

Sphingomonas solaris sp. nov., isolated from a solar panel in Boston, Massachusetts

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Abstract

Solar panel surfaces, although subjected to a range of extreme environmental conditions, are inhabited by a diverse microbial community adapted to solar radiation, desiccation and temperature fluctuations. This is the first time a new bacterial species has been isolated from this environment. Strain R4DWN^T belongs to the genus *Sphingomonas* and was isolated from a solar panel surface in Boston, MA, USA. Strain R4DWN^T is a Gram-negative, non-motile and rod-shaped bacteria that tested positive for oxidase and catalase and forms round-shaped, shiny and orange-coloured colonies. It is mesophilic, neutrophilic and non-halophilic, and presents a more stenotrophic metabolism than its closest neighbours. The major fatty acids in this strain are C_{18:1}ω7c/C_{18:1}ω6c, C_{16:1}ω7c/C_{16:1}ω6c, C_{14:0} 2OH and C_{16:0}. Comparison of 16S rRNA gene sequences revealed that the closest type strains to R4DWN^T are *Sphingomonas fennica*, *Sphingomonas formosensis*, *Sphingomonas prati*, *Sphingomonas montana* and *Sphingomonas oleivorans* with 96.3, 96.1, 96.0, 95.9 and 95.7 % pairwise similarity, respectively. The genomic G+C content of R4DWN^T is 67.9 mol%. Based on these characteristics, strain R4DWN^T represents a novel species of the genus *Sphingomonas* for which the name *Sphingomonas solaris* sp. nov. is proposed with the type strain R4DWN^T (=CECT 9811^T=LMG 31344^T).

In 1990, Yabuuchi *et al.* [1] described the genus *Sphingomonas* for the first time, with the type species being *Sphingomonas paucimobilis*. This genus is classified in the class *Alphaproteobacteria* [2] and is characterized by having ubiquinone Q-10 as the major respiratory quinone and by having an outer membrane that contains glycosphingolipids but lacks lipopolysaccharides [1, 3]. A total of 122 different *Sphingomonas* species have been described up to date (EzBioCloud [4]). They are Gram-negative, rod shaped, non-sporulating, strictly aerobic and display pigmented colonies that range from light yellow/whitish, to intense yellow and orange. Several members of the genus *Sphingomonas* have been shown to hold promise in bioremediation applications, including degradation of polycyclic aromatic hydrocarbon, bisphenol A and heavy metal pollutants [5–7].

In this study we have characterized a new isolate belonging to the genus *Sphingomonas* from the surface of a solar panel.

Solar panels from the Hunnewell Building at The Arnold Arboretum of Harvard University, Boston, MA, USA (42° 18' 28.3" N, 71° 07' 14.5" W), were sampled by cleaning the surfaces with sterile PBS and using a sterile window cleaner. The resulting liquid was collected in sterile tubes and transported to the laboratory on ice. The samples were then left to settle for 5 min in order to allow fungi to sediment, and serial dilutions were performed and plated on Luria–Bertani agar and Reasoner's 2A (R2A) agar. After incubation at room temperature for 6 days, individual colonies were selected and restreaked on fresh medium in order to obtain pure cultures. Strain R4DWN^T was among the isolates selected from the R2A agar plates.

The complete sequence of the 16S rRNA gene of the isolate was extracted from the draft genome and, according to the EzBioCloud online tool [4], the closest type strains to R4DWN^T are *Sphingomonas fennica* (96.3 %), *Sphingomonas*

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Abbreviations: ANIb, average nucleotide identity; CDS, coding sequences; dDDH, digital DNA–DNA hybridization; GGDC, Genome-to-Genome Distance Calculator; ML, maximum-likelihood; NJ, neighbour-joining; R2A, Reasoner's 2A; UBCG, up-to-date bacterial core gene set.

Colección Española de Cultivos Tipo (CECT), Belgian Co-ordinated Collections of Micro-organisms (BCCM/LMG). The GenBank/EMBL/DBJ accession number for the 16S rRNA gene sequence of strain R4DWN^T is MK569518, and the genome accession number is VNI000000000.

Two supplementary tables and one supplementary figure are available with the online version of this article.

formosensis (96.1 %), *Sphingomonas prati* (96.0 %), *Sphingomonas montana* (95.9 %) and *Sphingomonas oleivorans* (95.7 %). With the aim of establishing the accurate taxonomic position of R4DWN^T, this isolate was characterized using a polyphasic approach. For this, the reference strains of the two closest species, *S. fennica* and *S. formosensis*, were acquired from the DSMZ Collection (Leibniz Institute DSMZ, Germany) with reference numbers DSM 13665^T and DSM 24164^T, respectively. All three strains were grown on R2A medium at 25 °C for all studies (unless specified otherwise).

For temperature growth tests, all three strains were grown on R2A medium and incubated at 4, 15, 25, 30 and 37 °C. Salt tolerance was determined by cultivating the three strains on R2A medium supplemented with NaCl 0, 1, 2 and 3% (w/v). pH tolerance (between pH 4.0 and 11.0) was determined by cultivating the strains in liquid R2A media buffered with MES (pH 4–6), HEPES (pH 7–8) or CHES (pH 9–11). Catalase activity was determined by detecting bubble production when colonies were mixed with 30% (v/v) hydrogen peroxide. Oxidase activity was determined using Oxidase Sticks for microbiology (PanReac AppliChem), and Gram type was determined by assessing cell lysis in KOH 3% (w/v). All three strains were characterized using API 20NE and API ZYM strips (bioMérieux), as well as Biolog GENIII MicroPlates. The differential phenotypic characteristics between strain R4DWN^T and its closest species are shown in Table 1, and the detailed results obtained from the API galleries and Biolog GEN III utilization tests are detailed in the species description and in Table S1 (available in the online version of this article).

Strain R4DWN^T cells were observed to be Gram-negative, non-motile and rod-shaped (1.2–4.5 µm length x 1.2 µm wide). In old cultures, some cells grew in the form of a long rod shape of approximately 30 µm. Colonies were found to be round-shaped, shiny, orange-coloured, convex and 1 mm in diameter after 7 days of incubation at 25 °C. Strain R4DWN^T displayed several characteristics that allows it to be differentiated from other closely related species of the genus (Table 1), including growth at a smaller range of temperatures (growing only up to 25 °C as opposed to the 30 or 37 °C of other species), assimilation of potassium gluconate and malic acid, and valine arylamidase and β-glucosidase activities. Furthermore, Biolog assays revealed that strain R4DWN^T is only able to assimilate seven out of the 71 tested carbon sources, mainly organic acids and simple sugars (glucuronamide, acetoacetic acid, D-fructose-6-PO₄, L-malic acid, L-galactonic acid lactone, β-hydroxy-D,L-butyric acid and D-glucose-6-PO₄), whereas *S. fennica* DSM 13665^T and *S. formosensis* DSM 24164^T are able to assimilate 19 and 39 out of the 71 tested carbon sources, respectively. This suggests that strain R4DWN^T displays a more stenotrophic metabolism than its closest neighbours.

For fatty acid analysis, the three strains were grown on R2A plates at 25 °C for 5 days. Then, the cells were harvested and fatty acid profiles were obtained using the standard MIDI Microbial Identification System protocol [8]. Fatty acids were analysed on an Agilent 6850 gas chromatography system and using the MIDI method (TSBA6) [9]. The major fatty acids in

strain R4DWN^T were C_{18:1}ω7c/C_{18:1}ω6c (48.9 %), C_{16:1}ω7c/C_{16:1}ω6c (21.2 %), C_{14:0} 2OH (12.0 %) and C_{16:0} (10.3 %) (Table 2), a profile that is consistent with other members of the genus *Sphingomonas* [10, 11]. Nevertheless, the lack of C_{17:1}ω6c differentiates R4DWN^T from the type species *S. fennica* DSM 13665^T, whereas the large amount of C_{16:1}ω7c/C_{16:1}ω6c differentiates R4DWN^T from the type species *S. formosensis* DSM 24164^T, which displayed only low amounts of these fatty acids.

The total DNA of strain R4DWN^T was extracted using the protocol described by Latorre *et al.* [12], quantified using the Qubit dsDNA HS-high sensitivity kit (Invitrogen), and the 16S rRNA gene was amplified by PCR reaction using the following primers [13]: 8F (5'-AGAGTTTGATCCTG-GCTCAG-3'), 1492R (5'-GGTTACCTTGTACGACTT-3'), 1055F (5'-ATGGCTGTCGTCAGCT-3') and 341R (5'-CTGCTGCCTCCCGTAGG-3'). The almost-complete sequence of the 16S rRNA gene of the isolate was obtained through Sanger sequencing. The sequence length was 1470 base pairs, and it can be accessed in the GenBank/EMBL/DBJ databases under accession number MK569518. The online SINA (SILVA) tool [14] was used to perform a multiple alignment of the sequences, and the maximum-likelihood (ML) (Fig. 1) and neighbour-joining (NJ) (Fig. S1) trees were reconstructed using RaxML [15] and MEGA6 [16], respectively. The GTR algorithm was used for the ML tree, whereas Kimura's two-parameter model was used for the NJ tree. Reliability of the branch patterns was assessed using bootstrap analyses based on 1000 resamplings. Based on the 16S rRNA sequence analysis, R4DWN^T does not have a clear phylogenetic position within the genus *Sphingomonas*. The closest neighbour is *S. formosensis* in both the ML (Fig. 1) and NJ (Fig. S1) trees, whereas *S. fennica* (the closest neighbour according to the 16S rRNA sequencing) appears grouped with *S. oleivorans* forming an external group. Nevertheless, these branches are not supported by high bootstrap values.

The draft genome of strain R4DWN^T was sequenced using the MiSeq sequencer (Illumina), and the Nextera XT Prep Kit protocol was used for library preparation. FastQC was utilized to assess the quality of the sequence reads. Genome assembly of 284 541 paired reads was performed using SPAdes 3.12.0 [17]. The draft genome of R4DWN^T consists of 229 contigs yielding a total length of 4 444 219 bp, with a G+C content of 67.9mol% and an N50 value of 38 937 bp. This genomic G+C content is in agreement with the closest neighbours and confirms the adscription of R4DWN^T to the genus *Sphingomonas* [10, 11]. The maximum contig length was 136 617 bp, and all the contigs were annotated using the RAST tool kit (RASTtk) integrated in PATRIC version 3.5.41 (www.patricbrc.org). A total of 4455 coding sequences (CDS) were predicted, of which 2602 were proteins with functional assignments. A total of 45 tRNA and three rRNA genes (one single ribosomal operon) were identified. This Whole Genome Shotgun project has been deposited at GenBank/EMBL/DBJ under the accession VNUM00000000. The version described in this paper is version VNUM01000000. The completeness and levels of contamination of the genome were analysed

Table 1. Phenotypic comparisons of strain R4DWN^T and the type strains of closely related *Sphingomonas* species

Strains: 1, R4DWN^T; 2, *Sphingomonas fennica* DSM 24164^T; 3, *Sphingomonas formosensis* DSM 24164^T; 4, *Sphingomonas prati* DSM 103336^T; 5, *Sphingomonas montana* DSM 103337^T; 6, *Sphingomonas oleivorans* HAMBI 3659^T. Analysis of strains 1, 2 and 3 was conducted under the same conditions in this study, whereas data from strains 4, 5 and 6 was taken from the original species description papers [27–29]. All strains were positive for the following characteristics: alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, acid phosphatase and naphtol-AS-BI-phosphohydrolase. All strains were negative for the following characteristics: Gram reaction, nitrate reduction, glucose fermentation, activity of arginine dihydrolase, urease, gelatin hydrolysis, assimilation of adipic acid, trisodium citrate and phenylacetic acid, lipase (C14), *N*-acetyl- β -glucosaminidase, α -mannosidase, and α -fucosidase. +, Positive; –, negative; w, weakly positive.

Characteristic	1	2	3	4	5	6
Isolation source	Solar panel surface	Groundwater*	Soil†	Soil	Soil	Soil
Motility	No	No	No	No	Yes	No
Cell size (μm)	1.2–4.5×1.2	0.9–1.5×0.5–0.9*	1.4×0.4†	1.1×0.7	1.2×0.9	1.6–2.4×0.4–0.85
Colour	Orange	Light yellow	Yellow	Orange	Orange	Light yellow
Catalase	+	+	+	w	+	–
Oxidase	+	+	–	w	+	–
Growth temperature (°C)	4–25	4–30	4–37	4–30	4–30	4–37
pH range for growth	6–9	6–7	5–11	5–10	5–9	5–9
NaCl tolerance (% w/V)	0–1	0	0–3	0–1	0–1	0–2
Enzymatic activity (API 20NE):						
Indole production	–	–	–	w	–	–
Aesculin hydrolysis	w	–	+	+	+	–
β -Galactosidase	+	–	–	w	+	–
Enzymatic activity (API ZYM):						
Valine arylamidase	w	–	–	w	w	+
Cystein arylamidase	–	–	–	–	–	+
Trypsin	–	w	+	+	–	+
α -Chymotrypsin	–	–	–	w	–	–
α -Galactosidase	–	–	–	w	w	–
β -Galactosidase	+	–	–	–	+	+
β -Glucuronidase	–	–	+	–	–	–
α -Glucosidase	–	–	w	–	–	+
β -Glucosidase	+	–	+	+	+	–
Carbon source utilization (API 20NE):						
Glucose	+	–	+	–	–	–
Arabinose	+	–	+	–	+	–
Mannose	–	–	–	–	–	+
Manitol	+	–	–	–	–	+
<i>N</i> -Acetyl-glucosamine	+	–	+	–	–	+
Maltose	+	–	–	–	–	+

Continued

Table 1. Continued

Characteristic	1	2	3	4	5	6
Potassium gluconate	w	–	–	–	–	–
Capric acid	–	–	–	–	–	+
Malic acid	w	–	–	–	–	–

*Data from [10].

†Data from [11].

Table 2. Cellular fatty acid composition (%) of strain R4DWN^T and related type strains

Strains: 1, R4DWN^T; 2, *Sphingomonas fennica* DSM 13665^T; 3, *Sphingomonas formosensis* DSM 24164^T; 4, *Sphingomonas prati* DSM 103336^T; 5, *Sphingomonas montana* DSM 103337^T; 6, *Sphingomonas oleivorans* HAMBI 3659^T. Data from strains 1, 2 and 3 are from this study, whereas data from 4, 5 and 6 are from the original species description papers [27–29]. TR, <1.0%; –, not detected

Fatty acid	1	2	3	4	5	6
Saturated						
C _{14:0}	1.6	1.1	5.3	TR	TR	TR
C _{16:0}	10.3	15.6	12.6	4.5	7.0	14.6
C _{17:00}	–	–	–	–	–	1.1
C _{18:0}	–	–	1.1	–	TR	TR
Unsaturated						
C _{16:1} ω5c	1.2	1.1	4.7	1.9	1.3	TR
C _{17:1} ω6c	–	2.8	–	–	TR	14.0
C _{18:1} ω7c 11-methyl	3.5	1.5	10.3	1.5	3.1	4.0
C _{18:1} ω5c	–	TR	TR	–	1.3	1.0
C _{18:1} ω6c	–	–	–	–	–	43.1
C _{19:0} cyclo ω8c	–	6.9	TR	–	TR	TR
Hydroxy						
C _{14:0} 2OH	12.0	12.5	8.2	14.9	4.5	11.1
C _{16:0} iso 3OH	1.3	1.0	–	–	–	–
C _{15:0} 2OH	–	TR	–	–	–	3.2
C _{16:0} 2OH	–	–	–	1.5	–	1.3
C _{16:1} 2OH	–	–	–	–	1.0	–
C _{18:0} 2OH	–	–	–	1.1	–	–
C _{18:1} 2OH	–	–	–	–	1.3	TR
iso-16:0 3-OH	–	–	–	2.3	1.4	–
Summed features*						
3	21.2	14.7	1.3	48.1	36.7	TR
8	48.9	41.3	54.0	21.9	39.2	–

*Summed features represent groups of two or three fatty acids that could not be separated by GLC with the MIDI system. Summed feature 3 contains C_{16:1}ω7c/C_{16:1}ω6c; and summed feature 8 contains C_{18:1}ω7c/C_{18:1}ω6c.

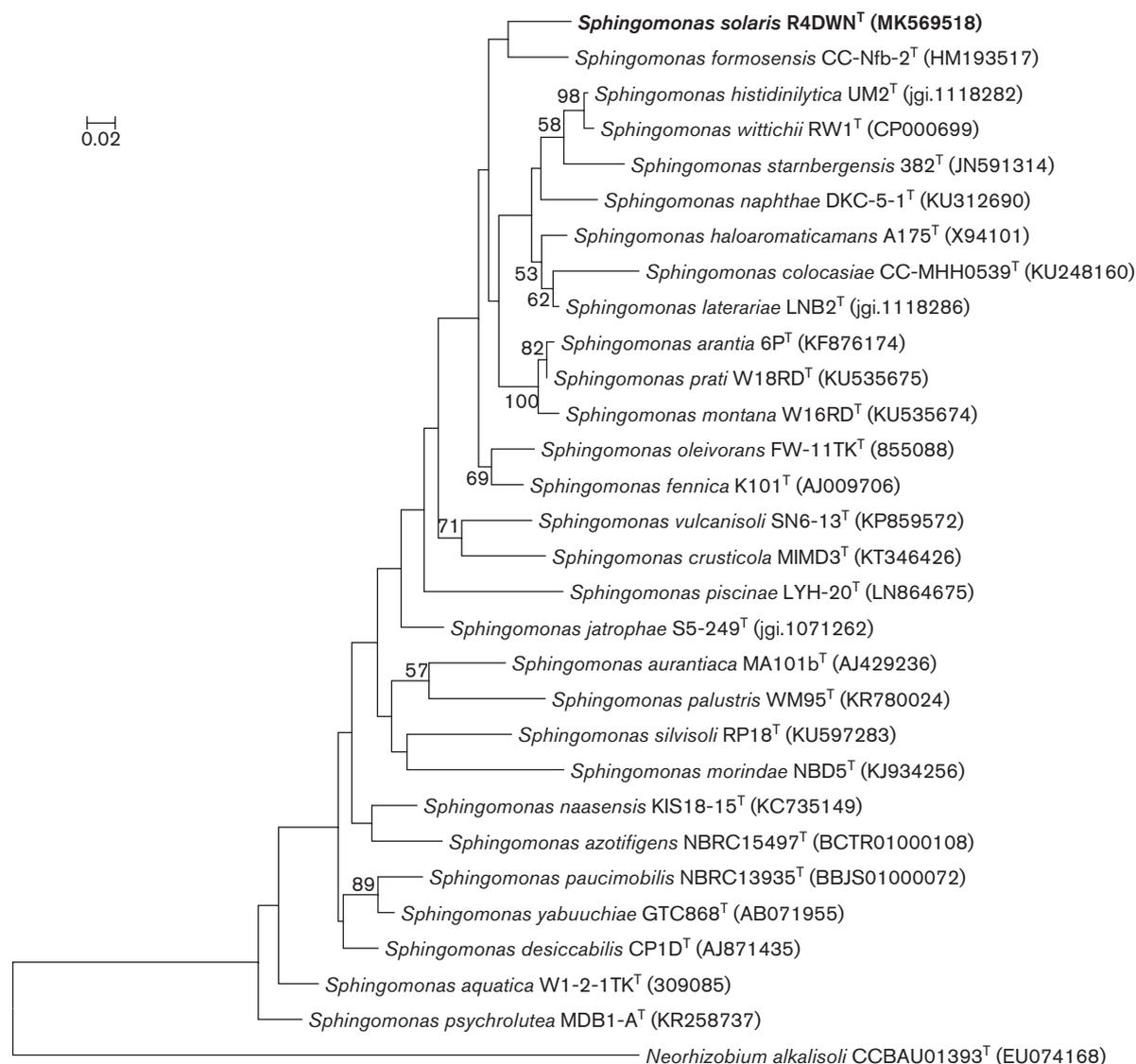


Fig. 1. Maximum-likelihood tree illustrating the phylogenetic position of strain R4DWN^T and related members of the genus *Sphingomonas* based on almost-complete 16S rRNA gene sequences. The optimal evolutionary model of nucleotide substitution applied is GTR. Bar, 0.02 expected nucleotide substitutions per site. *Neorhizobium alkalisolii* was used as an outgroup. Only bootstrap values above 50% are indicated (1000 resamplings) at branchings.

with the bioinformatic tool CheckM v1.0.6 [18], revealing values of 99.095% and 0.603, respectively. Therefore, the draft genome showed enough quality for further analyses [19]. The complete 16S rRNA gene was extracted from this draft genome and, according to the EZBioCloud online tool [4], the closest type strains of R4DWN^T are *S. fennica* K101^T, *S. formosensis* CC-Nfb-2^T, *S. prati* W18RD^T, *S. montana* W16RD^T and *S. oleivorans* FW-11^T with 96.3, 96.1, 96.0, 95.9 and 95.7% pairwise similarity, respectively. Taking into account that the similarity between R4DWN^T and the closest type strain (*S. fennica*) is lower than 98.7%, this isolate can be considered a new species [19, 20].

With the purposes of obtaining a more accurate phylogenetic inference of strain R4DWN^T, a phylogenomic tree based on

nucleotide sequences was generated. The UBCG version 3.0 pipeline (up-to-date bacterial core gene set) [21] was used to reconstruct an ML tree based on a multiple alignment of a set of 92 universal and single copy gene sequences with the tool FastTree version 2.10.1 (Fig. 2). According to the phylogenomic tree, the closest neighbour to R4DWN^T is *S. montana*, and this is supported by high bootstrap values. *S. fennica* and *S. oleivorans*, two of the closest neighbours according to the 16S rRNA gene sequence, have an external position with regards to the clade formed by *S. montana* and R4DWN^T, along with other species.

In order to investigate if our isolate belongs to a known species, pairwise average nucleotide identity values (ANI_b) [22] were calculated between strain R4DWN^T and its closest

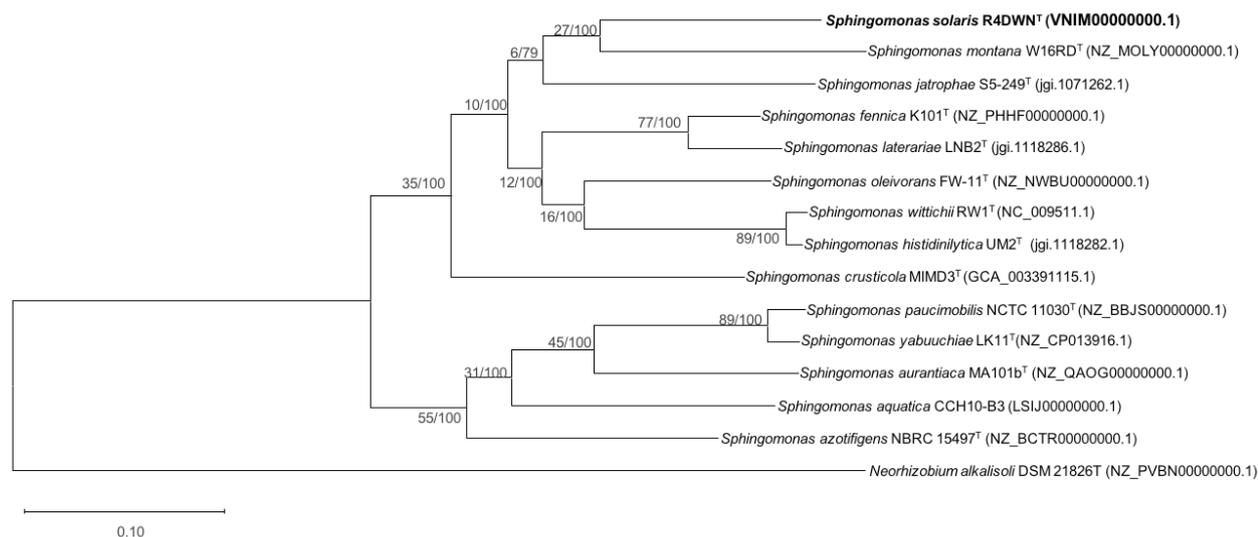


Fig. 2. Phylogenomic tree of strain R4DWN^T. Unrooted maximum-likelihood phylogenetic tree based on a multiple alignment of a set of 92 gene sequences (concatenation of 85764 nucleotides) from using the UBCG version 3.0 pipeline [21]. Bootstrap analysis was carried out using 100 replications. Gene support indices (max. value 92 genes) and percentage bootstrap values (max. value 100%) are given at branching points. Bar, 0.10 substitutions per position.

type strains, by using the JSpeciesWS online tool [23]. Additionally, digital DNA–DNA hybridization (dDDH) pairwise values were also obtained using the Genome-to-Genome Distance Calculator 2.1 (GGDC) tool [24]. As recommended for incompletely sequenced genomes, formula 2 was used for calculating the dDDH values [24]. The ANI and dDDH values between strain R4DWN^T and the type strains of phylogenetically close species were higher than the threshold established to circumscribe prokaryotic species (Table S2), namely 95% for ANI values [25] and 70% for dDDH [24]. Therefore, both genome-related indexes [26] confirmed the adscription of strain R4DWN^T to a hitherto unknown species.

Analysis of the draft genome of strain R4DWN^T allowed to predict its ability to synthesize phosphatidylethanolamine, diphosphatidylglycerol, phosphatidylglycerol, phosphatidylglycerolphosphate and a sphingolipid, due to the presence of genes coding for phosphatidylserine decarboxylase [EC 4.1.1.65], cardiolipin synthase A/B [EC:2.7.8.-], ribosomal-protein-serine acetyltransferase [EC 2.3.1.-], CDP-diacylglycerol-glycerol-3-phosphate 3-phosphatidyltransferase [EC 2.7.8.5] and serine palmitoyl transferase [EC 2.3.1.50]. This polar lipids profile is in agreement with the polar lipid analyses available for other species of the genus *Sphingomonas* with validly published names [10, 11]. As described previously in *S. fennica* [10], strain R4DWN^T is not able to synthesize phosphatidylcholine due to the absence of phosphatidylcholine synthase [EC 2.7.8.24], a unique feature of these closely related strains. Furthermore, spermidine synthase [EC 2.5.1.16] was detected in the draft genome of strain R4DWN^T, suggesting that this

strain could produce spermidine as the major polyamine. On the other hand, no genes related to homospermidine synthesis were detected. Strain R4DWN^T has all the enzymatic repertoire, including the enzymes 2-methoxy-6-polyprenyl-1,4-benzoquinol methylase [EC 2.1.1.201], ubiquinone biosynthesis monooxygenase Coq6 [EC 1.14.13.-] and 3-demethylubiquinol 3-O-methyltransferase [EC 2.1.1.64], to synthesize ubiquinones as the main isoprenoid quinone.

The comparison of the phenotypic, genomic and phylogenetic characteristics of strain R4DWN^T with those of its closest phylogenetic neighbours revealed that this strain represents a new species belonging to the genus *Sphingomonas* for which the name of *Sphingomonas solaris* sp. nov. is proposed.

DESCRIPTION OF *SPHINGOMONAS SOLARIS* SP. NOV.

Sphingomonas solaris (so.la.ris. N.L. fem. adj. *solaris*, pertaining to the sun, referring to the origin of the type strain, isolated from the surface of solar panels).

Cells are Gram-negative, non-motile and rod-shaped (1.2–4.5 µm long × 1.2 µm wide). In old cultures, some cells grow in the form of a long rod shape of approximately 30 µm. After 7 days of incubation at 25 °C, colonies are round-shaped, shiny, orange-coloured, convex and 1 mm in diameter. This species is able to grow between 4 and 25 °C (optimum, 15–25 °C), and tolerates up to 1% NaCl (w/v), with optimum at 0% NaCl (w/v). The pH for optimum growth ranges between 6 and 9, and oxidase and catalase tests were

positive. Alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, acid phosphatase, naphthol-AS-BI-phosphohydrolase, β -galactosidase and β -glucosidase activities are detected, whereas lipase (C14), cystine arylamidase, trypsin, α -chymotrypsin, α -galactosidase, β -glucuronidase, α -glucosidase, *N*-acetyl-beta-glucosaminidase, α -mannosidase and α -fucosidase activities are not detected. Using API 20NE test kit, this species is positive for the assimilation of glucose, arabinose, mannitol, *N*-acetyl-glucosamine and maltose; weak for the assimilation of potassium gluconate and malic acid; and negative for the assimilation of mannose, capric acid, adipic acid, trisodium citrate and phenylacetic acid. Using Biolog GENIII MicroPlates, this species is positive for the utilization of glucuronamide, acetoacetic acid, D-fructose-6-PO₄ and L-malic acid; weakly positive for the utilization of L-galactonic acid lactone, β -hydroxy-D,L-butyrac acid and D-glucose-6-PO₄; and negative for the utilization of raffinose, α -D-glucose, D-sorbitol, gelatin, pectin, *p*-hydroxy-phenylacetic acid, Tween 40, dextrin, lactose, D-mannose, D-mannitol, glycyl-L-proline, D-galacturonic acid, methyl pyruvate, γ -amino-butyrac acid, maltose, melibiose, D-fructose, D-arabitol, L-alanine, D-lactic acid methyl ester, α -hydroxy-butyrac acid, trehalose, methyl β -D-glucoside, D-galactose, myo-inositol, L-arginine, D-gluconic acid, L-lactic acid, cellobiose, D-salicin, 3-methyl glucose, glycerol, L-aspartic acid, D-gluconic acid, citric acid, α -keto-butyrac acid, gentiobiose, *N*-acetyl-D-glucosamine, D-fucose, L-glutamic acid, α -keto-glutaric acid, sucrose, *N*-acetyl- β -D-mannosamine, L-fucose, L-histidine, mucic acid, D-malic acid, propionic acid, turanose, *N*-acetyl-D-galactosamine, L-rhamnose, D-aspartic acid, L-pyroglytamic acid, quinic acid, acetic acid, stachyose, *N*-acetyl neuraminic acid, inosine, D-serine, L-serine, D-saccharic acid, bromo-succinic acid and formic acid. The major fatty acids are C_{18:1} ω 7c/C_{18:1} ω 6c, C_{16:1} ω 7c/C_{16:1} ω 6c, C_{14:0} 2OH and C_{16:0}. The type strain is R4DWN^T (=CECT 9811^T=LMG 31344^T), isolated from the surface of a solar panel in Boston, MA, USA. The genomic G+C content of the type strain is 67.9mol%.

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Conflicts of interest

The authors declare that there are no conflicts of interest.

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