *F. psychrophilum* and the second which was identified by 16S rRNA gene sequencing as *Myroides profundi*, which have been isolated from deep-sea sediment but present best growth with media supplemented with 1% NaCl (w/v) [5]).

Strain T11b^T grew well aerobically on nutrient rich media such as tryptone soy agar and nutrient agar (both Oxoid), 3.3×PYE agar (1.0% peptone from casein, 1.0% yeast extract, 1.5% agar, pH 7.2) at 28 °C and in the corresponding liquid medium and was also able to grow on Columbia III agar (BD Becton Dickinson) supplemented with 5% sheep blood but not on MacConkey II agar (BD Becton Dickinson). Growth on Columbia III agar supplemented with 5% sheep blood was not observed anaerobically.

Gram-staining was done as previously described according to Gerhardt *et al*. [6]. Cell morphological characters were observed under a Zeiss light microscope at ×1000. The ability of the strain to grow at various pH values was determined in nutrient broth (Oxoid) which was adjusted prior to sterilisation to pH 3–11 (at 0.5 pH unit intervals). Growth at different temperatures in the range of 4–60 °C (4, 10–60 °C in 5 °C intervals) was also investigated in nutrient broth. The strain grew well at temperatures between 10–35 °C and not at 4 and 40 °C and above. In addition, the strain grew well in a pH range of 5.0–9.5. Weak growth was observed at pH 4.5.

The physiological/biochemical characterisation was performed to assess the carbon source utilisation pattern, and hydrolysis of chromogenic substrates according to Kämpfer *et al*. [7] at 30 °C.

The morphological, physiological, and biochemical characteristics of strain T11b^T are given in detail in the species description and in Table 1.

In order to assemble the draft genome of strain T11b^T, libraries were constructed using the Nextera XT DNA library preparation kit (Illumina) and sequenced on a NextSeq 500 instrument using a 2×150 bp paired-end protocol, leading to 4349580 read pairs (185× average sequencing depth, 426 bp average insert size). Sequenced reads were trimmed, clipped and corrected, and next assembled with SPAdes [8]. The draft genome of strain T11b^T has a total size of 3516174 bps, represented in 73 scaffolds, with an N50 value of 123793 bps. The G+C content is 64.27%, in the range 60–72 mol% of the genus *Arthrobacter* [2]. Scaffold sequences were processed with Prokka [9] for gene prediction and annotation, which led to the detection of 3300 coding genes, 49 tRNAs and three rRNAs.

Table 1. Differential characteristics between strain T11b^T and the reference strains

Strain: 1, T11b^T; 2, *Pseudarthrobacter siccitolerans* DSM 28024^T; 3, *Pseudarthrobacter defluvii* DSM 18782^T; 4, *Arthrobacter alkaliphilus* DSM 23368^T; 5, *Arthrobacter methylotrophus* DSM 14008^T. All data from this study. +, Positive reaction; (+), weakly positive reaction; –, negative reaction.

Test	1	2	3	4	5
Hydrolysis of aesculin	+	–	–	–	–
Utilisation of:					
N-Acetyl-D-glucosamine	–	+	–	+	–
D-Xylose	–	+	(+)	(+)	–
D-Sorbitol	–	+	+	(+)	(+)
D-Ribose	+	–	–	+	+

For 16S rRNA gene based phylogenetic analyses, the nearly full-length 16S rRNA gene of strains T11b^T was PCR-amplified and sequenced by the Sanger method with universal primers fd1 and rp1 [10]. Pairwise 16S rRNA gene sequence similarities to highest related type strains was determined by BLAST analysis against the 16S rRNA gene sequence database in EzBioCloud [11]. Phylogenetic trees were calculated in ARB release 5.2 [12] using the 'All-Species Living Tree' Project (LTP [13]) database release LTPs132 (June 2018). Sequences not included in the database were aligned with SINA (version 1.2.9) according to the SILVA seed alignment [14] and imported into the database. The alignment of sequences selected for the phylogenetic analyses was checked and corrected manually including secondary structure information. Phylogenetic trees were reconstructed with the neighbour-joining method [15] and the Jukes–Cantor correction model [16], the maximum-likelihood method using RAxML version 7.04 [17] with GTR-GAMMA and rapid bootstrap analysis, and the maximum-parsimony method using DNAPARS version 3.6 [18]. Final trees based on 100 re-samplings (bootstrap analysis [19]) and 16S rRNA gene sequences between *E. coli* positions 89–1399 (*Escherichia coli* numbering according to Brosius *et al*. [20]) included several *Arthrobacter* type strains and all type strains of species in the genus *Pseudarthrobacter* including the type species of both genera.

The 16S rRNA gene sequence of strain T11b^T represented a continuous stretch of 1407 bp spanning *E. coli* positions 46–1470 nt according to Brosius *et al*. [20]. 16S rRNA gene sequence similarity for strain T11b^T to next related type strains was 98.1% to *Pseudarthrobacter siccitolerans* 4J27^T (GU815139) followed by 98.0% to *Arthrobacter methylotrophus* TGA^T (AF235090) and *Pseudarthrobacter phenanthrenivorans* Sphe3^T (AM176541). The 16S rRNA gene sequence similarities to 22 further *Pseudarthobacter/Arthrobacter* type strains were in the range of 97.0–98.0%. Maximum likelihood and neighbour-joining trees are shown in Figs 1 and S1, available in the online version of this article, respectively.

Pairwise average nucleotide identity (ANI) values were calculated with the fastANI tool [21] between the genome sequence of strain T11b^T and the currently available genome sequences of four *Pseudarthrobacter* and 23 *Arthrobacter* type strains, leading to ANI percentages ranging from 80.91 to 81.14% (*Pseudarthrobacter*) and from 76.91 to 80.99% (*Arthrobacter*). Pairwise *in silico* DNA–DNA hybridization (isDDH) values were also estimated using the GGDC web service (formula

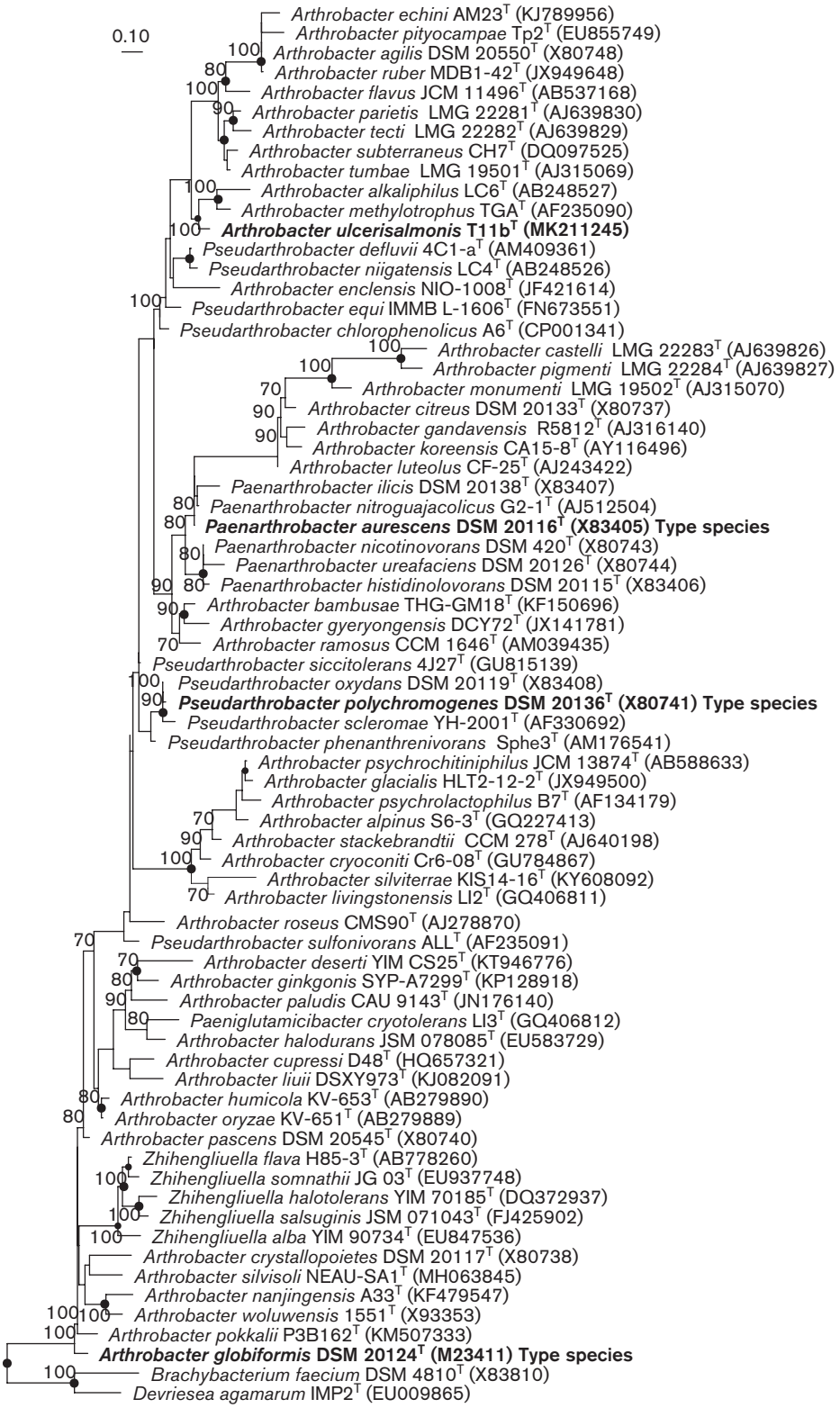

Fig. 1. Maximum-likelihood tree based on 16S rRNA gene sequences showing the relatedness of strain T11b^T to type strains of the species of the genera *Arthrobacter*/*Pseudarthrobacter*. The tree was generated in ARB using RAxML with the GTR-GAMMA model and rapid bootstrap analysis with 100 bootstraps. Type strains of the family *Dermabacteraceae* were used as outgroups. Numbers at nodes represent bootstrap values of 70% and above. Circles mark nodes which were also present in the maximum-parsimony and the neighbour-joining trees. Larger circles represent nodes supported with high bootstrap values (70% and above) in both alternative trees. Bar, 0.1 substitutions per nucleotide position.

2; ggdc.dsmz.de [22]), leading to percentages ranging from 19.30 to 22.00%. All these values were far below the generally accepted species delineation cut-off values (ANI, 95% [23]; isDDH, 70%).

The reconstruction of phylogenetic trees based on the nearly full-length 16S rRNA gene sequences showed independent of the applied treeing method that T11b^T formed a distinct cluster (supported by high bootstrap values; >70%) with the type strains of *Arthrobacter methylotrophus* and *Arthrobacter alkaliphilus*. The pairwise 16S rRNA gene sequence similarity to the latter one was only 97.2% (Acc. number AB248527). Strain T11b^T clustered neither with the type strain of the type species of the genus *Arthrobacter*, *Arthobacter globiformis*, nor of the genus *Pseudarthrobacter*, *Pseudarthrobacter polychromogenes*.

Isoprenoid quinones, polar lipids, diamino acid of the peptidoglycan and polyamines were extracted from biomass grown in 3.3×PYE broth (w/v; 1.0% peptone from casein, 1.0% yeast extract, pH 7.2) and harvested at the stationary growth phase except biomass for polyamine extraction which was harvested when the cells had reached the late exponential growth phase. Isoprenoid quinones and polar lipids were extracted and analysed according to the protocols of Tindall [24, 25] and Altenburger *et al.* [26]. The quinone system of strain T11b^T consisted of the major menaquinone MK-9(H_2) (85.5%), MK-10(H_2) (8.0%) and MK-8(H_2) (6.4%). Major menaquinone MK-9(H_2) is a characteristic of the genera *Pseudarthrobacter, Arthrobacter* and *Paenarthrobacter* [2]. The polar lipid profile (Fig. S2, supplementary data) was composed of the major lipids diphosphatidylglycerol, phosphatidylglycerol, monogalactosyldiacylglycerol, dimannosylglyceride and minor amouts of trimannosyldiacylglycerol and phosphatidylinositol. This polar lipid profile exhibits several characteristics also found in the type species of the genera *Arthrobacter* (*A. globiformis*) and *Pseudarthrobacter* (*P. polychromogenes*) but it is less complex than those of these two reference species [2]. Polyamines were extracted and analysed according to Busse and Auling [27] and Altenburger *et al.* [28]. The apparatus used for HPLC analyses was described by Stolz *et al.* [29]. The polyamine pattern of T11b^T contained the major component spermidine [3.01 µmol (g dry weight)$^{-1}$], minor amounts of putrescine [0.15 µmol (g dry weight)$^{-1}$], and traces of spermine and cadaverine [<0.1 µmol (g dry weight)$^{-1}$]. Polyamine patterns with the predominant compound spermidine were also reported for *P. polychromogenes* and *A. globiformis*.

The peptidoglycan was prepared and its detailed structure was analysed according to published protocols [30]. 1D- and 2D-TLC of the total hydrolysate of the peptidoglycan (4 N HCl, 16 h at 100 °C) revealed the presence of the amino acids lysine, alanine, glutamic acid, serine and threonine. After derivatization according to Protocol 10 [30], the approximate molar amino acid ratio was determined by gas chromatography (Shimadzu GC 14A) as follows: 2.5 Ala; 0.8 Thr; 0.9 Ser; 1.0 Glu; 0.8 Lys. Chiral amino acid analysis of the total hydrolysate (Protocol 11) resulted in the detection of L-Ala, D-Ala, L-Thr, L-Ser, D-Glu and L-Lys. 2D-TLC of the partial hydrolysate (4 N HCl, 100 °C, 45 min) of the peptidoglycan revealed the presence of the peptides L-Ala–D-Glu, L-Lys–D-Ala, L-Lys–L-Ser, L-Lys–L-Ser–L-Thr, D-Ala–L-Lys–L-Ser, D-Ala–L-Lys–L-Ser–L-Thr and L-Ser–L-Thr. On the basis of these results, the following peptidoglycan type of strain T11b^T was concluded: A3α L-Lys–L-Ser–L-Thr–L-Ala (A11.23 according to www.peptidoglycan-types.info). The peptidoglycan structure A11.23 is typical of the genus *Pseudarthrobacter* and is also shared by the related species *Arthrobacter alkaliphilus* ([31] and own data). However, despite of the even higher 16S rRNA gene sequence similarity to strain T11b^T, *A. methylotrophus* displays a different peptidoglycan structure (L-Lys–L-Ala$_{2-4}$ [32]).

Table 2. Cellular fatty acid compositions (%) of strain T11b^T and the reference strains

Strain: 1, T11b^T; 2, *Pseudarthrobacter siccitolerans* DSM 28024^T; 3, *Pseudarthrobacter defluvii* DSM 18782^T; 4, *Arthrobacter alkaliphilus* DSM 23368^T; 5, *Arthrobacter methylotrophus* DSM 14008^T.

Data were obtained with the Sherlock MIDI version 2.1 (TSBA version 4.1) with biomass obtained after growth on tryptone soy agar at 28 °C for 48 h. –, not detected. Data for (1) to (3) from this study. Data for *A. alkaliphilus* DSM 23368^T from Ding *et al.* [31] and for *A. methylotrophus* DSM 14008^T from Borodina *et al.* [32] obtained under exactly the same conditions.

Fatty acid	1	2	3	4	5
iso-$C_{14:0}$	1.5	2.9	7.7	0.7	1.9
$C_{14:0}$	–	–	2.7	0.2	0.9
$C_{15:0}$	–	–	–	–	0.2
iso-$C_{15:0}$	2.2	15.2	10.3	4.5	7.1
iso-$C_{16:1}$ H	–	1.5	1.6	–	–
anteiso-$C_{15:0}$	64.3	48.9	58.4	58.0	74.7
iso-$C_{16:0}$	10.5	11.2	9.2	7.1	5.7
iso-$C_{17:0}$	–	1.3	–	1.4	0.3
anteiso-$C_{17:0}$	16.6	11.9	4.2	20.1	6.8
$C_{16:1}$ω7*c* and/or iso-$C_{15:0}$ 2-OH	–	1.3	1.3	0.7	–
anteiso-$C_{17:1}$ω9*c*	–	1.9	–	–	–
$C_{16:0}$	5.0	3.9	3.3	1.1	1.6
$C_{18:1}$	–	–	–	–	0.7
$C_{18:3}$ω16,7/12*c*	–	–	1.4	–	–

Production of biomass, extraction and analysis of fatty acids was carried out as described by Kämpfer and Kroppenstedt [33]. The fatty acid profile (Table 2) was composed predominantly of anteiso- and iso-branched fatty acids, with anteiso-$C_{15:0}$, iso-$C_{16:0}$ and anteiso-$C_{17:0}$ as predominating fatty acids. This fatty acid profile was qualitatively quite similar to that of *Pseudarthrobacter* species such as *Pseudarthrobacter siccitolerans* DSM 28024^T and *Pseudarthrobacter defluvii* DSM 18782^T and also *A. alkaliphilus* DSM 23368^T and *A. methylotrophus*

DSM 14008^T but slight quantitative differences in the contents of several fatty acids were detected between the strains under comparison (Table 2).

The results of the comparative physiological characterisation using identical test conditions [7] for the type strains of the species *P. siccitolerans* DSM 28024^T, *P. defluvii* DSM 18782^T, *A. alkaliphilus* DSM 23368^T, and *A. methylotrophus* DSM 14008^T are shown in Table 1.

The results from 16S rRNA gene analyses, ANI calculations and isDDH estimates showed that T11b^T is different from known species of the genus *Arthrobacter*. Because strain T11b^T always clustered on the basis of 16S rRNA gene sequence analyses together with strains *A. alkaliphilus* DSM 23388^T and *A. methylotrophus* DSM 14008^T (Fig. 1), DNA–DNA hybridization (DDH) experiments were performed with strain T11b^T and the type strains *A. alkaliphilus* and *A. methylotrophus* according to the method of Ziemke *et al.* [34] (except that for nick translation 2 µg DNA was labelled during 3 h of incubation at 15 °C). Strain T11b^T showed moderate to low DNA–DNA similarities to *A. alkaliphilus* DSM 23388^T (34%) and *A. methylotrophus* DSM 14008^T (19%), therefore confirming the estimated isDDH values (see above).

Strain T11b^T agrees in its peptidoglycan structure and other chemotaxonomic characteristics to members of the genus *Pseudarthrobacter* and *A. alkaliphilus* but differs in its peptidoglycan structure from the related type strain of *A. methylotrophus* and does not show high 16S rRNA gene sequence similarities neither to the type strain of the type species *P. polychromogenes* nor to *A. globiformis*. Because of lacking support by the 16S rRNA gene phylogeny and the as-yet incomplete set of genome sequences available for the genera *Arthrobacter* and *Pseudarthrobacter*, we refrain at the time being from affiliating our isolate to the genus *Pseudarthrobacter* despite of existing chemotaxonomic arguments. Therefore it is proposed to classify strain T11b^T into the genus *Arthrobacter sensu lato* [2] as type strain of a new species *Arthrobacter ulcerisalmonis* sp. nov. and to emend the description of *Arthrobacter sensu lato* for the inclusion of the peptidoglycane type A11.23.

This is the first description of a member of *Arthrobacter* isolated from fish.

EMENDED DESCRIPTION OF THE GENUS *ARTHROBACTER* CONN AND DIMMICK 1947, EMEND. KOCH *ET AL.* 1995, EMEND. BUSSE 2016 *SENSU LATO*

Cells exhibit a rod-coccus cycle but exclusively coccoid cells may occur. The peptidoglycan type is A3α and comprises the variations Lys–Ala$_{1-4}$, Lys–Thr–Ala$_{1-3}$, Lys–Ala–Ser–Ala$_3$, Lys–Gly–Ala$_3$ and Lys–Ser–Thr–Ala. The peptidoglycan type A4α with the variations Lys–D-Asp and Lys–Ala–D-Glu may be present in some species. The quinone system usually contains MK-9(H$_2$) as predominant component but almost equal amounts of MK-9(H$_2$) and MK-8(H$_2$) or MK-8(H$_2$) as major components may occur. The polar lipid profile contains predominantly diphosphatidylglycerol, phosphatidylglycerol, phosphatidylinositol and dimannosylglyceride. The fatty acid profile is dominated by anteiso- and iso-methyl-branched acids. The major fatty is usually anteiso-C$_{15:0}$. Fatty acids iso-C$_{15:0}$, iso C$_{16:0}$ and anteiso-C$_{17:0}$ often contribute significantly to the profile. The type species is *Arthrobacter globiformis*.

DESCRIPTION OF *ARTHROBACTER ULCERISALMONIS* SP. NOV.

Arthrobacter ulcerisalmonis (ul.ce.ri.sal.mo'nis. L. neut. n. *ulcus*, *-eris* ulcer; L. masc. n. *salmo*, *salmonis* a salmon; N.L. gen. n. *ulcerisalmonis* of an ulcer of a salmon).

Cells are Gram-stain positive, non-spore-forming, coccoid and sometimes irregular non-motile rods, which grow aerobically. On TSA the strain produces creamy-whitish to beige, non-translucent colonies with a diameter of approximately 0.5 mm. The cells are not typical rods but coccoid to irregular rods. Oxidase-negative. Catalase-positive. Good growth occurs on nutrient rich media, like TSA and nutrient agar, PYE agar and blood agar but not on MacConkey agar. CAMP-negative with *S. aureus*. On nutrient agar growth is observed at temperatures between 10 and 35 °C and not at 4 °C and below and 40 °C and above. In addition, good growth at pH 5.0–9.5. Weak growth at pH 4.5.

The peptidoglycan is of the type A3α L-Lys–L-Ser–L-Thr–L-Ala (A11.23). Major respiratory quinone is menaquinone MK-9(H$_2$). The polyamine pattern contains predominantly spermidine. The polar lipid profile consists of the major lipids diphosphatidylglycerol, phosphatidylglycerol, monogalactosyl-diacylglycerol and dimannosylglyceride. Minor amounts of trimannosyldiacylglycerol and phosphatidylinositol are also detected. In the fatty acid profile, anteiso and iso branched fatty acids predominate (anteiso-C$_{15:0}$, iso C$_{16:0}$, anteiso-C$_{17:0}$).

N-Acetyl-D-glucosamine, D-fructose, D-galactose, D-gluconate, D-glucose, D-mannose, D-ribose, acetate, propionate, fumarate, citrate, and pyruvate are assimilated, but *N*-acetyl-D-galactosamine, L-arabinose, p-arbutin, cellobiose, α-melibiose, L-rhamnose, sucrose, salicin, D-xylose, adonitol, i-inositol, maltitol, D-mannitol, D-sorbitol, putrescine, *cis*-aconitate, *trans*-aconitate, adipate, 4-aminobutyrate, azelate, glutarate, DL-3-hydroxybutyrate, itaconate, mesaconate, oxoglutarate, suberate, L-alanine, ß-alanine, L-leucine, L-ornithine, L-phenylalanine, L-proline, L-tryptophane, 3-hydroxybenzoate, 4-hydroxybenzoate, and phenylacetate are not. Acid is produced (weakly) from glucose, but not from lactose, sucrose, D-mannitol, dulcitol, salicin, adonitol, inositol, sorbitol, L-arabinose, raffinose, rhamnose, maltose, D-xylose, trehalose, cellobiose, methyl-D-glucoside, erythritol, melibiose, D-arabitol, and D-mannitol. Aesculin, bis-pNP-phosphate, pNP-phenyl-phosphonate, and 2-deoxythymidine-5'-pNP-phosphate are hydrolysed. oNP-ß-D-Galactopyranoside, pNP-ß-D-glucuronide, pNP-alpha-D-glucopyranoside, pNP-ß-D-glucopyranoside,

pNP-ß-D-xylopyranoside, pNP-phosphoryl-choline, 2-deox ythymidine-5'-pNP-phosphate, and L-glutamate-gamma-3-carboxy-pNA are not hydrolysed.

The type strain is strain T11b^T (=CIP 111621^T=CCM 8854^T=LMG 30632^T=DSM 107127^T) from an ulcer of a farmed Atlantic salmon (*Salmo salar*).

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

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