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TAXONOMIC DESCRIPTION

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Lysobacter silvestris sp. nov., isolated from alpine forest soil, and reclassification of *Luteimonas tolerans* as *Lysobacter tolerans* comb. nov.

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Abstract

A Gram-stain-negative, rod-shaped, motile, catalase-positive and cytochrome *c* oxidase-positive bacterial strain, designated AM20-91^T, was isolated from alpine forest soil. Phylogenetic analysis based on 16S rRNA gene sequencing showed that strain AM20-91^T was related to the genus *Lysobacter* and had highest 16S rRNA gene sequence similarities to the type strains of *Lysobacter novalis* THG-PC7^T (97.8 %), *Luteimonas tolerans* UM1^T (97.7 %) and *Lysobacter ximonensis* XM415^T (97.0 %). The strain contained ubiquinone 8 as the predominant respiratory quinone; its polar lipid profile contained phosphatidylethanolamine, phosphatidylglycerol, diphosphatidylglycerol and two unidentified aminophospholipids. The major cellular fatty acids (>10 %) were iso-$C_{15:0}$, iso-$C_{11:0}$ 3-OH and iso-$C_{11:0}$. The DNA G+C content was 63.35 % (draft genome sequence). The combined results of phylogenetic, phenotypic, DNA–DNA relatedness and chemotaxonomic analyses demonstrated that strain AM20-91^T represents a novel species of the genus *Lysobacter*, for which the name *Lysobacter silvestris* sp. nov. is proposed. The type strain is AM20-91^T (=DSM 104734^T=LMG 30011). In this study, it is also proposed that *Luteimonas tolerans* be reclassified as member of the genus *Lysobacter*.

The genus *Lysobacter* was first proposed by Christensen and Cook [1] and belongs to the family *Xanthomonadaceae* of the *Gammaproteobacteria*. At the time of writing, this genus comprises 46 species with validly published names. Cells of the members of the genus *Lysobacter* stain Gram-negative, are aerobic and rod-shaped with variable motility, chemoorganotrophic, negative for urease and indole production, contain ubiquinone 8 as the major respiratory quinone and have high DNA G+C contents. Strains of this genus have been isolated from various environmental sources, including soil, sediments and aqueous habitats. In this study, we describe a novel representative of the genus *Lysobacter* isolated from alpine forest soil.

Strain AM20-91^T was isolated in the course of a study on microbial diversity in forest soils along an altitude gradient in South Tyrol in the Alps [2]. The strain was isolated from soil collected in Montiggl, South Tyrol, Italy, at 545 m above sea level in Autumn 2014. Ten grams of sample were shaken with 90 ml of sterile 0.1 % sodium pyrophosphate for 15 min at 150 r.p.m. Appropriate dilutions, prepared with sterile saline solution (0.9 % w/v), were plated on Reasoner's 2A (R2A) agar [3] amended with cycloheximide to exclude fungal growth and were incubated at 20 °C. One of the pure cultures was designated strain AM20-91^T. The strain was routinely cultured on R2A agar at 25 °C and stored at −80 °C in R2A broth supplemented with 15 % (w/v) glycerol. *Lysobacter ximonensis* DSM 23410^T [4], *Lysobacter novalis* CCTCC AB2014319^T [5] and *Luteimonas tolerans* DSM 28473^T [6], were used as reference strains in this study and were routinely grown on R2A agar at 25 °C.

Total genomic DNA was extracted as described previously [7]. The 16S rRNA gene was amplified by PCR with the forward primer 5′-AGAGTTTGATCCTGGCTCAG-3′ and the reverse primer 5′-AAGGAGGTGATCCAGCCGCA-3′. PCR-amplification of the 16S rRNA gene was carried out as described previously [8]. The PCR product was purified and the 16S rRNA gene sequence was determined by Sanger sequencing (Macrogen). On the basis of pairwise comparisons

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Keywords: alpine; forest; *Lysobacter*; *Luteimonas*.
Abbreviations: ML, maximum-likelihood; NA, nutrient agar; NJ, neighbour-joining; R2A, Reasoner's 2A; TSA, trypticase soy agar.
The GenBank accession number for the 16S rRNA gene sequence of *Lysobacter silvestris* AM20-91^T is KP899165. The draft genome accession number for strain AM20-91^T is NPZB00000000.
Three supplementary tables and three supplementary figures are available with the online version of this article.

of the 16S rRNA gene sequences using the recent version of the EzTaxon program [9], strain AM20-91^T was most similar to *Lysobacter novalis* THG-PCT7^T (97.8 %), *Luteimonas tolerans* UM1^T (97.7 %) and *Lysobacter ximonensis* XM415^T (97.0 %). Multiple sequence alignments were performed using the CLUSTAL_W program integrated in MEGA version 6.0 [10]. Phylogenetic trees were reconstructed by using the neighbour-joining (NJ) and maximum-likelihood (ML) algorithms using MEGA version 6.0 [11]. For the NJ and ML algorithms, genetic distances were calculated using the Kimura two-parameter model [12] and the pairwise deletion option was used. The tree topologies generated from two methods were evaluated by bootstrap analysis based on 1000 replicates. The reconstructed phylogenetic tree based on the NJ algorithm revealed that strain AM20-91^T grouped with the members of the genus *Lysobacter* and formed a coherent cluster with *Lysobacter novalis* THG-PC7^T, *Luteimonas tolerans* UM1^T and *Lysobacter ximonensis* XM415^T (Fig. 1). This phylogenetic position was confirmed in the tree generated using the ML algorithm (Fig. S1, available in the online version of this article).

Cell morphology was examined by phase-contrast microscopy and by transmission electron microscopy (Zeiss Libra 120 EFTEM) of cells grown on R2A agar. Motility was examined by microscopy (×1000) and on soft agar (0.3 % agar) plates. Gram-staining was tested by using the bioMérieux Gram-stain kit. Catalase activity was determined by bubble production in 3 % (v/v) H_2O_2 and cytochrome *c* oxidase activity was determined using 1 % (w/v) *N*,*N*,*N*′,*N*′-tetramethyl-*p*-phenylenediamine. Physiological and biochemical characteristics and enzyme activities were determined with the API ZYM (4 h of incubation at 30 °C) and API 20 NE (up to 4 days of incubation at 25 °C) systems (bioMérieux). Degradation of starch (amylase), skimmed milk (protease), carboxymethyl cellulose (cellulase) and Tween 80 (lipase–esterase) was tested after 4–7 days at 25 °C on R2A agar supplemented with the appropriate substrates as described previously [13]. The assimilation of a number of compounds as the sole carbon source (see species description) at a final concentration of 0.2 % (w/v) was tested after 4–7 days at 25 °C in liquid culture in phosphate-buffered pH-neutral mineral medium supplemented with trace elements and vitamins [14]. Fermentative metabolism of glucose was determined on Hugh and Leifson's OF basal medium (1 % glucose, 0.2 % peptone, 0.1 % yeast extract, 0.5 % NaCl, 0.02 % K_2HPO_4, 0.008 % bromothymol blue, 0.3 % agar) covered with oil. Aerobic growth on different media was assessed at 25 °C on R2A agar, nutrient agar (NA; 0.5 % peptone, 0.3 % meat extract, 1.5 % agar; pH 7) and trypticase soy agar (TSA; 1.5 % casein peptone, 0.5 % soy peptone, 0.5 % sodium chloride, 1.5 5 agar; pH 7). Growth under anaerobic conditions was examined after 7 days of incubation at 25 °C in an anaerobic jar [containing Anaerocult A (Merck) to produce anaerobic conditions] on R2A agar and on NA, each supplemented with 10 mM KNO_3. Growth at 0, 5, 10, 15, 20, 25, 30, 35 and 40 °C was determined in R2A broth and on R2A agar. Growth at pH 5.0, 5.5, 6.0, 6.5, 7.0, 8.5, 9.0, 9.5 and 10.0 (using medium buffered with citrate buffer for pH 5, phosphate buffer for pH 6–7, Tris buffer for pH 8–10) was determined in R2A broth. Growth in the presence of 0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5 4.0, 4.5 and 5.0 % (w/v) NaCl was determined in R2A broth. All tests were carried out simultaneously with strain AM20-91^T, *Lysobacter ximonensis* DSM 23410^T, *Lysobacter novalis* CCTCC AB2014319^T and *Luteimonas tolerans* DSM 28473^T. The morphological, physiological and biochemical characteristics of strain AM20-91^T are given in the species description, and the features that differentiate the investigated strain from the reference strains are given in Table 1.

For chemotaxonomic analyses, strain AM20-91^T and the reference strains *Lysobacter ximonensis* DSM 23410^T, *Lysobacter novalis* CCTCC AB2014319^T and *Luteimonas tolerans* DSM 28473^T were grown in R2A broth until the late exponential phase at 25 °C. Cells were harvested by centrifugation and washed in 0.1 M Tris-HCl, pH 7.5, before subsequent analyses. Fatty acid methyl esters (FAMEs) were obtained from fresh wet biomass, separated, identified and quantified with the standard MIS Library Generation Software, version 6.0, aerobe TSBA method (Microbial ID) as described previously [15]. The major fatty acids of the novel species represented by strain AM20-91^T were primarily composed of branched chain iso- and anteiso-fatty acids, as those of other closely related species of the genus *Lysobacter* and the closely related *Luteimonas tolerans*. However, the fatty acid composition of the species examined was distinct for each species, mainly due to the values obtained for iso-$C_{15:0}$, anteiso-$C_{15:0}$, iso-$C_{11:0}$ 3-OH and iso-$C_{15:1}$ F (Table S1).

Respiratory lipoquinones were extracted from freeze-dried cells and purified by thin-layer chromatography (TLC). The purified lipoquinones were separated by high-performance liquid chromatography as described previously [16]. The major respiratory lipoquinone was ubiquinone 8, as identified in all members of the family *Lysobacteraceae* examined in this study and in line with previous descriptions [4–6].

Polar lipids were extracted from freeze-dried cells and the individual polar lipids were separated by two-dimensional TLC. To visualize phospholipids, aminolipids, glycolipids and total lipids, the following reagents were used, respectively: molybdenum blue, ninhydrin, α-naphthol-sulfuric acid and molybdophosphoric acid [17]. The major polar lipid profile of strain AM20-91^T revealed the presence of phosphatidylethanolamine, phosphatidylglycerol and diphosphatidylglycerol; two unidentified aminophospholipids were also detected. The polar lipid patterns of the type strains of *Lysobacter novalis*, *Lysobacter ximonensis* and *Luteimonas tolerans* were basically similar to that of strain AM20-91^T (Fig. S2).

DNA–DNA hybridizations were done by the spectrophotometric renaturation method [18] as modified by Huss *et al.* [19]. DNA–DNA hybridizations were carried out in 2×SSC at 79 °C and each determination was done in triplicate. Both experiments were performed at 260 nm with a model Lambda 35 UV/VIS spectrometer equipped with a Peltier

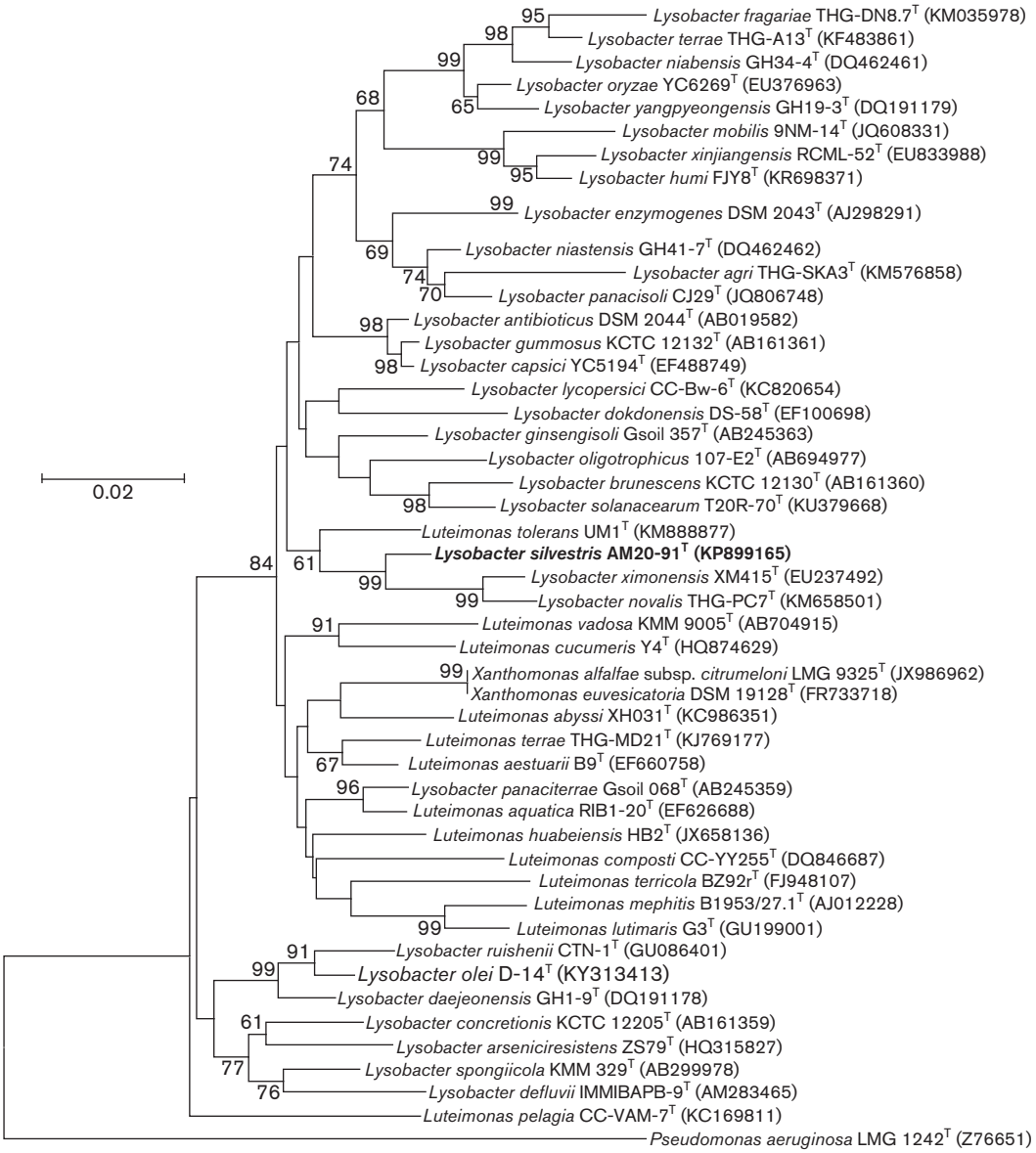

Fig. 1. Neighbour-joining tree, based on 16S rRNA gene sequence data, showing the phylogenetic position of strain AM20-91^T, other members of the genus *Lysobacter*, and representatives of some related taxa of the family *Xanthomonadaceae*. Bootstrap values (%) are based on 1000 replicates and are shown for branches with more than 50 % support. The 16S rRNA gene sequence of *Pseudomonas aeruginosa* LMG 1242^T was used as an outgroup. GenBank accession numbers of 16S rRNA sequences are given in parentheses. Bar, 0.02 substitutions per nucleotide position.

System (PTP 1+1) (Perkin–Elmer). The DNA–DNA hybridization experiments revealed that strain AM20-91^T shared 41 % DNA relatedness with *Lysobacter ximonensis* DSM 23410^T, 29 % with *Lysobacter novalis* CCTCC AB2014319^T and 34 % *Luteimonas tolerans* DSM 28473^T (Table S2). All these values were well below the 70 % cut-off point recommended for the assignment of strains to the same genospecies [20].

The draft genome of strain AM20-91^T was obtained by extraction of total genomic DNA following the method of Nielsen *et al.* [7]. The DNA was prepared with the Nextera XT DNA Library Preparation Kit and sequenced using paired-end 2×300 bp on the MiSeq (Illumina). Sequenced reads were quality filtered with Trimmomatic [21] and assembled with SPAdes (version 3.9.0; [22]). Resulting contigs were annotated with Prokaryotic Genome Prediction (PGP) [23]. Genome-estimated completeness and contamination were verified with CheckM (version 1.0.7) [24]. 16S rRNA gene analysis was performed with RNAmmer (version 1.2) [25].

Table 1. Characteristics that differentiate strain AM20-91^T from type strains of phylogenetically closely related species

Strains: 1, AM20-91^T; 2, *Lysobacter novalis* CCTCC AB2014319^T; 3, *Luteimonas tolerans* DSM 28473^T; 4, *Lysobacter ximonensis* DSM 23410^T. All data are from this study. All strains are positive for aerobic growth, growth on R2A and NA, catalase, cytochrome *c* oxidase, alkaline phosphatase, acid phosphatase, esterase lipase (C8), leucine arylamidase, valine arylamidase, cysteine arylamidase (weak), trypsin, α-chymotrypsin (weak), naphthol-AS-Bi-phosphohydrolase and α-glucosidase in the API ZYM and API 20NE systems and utilize yeast extract as sole source of carbon and energy. All strains are negative for anaerobic growth, nitrate reduction, indole production, α-galactosidase, β-glucuronidase, α-mannosidase, α-fucosidase, arginine dihydrolase and urease in the API ZYM and API 20NE systems, hydrolysis of starch (amylase) and carboxymethylcellulose (cellulase) on agar plates, glucose fermentation, utilization of L-arabinose, glucosamine, D-xylose, cellobiose, lactose, sucrose, glycerol, benzoate, fumarate and DL-lactate. +, Positive; W, weak; –, negative.

Characteristic	1	2	3	4
(Polar) flagellum	+	–*	–†	–‡
DNA G+C content (%)	63.4	62.5*	64.3†	63.5‡
Growth at/with:				
Temperature range (°C)	5 (weak)–30	10–35	10–35	10–35
2–3 % (w/v) NaCl	–	–	+	–
Enzyme assays (API ZYM, API 20NE):				
Lipase (C14)	–	–	+	–
β-Galactosidase	+	+	–	+
β-Glucosidase	+	–	–	+
N-acetyl-β-D-glucosaminidase	+	+	–	+
Hydrolysis on agar plates:				
Skimmed milk (protease)	–	+	W	+
Utilization as sole carbon source:				
N-acetyl-β-D-glucosamine	+	+	–	+
Fructose	–	W	–	–
Galactose	–	–	–	+
D-Glucose	+	+	–	–
Maltose	+	+	–	+
Trehalose	W	–	–	–
Pyruvate	+	+	–	+
Succinate	W	–	–	–

*Data from Singh *et al.* [5].

†Data from Rani *et al.* [6].

‡Data from Wang *et al.* [4].

Pairwise average nucleotide identity analysis was conducted with JSpecies [26] with *Luteimonas tolerans* UM1^T although the closest *Lysobacter* genomes, *L. ximonensis* and *L. novalis*, were not available for this analysis. The AM20-91^T DNA genome run generated 4 683 201 paired-end reads of which 3 278 083 high-quality reads remained after quality filtering. The *de novo* read assembly produced 3 contigs with an N50 size of 1 664 168 bp (Table 2). The high-quality draft assembled genome sequence consisted of 2 847 002 bp with a DNA G+C content of 63.35 %, which is within the reported range of DNA G+C contents of species of the genus *Lysobacter* (between 61.7 and 70.7 %). CheckM estimated the genome to be near-completion (98.67 %) and the level of contamination to be extremely low (0.87 %). No contamination was detected for the 16S rRNA gene. The genome had a total of 2599 genes, including 2549 protein-coding genes, 47 tRNA genes and three rRNA genes (one 5S, one 16S and one 23S) (Table 2). The draft genome comprised 2255 genes with putative functions (~89 % of total protein-coding genes) and 1649 allocated to COG functional categories (~73 % of total protein-coding genes). The most abundant COG-identified category was 'translation, ribosomal structure and biogenesis' followed by 'amino acid transport and metabolism' and 'cell wall/membrane biogenesis' (Table S3). The average nucleotide identity value between AM20-91^T and *Luteimonas tolerans* UM1^T was 72.88 % (based on a 42.17 % alignment of the genome), indicating that the organisms represented two species.

A phylogenetic tree of core proteins was reconstructed to better understand the phylogenic relationships of the new organism to other members of the genera *Lysobacter* and *Luteimonas*. PhyloPhlAn 0.99 [27] was used to identify 400 universally conserved proteins from genomes available in the NCBI database by translated mapping with USEARCH 5.1 [28]. Each protein was aligned with Muscle 3.8 [29] to the conserved proteins and the most informative amino acid positions were concatenated. The concatenated alignment was used to reconstruct an ML phylogenetic tree with the Jones–Taylor–Thorton amino acid substitution model, using FastTree 2.1 [30]. Moreover, the CAT model and gamma correction were used to optimize and rescale the tree. The resulting tree, visualized using MEGA 6.06 [10], is shown in Fig. 2.

Multigene phylogenetic analysis was performed with the closest representatives of the genera *Lysobacter* and *Luteimonas* whose genomes are available in the NCBI database, namely (*Lysobacter silvestris* (NPZB00000000), *Lysobacter capsici* 55 (GCF_001442785.1), *Lysobacter gummosus* 3.2.11 (GCF_001442805.1), *Lysobacter antibioticus* ATCC 29479^T (GCF_001442535.1), *Lysobacter enzymogenes* ATCC 29487^T (GCF_900106525.1), *Lysobacter daejeonensis* GH1-9^T (GCF_000768355.1), *Lysobacter concretionis* DSM 16239^T (GCF_000768345.1), *Lysobacter arseniciresistens* ZS79^T (GCF_000768335.1), *Lysobacter defluvii* DSM 18482^T (GCF_000768335.1) and *Lysobacter dokdonensis* DS-58 (GCF_000770795.1). Three genomes from the genus *Luteimonas* were also included, namely *Luteimonas tolerans* UM1^T (GCF_900155935.1), *Luteimonas huabeiensis* HB-2^T (GCF_000559025.1) and *Luteimonas abyssi* XH031^T (GCF_001482195.1), two genomes from the genus *Xanthomonas* (*Xanthomonas alfalfae* subsp. *alfalfae* CFBP 3836 (GCF_000488955.1) and *Xanthomonas campestris* pv. *vesicatoria* str. 85-10 (GCF_001854165.1) and the outgroup

Table 2. Genome sequencing project information and statistics of strain AM20-91^T

MIGS ID*	Attribute	Value/comment
MIGS-28	Libraries used	Illumina paired-end library (2×300 bp insert size)
MIGS 29	Sequencing platforms	Illumina MiSeq
	Size of raw data included in the assembly process (Mbp)	1390
MIGS 30	Assembler	Spades version 3.9.0
MIGS 31	Finishing quality	High-quality draft
MIGS 31.2	Sequencing depth of coverage	480×
MIGS 31.3	Number of contigs	3
MIGS 32	Gene calling method	PGP
	N50 (bp)	1 664 168
	Estimated genome completeness (%)	98.67
	Assembled genome size (bp)	2 847 002
	DNA coding (bp)	2 680 841
	DNA G+C (bp)	1 151 283
	DNA G+C (%)	63.35
	Total genes	2599
	Protein-coding genes	2549
	RNA genes	50
	tRNA genes	47
	rRNA genes	3
	5S	1
	16S	1
	23S	1
	Genes with function prediction	2255
	Genes assigned to COGs	1649
	Genes with Pfam domains	2077
	Genes with Tfam domains	901
	CRISPR repeats	0
	Estimated contamination (%)	0.87
	Authenticity of strain checked by	16S (rRNA gene from Sanger and genome sequencing)
	Accession number of the assembly	NPZB00000000
	Accession number of raw data the assembly	SRR5990291

*Based on MIGS recommendations [31].

Pseudomonas aeruginosa DSM 50071^T (GCF_001045685.1). This phylogenetic approach corroborated the results of the 16S rRNA sequence analysis and showed that *Luteimonas tolerans* was most closely related to strain AM20-91^T.

In view of the results obtained above, we propose that strain AM20-91^T is a representative of the genus *Lysobacter* and can be distinguished from all three reference strains (*Lysobacter ximonensis* DSM 23410^T, *Lysobacter novalis* CCTCC AB2014319^T and *Luteimonas tolerans* DSM 28473^T) by its flagellum-induced motility, its ability to utilize succinate as sole carbon source, and its inability to grow at 35 °C and to hydrolyse skimmed milk on agar plates (Table 1). In addition, strain AM20-91^T has different cellular fatty acid contents (regarding iso-$C_{15:0}$, anteiso-$C_{15:0}$, iso-$C_{11:0}$ 3-OH and iso-$C_{15:1}$ F; Table S1), different enzyme and carbon utilization patterns compared to the reference strains. Moreover, *Lysobacter novalis* TGH-PCT7^T, *Luteimonas tolerans* UM1^T, *Lysobacter ximonensis* XM415^T and strain AM20-91^T formed a phylogentic group. *Luteimonas tolerans* UM1^T is reclassified as member of the genus *Lysobacter* as *Lysobacter tolerans* comb. nov. (type strain UM1^T=DSM 28473^T=MCC 2572^T=KCTC 42936^T).

DESCRIPTION OF *LYSOBACTER SILVESTRIS* SP. NOV.

Lysobacter silvestris (sil.ves′tris. L. masc. adj. *silvestris* from forest).

Cells stain Gram-stain-negative and are rods with polar flagella, 0.4–0.5×1.1–1.7 µm in size after 2 days at 20 °C on R2A agar (Fig. S3). Colonies on R2A agar are light yellow, circular, convex and with an entire margin. Grows under aerobic conditions, unable to grow under anaerobic conditions. Grows on R2A agar and NA (weak), no growth on TSA. Grows well in R2A broth and on plates at 10–30 °C, with optimal growth

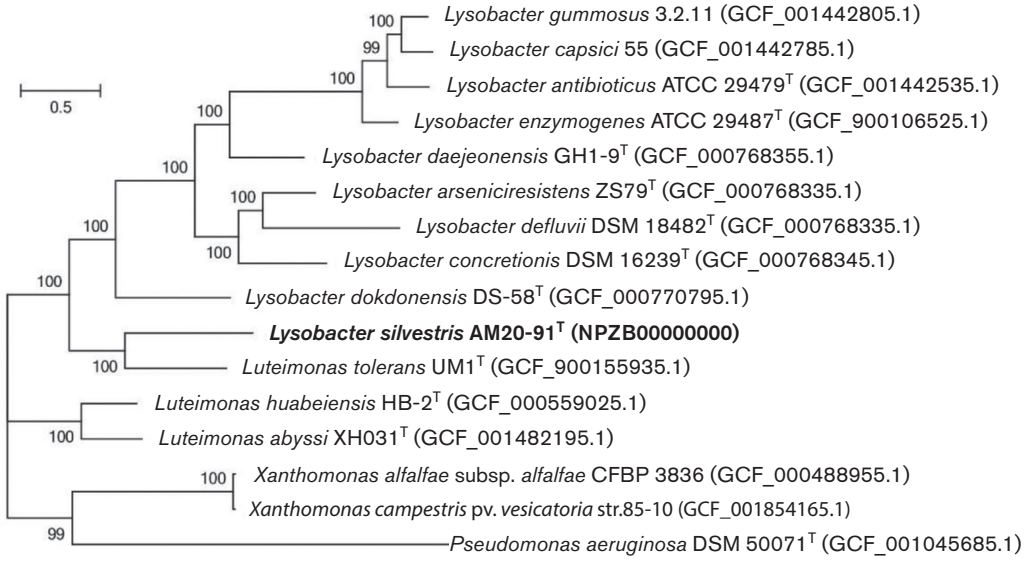

Fig. 2. Phylogenetic placement of strain AM20-91^T to other members of the genus *Lysobacter*, and representatives of some related taxa of the genera *Luteimonas* and *Xanthomonas* based on a set of 400 conserved bacterial genes. *Pseudomonas aeruginosa* DSM 50071^T was used as an outgroup. GenBank accession numbers of the genomes are given in parentheses. Bootstrap values were calculated based on 1000 replicates. The scale indicates the number of amino acid substitutions per site.

(in terms of fastest growth rates) at 25 °C and highest cell densities at 10–15 °C; growth is weak at 5 °C and absent at 0 °C and 35 °C. Grows at pH 6–7 (optimal growth at pH 6.5) and in the presence of 0–1.5 % (w/v) NaCl (optimal growth at 0 %). Positive for catalase, cytochrome *c* oxidase, alkaline phosphatase, acid phosphatase, esterase lipase (C8), leucine arylamidase, valine arylamidase, cysteine arylamidase (weak), trypsin, α-chymotrypsin (weak), naphthol-AS-Bi-phosphohydrolase, α-glucosidase, β-galactosidase, β-glucosidase and *N*-acetyl-β-D-glucosaminidase in API ZYM and API 20NE assays, and for utilization of yeast extract, glucose, *N*-acetyl-β-D-glucosamine, maltose, trehalose (weak), pyruvate and succinate (weak) as sole source of carbon and energy. Negative for nitrate reduction, indole production, lipase (C14), gelatinase, α-galactosidase, β-glucuronidase, α-mannosidase, α-fucosidase, arginine dihydrolase and urease in API ZYM and API 20NE assays, hydrolysis of starch skimmed milk (protease), starch (amylase), Tween 80 (lipase-esterase) and carboxymethylcellulose (cellulase) on agar plates, glucose fermentation, utilization of L-arabinose, D-fructose, galactose, glucosamine, D-xylose, cellobiose, lactose, sucrose, glycerol, benzoate, fumarate and DL-lactate. The predominant cellular fatty acids (>10 %) are iso-$C_{15:0}$, iso-$C_{11:0}$ 3-OH and iso-$C_{11:0}$. The polar lipid profile contains phosphatidylethanolamine, phosphatidylglycerol, diphosphatidylglycerol and two unidentified aminophospholipids. The major respiratory lipoquinone is ubiquinone 8.

The type strain is AM20-91^T (=DSM 104734^T=LMG 30011) and was isolated from alpine forest soil in Montiggl in South Tyrol, Italy. The genomic DNA G+C content is 63.35 %.

DESCRIPTION OF *LYSOBACTER TOLERANS* COMB. NOV.

Lysobacter tolerans [to'le.rans. L. part. adj. *tolerans* tolerating, referring to its ability to tolerate HCH (hexachlorocyclohexane)].

Basonym: *Luteimonas tolerans* Rani *et al.* 2016.

The description is identical to that given for *Luteimonas tolerans* by Rani *et al.* [6]. The type strain is UM1^T (=DSM 28473^T=MCC 2572^T=KCTC 42936^T).

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

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