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Modestobacter excelsi sp. nov., a novel actinobacterium isolated from a high altitude Atacama Desert soil

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ABSTRACT

A polyphasic study was undertaken to establish the taxonomic status of three *Modestobacter* strains isolated from a high altitude Atacama Desert soil. The isolates, strains 1G6^T, 1G14 and 1G50, showed chemotaxonomic and morphological properties characteristic of members of the genus *Modestobacter*. The peptidoglycan contained *meso*-diaminopimelic acid, the whole cell sugars were glucose and ribose (diagnostic sugars) and arabinose, the predominant menaquinone was MK-9(H_4), polar lipid patterns contained diphosphatidylglycerol, glycophosphatidylinositol, phosphatidylethanolamine (diagnostic component), phosphatidylglycerol and phosphatidylinositol while whole cellular fatty acid profiles consisted of complex mixtures of saturated, unsaturated iso- and *anteiso*-components. The isolates were shown to have different BOX-PCR fingerprint and physiological profiles. They formed a distinct phyletic line in *Modestobacter* 16S rRNA gene trees, were most closely related to the type strain of *Modestobacter italicus* (99.9 % similarity) but were distinguished from this and other closely related *Modestobacter* type strains using a combination of phenotypic properties. Average nucleotide identity and digital DNA:DNA hybridization similarities between the draft genome sequences of isolate 1G6^T and *M. italicus* BC 501^T were 90.9 % and 42.3 %, respectively, indicating that they belong to different species. Based on these phenotypic and genotypic data it is proposed that the isolates be assigned to a novel species in the genus *Modestobacter*, namely as *Modestobacter excelsi* with isolate 1G6^T (=DSM 107535^T =PCM 3004^T) as the type strain. Analysis of the whole genome sequence of *M. excelsi* 1G6^T (genome size of 5.26 Mb) showed the presence of genes and gene clusters that encode for properties that are in tune with its adaptation to extreme environmental conditions that prevail in the Atacama Desert biome.

Abbreviations: A_2pm, diaminopimelic acid; AL, aminolipids; APL, aminophospholipids; ANI, average nucleotide identity; ATP, adenosine triphosphate; BLAST, Basic Local Alignment Search Tool; CO, carbon monoxide; dDDH, digital DNA–DNA hybridization; DDH, DNA–DNA hybridization; DNA, deoxyribonucleic acid; DPG, diphosphatidylglycerol; GGDC, genome to genome distance calculator; GL, glycolipid; GPI, glycophosphoinositol; ECLs, equivalent chain lengths; IF, inoculating fluid; IMG/M, Integrated Microbial Genomes and Microbiomes System; ISP, International *Streptomyces* Project; IUPAC, International Union of Pure and Applied Chemistry; L, unidentified lipid; M., *Modestobacter*; MIDI, Microbial Identification System; MK, menaquinones; NCBI, National Center for Biotechnology Information; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; PI, phosphatidylinositol; PIM, phosphoinositolmannoside; PL, unidentified phospholipid; PYGV, peptone-yeast extract-glucose-vitamins agar; rRNA, Ribosomal RNA; T, transmitance; TLC, thin-layer chromatography TYGS Type (Strain) Genome Server; UV, ultraviolet.

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Introduction

The actinobacterial genus *Modestobacter* was proposed by Mevs et al. [46] and the description of the taxon subsequently emended by Reddy et al. [61], Xiao et al. [81], Qin et al. [59] and Montero-Calasanz et al. [49]. The genus is classified in the family *Geodermatophilaceae* [53] of the order *Geodermatophilales* [69] together with the genera *Blastococcus* [1], *Cumulibacter* [26], *Klenkia* [48] and *Geodermatophilus* [40]. *Modestobacter* strains can be distinguished from members of all of these taxa using a combination of genotypic and phenotypic features [48,49].

In general, *Modestobacter* strains are aerobic, Gram-stain-positive, non-spore-forming, heterotrophic, psychrotolerant actinobacteria which form rod- and coccoid-like elements that have a tendency to remain aggregated and produce short, multiseptate filaments; the diagnostic diamino acid is *meso*-diaminopimelic acid, the major fatty acid iso-$C_{16:0}$, the predominant respiratory quinone tetrahydrogenated menaquinone with nine isoprene units, a polar lipid profile containing diphospatidylglycerol, phosphatidylethanolamine and phosphatidylinositol, the characteristic whole-cell sugar pattern consists of glucose and ribose while the presence of arabinose, galactose, mannose and rhamnose is variable, and the genomic G + C content falls with the range 70–74 mol% [10,49].

The genus *Modestobacter* currently encompasses nine validly published species: *Modestobacter multiseptatus* [46,49,61], the type species, *Modestobacter caceresii* [10], *Modestobacter italicus* [49], *Modestobacter lacusdianchii* [85], *Modestobacter lapidis* [75], *Modestobacter marinus* [49,81], *Modestobacter muralis* [75], *Modestobacter roseus* [49,59] and *Modestobacter versicolor* [49,61]. Members of these taxa have been recovered from diverse habitats through they seem to be associated with extreme biomes, as exemplified by the isolation of *M. caceresii* from extreme hyper-arid Atacama Desert soils [10], *M. lapidis*, *M. muralis* and *M. italicus* from deteriorating sandstone [49,74], *M. marinus* from deep-sea sediment [81] and *M. multiseptatus* from an Antarctic surface soil [46]. Culture-independent surveys show that *Modestobacter* strains are a common feature of the Atacama Desert landscape [9,27] while interrogation of whole-genome sequences of *Geodermatophilaceae* strains, including that of the type strain of *M. caceresii*, show the presence of stress-related genes that provide an insight into how these microorganisms adapt to harsh environmental conditions associated with this desert biome [10,11,12]. It has been shown that *M. italicus* BC 501^T, previously misclassified as *M. multiseptatus* [23,70] and as *M. marinus* [55], is highly resistant to desiccation and to γ- and UV-radiation [23,70]. The genomes of *Modestobacter* strains contain multiple copies of several genes, such as *coxSML* (carbon monoxide dehydrogenase), *katA* (manganese-containing catalase) and *uvrACD* [10,55,70].

The present study, a continuation of our previous surveys on actinobacterial diversity in the Atacama Desert biome [8–12], was designed to establish the taxonomic status of three presumptive *Modestobacter* strains isolated from an arid high altitude soil. The strains, isolates 1G6^T, 1G14 and 1G50, were compared with reference strains of *Modestobacter* species using a combination of genotypic and phenotypic properties known to be of value in the delineation of *Modestobacter* species. The isolates were found to belong to a novel species of *Modestobacter*; the name proposed for this taxon is *Modestobacter excelsi* with isolate 1G6^T as the type strain.

Materials and methods

Isolation of strains

Three presumptive *Modestobacter* strains were isolated from a surface soil sample (2 cm depth) collected at 3018 m above sea level on Cerro Chajnantor (23°04′39″S/67°57′43″W), adjacent to the Atacama Large Millimeter Array (ALMA), east of San Pedro de Atacama, Chile in November 2012 [27]. The physicochemical properties of the soil sample (pH 7.08, 360 mv, moisture content 0 % and organic matter content 1.67 %) were determined by Bull et al. [9]. One gram of soil sample was diluted ten-fold with ¼ strength Ringer's solution (Oxoid) prior to preparing a 10^{-2} dilution using the same diluent. Aliquots (100 μl) of each dilution were spread, in triplicate, over plates of Gauze's No. 1 medium [84] supplemented with cycloxehimide and nystatin (each at 50 μg ml^{-1}), which had been dried for 15 min at room temperature prior to inoculation as recommended by Vickers and Williams [79]. After incubation at 28 °C for 3 weeks, the presumptive *Modestobacter* isolates were subcultured onto Gauze's agar plates to check their purity.

Maintenance and cultural conditions

Isolates 1G6^T, 1G14 and 1G50 were maintained on modified Bennett's agar slopes [28], pH 7.5, at room temperature and as suspensions of cells in 20 %, v/v glycerol at −80 °C. Biomass for most of the chemotaxonomic analyses and for the molecular systematic studies were harvested from 500 ml of modified Bennett's broth cultures which had been shaken at 150 rpm at 28 °C for 7 days following inoculation with 1 ml of each of the isolates prepared in the same medium. The resultant biomass preparations were washed three times with sterile distilled water and those for the molecular systematic analyses were stored at room temperature; biomass preparations for the chemotaxonomic studies were freeze dried. Biomass preparations of the isolates and *M. caceresii* KNN 45-2b^T, *M. italicus* BC 501^T, *M. lacusdianchii* KCTC 39600^T, *M. lapidis* MON 3.1^T, *M. marinus* DSM 45201^T, *M. multiseptatus* DSM 44406^T, *M. muralis* MDVD1^T, *M. roseus* DSM 45764^T and *M. versicolor* DSM 16678^T for the fatty acid analyses were prepared from plates of peptone-yeast extract-glucose-vitamins agar (PYGV, DSM medium 621) that had been incubated for 16 days at 20 °C.

Phylogenetic analyses

Genomic DNA was extracted from isolates 1G6^T, 1G14 and 1G50 and PCR-mediated amplification of 16S rRNA genes carried out following the procedures described by Golinska et al. [19,20]. PCR-products were purified using a PCR purification kit (Qiagen), according to the protocol of the manufacturer, checked for quality by using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific) and sequenced at the Institute of Biochemistry and Biophysics (IBB) of the Polish Academy of Sciences, Warsaw, Poland using an ABI 3730xl Genetic Analyzer (Applied Biosystems). The resultant 16S rRNA gene sequences (1400–1526 bp) were aligned using CLUSTAL W [33] against corresponding sequences of the type strains of *Modestobacter* species retrieved from the GenBank database using the EzBioCloud server [82].

Maximum-likelihood (ML) and maximum-parsimony (MP) phylogenetic trees based on the 16S rRNA gene sequences were inferred using the genome-to-genome distance calculator (GGDC) web server [44] adapted to single genes; the server was also used to calculate pairwise sequence similarities [42,45]. Multiple sequence alignments were generated using MUSCLE software [17]. The ML tree was inferred from the alignments with RAxML [72] 81) using rapid bootstrapping together with the auto maximal-relative-error (MRE) bootstrapping criterion [58]. The MP tree was inferred from the alignments with the Tree Analysis using New Technology (TNT) program [21] using 1000 bootstraps together with tree bisection and reconnection branch swapping and 10 random sequence replicates. The sequences

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were checked for computational bias using the x^2 test implemented in PAUP* [73]. A third phylogenetic tree was inferred using the neighbour-joining [66] algorithm with 1000 bootstrap replicates [18] and the MEGA 7 software package [32]. Evolutionary distances were calculated using the two-parameter model of Kimura [30]. The phylogenetic positions of the isolates, in all trees, were established by comparison with corresponding sequences from representative members of the family *Geodermatophilaceae*.

BOX typing

BOX-PCR fingerprints were generated from DNA extracted from the three isolates using the BOXAIR primer [78] and the experimental conditions described by Trujillo et al. [75].

Whole-genome sequencing

A colony of strain 1G6^T was used to inoculate 50 ml of modified Bennett's broth [28] and the preparation incubated at 28 °C in a shake flask (180 rpm) for 72 h. Genomic DNA was extracted from the harvested biomass and sequenced at MicrobesNG (http://www.microbesng.uk) on a MiSeq instrument (Illumina). The reads were trimmed using Trimmomatic [5] and their quality assessed using in-house scripts and Samtools [35,37], BedTools [60] and bwa-mem [36] software. The reads were assembled into contigs with Spades 3.6.2 software [57], contigs under 200 bp were discarded. The draft genome assembly was annotated using the RAST server [2] with default options and submitted to GenBank (accession no. SJEX00000000). The genome sequences of its closest phylogenetic neighbours, *M. italicus* BC 501^T and *M. caceresii* KNN 45-2b^T, were obtained from GenBank (accession numbers: FO203431 and JPMX00000000, respectively), that of *M. roseus* DSM 45764^T from the Integrated Microbial Genomes and Microbiomes System (IMG/M) [13] (IMG genome ID: 2585427561) while the sequence of *M. marinus* DSM 45201^T was provided by Vartul Sangal from Northumbria University, UK (IMG genome ID: 2820994125).

The digital DNA-DNA hybridization (dDDH) value between the draft genome of strain 1G6^T and that of the type strain of *M. italicus*, its closest phylogenetic neighbour, was determined using the GGDC server [42] and the corresponding values between the draft genome of strain 1G6^T and those of the three remaining strains mentioned above were calculated using the TYGS platform [43]. The average nucleotide identity (ANI) values between the draft genome of strain 1G6^T and those of its four closest phylogenetic neighbours were calculated according to Rodriguez and Konstantinidis [63]. Gene sequences encoding proteins involved in stress responses were sought in the genome of strain 1G6^T using the SEED server with default settings [3]. In addition, the genome of strain 1G6^T was examined for gene clusters encoding for natural products using anti-SMASH 4.0 software [4].

Chemotaxonomy

Standard chromatographic procedures were used to detect diagnostic chemical markers of the isolates from freeze-dried biomass. Analysis of the isomers of diaminopimelic acid (A_2pm) was achieved after Lechevalier & Lechevalier [34] and Hasegawa et al. [24]. Menaquinones extracted following Collins et al. [15] were analysed by high performance liquid chromatography [31] and extracted polar lipids identified by two-dimensional thin-layer chromatography (TLC), as described by Minnikin et al. [47]. Extracted whole-organism sugars were analysed following the protocol of Hasegawa et al. [24]; the sugars were separated by TLC on Merck cellulose plates and detected by spraying with acid aniline phthalate. Fatty acids extracted from the isolates and the reference strains of their closest neighbours were methylated and analysed using the protocol of the Sherlock Microbial Identification (MIDI) system, version 5 [68] and the resultant peaks named using the ACTIN6 database. The annotation of the fatty acids in the ACTIN6 peak naming table is consistent with IUPAC nomenclature (i.e. double bond positions identified with reference to the carboxyl group of the fatty acid), but to be in line with other publications this has been changed to numbering from the aliphatic end of the molecule (i.e. $C_{16:1}$ CIS 9 becomes $C_{16:1}$ ω7c and $C_{17:1}$ CIS 9 becomes $C_{17:1}$ ω8c).

Cultural and morphological properties

The isolates were examined for motility, Gram stain, cultural and morphological properties using procedures described by Trujillo et al. [74]. Cultural properties of the isolates were recorded on tryptone-yeast extract, yeast extract-malt extract, oatmeal, inorganic salts-starch, glycerol-asparagine, peptone-yeast extract iron and tyrosine agar plates (ISP media 1–7) [71] following incubation at 28 °C for 14 days. Colony pigments were determined by comparison against chips from Inter-Society Color Council National Bureau of Standard Colour charts [29]. Growth of the isolates at different temperatures (4, 10, 15, 20, 25, 28, 30, 35, 40 and 45 °C), from pH 4.0–12.0 (at intervals of 0.5 pH unit) and in the presence of 0–10 % NaCl (w/v) were determined on glucose yeast extract-malt extract (ISP2) agar medium [71]; KH_2PO_4/HCl, KH_2PO_4/K_2HPO_4 (0.1 M) and K_2HPO_4/NaOH buffer systems were used to adjust pH values.

Phenotypic properties

The isolates and the type strains of *Modestobacter* species were screened for a combination of biochemical, degradation and physiological properties found to be of value in the circumscription of *Modestobacter* species [10,49,74]. All of these tests were carried out in duplicate using a standard inoculum equivalent to 5.0 on the McFarland scale [51]. The ability of the strains to oxidise diverse carbon and nitrogen sources and to show resistance to inhibitory compounds were determined, in duplicate, using GEN III microplates in an Omnilog device (BIOLOG Inc., Haywood, USA) following incubation at 28 °C for 7 days. Briefly, the isolates were grown on GYM *Streptomyces* agar plates at 28 °C, cell suspensions prepared in a viscous inoculating fluid (IF C) at 83 % transmittance (T) for the type strains, at 92 % T for isolate 1G6^T, at 80 % T for isolate 1G14 and at 91 % T for isolate 1G50 and the microplates inoculated according to the protocol of the manufacturer. Data were exported and analysed using the opm package for R v.1.0.6 [76,77]. In addition, the enzymatic activities of the isolates were determined using API ZYM kits (bioMerieux) by following the manufacturer's instructions. In all cases conflicting results between duplicated cultures were scored as variable.

Results and discussion

Phylogeny

Nearly complete 16S rRNA gene sequences of isolates 1G6^T, 1G14 and 1G50 (1526, 1416 and 1417 nucleotides [nt], respectively) were determined (GenBank accession numbers: MH430528, MH430529 and MH430530, respectively). Isolates 1G6^T and 1G14 were found to have identical 16S rRNA gene sequences and shared a 99.86 % sequence similarity with isolate 1G50, a value corresponding to two nt differences at 1414 and 1416 locations. The isolates formed a distinct lineage within the evolutionary radiation occupied by the genus *Modestobacter* that was supported by

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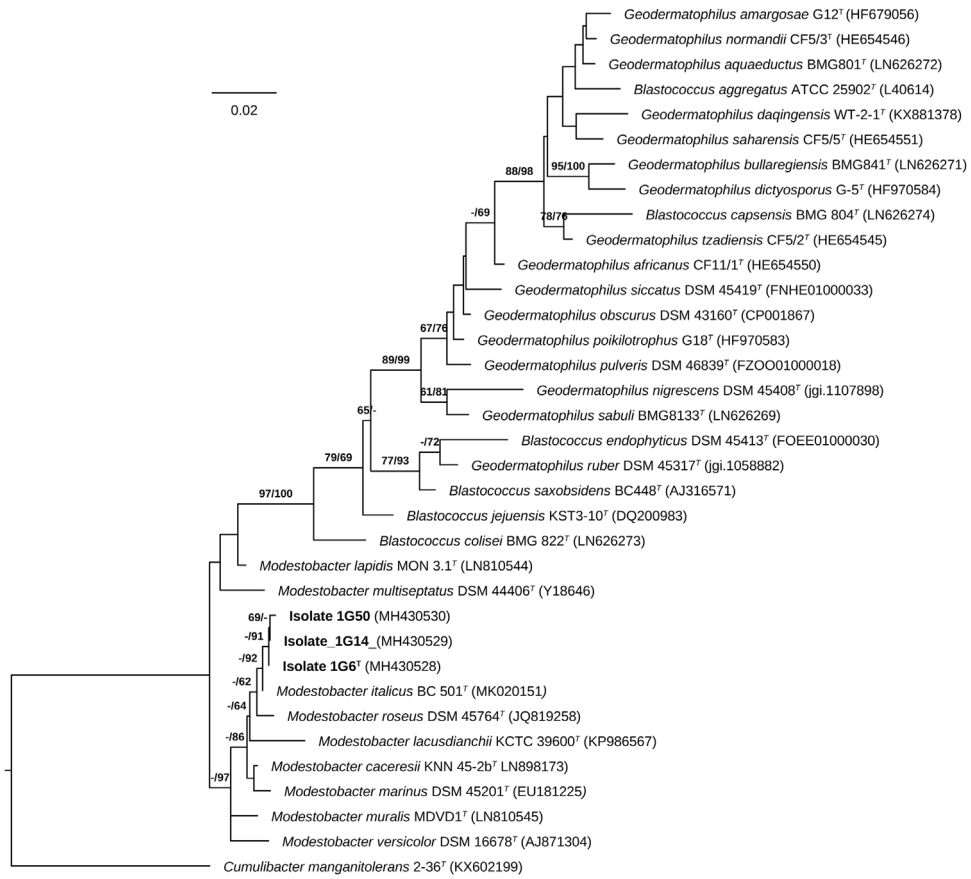

Fig. 1. Maximum-likelihod and maximum-parsimony tree based on nearly complete 16S rRNA gene sequences showing relationships between isolates 1G6^T, 1G14 and 1G50 and between them and the type strains of *Modestobacter* species. The numbers above the branches are support values when larger than 60% from ML (left) and MP (right) bootstrapping. Bar; 0.02 substitutions per nucleotide position. The root position of the tree was determined using *Cumulibacter manganitolerans* 2-36^T as the outgroup.

the maximum-likelihood, maximum-parsimony and neighbour-joining algorithms (Fig. 1, Fig. S1). The isolates showed diverse BOX-PCR profiles (Fig. S2) indicating that they are not clones.

All of the isolates were most closely related to *M. italicus* BC 501^T sharing a 99.8–99.9 % 16S rRNA gene similarity with the latter, this corresponds to 1–3 nt differences at between 1416–1508 locations. The isolates were also closely related to *M. caceresii* KNN 45-2b^T (99.6 % similarity), *M. roseus* DSM 45764^T (99.4–99.5 % similarity) and *M. marinus* DSM 45201^T (99.3–99.5% similarity) but less so to *M. versicolor* DSM 16678^T (98.6–98.7% similarity), *M. muralis* MDVD1^T (98.5–98.7% similarity) and *M. lacusdianchii* KCTC 39600^T (98.2–98.6 % similarity). According to Meier-Kolthoff et al. [42] an actinobacteria-specific 16S rRNA threshold of 99.0 % with a 1.0 % maximum probability of error is equivalent to a DNA–DNA hybridization (DDH) value at the 70 % threshold recommended for the assignment of closely related strains to the same species [80]. Information drawn from whole-genome sequences is being used to distinguish between members of closely related prokaryotic species [42,56,67,83], as exemplified by ANI and dDDH values used to distinguish between closely related strains classified in the genera *Blastococcus* and *Geodermatophilus* [11,12].

Comparison of the draft genome of isolate 1G6^T with those of its closest phylogenetic neighbours

The draft assembly of the genome sequence of isolate 1G6^T (GenBank accession number: SJEX00000000) was composed of 178 contigs giving a total genome size of 5255906 bp with a digital DNA G + C content of 73.7 mol%. The total number of reads was 725876 (N50 = 48913, L50 = 32) and the genome sequencing coverage 60 ×. The whole genome was annotated to include 5273 protein coding sequences and 50 RNA genes. Digital DDH values between isolate 1G6^T and the type strains of *M. caceresii, M. italicus*, *M. marinus* and *M. roseus*, its closest phylogenetic relatives, were 26.8 %, 42.3 %, 26.9 % and 25.6 % respectively, values well below the previously mentioned 70 % threshold introduced by Wayne et al. [80]. Similarly, the corresponding ANI similarities between isolate 1G6^T and the type strains of *M. italicus*, *M. caceresii, M. marinus* and *M. roseus* were 90.7 %, 84.28 %, 84.1 % and 82.5 % respectively, values well below the 95–96 % threshold used to distinguish between members of closely related species [14,22].

Chemotaxonomic, cultural and morphological properties

In general, the chemotaxonomic, cultural and morphological properties of the isolates were in accord with their classification in the genus *Modestobacter* [46,49,54,74]. The isolates were found to be aerobic, Gram-stain-positive, non-motile, formed short rods and coccoid-shaped cells which tended to remain aggregated. The isolates grew well on all of the ISP agar media, mainly forming black, greenish-yellow, olive and brown colonies (Table 2). They produced whole-organism hydrolysates rich in *meso*-A_2pm, glucose and ribose (diagnostic sugars) and arabinose, contained MK-9(H_4) as the predominant isoprenologue (77.4–91.3 % of total menaquinone composition) with minor amounts of MK-8(H_4) (8.7–22.5 %) and polar lipid patterns containing diphosphatidylglycerol, glycophosphatidylinositol, phosphatidylethanolamine (diagnostic component), phosphatidylglycerol, phosphatidylinositol, and as exemplified in Fig. S3. Glycophosphatidylinositol, previously annotated as phosphatidylinositol mannoside (PIM) [10,59,74], is a

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Table 1
Fatty acid profiles (%) of the isolates and their closest relatives after growth on peptone-yeast extract-glucose-vitamins agar plates for 16 days at 20 °C. Values are percentages of total fatty acids; -, not detected.

	Modestobacter strains							
Fatty acids	1G6^T	1G14	1G50	*M. caceresii* KNN 45-2b^T	*M. italicus* BC 501^T	*M. marinus* DSM 45201^T	*M. roseus* DSM 45764^T
$C_{9:0}$	–	–	–	–	0.1	–	–
$C_{10:0}$	–	–	–	–	0.1	–	–
$C_{12:0}$	–	–	0.4	–	–	–	–
$C_{12:0}$ 3OH	–	–	–	–	–	–	0.1
$C_{14:0}$	0.4	0.9	1.5	0.3	0.3	0.2	0.2
$C_{15:0}$	–	–	–	0.4	0.1	0.2	2.4
$C_{15:0}$ 2OH	–	–	–	–	–	–	0.1
$C_{16:0}$	1.6	1.7	7.9	3.1	1.0	4.1	0.3
$C_{16:0}$ 2OH	–	–	–	0.1	–	–	–
$C_{17:0}$	0.3	0.3	1.5	0.3	0.2	1.1	1.7
$C_{18:0}$	0.9	3.9	4.5	–	0.4	0.2	–
$C_{14:1}$ ω5c	0.1	0.2	–	–	–	–	–
$C_{15:1}$ ω5c	–	0.2	–	–	–	–	–
$C_{15:1}$ ω6c	0.5	0.4	–	–	–	0.5	–
$C_{15:1}$ B	–	–	–	0.5	0.1	–	1.2
$C_{16:1}$ B	–	–	–	–	0.2	–	–
$C_{16:1}$ cis 9	–	–	–	23.5	5.7	–	5.4
$C_{17:0}$ cyclo	–	–	–	2.6	–	1.7	1.5
$C_{17:1}$ ω8c	3.3	3.0	5.2	–	–	7.6	–
$C_{17:1}$ cis 9	–	–	–	7.6	4.5	–	10.9
$C_{18:1}$ ω6c	0.4	0.7	1.7	–	–	–	–
$C_{18:1}$ ω9c	7.3	8.0	12.2	–	–	4.1	–
$C_{18:1}$ cis 9	–	–	–	3.8	17.3	–	0.4
$C_{20:1}$ ω9c	0.2	–	–	–	–	–	–
$C_{20:1}$ cis 11	–	–	–	0.1	–	–	–
$C_{16:0}$ 9-methyl	–	–	–	1.8	1.5	–	4.4
$C_{17:0}$ 10-methyl	–	–	–	1.8	4.4	6.0	0.9
$C_{18:0}$ 10-methyl, TSBA	–	–	1.3	–	–	–	–
anteiso-$C_{11:0}$	–	–	0.5	–	0.2	–	–
anteiso-$C_{13:0}$	–	0.2		–	–	–	–
anteiso- $C_{15:0}$	5.8	12.5	14.5	0.4	1.2	0.7	0.9
anteiso-$C_{15:0}$ A	0.6	0.5	0.5	–	–	–	–
anteiso-$C_{15:0}$ 2OH	–	–	–	–	–	–	0.4
anteiso-$C_{15:1}$ A	–	–	–	–	0.2	0.2	–
anteiso-$C_{16:0}$	0.3	0.7	0.9	0.1	–	–	–
anteiso- $C_{17:0}$	–	–	–	0.5	1.9	0.7	0.5
anteiso- $C_{17:1}$	6.3	7.6	11.6	–	–	–	–
anteiso- $C_{17:1}$ C	–	–	–	0.3	0.5	–	1.0
anteiso-$C_{17:1}$ ω9c	3.8	4.3	1.3	–	–	0.7	–
iso-$C_{10:0}$	–	–	–	–	1.3	–	–
iso-$C_{11:0}$	–	–	–	–	0.4	–	–
iso-$C_{12:0}$	–	–	–	–	0.1	–	–
iso-$C_{13:0}$	0.1	0.2	–	–	0.1	–	0.1
iso-$C_{14:0}$	1.4	1.0	1.1	1.7	1.4	2.3	3.1
iso-$C_{15:0}$	18.7	20.8	10.7	3.2	6.9	2.9	16.0
iso-$C_{15:1}$ G	8.1	6.1	2.3	3.1	4.4	3.0	–
iso-$C_{16:0}$	16.3	7.4	7.5	28.1	32.8	32.5	25.7
iso-$C_{16:0}$ 2OH	–	–	–	–	2.0	–	1.7
iso-$C_{16:1}$ G	–	–	–	–	5.6	–	–
iso-$C_{16:1}$ H	5.8	2.3	–	14.9	–	16.7	9.4
iso-$C_{17:0}$	1.7	1.4	2.7	0.6	1.9	1.4	2.4
iso-$C_{17:0}$ 2OH	–	–	–	0.6	0.3	–	3.7
iso-$C_{17:1}$ ω9c.	5.9	4.5	0.9	–	–	1.7	–
iso-$C_{18:0}$	0.1	–	–	–	0.9	0.4	–
iso-$C_{18:1}$ H	–	–	–	–	0.3	0.4	–
iso-$C_{19:1}$ I	–	–	–	–	0.1	–	–
Sum in feature 2	–	–	–	–	–	–	0.5
Sum in feature 3	9.1	10.2	5.2	–	–	8.5	–
Sum in feature 4	–	–	–	–	–	–	2.6
Sum in feature 6	–	–	–	0.4	–	–	–
Sum in feature 7*/**	1.0*	1.2*	4.2*	0.3**	0.8**	0.6*	0.1**
Sum in feature 9	–	–	–	0.2	0.8	–	–

*As indicated by Montero-Calasanz et al. [50] summed features are groups of two or three fatty acids that are treated together for the purpose of evaluation in the MIDI system and include both peaks with discrete ECLs as well as those where the ECLs are not reported separately.
Summed feature 2 comprises iso-$C_{15:1}$ I and $C_{13:0}$ 3OH, summed feature 3 $C_{16:1}$ ω7c and $C_{16:1}$ ω6c; summed feature 4 iso-$C_{15:0}$ 2OH and $C_{16:1}$ t9; summed feature 6 anteiso-$C_{18:0}$ and $C_{18:2}$ cis; summed feature 7* $C_{19:0}$ cyclo ω10c and/or 19ω6; summed feature 7** $C_{18:1}$ trans 9 and $C_{18:1}$ trans 6 and $C_{18:1}$ cis; summed feature 9 $C_{19:0}$ cyclo C9-10 and undefined fatty acid.

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Table 2
Cultural and phenotypic properties that distinguish between the isolates.

Characteristics	Isolates					
	1G6^T		1G14		1G50	
Growth on media:						
Tryptone - yeast extract agar (ISP 1)	++	Dark olive	++	Black	+++	Light olive
Yeast extract - malt extract agar (ISP 2)	+++	Black	+++	Black	++	Strong yellow
Oatmeal agar (ISP 3)	++	Black	++	Black	++	Black
Inorganic salts starch agar (ISP 4)	+	Black	+	Black	+	Brown
Glycerol-asparagine agar (ISP 5)	+	Dark olive	+	Black	+	Pale greenish yellow
Peptone - yeast extract iron agar(ISP 6)	+++	Strong brown	+++	Deep brown	++	Pale greenish yellow
Tyrosine agar (ISP 7)	+	Black	+	Black	+	Pale greenish yellow
API-ZYM tests:						
α-Fucosidase	–		–		+	
α-Galactosidase	–		–		+	
β-Galactosidase	–		–		+	
Lipase (C14)	–		–		+	
α-Mannosidase	–		–		+	
BIOLOG GEN III microplate tests						
Assimilation of:						
D-Cellobiose	+		–		+	
D-Fructose	+		+		–	
L-Fucose	+		–		–	
L-Galactonic acid-γ-lactone	–		+		–	
β-Gentiobiose	+		–		+	
D-Gluconic acid	–		+		–	
L-Glucuronic acid	+		–		–	
D-Glucose-6-phosphate	+		+		–	
D-Mannose	+		+		–	
Pectin	–		+		+	
D-Turanose	+		–		+	
Citric acid	+		–		+	
Sodium lactate (1 %)	+		+		–	
Gelatin	–		+		–	
Temperature growth range (°C)	4-30		10-35		15-35	

Growth: +++, abundant; ++, good; +, weak. None of the isolates formed diffusible pigments on the growth media. +, positive; -, negative.
The isolates were positive for acid and alkaline phosphatase, α-chymotrypsin, cystine arylamidase, esterase (C4), esterase lipase (C8), *N*-acetyl-β-glucosaminidase, α- and β-glucosidases, leucine arylamidase, naphthol-AS-BI-phosphohydrolase, trypsin and valine arylamidase (API-ZYM tests); oxidised D-serine#2 (amino acid), acetic acid, acetoacetic acid, butyric acid, α- and β-*hydroxy*-butyric acid, α-*keto*-butyric acid, D-galacturonic acid, α-*keto*-glutaric acid, L-malic acid and propionic acid (organic acids), dextrin, D-fructose-6-phosphate, D-glucose, glucuronamide, D-maltose, D-raffinose, D-sorbitol and D-trehalose (sugars), Tween 40 (polymer) and grew in the presence of aztreonam, fusidic acid, guanidine hydrochloride, lincomycin, lithium chloride, minocycline, nalidixic acid, niaproof, potassium tellurite, rifamycin SV, sodium bromate, sodium chloride (1, 4 and 8 %), tetrazolium blue, tetrazolium violet, troleandomycin and vancomycin (Biolog tests). In contrast, the isolates were negative for β-glucuronidase (API-ZYM tests), did not metabolise L-alanine, L-arginine, D- and L-aspartic acid, bromo-succinic acid, γ-amino-*n*-butyric acid, L-glutamic acid, L-histidine, D-serine#1 or L-serine (amino acids), L-lactic acid, D-lactic acid methyl ester, D-malic acid, mucic acid, *N*-acetyl-neuraminic acid, *p*-*hydroxy*-phenylacetic acid, glycyl-L-proline, pyroglutamic acid, methyl-pyruvate, quinic acid or D-saccharic acid (organic acids), D-arabitol, D-fucose, *N*-acetyl-D-galactosamine, D-galactose, *N*-acetyl-D-glucosamine, 3-*O*-methyl-D-glucose, β-methyl-D-glucoside, glycerol, inosine, *myo*-inositol, α-D-lactose, D-mannitol, *N*-acetyl-β-D-mannosamine, D-melibiose, L-rhamnose, D-salicin, D-stachyose or D-sucrose (sugars) or grow in the presence of sodium formate (Biolog tests).

common component in chromatographic profiles of *Modestobacter* species, except for *M. multiseptatus* DSM 44406^T, which it contains an unidentified glycolipid [49]. In this context, the polar lipid profiles of the isolates are in accordance with polar lipid patterns found in the type strains of *M. caceresii, M. muralis, M. lapidis, M. roseus* and *M. versicolor* [10,49,74].

In general, the isolates had fatty acid profiles that distinguish them from those of their closest phylogenetic neighbour, as exemplified by relatively high proportions of $C_{18:1}$ ω9c (7.3–12.2 %), anteiso-$C_{15:0}$ (5.8–14.5 %), anteiso-$C_{17:1}$ (6.3–11.6 %), iso-$C_{15:0}$ (10.7–20.8 %) and summed feature 3 (5.2–10.2 %). In contrast, *M. caceresii, M. italicus, M. marinus* and *M. roseus* were characterized by much higher proportions of iso-$C_{16:0}$ (25.7–32.8 %); the corresponding range for the isolates was 7.4–16.3 %. Qualitative and quantitative differences were also found between the isolates; the predominant fatty acid in isolates 1G6^T and 1G14 was iso-$C_{15:0}$ (18.7–20.8 %, respectively) whereas the predominant component in isolate 1G50 was anteiso-$C_{15:0}$ (14.5 %); much lower levels of this fatty acid were found in isolates 1G6^T and 1G14 (with 5.8 and 12.5 %, respectively). In general, the polar lipid profiles of the isolates are in line with these found in the type strains of *Modestobacter* species, as shown in Table 3.

Phenotypic tests

The duplicated cultures of the isolates gave the same results for all of the API-ZYM tests though variable results were recorded for some of the Biolog tests, as shown in Table 2.

It can also be seen from Table 2 that the isolates have many phenotypic properties in common, namely 83 %, though several features can be weighted to distinguish between them thereby providing further evidence that the isolates are not clones. Isolate 1G6^T, for instance, can be separated from the other two strains by its ability to metabolize L-fucose and L-glucuronic acid while only isolate 1G50 was positive for α-fucosidase, α- and β-galactosidase, lipase (C14) and α-mannosidase. Only isolate 1G14 was found to be positive for D-gluconic acid and gelatin and negative for the assimilation of D-cellobiose, citric acid β–gentiobiose and D-turanose (Table 2).

It can be seen from Table 3 that although some of the duplicated cultures gave variable results, a combination of phenotypic properties can be weighted to distinguish between the isolates and the type strains of *Modestobacter* species. In particular, the isolates can be separated from *M. italicus* BC 501^T, their nearest phylogenetic neighbour, by an ability to oxidise acetic acid, acetoacetic acid, α-*hydroxy*-butyric acid, D-fructose-6-phosphate, D-galacturonic acid,

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Table 3
Phenotypic properties that distinguish the isolates from the type strains of *Modestobacter* species.

	1	2	3	4	5	6	7	8	9	10
BIOLOG GEN III microplate tests Assimilation of:										
Acetic acid	+	+	–	+	+	–	+	+	+	+
Acetoacetic acid	+	+	–	+	+	–	+	+	+	+
Bromo-succinic acid	–	–	–	–	–	–	–	–	+	–
Butyric acid	+	–	+	+	–	–	–	–	+	–
γ-amino-*n*-Butyric acid	–	+	–	–	–	–	+	–	–	+
α-*hydroxy*-Butyric acid	+	+	–	–	+	–	–	–	–	–
β-*hydroxy*-Butyric acid	+	+	–	–	–	–	+	–	–	+
Dextrin	+	+	+	+	+	+	–	–	+	–
D-Fructose-6-phosphate	+	+	–	–	–	+	–	+	–	+
D-Fucose	–	+	–	–	+	–	+	–	–	+
D-Galactose	–	+	–	+	+	+	+	+	–	+
D-Galacturonic acid	+	–	–	+	+	–	+	–	–	–
N-Acetyl-D-glucosamine	–	+	–	+	+	+	+	+	+	+
β-Methyl-D-glucoside	–	+	–	+	+	+	+	–	–	–
Glucuronamide	+	+	–	–	+	–	+	–	–	–
Glycerol	–	+	+	+	–	+	+	+	+	+
Glycyl-L-proline	–	–	–	–	–	–	+	–	–	–
Inosine	–	–	–	–	–	+	–	–	–	–
D-Lactic acid methyl ester	–	+	–	–	–	–	–	–	–	+
α-D-lactose	–	–	–	+	+	+	+	+	+	–
D-Malic acid	–	–	–	+	–	–	+	+	+	–
L-Malic acid	+	–	–	+	+	+	+	+	+	+
D-Maltose	+	+	–	–	+	+	+	+	+	–
D-Melibiose	–	–	–	–	+	–	+	+	–	–
p-hydroxy-Phenylacetic acid	–	+	–	–	–	–	–	–	+	–
Propionic acid	+	+	–	+	+	–	+	–	+	+
L-Pyroglutamic acid	–	–	–	–	–	+	+	–	–	–
Methyl pyruvate	–	–	–	–	–	–	–	–	+	–
Quinic acid	–	–	–	–	–	–	–	–	+	–
D-Raffinose	+	–	–	+	+	–	–	+	–	–
L-Rhamnose	–	+	+	+	+	+	+	+	+	+
D-Saccharic acid	–	–	–	–	–	+	–	–	+	–
D-Serine#2	+	–	–	–	–	–	–	–	–	–
L-Serine	–	–	–	+	–	+	–	–	–	–
D-Sorbitol	+	+	–	+	+	+	–	+	–	+
D-Stachyose	–	–	–	–	+	+	+	–	–	–
D-Sucrose	–	+	–	+	+	+	+	+	+	+
D-Trehalose	+	+	–	+	+	+	+	+	+	+
Tween 40	+	+	+	+	+	–	+	+	+	–
Growth in presence of inhibitory compounds:										
Fusidic acid	+	–	–	–	–	–	–	–	–	–
Guanidine hydrochloride	+	–	–	–	–	–	–	–	–	–
Lincomycin	+	–	–	–	–	–	–	–	–	–
Minocycline	+	–	+	–	–	–	–	–	–	–
Nalidixic acid	+	–	+	+	+	+	–	+	+	+
Niaproof	+	–	–	–	–	–	–	–	–	–
Sodium bromate	+	–	+	+	–	–	–	+	+	–
Sodium chloride 1 %	+	–	+	+	+	+	–	+	+	–
Sodium chloride 4 %	+	–	–	+	–	–	–	–	+	–
Sodium chloride 8 %	+	–	–	+	–	–	–	–	–	–
Tetrazolium blue	+	–	–	–	–	–	–	–	–	–
Tetrazolium violet	+	–	–	+	–	–	–	–	–	–
Troleandomycin	+	–	–	–	–	–	–	–	–	–
Vancomycin	+	–	–	–	–	–	–	–	–	–
growth at pH 6	+	–	–	–	–	+	–	–	–	–
Polar lipids[a]	DPG, PG, PE, PI, GPI, 2L	DPG, PG, PE, PI, PIM	DPG, PE, PI, GPI	DPG, PE, PI, PIM, PL	DPG, PG, PE, PI, PIM	DPG, PG, PE, PI, APL, GL, PL	DPG, PE, PI, GL, 2APL, 3L	DPG, PG, PE, PI, PIM	DPG, PG, PE, PI, GPI, AL, 2APL	DPG, PG, PE, PI, PL, GPI, 4L

Strains: 1, Isolates 1G6^T, 1G14 and 1G50; 2, *M. caceresii* KNN 45-2b^T; 3, *M. italicus* BC 501^T; 4, *M. lacusdianchii* KCTC 39600^T; 5, *M. lapidis* MON 3.1^T; 6, *M. marinus* DSM 45201^T; 7, *M. multiseptatus* DSM 44406^T; 8, *M. muralis* MDVD1^T; 9, *M. roseus* DSM 45764^T; 10, *M. versicolor* DSM 16678^T. All data are from this study. +, positive; –, negative.
Codes: DPG, diphosphatidylglycerol; PG, phosphatidylglycerol; PE, phosphatidylethanolamine; PI, phosphatidylinositol; GPI, glycophosphoinositol; PIM, phosphoinositol-mannoside; AL, aminolipids; APL, aminophospholipids; GL, glycolipid; PL, unidentified phospholipid; L, unidentified lipid.
All of the strains oxidized D-glucose, but not D-arabitol, D-aspartic acid, L-histidine, mucic acid, *N*-acetyl-neuraminic acid or D-serine#1, and did not grow in the presence of sodium formate or at pH 5.
Between one and three of the strains gave variable results for the following duplicated tests: L-alanine, L-arginine, L-aspartic acid, α-*keto*-butyric acid, *N*-acetyl-D-galactosamine, 3-*O*-methyl-D-glucose, L-glutamic acid, α-*keto*-glutaric acid, *myo*-inositol, L-lactic acid, D-mannitol, *N*-acetyl-β-D-mannosamine, D-salicin, and for growth in the presence of aztreonam, lithium chloride, pottasium tellurite and rifamycin SV.

[a] Data for strain 2 are from Busarakam et al. [10]; for 3, 6, 7 and 9 from Montero-Calasanz et al. [49]; for 4 from Zhang et al. [85]; for 5 and 8 from Trujillo et al. [74].

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glucuronamide, L-malic acid, D-maltose, propionic acid, D-raffinose, D-sorbitol and D-trehalose and by a pronounced ability to grow in the presence of inhibiting compounds. In contrast, the *M. italicus* strain, unlike the isolates, assimilated L-rhamnose and glycerol. Similar combinations of phenotypic properties can be used to distinguish the isolates from the remaining *Modestobacter* type strains and the latter from one another.

Genes associated with stress responses

It is evident from the SEED analyses that the draft genome of isolate 1G6^T contains 59 stress-related genes, as exemplified by the presence of *dnaK* and *dnaJ* gene clusters and *hrcA*, *grpE* and *Hsp* genes that are linked to heat shock responses [38] and by genes encoding for the Csp family of proteins which are associated with cold shock responses [16]. The draft genome also contains a *KatA* and a *KatE* gene encoding for enzymes associated with protection against reactive oxygen species [55], as well as a *sox* gene cluster and several genes coding for betaine biosynthesis and for betaine and choline uptake, all of these genes are involved in responses to oxidative stress [6,7,52]. In turn, the presence of a carbon storage regulator gene (*Csr*) (fig|6666666.388060.peg.4837) is associated with multiple biosynthetic pathways, including glycogen biosynthesis [64,65]. Two copies of an *uvrD* gene encode ATP dependent DNA helicase were detected; these genes are involved in the UV-resistance of *M. italicus* BC 501^T (formerly *M. marinus*) [55]. Genes linked with responses to desiccation stress were not found though multiple copies of genes involved in the uptake of trehalose and associated with tolerance to desiccation and temperature in bacteria [62] were detected. Similarly, genes linked with stabilizing genomes, namely *recO*, *recF* and *recQ* helicase [25,41], were found. Two copies of *coxD*, *coxE* and *coxG* genes and a *coxLSM* cluster which encode for different subunits of carbon monoxide (CO) dehydrogenase were highlighted in a BLAST search of the 1G6^T genome; these genes encode for the uptake of carbon monoxide indicating that this isolate may have a chemolithoautotrophic lifestyle [39]. Similar profile of stress-related genes have been detected in the genomes of the type strains of *Blastococcus atacamensis* [11], *G. chilensis* [12] and *M. caceresii* [10], all of which were isolated from Atacama Desert soils.

Biosynthetic gene clusters

Mining of the draft genome of isolate 1G6^T using the antiSMASH server [4] revealed the presence of several putative biosynthetic gene clusters. Two of the clusters coded for type 2 and type 3 polyketide synthases while others were associated with the synthesis of betalactone and terpenes; these results are in line with corresponding studies on the type strains of *G. chilensis* [12] and *M. caceresii* [10]. However, improved genome alignments are needed to achieve a better understanding of the genomes of isolate 1G6^T and those of the type strains of *G. chilensis* and *M. caceresii*.

Conclusions

The chemotaxonomic, cultural, morphological and phenotypic data show that isolates 1G6^T, 1G14 and 1G50 are not clones but are *bone fide* members of the genus *Modestobacter* and belong to the same species. The isolates can be separated readily from the type strains of *Modestobacter* species by a wealth of genomic and phenotypic data. In addition, isolate 1G6^T can be distinguished from *M. italicus* BC 501^T, its closest phylogenetic neighbour, by low ANI and dDDH values. Consequently, it is proposed that the three isolates be recognised as a novel species of *Modestobacter*, namely as *Modestobacter excelsi*. It is also interesting that the genome of isolate 1G6^T is rich in stress-related genes associated with cold and heat stress responses, oxidative stress, resistance to UV-radiation and with an ability to use carbon monoxide as a source of carbon and energy while the presence of a few natural product biosynthetic gene clusters show that it has the capacity to produce specialized metabolites; these observations provide support for the view that the competitive success of *Geodermatophilaceae* strains in extreme, sparsely populated biomes may be more related to stress resistance than to antibiosis [8].

Description of *Modestobacter excelsi* sp. nov

Modestobacter excelsi *(ex.cel' si. L. gen. n.* excelsi *of a high place)*

Aerobic, Gram-stain-positive, non-motile actinobacteria which form short rods and coccoid-like elements that tend to remain aggregated. Grows between 4 and 35 °C, optimally around 28 °C, from pH 6 to 8.5, optimally around pH 8 and in presence of up to 8 % (w/v) NaCl. Aesculin is hydrolysed but not allantoin, arbutin or urea. Tweens 40 and 60 are degraded but not adenine, casein, chitin, elastin, gelatin, guanine, hypoxanthine, starch, Tweens 20 and 80, L-tyrosine, uric acid, xanthine or xylan. Positive for acid and alkaline phosphatase, α-chymotrypsin, cystine arylamidase esterase (C4), esterase lipase (C8), *N*-acetyl-β-glucosaminidase, α- and β-glucosidases, leucine arylamidase, naphthol-AS-BI-phosphohydrolase, trypsin, valine arylamidase and negative for β-glucuronidase. Oxidizes dextrin, D-fructose-6-phosphate, D-glucose, glucuronamide, D-maltose, D-raffinose D-sorbitol and D-trehalose, but not D-arabitol, D-fucose, *N*-acetyl-D-galactosamine, D-galactose, *N*-acetyl-D-glucosamine, 3-*O*-methyl-D-glucose, β-methyl-D-glucoside, glycerol, inosine, *myo*-inositol, α-D-lactose, D-mannitol, *N*-acetyl-β-D-mannosamine, D-melibiose, L-rhamnose, D-salicin, D-stachyose or D-sucrose. Acetic acid, acetoacetic acid, butyric acid, α- and β-*hydroxy*-butyric acid, α-*keto*-butyric acid, D-galacturonic acid, α-*keto*-glutaric acid, L-malic acid and propionic acids are metabolised, but not L-alanine, L-arginine, D- or L-aspartic acid, bromo-succinic acid, γ-amino-*n*-butyric acid, L-glutamic acid, L-histidine, L-lactic acid, D-lactic acid methyl ester, D-malic acid, mucic acid, *N*-acetyl-neuraminic acid, *p-hydroxy*-phenylacetic acid, glycyl-L-proline, L-pyroglutamic acid, methyl pyruvate, quinic acid, D-saccharic acid, D-serine#1 or L-serine. Grows in the presence of aztreonam, fusidic acid, guanidine hydrochloride, lincomycin, lithium chloride, minocycline, nalidixic acid, niaproof, potassium tellurite, rifamycin SV, sodium bromate, tetrazolium blue, tetrazolium violet, troleandomycin and vancomycin, but not in the presence of sodium formate. Additional phenotypic properties are cited in the text and in Tables 1–3. The cell wall peptidoglycan contains *meso*-A_2pm, the whole-cell sugars are arabinose, glucose and ribose, the major fatty acids are anteiso-$C_{15:0}$, iso-$C_{15:0}$, iso-$C_{16:0}$, anteiso-$C_{17:1}$and and $C_{18:1}\omega$9c, the predominant menaquinone is MK-9(H_4) and the diagnostic phospholipid phosphatidylethanolamine. The genome size of the type strain is around 5.25 Mbp and the genomic DNA G + C content 73.7 mol%.

The type strain 1G6^T (=PCM 3004^T, =DSM 107535^T) was isolated from a surface soil sample (2 cm depth) collected from a high altitude Atacama Desert soil. The GenBank 16S rRNA gene sequence accession number for isolate 1G6^T is MH430528 and the corresponding GenBank NCBI accession number of the genome sequence SJEX00000000. The digital protologue number is TA01023.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.syapm.2019.126051.

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