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TAXONOMIC DESCRIPTION

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# *Tundrisphaera lichenicola* gen. nov., sp. nov., a psychrotolerant representative of the family *Isosphaeraceae* from lichen-dominated tundra soils

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**Abstract**

Two strains of aerobic, budding, pink-pigmented bacteria, P12$^T$ and P515, were isolated from a lichen-dominated peatland and a forested tundra soil of north-western Siberia, respectively. Cells of these isolates were represented by non-motile spheres that occurred singly or were arranged in short chains and aggregates. While growing on solid media, cells of strains P12$^T$ and P515 attached to the surface by means of holdfast-like appendages. These isolates were mildly acidophilic (optimum growth at pH 5.5–6.0), psychrotolerant bacteria, which displayed tolerance of low temperatures (4–15 °C), grew optimally at 15–22 °C and did not grow at temperatures above 28 °C. The preferred growth substrates were sugars and some heteropolysaccharides. The major fatty acids were $C_{18:1}\omega9c$, $C_{16:0}$ and $C_{14:0}$. Trimethylornithine lipid was the major polar lipid. The only quinone was MK-6, and the G+C content of the DNA was 61.2–62.2 mol%. Strains P12$^T$ and P515 possessed identical 16S rRNA gene sequences, which affiliated them with the family *Isosphaeraceae*, order *Planctomycetales*, and these displayed the highest similarity (93–94 %) to 16S rRNA gene sequences from members of the genus *Singulisphaera*. However, the signature fatty acid of species of the genus *Singulisphaera*, i.e. $C_{18:2}\omega6c$,12*c*, was absent in cells of strains P12$^T$ and P515. They also differed from members of the genus *Singulisphaera* by substrate utilization pattern and a number of physiological characteristics. Based on these data, the novel isolates should be considered as representing a novel genus and species of planctomycetes, for which the name *Tundrisphaera lichenicola* gen. nov., sp. nov, is proposed. The type strain is P12$^T$ (=LMG 29571$^T$=VKM B-3044$^T$).

The family *Isosphaeraceae* belongs to the order *Planctomycetales* and accommodates stalk-free planctomycetes with spherical cells, which can be assembled in short chains, long filaments or shapeless aggregates [1]. At present, this family includes four described genera, i.e. *Isosphaera* [2], *Singulisphaera* [3, 4], *Aquisphaera* [5] and *Paludisphaera* [1]. *Isosphaera pallida* was the first member of this family to be described taxonomically and is the only thermophilic member. Three other described genera accommodate mesophilic or cold-adapted planctomycetes. Members of the family *Isosphaeraceae* are especially abundant and diverse in boreal peatlands, where they appear to be involved in degradation of *Sphagnum*-derived litter [6–8]. The presence of hydrolytic potential in these bacteria was confirmed by the comparative genome analysis of several mesophilic planctomycetes of the family *Isosphaeraceae* [9]. Our recent molecular survey of planctomycete diversity in lichen-dominated tundra soils within the zone of forested tundra and discontinuous permafrost of northwest Siberia showed that representatives of the family *Isosphaeraceae* are common in these cold ecosystems as well [10]. Two isolates of bacteria resembling members of the genus *Singulisphaera*, strains P12$^T$ and P515, were isolated from these tundra environments. In general, phenotypic properties of these isolates were similar to those defined for members of the genus *Singulisphaera* [4], although their exact taxonomic identification required obtaining additional chemotaxonomic and genotypic data. This study, therefore, was initiated in order to determine the taxonomic position of these planctomycetes.

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**Keywords:** the phylum *Planctomycetes*; family *Isosphaeraceae*; *Tundrisphaera lichenicola* gen. nov., sp. nov.; lichen-dominated tundra soils.

**Abbreviation:** IPL, intact polar lipid.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of *Tundrisphaera lichenicola* P12$^T$ is KX943553.

One supplementary table is available with the online Supplementary Material.

Strains P12$^T$ and P515 were obtained from the upper oxic layer (0–10 cm) of a shallow peatland (65° 35′ 01.3″ N 73° 03′ 10″ E) and lichen-dominated forested tundra soil (65° 36′ 07.1″ N 72° 44′ 39.5″ E), respectively, in Nadym region, Yamalo-Nenets Autonomous Okrug, Russia. The enrichment strategy and the isolation approach have been described elsewhere [10]. The isolates were maintained routinely at 20 °C on medium M31 (modification of medium 31 described by Staley *et al.* [11]), solidified with 10 g phytagel (Sigma-Aldrich) and containing (per litre distilled water) 0.1 g $KH_2PO_4$, 20 ml Hutner's basal salts, 1.0 g *N*-acetylglucosamine, 0.2 g ampicillin (sodium salt), 0.1 g peptone and 0.1 g yeast extract, pH 5.8. The strains were sub-cultured at 2-month intervals.

Morphological observations and cell size measurements were made with a Zeiss Axioplan 2 microscope and Axiovision 4.2 software (Zeiss). For negative staining, cells were dried onto grids and treated with 1 % (w/v) phosphotungstic acid. The specimen samples were examined with a JEM-1011 (JEOL) transmission electron microscope. For scanning electron microscopy, a small piece of solid medium with bacterial cells was fixed in glutaraldehyde vapour for 12 h at 4 °C and was then post-fixed in vapours of osmium tetroxide for 24 h at 20 °C. The samples were then critical-point dried on a Dryer JEE-4X (JEOL), coated with the Au alloy on a JFC 1100 (JEOL) and examined with a JSM-6510LV scanning electron microscope (JEOL).

On phytagel-solidified medium M31, strains P12$^T$ and P515 formed small (1–2 mm), circular, pink-pigmented colonies with an entire edge and a smooth surface. These colonies were composed of non-motile, spherical cells, which varied in size from 2.2 to 3.0 µm and reproduced by budding (Fig. 1a). The buds separated from the mother cells were non-motile. While colonizing solid media, cells of strains P12$^T$ and P515 attached to the surface by means of thick holdfast appendages (Fig. 1b–d). These appendages were mostly observed in old (4–6 weeks) cultures. The examination of negatively stained cells using electron microscopy revealed the presence of numerous crateriform pits, which were uniformly scattered over the cell surface (data not shown). Liquid cultures of the novel isolates displayed pink turbidity.

Physiological tests were performed in liquid medium M31. Growth of strains P12$^T$ and P515 was monitored by nephelometry at 600 nm in an Eppendorf BioPhotometer for 2–3 weeks under a variety of conditions, including temperatures of 4–37 °C, pH 3.8–7.9 and NaCl concentrations of 0–3.0 % (w/v). Incubations at various temperatures were made under static conditions in triplicate; optical density at 600 nm ($OD_{600}$) was determined after 2 weeks of incubation. Variations in pH were achieved by using MES (pH 4.0–6.5) and MOPS (pH 6.5–7.9) buffer systems. The pH range of pH 3–4 was achieved by adjusting the medium pH with 0.1 M $H_2SO_4$. Strains P12$^T$ and P515 were capable of growth at pH values of between pH 4.5 and 6.8 (with an optimum at pH 5.5–6.0), and at temperatures of between 4 and 28 °C (with an optimum at 15–22 °C). The specific growth rate displayed by these planctomycetes at 10 °C ($\mu$=0.014 $h^{-1}$; $T_d$=49.8 h) was close to that observed at 22 °C ($\mu$=0.020 $h^{-1}$; $T_d$=35.3 h). Slow, but consistent, growth was also detected at 4 °C ($\mu$=0.008 $h^{-1}$; $T_d$=82 h). In contrast to the previously described planctomycetes of the family *Isosphaeraceae*, strains P12$^T$ and P515 did not grow at temperatures above 28 °C. These planctomycetes are, therefore, psychrotolerant micro-organisms. NaCl inhibited growth at concentrations above 0.1 % (w/v).

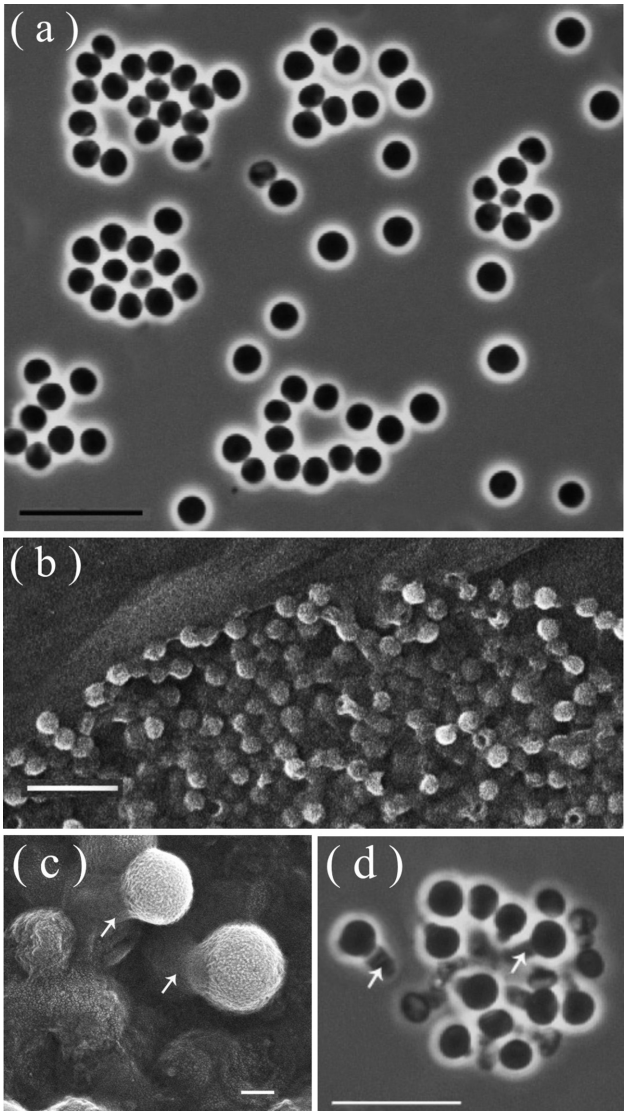


**Fig. 1.** (a) Phase-contrast image of cells of strain P12$^T$ grown for 14 days on solid medium M31; (b) a mono-layer of cells formed by strain P12$^T$ on the surface of a solid medium; (c and d) thick holdfast appendages (indicated by white arrows) observed in old cultures of strain P12$^T$ by electron (c) or phase-contrast (d) microscopy. Bars, 10 µm (a, b, d); 1 µm, (c).

Carbon source utilization was determined using mineral medium M1 supplemented with 0.005 % yeast extract and

the individual carbon sources given in the species description at a concentration 0.05 % (w/v). Medium M1 contained (grams per litre of distilled water): $KH_2PO_4$, 0.1; $(NH_4)_2SO_4$, 0.1; $MgSO_4 . 7H_2O$, 0.1; $CaCl_2 . 2H_2O$, 0.02; 1 ml of trace element solution '44' and 1 ml Staley's vitamin solution [11]; pH 4.8–5.5. Cultivation was done in 120 ml flasks containing 10 ml medium, which were incubated at 22 °C for 2–3 weeks on a shaker. The capability to degrade different biopolymers was examined by measuring the rate of $CO_2$ production in tightly closed 160 ml serum bottles containing 10 ml of liquid medium M1 with 0.005 % yeast extract as a growth factor and 0.05 % (w/v) of the corresponding polymer substrate for 1 month at 22 °C. Control incubations were run in parallel under the same conditions but without a polymer substrate. $CO_2$ concentration was measured with an Infralit non-dispersive infra-red gas-analyser. All experiments were performed in triplicate. Oxidative and fermentative utilization of carbohydrates was determined as described for the Hugh–Leifson test [12]. Nitrogen sources were tested using liquid medium M1 in which $(NH_4)_2SO_4$ was replaced with one of the following compounds at a concentration of 0.01 % (w/v): $KNO_3$, $KNO_2$, urea, *N*-acetylglucosamine, Bacto peptone, Bacto yeast extract or one of the amino acids listed in the species description. Analyses of enzymic profiles, gelatin and urease hydrolysis, and indole production were made with API ZYM and API 20NE kits (bioMérieux). A catalase test was carried out by standard methods [12]. Oxidase was tested using REF 55 635 Oxidase reagent (bioMérieux). Cultures were tested for growth under anaerobic conditions in anaerobic jars by using AnaeroGen anaerobic system envelopes (Oxoid), which absorb atmospheric oxygen with the simultaneous generation of $CO_2$ (up to 9–13 %, v/v). Strains P12$^T$ and P515 were obligately aerobic chemoheterotrophs and did not grow under anoxic conditions. Both strains were catalase positive, but cytochrome oxidase- and urease-negative. Dissimilatory nitrate reduction was negative. The preferred growth substrates were various sugars, including *N*-acetylglucosamine, and some heteropolysaccharides, such as aesculin, arabinogalactan, dextrin, lichenan, locust bean gum, starch, xanthan gum, xylan and gelatin (see the species description). Notably, the growth rates on xylan and lichenan were comparable to those on sucrose. Organic acids were not utilized. Cellulose, casein, chondroitin sulfate, chitin, chitosan, laminarin and pectin were not hydrolyzed. Strains P12$^T$ and P515 utilized nitrate, ammonia, Bacto yeast extract, glutamine, asparagine, serine, valine and lysine as nitrogen sources. The following enzymic activities (API ZYM test) were detected in these bacteria: alkaline and acid phosphatase, esterase, esterase lipase, leucine arylamidase, valine arylamidase, phosphohydrolase, *N*-acetyl-$\beta$-glucosaminidase, $\alpha$-glucosidase and $\beta$-galactosidase. The following enzymic activities were not detected: lipase, trypsin, chymotrypsin, cystine arylamidase, $\alpha$-galactosidase, $\beta$-glucosidase, $\beta$-glucuronidase, $\alpha$-fucosidase and $\alpha$-mannosidase.

**Table 1.** Fatty acid contents (percentages; normalized by their sum) released after acid hydrolysis of cell material

Strains: 1, P12$^T$; 2, P515; 3, *Singulisphaera rosea* S26$^T$ [4]; 4, *Singulisphaera acidiphila* MOB10$^T$ [3]. Major components are given in bold type. –, Not detected.

| Fatty acid | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| $nC_{14:1}\omega5c$ | 1.0 | 1.2 | – | – |
| $nC_{14:0}$ | **11.5** | **12.9** | 5.2 | 1.8 |
| $nC_{15:0}$ | 0.9 | 1.0 | 0.3 | 0.4 |
| iso-$C_{16:0}$ | 0.9 | – | – | 0.5 |
| $nC_{16:1}\omega7c$ | 2.0 | 2.3 | 0.6 | 1.3 |
| $nC_{16:1}\omega5c$ | 1.0 | 1.2 | – | – |
| $nC_{16:0}$ | **21.2** | **20.5** | **28.3** | **33.1** |
| $nC_{17:1}\omega8c$ | – | 0.6 | – | – |
| $nC_{18:2}\omega6c,12c$ | – | – | **13.3** | **11.9** |
| $nC_{18:1}\omega9c$ | **51.6** | **50.4** | **40.2** | **42.8** |
| $nC_{18:1}\omega7c$ | 2.0 | 1.6 | – | – |
| $nC_{18:0}$ | 7.9 | 8.2 | 6.5 | 6.5 |

Susceptibility to antibiotics was determined on solid medium M31 using discs (Oxoid) containing the following antibiotics: ampicillin (10 µg), gentamycin (10 µg), kanamycin (30 µg), neomycin (10 µg), novobiocin (30 µg), streptomycin (10 µg), chloramphenicol (30 µg) and lincomycin (10 µg). Growth of strains P12$^T$ and P515 and occurrence of growth inhibition zones around these discs were assessed after 4 weeks of incubation at 22 °C. Only the inhibition zones exceeding 2 mm were taken into account. Both strains were resistant to ampicillin, chloramphenicol, streptomycin, lincomycin and novobiocin, but sensitive to kanamycin, neomycin and gentamicin.

For the analysis of total lipids (including fatty acids), cells of strains P12$^T$ and P515 were grown in liquid medium M31 and harvested in the late exponential growth phase. Lipids were analysed after acid hydrolysis of the cell material following the procedure described by Kulichevskaya *et al.* [4]. The major fatty acids detected in strains P12$^T$ and P515 were $nC_{14:0}$, $nC_{16:0}$ and $nC_{18:1}\omega9$ (Table 1). In general, these fatty acid profiles were somewhat similar to those of members of the genus *Singulisphaera* (Table 1). The key difference, however, was that the signature fatty acid of species of the genus *Singulisphaera*, $nC_{18:2}\omega6c,12c$, was missing from cells of strains P12$^T$ and P515. Also, the content of $nC_{14:0}$ in the novel isolates (11.5–12.9 %) was higher than that in members of the genus *Singulisphaera* (1.8–5.2 %). In addition, smaller amounts of a suite of long-chain hydroxyl fatty acids and the neutral lipid, $nC_{31:9}$ alkene were present in both strains (Table S1, available in the online Supplementary Material). The occurrence of these latter components is more widespread in planctomycetes [1, 3, 4, 13–15].

The intact polar lipids (IPLs) in strains P12$^T$ and P515 were analysed as described by Moore *et al.* [16]. Trimethylornithine IPLs were the major constituents, while smaller

**Table 2.** Relative abundances and fatty acid composition of intact polar lipids of strains P12$^T$ and P515

| IPL* | P12$^T$ | P515 | Fatty acid composition† |
|---|---|---|---|
| PG | +‡ | + | ($C_{36:2}$, $C_{34:1}$, $C_{32:1}$) |
| PC | + | + | ($C_{36:1}$, $C_{34:1}$, $C_{32:1}$) |
| TMO | +++ | +++ | ($C_{18:1}$, $\beta$OH-$C_{18}$) |

*Listed in order of elution: PG, phosphoglycerol; PC, phosphocholine; TMO, trimethylornithine lipid.

†The predominant fatty acid composition is reported as the total number of carbon atoms of the acyl moieties and the number of double bonds.

‡The abundance is relative to major peaks in the LC/MS base peak chromatogram: +++, base peak; ++, 50–100 % of base peak; +, 10–50 % of base peak. Note that the mass spectral response factors for different IPL groups can be quite different.

amounts of phosphatidylglycerol and phosphatidylcholine were also detected (Table 2).

Isoprenoid quinones were extracted according to Collins [17] and analysed using a tandem-type mass spectrometer LCQ ADVANTAGE MAX and a Finnigan Mat 8430 ionization mass spectrometer. Similar to other members of the order *Planctomycetales* [18], strains P12$^T$ and P515 contained menaquinone-6 (MK-6) as the only isoprenoid quinone.

The DNA base composition of the novel isolates were determined by thermal denaturation using a Cary-100 UV-VIS spectrophotometer (Varian) at a heating rate of 0.5 °C min$^{-1}$.

The DNA G+C content (mol%) was calculated according to the method of Owen *et al.* [19]. DNA of *Escherichia coli* K-12 (DNA G+C content 51.7 mol%) was used as the standard. The DNA G+C contents of strains P12$^T$ and P515 were 61.2 and 62.2 mol%, respectively.

PCR-mediated amplification of the 16S rRNA gene from positions 28 to 1491 (numbering according to the International Union of Biochemistry nomenclature for *Escherichia coli* 16S rRNA) was performed using primers 9f and 1492r and reaction conditions described by Weisburg *et al.* [20]. The 16S rRNA gene amplicons were purified using QIAquick spin columns (Qiagen) and sequenced on an ABI Prism 377 DNA sequencer using BigDye terminator chemistry, as specified by the manufacturer (PE Applied Biosystems). Phylogenetic analysis was carried out using the ARB program package [21]. The significance levels of interior branch points obtained in the neighbour-joining analysis were determined by bootstrap analysis (based on 1000 data resamplings) using PHYLIP [22]. The comparative 16S rRNA gene-based analysis confirmed that strains P12$^T$ and P515 possessed identical 16S rRNA gene sequences, which were affiliated with the family *Isosphaeraceae*, order *Planctomycetales*, and displayed highest similarity (93–94 %) to 16S rRNA gene sequences from members of the genus *Singulisphaera* (Fig. 2). The 16S rRNA gene sequence similarity to other currently described representatives of the family *Isosphaeraceae* was 90–92 %.

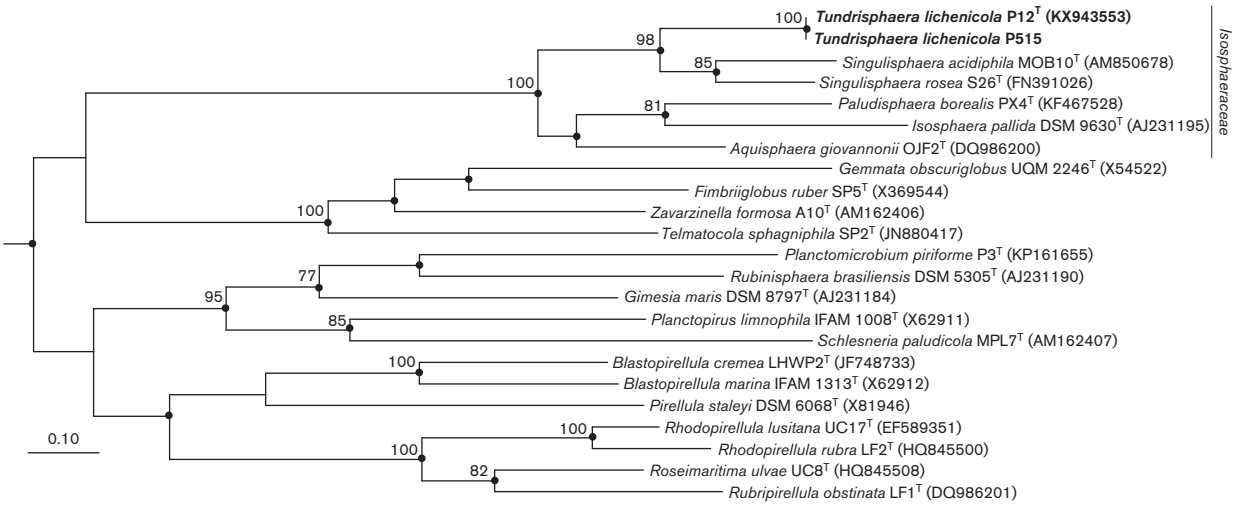


**Fig. 2.** 16S rRNA gene-based neighbour-joining tree (Jukes–Cantor correction) showing the phylogenetic relationship of strains P12$^T$ and P515 to representative members of the order *Planctomycetales*. The boundaries of the family *Isosphaeraceae* are shown on the right. The significance levels of interior branch points obtained in neighbour-joining analysis were determined by bootstrap analysis (1000 data re-samplings). Bootstrap values (1000 data resamplings) of >70 % are shown. Filled circles indicate that the corresponding nodes were also recovered in the maximum-likelihood and maximum-parsimony trees. The root (not shown) was composed of five 16S rRNA gene sequences from anammox planctomycetes (AF375994, AF375995, AY254883, AY257181 and AY254882). Bar, 0.1 substitutions per nucleotide position.

**Table 3.** Major characteristics that distinguish *Tundrisphaera* gen. nov. and other described genera of the *Isosphaeraceae*

Genera: 1, *Tundrisphaera* gen. nov.; 2, *Singulisphaera* (data from [3, 4, 23]); 3, *Paludisphaera* (data from [1, 9]); 4, *Aquisphaera* (data from [8]); 5, *Isosphaera* (data from [2, 24]). +, Positive; −, negative; ND, not determined; V, variable.

| Characteristic | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| Arrangement of cells | Single, in pairs or short chains | Single or in pairs | Single, in pairs or short chains | Single or aggregates | Filaments |
| Holdfast-like appendages | + | − | − | − | − |
| Gliding motility | − | − | − | − | + |
| Photo-taxis | − | − | − | − | + |
| Habitat | Lichen-dominated tundra soils | Wetlands | Wetlands | Freshwater | Hot springs |
| Colony colour | Pink | Colourless or pink | Pink | Pink | Pink |
| Respiration | Strictly aerobic | Aerobic or microaerophilic | Aerobic or microaerophilic | Strictly aerobic | Strictly aerobic |
| Hydrolysis of: | | | | | |
| Phytagel | − | − | + | ND | ND |
| Aesculin | + | + | + | − | ND |
| Starch | + | V | − | + | ND |
| Xylan | + | V | + | − | ND |
| Temperature for growth | | | | | |
| Range (°C) | 4–28 | 4–33 | 6–30 | 10–35 | 34–55 |
| Optimum (°C) | 15–22 | 15–28 | 15–25 | 30–35 | 40–50 |
| pH range for growth | 4.5–6.8 | 4.2–7.5 | 3.5–6.5 | 6.5–9.5 | ND |
| pH optimum for growth | 5.5–6.0 | 5.0–6.2 | 5.0–5.5 | 7.5–8.5 | 7.8–8.8 |
| Oxidase | − | − | − | + | ND |
| Vitamin requirement | None | None | None | $B_{12}$ | ND |
| Presence of $C_{18:2}\omega6c,12c$ | − | + | − | − | ND |
| DNA G+C content (mol%)* | 61.2–62.2 | 62.0 | 66.3 | 70.0 | 62.4 |

*Values given for the genera *Paludisphaera*, *Singulisphaera* and *Isosphaera* are based on genome sequence analyses.

In summary, strains P12$^T$ and P515 displayed some phenotypic similarity and were related phylogenetically to planctomycetes of the genus *Singulisphaera*. However, cells of the novel isolates formed holdfast-like appendages, which were not observed in species of the genus *Singulisphaera*, and displayed significant differences in the fatty acid composition. Other characteristics that differentiate strains P12$^T$ and P515 from members of the genus *Singulisphaera* as well as other described genera of the family *Isosphaeraceae* are listed in Table 3. Given these differences, we propose to classify the novel isolates as members of a novel genus and species of planctomycetes, for which the name *Tundrisphaera lichenicola* gen. nov., sp. nov, is proposed.

## DESCRIPTION OF *TUNDRISPHAERA* GEN. NOV.

*Tundrisphaera* (Tun.dri.sphae′ra. N.L. n. *tundra* tundra, a cold treeless region; L. fem. n. *sphaera* a ball, globe sphere; N.L. fem. n. *Tundrisphaera* a spherical cell from tundra).

Spherical cells that occur singly, in pairs, in short chains or in shapeless aggregates. Non-motile. Reproduce by budding. Daughter cells are non-motile. Crateriform pits are scattered all over the cell surface. Attach to surfaces by means of thick holdfast-like appendages. Chemoheterotrophic aerobes. Moderately acidophilic and psychrotolerant. Sensitive to NaCl. The major quinone is MK-6. The major fatty acids are $C_{18:1}\omega9c$, $C_{16:0}$ and $C_{14:0}$. Trimethylornithine lipid is the major polar lipid. The genus is a member of the phylum *Planctomycetes*, order *Planctomycetales*, family *Isosphaeraceae*. The type species is *Tundrisphaera lichenicola*.

## DESCRIPTION OF *TUNDRISPHAERA LICHENICOLA* SP. NOV.

*Tundrisphaera lichenicola* [li.che.ni′cola. L. n. *lichen* lichen; L. suff. *-cola* (from L. n. *incola*) inhabitant, dweller; N.L. n. *lichenicola* inhabitant of lichens).

Exhibits the following properties in addition to those given in the genus description. Colonies are pink. Mature spherical cells are 2.2–3.0 µm in size. Catalase-positive and cytochrome- oxidase and urease-negative. Dissimilatory nitrate reduction and glucose fermentation are negative. Cannot produce indole from tryptophan. Carbon sources include arabinose, cellobiose, glucose, galactose, fructose, lactose, leucrose, maltose, mannose, melibiose, rhamnose, ribose, sucrose, trehalose, xylose, salicin and *N*-acetylglucosamine.

Capable of hydrolysing aesculin, arabinogalactan, dextrin, lichenan, locust bean gum, starch, xanthan gum, xylan and gelatin. Cannot utilize melizitose, raffinose, sorbose, fucose, glycerol, gluconate, methanol, ethanol, galacturonate, acetate, benzoate, caproate, citrate, formate, formaldehyde, fumarate, glutarate, galacturonate, lactate, malate, succinate, pyruvate, propionate, tartrate, adonitol, dulcitol, mannitol, sorbitol, alanine, arginine, asparagine, aspartate, cysteine, cystine, glutamine, glycine, histidine, isoleucine, leucine, lysine, methionine, norleucine, ornithine, phenylalanine, proline, serine, threonine, tryptophan, tyrosine or valine. Cannot hydrolyse casein hydrolysate, chondroitin sulfate, chitosan, chitin, cellulose, laminarin or pectin. Shows the following enzyme activities: alkaline and acid phosphatase, esterase, esterase lipase, leucine arylamidase, valine arylamidase, phosphohydrolase, *N*-acetyl-$\beta$-glucosaminidase, $\alpha$-glucosidase and $\beta$-galactosidase (API ZYM test). The following enzyme activities are not present: lipase, trypsin, chymotrypsin, cystine arylamidase, $\alpha$-galactosidase, $\beta$-glucosidase, $\beta$-glucuronidase, $\alpha$-fucosidase and $\alpha$-mannosidase. Utilizes nitrate, ammonia, Bacto yeast extract, glutamine, asparagine, serine, valine and lysine as nitrogen sources. Resistant to ampicillin, chloramphenicol, streptomycin, lincomycin and novobiocin, but sensitive to kanamycin, neomycin and gentamicin. Growth occurs at pH 4.5–6.8 (optimum, pH 5.5–6.0) and at temperatures between 4 and 28 °C (optimum, 15–22 °C). NaCl inhibits growth at concentrations above 0.1 % (w/v). The G+C content of the DNA is 61.2–62.2 mol%.

The type strain is P12$^T$ (=LMG 29571$^T$=VKM B-3044$^T$), which was isolated from a shallow tundra peatland in Nadym region, Yamalo-Nenets Autonomous Okrug, Russia.

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

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