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BRIEF REPORT

ENVIRONMENTAL MICROBIOLOGY

Genome analysis and description of *Tunturibacter* gen. nov. expands the diversity of *Terriglobia* in tundra soils

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Abstract

Increased temperatures in Arctic tundra ecosystems are leading to higher microbial respiration rates of soil organic matter, resulting in the release of carbon dioxide and methane. To understand the effects of this microbial activity, it is important to better characterize the diverse microbial communities in Arctic soil. Our goal is to refine our understanding of the phylogenetic diversity of *Terriglobia*, a common but elusive group within the *Acidobacteriota* phylum. This will help us link this diversity to variations in carbon and nitrogen usage patterns. We used long-read Oxford Nanopore MinION sequences in combination with metagenomic short-read sequences to assemble complete *Acidobacteriota* genomes. This allowed us to build multi-locus phylogenies and annotate pangenome markers to distinguish *Acidobacteriota* strains from several tundra soil isolates. We identified a phylogenetic cluster containing four new species previously associated with *Edaphobacter lichenicola*. We conclude that this cluster represents a new genus, which we have named *Tunturibacter*. We describe four new species: *Tunturibacter lichenicola* comb. nov., *Tunturibacter empetritectus* sp. nov., *Tunturibacter gelidoferens* sp. nov., and *Tunturibacter psychrotolerans* sp. nov. By uncovering new species and strains within the *Terriglobia* and improving the accuracy of their phylogenetic placements, we hope to enhance our understanding of this complex phylum and shed light on the mechanisms that shape microbial communities in polar soils.

INTRODUCTION

Approximately one third of the global soil carbon stock is stored in Arctic soils (Hugelius et al., 2014; Loya & Grogan, 2004), and despite sub-zero temperatures, microbial activity persists throughout the long winters, albeit at a slower rate (Gadkari et al., 2020; Natali et al., 2014; Nikrad et al., 2016; Oechel et al., 1997; Pessi et al., 2022; Poppeliers et al., 2022; Welker et al., 2000). Microbes play important roles in nutrient cycling as they decompose soil organic matter (SOM). As polar soils warm due to climate change, it is of concern that enhanced microbial activity will increase the rate of SOM degradation and consequently greenhouse gas emissions (Campbell et al., 2010; Graham et al., 2012; Natali et al., 2014; Welker et al., 2000). SOM degradation usually increases in the short summer season, with climate change resulting in faster and longer soil decomposition and increased greenhouse gas emissions that contribute to a positive warming feedback loop (Bond-Lamberty & Thomson, 2010; Koven et al., 2011; Schuur et al., 2008). However, the mechanisms by which climate change affects gas emissions are complex and site-specific, likely determined by for example, vegetation type and microbial community structure (Fry et al., 2023).

The microbial community diversity of Arctic environments, like the tundra, is shaped by soil abiotic factors (e.g., pH, SOM, temperature and water activity) and the

extreme conditions of the Arctic (e.g., intense UV radiation, drought, long periods of sub-zero temperatures interspersed by freeze–thaw events; Männistö et al., 2009; Taş et al., 2018; Tveit et al., 2014; Viitamäki et al., 2022; Weintraub & Schimel, 2003). Despite these harsh conditions, there is tremendous bacterial diversity in tundra soils, with the bacterial communities dominated by *Acidobacteriota*, *Actinomycetota*, and *Pseudomonadota* (*Proteobacteria*; Chu et al., 2010; Kim et al., 2014; Männistö et al., 2007, 2013; Viitamäki et al., 2022; Voříšková et al., 2019). Members of these phyla change in abundance, composition, and activity in response to environmental variables such as seasonal changes (freeze–thaw cycles), vegetation, and soil pH (Männistö et al., 2009, 2013; McMahon et al., 2011; Viitamäki et al., 2022; Zinger et al., 2009). The ubiquitous but elusive *Acidobacteriota* are particularly susceptible to changes in soil pH and different members of the phylum thrive at different pH levels. Members of the Class *Terriglobia* (formerly *Acidobacteriia*; Sub-division 1 [SD1] *Acidobacteriota*) are particularly abundant in the cold, nutrient-poor, acidic soils such as those in Arctic tundra and boreal forest biomes (Belova, Ravin, et al., 2018; Campbell et al., 2010; Ivanova et al., 2020; Kim et al., 2014; Männistö et al., 2007, 2009, 2018).

The *Acidobacteriota* is one of the most abundant phyla in soils around the globe; however, the diversity within this phylum is still largely uncharacterized (Zhang et al., 2022). Initial culture-independent methods initially delineated 26 subdivisions of *Acidobacteria* (Barns et al., 2007). More recently, these subdivisions were refined into 15 class-level units (Dedysh & Yilmaz, 2018). Of these, the classes *Terriglobia*, *Blastocatellia*, and *Vicinamibacteria* are most abundant in soils (Janssen, 2006; Jones et al., 2009). Furthermore, members of the *Terriglobia* have been the most successfully cultivated group with over 40 named and published species to date (Göker, 2023; Zhang et al., 2022).

The family *Acidobacteriaceae* currently encompasses over a dozen named genera; however with faster and more advanced sequencing technologies a greater number of *Acidobacteriota* species and strains are being described (Kalam et al., 2020; Zhang et al., 2022). The analysis of multiple genes from isolate genomes and environmental metagenomes has contributed towards a better understanding of the diversity of *Acidobacteriota* in multiple ecosystems without the need for cultivation (Dedysh et al., 2022; Kalam et al., 2020; Kielak et al., 2016; Parsley et al., 2011). Genome analysis has indicated a variety of metabolic functions within the *Acidobacteriota* including complex carbohydrate degradation (xylan, cellulose, hemicelluloses, pectin, starch, and chitin), nitrogen metabolism (nitrate, nitrite, and nitric oxide reduction), genes for oxygen utilization in hypo- and hyperoxic conditions, as well as the ability to oxidize methanol (Diamond et al., 2019; Eichorst et al., 2007; Kalam et al., 2020; Rawat et al., 2012; Ward et al., 2009). Some *Acidobacteriota* is equipped with regulatory genes in response to stressors like starvation, oxidative stress, heat stress, as well as acid resistance systems (Challacombe et al., 2011; Kalam et al., 2020; Kielak et al., 2016; Ward et al., 2009). Secondary metabolites from biosynthetic gene clusters were also found within *Acidobacteriota*. Specifically, non-ribosomal peptide synthetases and polyketide synthases were found within *Candidatus* Angelobacter (a proposed *Terriglobia*), indicating mechanisms for interbacterial competition (Crits-Christoph et al., 2022).

There may be several reasons for such a high taxonomic and functional diversity of *Acidobacteriota* in terrestrial systems. Primarily, soils create complex and spatially/temporally heterogeneous environments, with this disequilibrium ensuring that no one species dominates over others (Ghoul & Mitri, 2016; Lennon et al., 2012). Additionally, ecological drivers, such as resource partitioning, selective predation, and temporal separation, most likely shape the diversity of *Acidobacteriota* and other soil phyla (Chesson, 2000; Chesson & Huntly, 1997). To better understand how *Acidobacteriota* activity is shaped by environmental and ecological factors we need to identify the yet uncharacterized species/strains within this phylum and compare their genomes to elucidate metabolic potential. In this study, we sequenced several new tundra soil *Acidobacteriota* isolates from Malla Nature Reserve, Kilpisjärvi, Finland using both Illumina short-read and Oxford Nanopore long-read technologies. Through rRNA operon and full genome analysis, we expand the current phylogenetic diversity of the order *Terriglobales* in the *Acidobacteriota*. We also delineate and name a novel genus, *Tunturibacter*, containing four new species in phylogenetic proximity to other species within the genera *Terriglobus* (Eichorst et al., 2007; Männistö et al., 2011; Podar et al., 2019; Rawat et al., 2012), *Granulicella* (Männistö et al., 2012; Pankratov & Dedysh, 2010; Rawat et al., 2013, 2014), and *Edaphobacter* (Koch et al., 2008; Wang et al., 2016). With functional annotation and comparison of this new genus to known *Acidobacteriota*, the core and unique genes of the genera within this group can be identified. Our phylogenetic analysis demonstrates that a complex diversity of the *Terriglobales* can be uncovered. Additionally, understanding how novel genera differ within *Acidobacteriota* can help further elucidate why such diversity exists in soil environments.

EXPERIMENTAL PROCEDURES

Acidobacteriota isolation and DNA extraction

Acidobacteriota strains were isolated from tundra soil samples collected from Malla Nature Reserve,

Kilpisjärvi, Finland (69°01′ N, 20°50′ E) in July 2010 (strain codes that begin with 'M') and July 2012 (strain codes that begin with 'X'). Several carbon substrates were tested in an attempt to isolate novel members of the *Acidobacteriota*. Soil samples were diluted in VL55 mineral medium (Davis et al., 2005) and dilution plated on the different media. Plates were incubated at 4°C for up to 3 months and inspected every 2 weeks. To isolate *Acidobacteriota* and other slow-growing oligotrophs, only colonies that formed after 1–2 months of incubation were picked and streaked to new media. After purification, isolated strains were identified by Sanger sequencing of the 16S rRNA gene. DNA was extracted from the isolates using the DNeasy UltraClean Microbial Kit (Qiagen) according to the manufacturer's instructions. 16S rRNA genes were amplified using 27f and 1525r primers (Lane, 1991) and the polymerase chain reaction (PCR) products were sequenced by LGC Genomics (Berlin, Germany) using the forward primer 27 f. Approximately 800 bp sequences were compared with those in the EzTaxon database (Yoon et al., 2017) and those identified as members of the *Acidobacteriota* were selected for further studies.

Strains M8UP20, M8UP22, M8UP23, M8UP27, M8UP28, M8UP30, and M8UP39 were isolated using a mixture of carboxy methyl cellulose (CMC), xylan, pectin, and starch (each 0.25 g L^{-1}) in VL55 mineral salt medium amended with yeast extract (0.1 g L^{-1}) and agar (20 g L^{-1}). Strain MP8S11 was isolated using cellobiose, trehalose, and sucrose (each 0.25 g L^{-1}) in VL55 mineral salt medium amended with yeast extract (0.1 g L^{-1}) and agar (20 g L^{-1}). Strains X4BP1, X5P3, X5P6, and X4EP2 were isolated using xylan (0.5 gL^{-1}), cellobiose (0.25 g L^{-1}), and xylose (0.25 g L^{-1}) in VL55 mineral salt medium amended with MEM essential and non-essential amino acids (Sigma-Aldrich®). VL55 mineral salt solution was prepared as described by Davis et al. (2005), pH was adjusted either to 4.0 or 5.5. All strains were maintained at pH 5.5 using GY medium containing glucose (1 g L^{-1}) and yeast extract (0.5 g L^{-1}) in VL55. Isolation of *Granulicella arctica* MP5ACTX2 has been described earlier (Männistö et al., 2012).

Phenotypic and chemotaxonomic analyses

Growth of strains M8UP23, M8UP39, and X5P6 on GY medium was tested at different temperatures and pH. The temperature range was evaluated by growth on GY-agar incubated at 2, 4, 10, 15, 20, 25, and 30°C. The plates were checked every 1–2 days for growth. Visual differences in growth at different temperatures were recorded. The effect of pH on growth was evaluated by growing the strains in liquid GY medium at pH 3.0–9.0 (in 0.5 pH unit increments) in 96 well plates. Carbon source utilization of the three strains was analysed in 96-well plates for up to 10 days at 20°C with VL55 mineral medium supplemented with 100 mg L^{-1} yeast extract and 10 mM of each carbon source. Yeast extract was required for good growth on single carbon sources. The control contained only yeast extract. Growth was measured at 620 nm using a Multiscan FC microplate reader (Thermo Scientific). Hydrolysis of different polysaccharides (starch, CMC, xylan, lichenan, pectin, xanthan, and gum arabic) was determined at room temperature by observing CO_2 production for up to 20 days and analysed as described in Männistö et al. (2012).

Cellular fatty acids were analysed by gas chromatography as described in Männistö et al. (2012). Analysis of respiratory quinones and polar lipids was carried out by the Identification Service, DSMZ, Braunschweig, Germany. For the analysis, cells were cultivated on GY medium, collected by centrifugation, washed with PBS buffer, and freeze-dried. Polar lipids were extracted from 200 mg of freeze-dried cells and separated by thin-layer chromatography (German Collection of Microorganisms and Cell Cultures GmbH: Polar Lipids, n.d. https://www.dsmz.de/services/microorganisms/biochemical-analysis/polar-lipids). Respiratory quinones were extracted from 50 mg of freeze-dried cells and analysed by HPLC (German Collection of Microorganisms and Cell Cultures GmbH: Respiratory Quinones, n.d. https://www.dsmz.de/services/microorganisms/biochemical-analysis/respiratory-quinones).

Genome sequencing and assembly

A total of 13 *Acidobacteriota* isolates were used for whole genome sequencing via the Oxford Nanopore MinION. Sequence libraries were prepared using R 9.4 chemistry and the MinION Rapid Sequencing kit (SQK-RAD004). Libraries were run on a MinION R9.4 Flongle for ~24 h. Fast5 files were basecalled using Guppy (V 6.0.1; Oxford Nanopore Technologies Ltd.) in high accuracy mode and the FastA reads were used for genome assembly with the Trycycler assembler package (V 0.5.3; Wick et al., 2021), which allows for multiple assemblies specific to Nanopore long read sequences. For these genomes, the assemblers Flye—nano-hq (V 2.9; Kolmogorov et al., 2019; Lin et al., 2016), Minipolish (V 0.1.2; Wick & Holt, 2019), and Raven (V 1.8.1; Vaser & Šikić, 2021) were employed using default settings. The contigs were put into clusters and multiple sequence alignments were generated to produce a consensus or final assembly using Medaka (V 1.6.0; © 2018 Oxford Nanopore Technologies Ltd.).

In addition, several of the assemblies were run through PolyPolish (V 0.5.0; Wick & Holt, 2022) to close and complete the genomes. Of the 13 isolates used for

genome assembly, 6 also had Illumina short-read sequences publicly available via the JGI Genome Portal (see Project IDs in Table S1), and 4 (MP8S11, M8UP39, X5P6, and M8UP23) were previously sequenced via Illumina (see Supporting information S1, Methods and Results). These short reads along with our Trycycler-Medaka assemblies were used in the PolyPolish pipeline (default parameters). Genome assembly completeness and contamination for all 13 isolates were analysed via CheckM (V 1.0.18; Parks et al., 2015). Percent GC was calculated via QUAST (V 4.4; Gurevich et al., 2013). For each assembly with greater than one contig, the second longest contig was searched against the plasmid database PLSDB (V 2023_11_03_v2; Schmartz et al., 2021). This search was conducted via the PLSDB online API tool using Mash (V 2.3; Ondov et al., 2016) to search against the PLSDB database (parameters used: maximal *p*-value 0.1, maximal distance 0.1, minimal identity 0.70). Gene prediction was run via Prokka (V 1.14.5; Seeman, 2014). To find annotations to carbohydrate-active enzymes (CAZy), genes annotated via Prokka were scanned using a set of Hidden Markov Models (HMMs) from the dbCAN2 CAZy collection (dbCAN HMM database v10; Zhang et al., 2018) using HMMER (v 3.3.2; Eddy, 2011). The minimum *e*-value for this search was $1e-15$ and the minimum coverage of the model length was set at 90%. The Genome Taxonomy Database (GTDB; releases 207 and 214; GTDB R07-RS207 and R08–RS214; Parks et al., 2022) was used to taxonomically classify the genomes via the GTDB-Tk tool (v 2.3.2).

Genome phylogenies and pangenome analysis

A single-copy gene (SCG) phylogeny including the 13 new tundra soil isolate genomes and known Class *Terriglobia* (SD1 *Acidobacteriota*) species was analysed via the GToTree program (V 1.7.05; Lee, 2019). The program was run with default settings for alignment (MUSCLE V 5.1; Edgar, 2021) and approximately maximum-likelihood phylogenetic tree building (FastTree V 2.1.11; Price et al., 2010). The '-H Bacteria' parameter was used to identify 74 bacterial SCGs across all genomes analysed (listed in Supporting information S1 and S2). Another multi-locus tree for the same genomes was built via OrthoFinder (V 2.5.4; Emms & Kelly, 2019). The Orthofinder tree also utilized a MUSCLE (V 5.1; Edgar, 2021) alignment and phylogenetic tree building with FastTree (Price et al., 2010). Both SCG and OrthoFinder trees were viewed via the iTOL interface (V6; Letunic & Bork, 2021). These trees were compared with 16S rRNA gene and rRNA-operon trees, which included a more complete representation of the *Terriglobia* and the novel *Acidobacteriota* isolates included in the rRNA operon analysis (see Supporting information S1, Methods and Results). Genome alignment visualizations were conducted via PGV-Mummer (default setting; V 0.3.2; Shimoyama, 2022) and progressive MAUVE (Geneious plugin V 1.1.1) with 15 match seed weight, minimum 5000 Locally Collinear Blocks score, full alignment, and MUSCLE 3.6 gapped aligner (Darling et al., 2004).

Genome assemblies of the new tundra isolates along with some select *Terriglobia* were further compared through the Anvi'o pangenome analysis pipeline (Eren et al., 2021). A contig database for each genome was created with the following additions: HMM search, SCG taxonomy, tRNAs scan, NCBI cogs search, and KEGG Kofam search. Average nucleotide identity across the compared genomes was calculated via pyANI (Pritchard et al., 2015) program plugin within the Anvi'o pangenome pipeline (command: 'anvi-compute-genome-similarity'). The pangenome was then visualized via the Anvi'o interactive display, organizing samples by a gene cluster frequencies tree. Functional enrichment between strain categories within the pangenome analysis was computed via anvi-compute-functional-enrichment-in-pan using the KEGG_Class and COG20_PATHWAY annotation sources (Shaiber et al., 2020).

Analysis of *Acidobacteriota* community in Malla tundra heath soils

Soil samples were collected from tundra heaths of Mt. Pikku Malla in Malla Nature Reserve, Kilpisjärvi (69°03′ 50″N, 20°44′40″ E), with differences in topography that dramatically influence snow accumulation. Four plots representing windswept slopes and four plots corresponding to snow-accumulating biotopes were sampled at a depth of <5 cm in February 2013 as described previously (Männistö et al., 2024). Composite soil samples of five soil cores were taken from each plot with three subsamples from each composite sample used for DNA extraction with a CTAB-based method.

Near full-length bacterial rRNA operons were amplified from extracted DNA using 16S rRNA-27 Forward and 23S rRNA-2241R primers, <10 ng template DNA, and a High-Fidelity Taq Polymerase (Biomake Inc., CA, USA; Kerkhof et al., 2017). PCR conditions were: Initial denaturation for 3 min at 94°C; followed by 25 cycles of 98°C/10 s denaturation, 60°C/15 s primer annealing and 72°C/240 s extension; and a final extension at 72°C for 5 min. Barcoded rRNA operon amplicons were visualized and quantified by agarose gel electrophoresis and stored at −20°C until library preparation. Library construction utilized the SQK-LSK108 sequencing kit and sequencing via the Oxford Nanopore MinION. The fast5 files were basecalled using Guppy (3.2.0). Raw

reads were demultiplexed with Guppy and sized (3700–5000 bp) using Geneious (11.1.5). FastA files were initially screened via MegaBLAST (2.10.0) against the ribosomal RNA operon database (rOPDB; Kerkhof et al., 2022) to determine the raw reads associated with the *Acidobacteriota*. These *Acidobacteriota* reads were re-screened against a modified database using the original *Acidobacteriota* rRNA operons from the rOPDB, amended with rRNA operons from the new *Tunturibacter* and *Granulicella* strains described in this study. Best BLAST hits (BBHs) were identified using the following settings: word size −60, match/mismatch cost −2/−3, gap open/extend −0/−4, and *e*-value of 1×10^{-10}. Relative abundance of the *Acidobacteriota* BBHs to the updated database was calculated and bubble plots were generated in RStudio (2023.06.0 + 421) using ggplot2 and reshape2.

RESULTS AND DISCUSSION

Novel tundra *Acidobacteriota* isolates

Acidobacteriota strains were isolated from tundra heath soil samples from Malla Nature Reserve using different carbon substrate combinations. Initial analysis of partial 16S rRNA sequences (data not shown) indicated that these were members of the *Terriglobia*, closely related to *Edaphobacter* and *Granulicella* species. Physiological comparisons of our isolates to known *Edaphobacter* and *Granulicella* strains showed similarities in the utilization of various organic compounds and slight differences in temperature and pH range. Further investigation utilizing long-read Oxford Nanopore sequencing to assemble full genomes uncovered phylogenetic differences between the isolates and other members of the *Terriglobia*. The consistent phylogenetic placement across several comparative tools (single-gene trees, multi-locus trees, pangenome analysis) clearly separates the tundra heath isolates from known *Edaphobacter* and *Granulicella* species. Therefore, these isolates ultimately represent a novel genus within *Terriglobia* for which we propose the name *Tunturibacter*. Here, we present the genomic, phylogenetic, and phenotypic characterization of four novel species within the *Tunturibacter* genus.

Genome assemblies

The 13 new *Acidobacteriota* genome assemblies are listed in Table 1. Of these, 10 included Illumina short reads used to polish the genomes to >99% completion. Three of the 10 complete genomes had only one scaffold/contig, while the remainder had two or more scaffolds/contigs, with the longer scaffold representing the bacterial chromosome and the shorter contigs representing smaller genetic elements, that is, plasmids. To examine whether these shorter contigs could be plasmids, we searched the shorter contigs from assemblies with more than one contig against the PLSDB plasmid database. For each assembly, the second longest contig had one or more hits with an average of 75% identity to an already annotated plasmid from the database (Table S2). Their predominant alignment to plasmids from *Granulicella tundricola* at only around 75% identity indicates these are novel plasmids belonging to the *Tunturibacter*. These plasmids may code for a few extra genes that are not necessary for *Tunturibacter* growth, reproduction, or existence, but may offer some resistance strategies beneficial for survival.

The assembled genomes of the *Tunturibacter* strains had between 3600 and 7400 predicted genes, of which >98% were protein-coding genes for each assembly (Table 1). Of these genes, on average ∼44% were annotated as non-hypothetical. Full assembly statistics for these genomes are included in Table S1. Based on GTDB annotation, 10 out of 13 assemblies were classified as most similar to *Edaphobacter lichenicola* DSM 104462 with ANI values ranging from 89% to 100% and amino acid (AA) similarities from 76% to 94%. Of the remaining three assemblies, two were classified as most similar to *G. arctica* MP5ACTX2 (DSM 23128; 79%–100% ANI and 86%–94% AA) and one to *Granulicella mallensis* MP5ACTX8 (100% ANI and 94% AA).

Multi-locus phylogeny of the SD1 *Acidobacteriota*

To determine the taxonomic placement of the new tundra *Acidobacteriota* isolates we compared 16S rRNA gene, rRNA operon, and single copy gene phylogenies. Utilizing the full genomes of members of the *Terriglobia*, we phylogenetically compared the genome assemblies using 74 selected SCGs (Figure 1A). The resulting SCG tree more accurately groups the *Edaphobacter*, *Granulicella*, and *Terriglobus* species than the rRNA operon or 16S rRNA gene trees alone (Figures S1A,B and S2A,B). Importantly, the assemblies grouping together with *E. lichenicola* DSM 104462 were phylogenetically separated from the other *Edaphobacter* species, including the type species *Edaphobacter modestus*, and would thus represent the new genus *Tunturibacter*. As can be seen from the SCG tree, this new genus appears to comprise four species, each with several strains.

The phylogeny is more evident in the SCG sub-tree showing the members of the *Terriglobia* most closely related to the proposed *Tunturibacter* genus (Figure 1B). The SCG tree also more accurately clusters the *Granulicella* species. Another potential new

TABLE 1 Genome assemblies of the 13 *Acidobacteriota* isolates from Malla Nature Reserve, Kilpisjärvi, Finland.

	Strain												
Characteristics	**M8UP23**	**M8UP22**	**M8UP27**	**M8UP20**	**M8UP39**	**M8UP30**	**M8UP28**	**X5P6**	**X4BP1**	**MP8S11**	**X5P3**	**X4EP2**	**MP5ACTX2**
% Completion	99.78	99.78	100	89.31	100	100	91.42	100	100	100	100	100	95.52
Contamination	0	0	0.05	0	0.86	0.86	0.86	0.86	0.86	1.72	2.63	1.71	0.86
% GC	57.82	57.76	58.43	58.41	57.42	57.56	57.08	56.72	56.7	56.26	57.83	58.26	57.68
Total number of genes predicted	4280	4377	4199	5345	4835	4508	7422	4845	5386	5367	5266	3696	5646
% Protein coding genes	98.74	98.79	98.67	98.93	98.86	98.82	99.29	98.93	98.96	98.99	99.01	98.59	99.08
% Genes with non-hypothetical function	44.39	44.16	44.61	38.02	41.84	43.06	35.29	42.84	41.57	41.33	43.35	47.35	38.24
Total number of CAZy genes	486	513	519	471	542	504	611	687	703	637	834	444	561
Number of contigs	3	2	2	2	2	2	2	2	1	2	1	1	6
Chromosome total size (bp)	4,895,849	5,073,717	4,841,149	4,830,045	5,450,518	5,148,408	6,616,843	5,616,891	6,129,460	5,517,693	6,509,459	4,305,847	5,272,918
Second longest contig size (bp)	114,874	15,020	55,309	78,140	128,519	138,883	213,906	16,651	Na	756,046	Na	Na	101,209

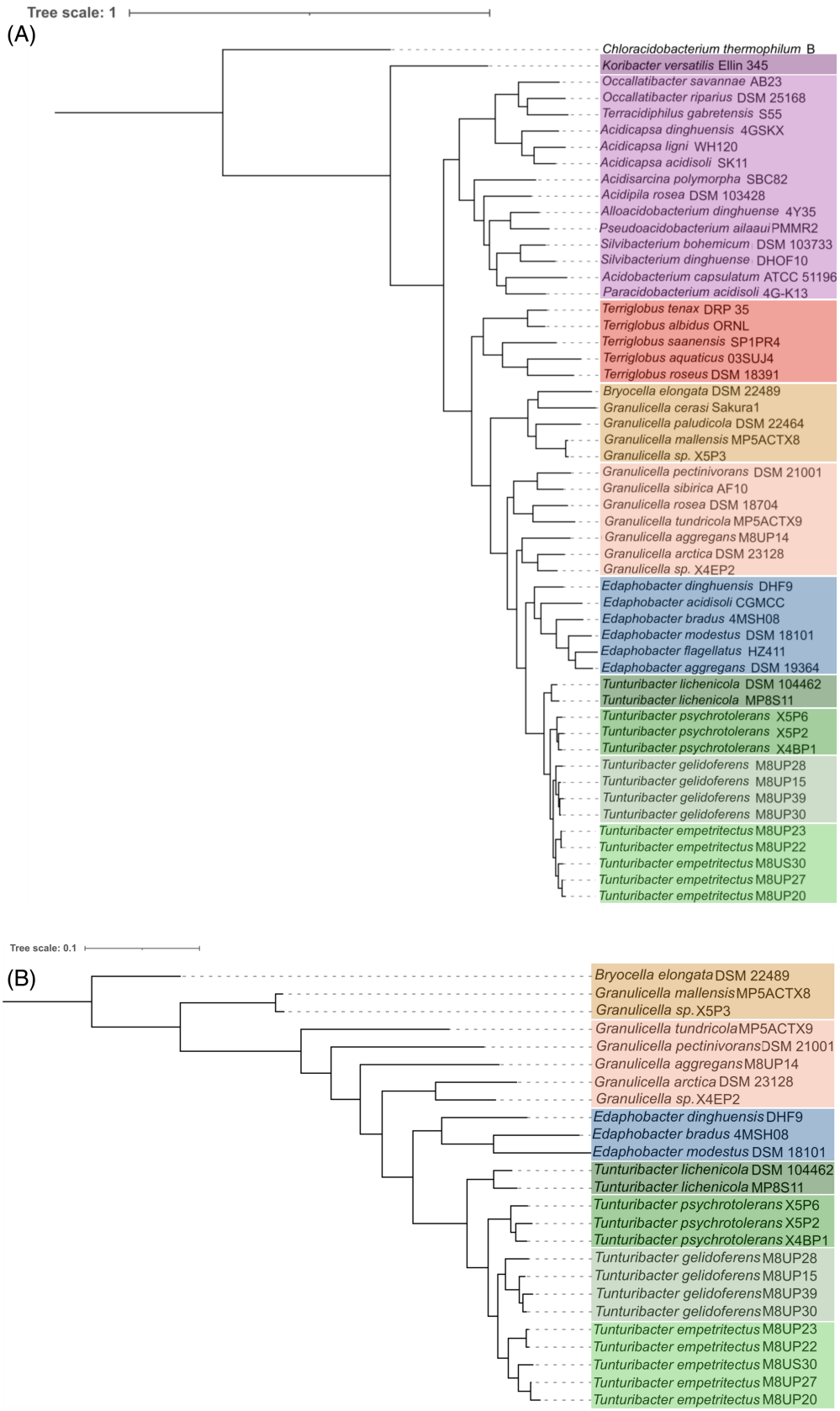


FIGURE 1 (A) Single copy gene phylogeny of *Terriglobia* genomes. (B) Sub-tree of the phylogenetic placement of the new *Tunturibacter* genus with more closely related genera. Accession numbers for genomes available from NCBI are listed in Table S3.

genus may be represented by *G. mallensis*, *Granulicella paludicola*, and *Granulicella cerasi*, which group with *Bryocella elongata*, phylogenetically distinct from the other species in the *Granulicella* cluster, including the type species *G. paludicola* (Figure 1A). A comparison of these genomes via a multi-locus phylogeny based on orthogroups and orthologs (Orthofinder) also resulted in a similar phylogenetic structure as the SCG tree (Figure S3).

Overall, compared with the rRNA operon tree, phylogenies built on multiple genes from fully assembled genomes more accurately delineated the *Acidobacteriota* genera and species. However, the rRNA operon tree was still able to differentiate the various novel clusters, revealing the polyphyletic nature of some of these genera, supporting the separation of *E. lichenicola* and three new species as the proposed new genus *Tunturibacter*.

Pangenome analysis

Pangenome analysis was used to compare gene frequencies from the COG, KEGG, SCG, and Kofam annotations of the input genomes (Figures 2 and 3). The gene frequency tree created from this analysis (Figure 2, right side) is similar to the SCG tree, again supporting the separation of two new potential genera in the *Terriglobia*. The proposed *Tunturibacter* genus is present as its own cluster, as is the cluster which groups several *Granulicella* species that affiliate with *B. elongata* (Figure 2). The very last row indicating the

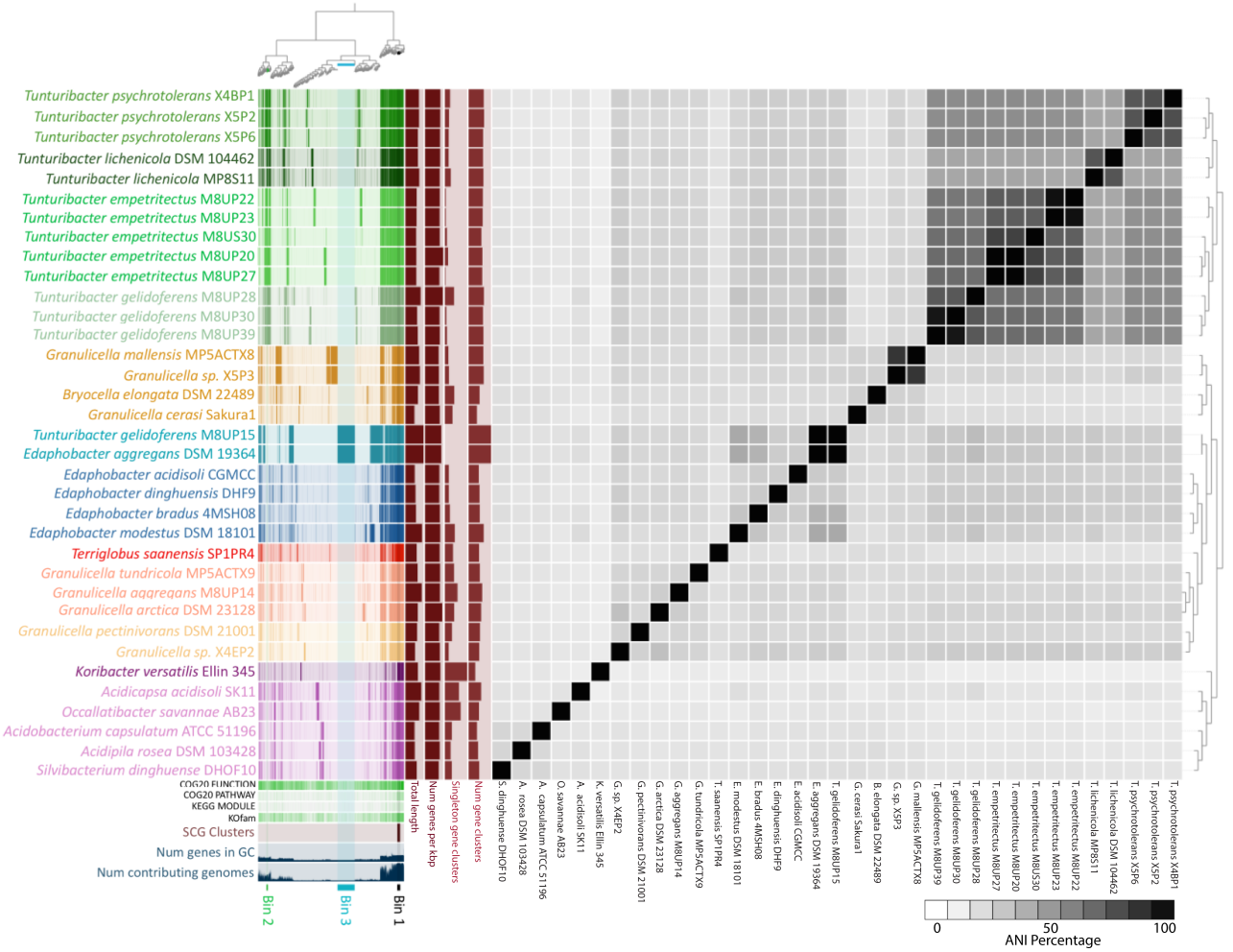
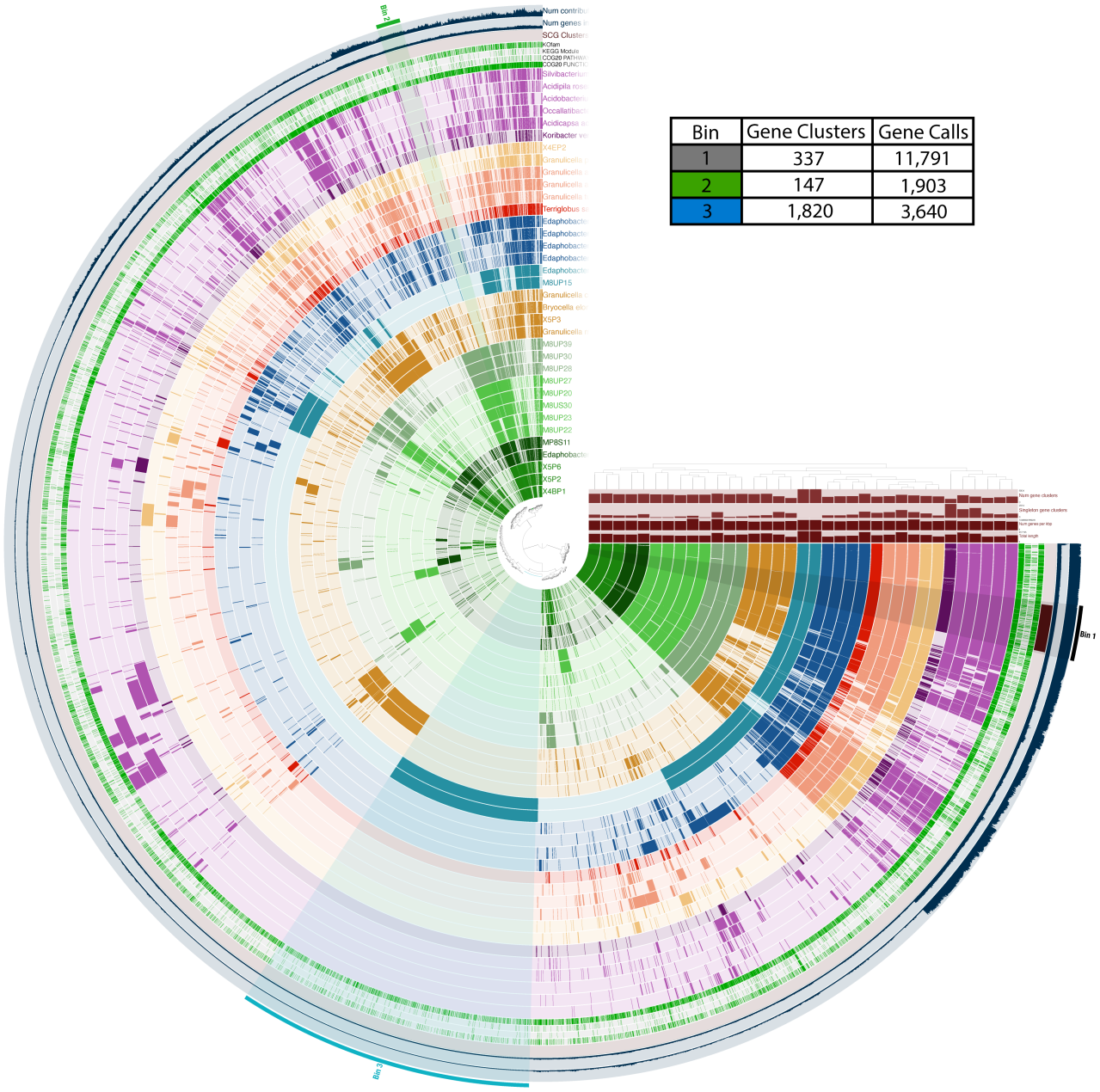


FIGURE 2 Pangenome analysis of the *Terriglobia* in the *Acidobacteriota*. Comparison of gene clusters between the 13 assembled tundra soil isolates and known *Terriglobia*. Each row designating an *Acidobacteriota* strain starts with information on the presence of gene clusters (gene clusters are marked by the darker-coloured regions within the row). This is followed by the red/maroon columns indicating levels of genome total length, number of genes per kbp, singleton gene clusters, and number of gene clusters. These columns are followed by the ANI data from the pangenome analysis, and the grouping of the *Acidobacteriota* based on gene cluster frequency (right-hand tree). Under the gene cluster presence rows are rows indicating COG20, KEGG, and Kofam annotations, SCG clusters, and the number of genes and contributing genomes in the gene cluster.



Bin	Gene Clusters	Gene Calls
1	337	11,791
2	147	1,903
3	1,820	3,640

FIGURE 3 Circularized Anvio pangenome of the *Terriglobia*.

number of contributing genomes (Figure 2, bottom left) shows that the area of the pangenome comparison with the most contributing genomes also includes the SCG clusters, representing the core genome of the *Acidobacteriota* analysed (Figure 3; Bin 1, 337 clusters, 11,791 gene calls).

Except for strain M8UP15, ANI analysis clearly separated the proposed new *Tunturibacter* species from the other *Edaphobacter* species, with *E. modestus* as the type species. The ANI similarities, along with the phylogenetic clusters of this new genus in the SCG tree (Figure 1) support the separation of four species within the new *Tunturibacter* genus with their respective type strains: *E. lichenicola* DSM 104462 transferred to the genus as *Tunturibacter lichenicola* comb. nov. (includes strain MP8S11), *Tunturibacter psychrotolerans* sp. nov. X5P6 (includes strains X4BP1 and X5P2), *Tunturibacter empetritectus* sp. nov. M8UP23 (includes strains M8UP22, M8US30, M8UP20, and M8UP27), and *Tunturibacter gelidoferens* sp. nov. M8UP39 (includes strains M8UP30 and M8UP28). Bin 2 captures the gene clusters unique to this new genus (Figure 3; Bin 2, 147 clusters, 1903 gene calls).

One major difference in this analysis compared with the SCG tree, is the grouping of genome M8UP15 with *E. aggregans* DSM 19364 rather than the *Tunturibacter* genus. These two genomes have the highest number of gene clusters, with one area sharing

multiple genes unique to these two genomes (Figure 3; Bin 3, 1820 clusters, 3640 gene calls). The high ANI similarity of these two genomes indicates that strain M8UP15 is most closely related to *E. aggregans* DSM 19364. However, out of all the genomes in this analysis, M8UP15 and *E. aggregans* DSM 19364 share the highest number of partial genes (416), indicating that their genomes are not complete. Since the SCG and operon trees did not group these two genomes closely, it is unclear whether this result is driven by their unique genes or their incomplete genomes. The taxonomic placement of strain M8UP15 may thus require future reassessment.

Physiological comparison of *Tunturibacter* species

The phenotypic properties of the proposed type-strains for the new species, *Tunturibacter empetritectus* M8UP23, *T. gelidoferens* M8UP39, and *T. psychrotolerans* X5P6 were compared with *Tunturibacter* (*Edaphobacter*) *lichenicola* (Belova, Suzina, et al., 2018). Similarities were found for all strains based on their utilization of various organic compounds (Table 2), as well as hydrolysis of polysaccharides, enzyme activities (API ZYM tests), and composition of quinones and major cellular fatty acids (Table S4). The temperature growth range for strains *T. empetritectus* M8UP23, *T. gelidoferens* M8UP39, and *T. psychrotolerans* X5P6 was 2–30°C, while the growth range of *T. lichenicola* DSM 104462 was different at 7–37°C. These *Tunturibacter* species/strains tolerate cold conditions, similar to *Terriglobus* (4–30°C; Eichorst et al., 2007; Männistö et al., 2011) and *Granulicella* species (4–28°C; Männistö et al., 2012). The growth pH range for *T. empetritectus* M8UP23, *T. gelidoferens* M8UP39, and *T. psychrotolerans* X5P6 was 3.5–6.5 and for *T. lichenicola* DSM 104462 was 3.4–7.0. These ranges are most similar to those of *G. tundricola* and *G. mallensis* (pH 3.5–6.5; Männistö et al., 2011) and can tolerate more acidic conditions than *Terriglobus* (pH 4.5–7.5; Eichorst et al., 2007; Männistö et al., 2012).

Genome comparisons of *Tunturibacter* species

Genome alignments at various taxonomic levels further support the designations of the new *Tunturibacter*

TABLE 2 Utilization of various carbon substrates by *Tunturibacter* species.

Utilization of	*T. empetritectus* M8UP23	*T. gelidoferens* M8UP39	*T. psychrotolerans* X5P6	*T. lichenicola* (Belova, Suzina et al., 2018)
Acetate	–	–	–	
Arabinose	–	–	–	–
Benzoate	–	–	–	
Cellobiose	+	+	+	+
Dulcitol	–	–	–	
Xylose	+	+	+	+
Fructose	+	+	+	+
Fucose	+	+	+	
Galacturonic acid	–	–	–	
Glucosamine	+	+	w	
Glucose	+	+	+	+
Lactulose	–	–	–	+
L-glutamic acid	w	w	w	
L-glutamine	–	–	–	
Maltose	+	+	+	+
Mannose	+	+	+	+
Mannitol	–	–	–	w
N-acetyl-glucosamine	+	+	w	
Oxalate	–	–	–	+
Pyruvate	–	–	–	
Salicin	+	+	+	+
Sorbitol	–	–	–	
Trehalose	+	+	+	+

Note: +, positive reaction; –, negative reaction; w, weak positive reaction.

species and strains (Figure 4). Only the longest assembled scaffold for each genome was used for the alignment. At the genus level we compared *T. lichenicola* DSM 104462 (5,662,239 bp), *G. arctica* DSM 23128 (4,736,692 bp), *E. modestus* DSM 18191 (6,121,180 bp), and *Terriglobus saanensis* SP1PR4

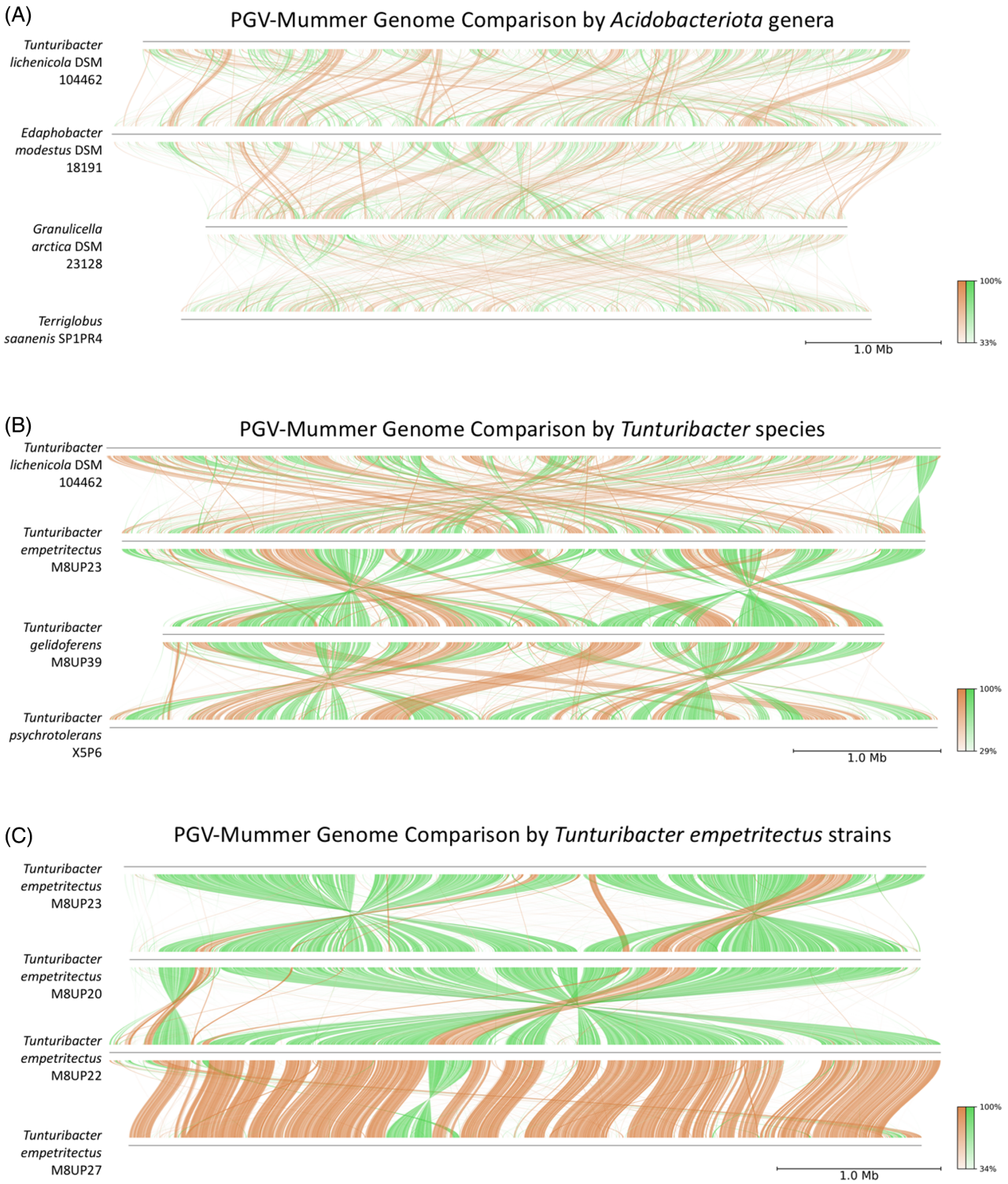


FIGURE 4 Genome comparisons at various taxonomic levels. (A) Comparison of four SD1 *Acidobacteriota* including *Tunturibacter lichenicola*. (B) Comparison of the four species within the *Tunturibacter* (each species represents the type strain). (C) Comparison of four strains within the *Tunturibacter empetritectus*. Genome comparisons were viewed via PGV-Mummer. Black horizontal lines indicate the span of the genome being compared, green lines connect homologous regions between the genomes in the same orientation (normal link), and brown lines connect homologous regions between the genomes in reverse orientation (inverted link). The shade of green and brown indicate percent homology (bottom right legend, dark colour means higher percent homology).

(5,095,225 bp). At the species level we compared *T. lichenicola* DSM 104462 (5,662,239 bp), *T. empetritectus* M8UP23 (4,898,072 bp), *T. gelidoferens* M8UP39 (5,453,280 bp), and *T. psychrotolerans* X5P6 (5,619,635 bp). At the strain level, we also compared *T. empetritectus* strains M8UP23 (4,898,072 bp), M8UP20 (4,830,045 bp), M8UP22 (5,076,618 bp), and M8UP27 (4,842,676 bp).

These alignments show decreased homology when comparing the *Tunturibacter* genomes against other genera in the *Terriglobia* (Figure 4A), compared with increased homology when comparing the genomes of the *Tunturibacter* species against each other (Figure 4B,C). The strength of homology increases with species and strain level alignments, with strain level alignments (within the *T. empetritectus* strains) showing the least amount of genome rearrangements (Figure 4C). These trends are also apparent when using another genome alignment visualization tool, Mauve (Figure S4A–C), which results in longer homology segments within alignments at the proposed strains compared with the species and genus level alignments.

Unique pathways and phenotypic data of *Tunturibacter* species

The *Tunturibacter* strains had between 3600 and 7400 predicted genes, of which >98% were protein-coding genes (Table 1). All strains had at least one successful alignment to a gene family in the CAZy HMM database within the following CAZy classes: glycoside hydrolases, glycosyl transferases, carbohydrate-binding modules, carbohydrate esterases, polysaccharide lyases, and auxiliary activities. For each assembled genome the number of CAZy gene alignments includes one or more hits to unique CAZy genes spanning numerous functions (Table 1 and Figure S5). In the different strains, 8%–16% of the total number of predicted genes was coded for modules of the CAZy family, with genes for glycoside hydrolases being the most abundant. While these hits represent mostly partial alignments to CAZy genes, this indicates a wide set of unique genes involved in the build-up and breakdown of complex carbohydrates.

Compared with the other *Acidobacteriota* genomes in the pangenome analysis, several pathways were significantly enriched ($p < 0.05$) in members of the *Tunturibacter* genus (Table 3). Based on KEGG Class and COG20 Functional annotations, *Tunturibacter* genomes are more enriched in functional pathways involving the metabolism of amino acids, such as tryptophan, betaine, and lysine. The enriched GABA (γ-aminobutyric acid) biosynthesis pathway suggests a pH resistance strategy within the *Tunturibacter* spp. (Dhakal et al., 2012). This genus is also enriched in genes within pathways involving the metabolism and biosynthesis of cofactors and vitamins such as menaquinone, cobalamin, biotin, and molybdopterin. These (COG20 Pathway) annotations do not, however, support the presence of the full pathway within the *Tunturibacter*. The specific KEGG and COG20 genes annotated from the enriched functional pathways can be found in Table S5.

Additionally, there is a lack of evidence for prominent vitamin and cofactor biosynthesis genes within many members of the *Terriglobia*. Menaquinone has been found in *Acidobacterium capsulatum* (Kishimoto et al., 1991), cobalamin (B12) transport has only been speculated in SD4 and SD8 *Acidobacteriota* and *Bryocella* species (Kielak et al., 2016). An uncultivated

TABLE 3 Enriched functional pathways within the *Tunturibacter* species compared with other *Acidobacteriota* genomes.

Annotation	Enrichment score	Adjusted *q*-value	Accession
KEGG module			
Aromatic amino acid metabolism: Tryptophan metabolism, tryptophan = >kynurenine = >2-aminomuconate; NAD biosynthesis, tryptophan = >quinolinate = >NAD	15.51	0.01	M00038; M00912
Amino acid metabolism: Betaine biosynthesis, choline = > betaine; Lysine degradation, lysine = > saccharopine = > acetoacetyl-CoA; GABA biosynthesis, eukaryotes, putrescine = > GABA	10.79	0.03	M00555; M00032; M00135
COG20 pathway			
COG20 Pathway: Menaquinone biosynthesis; Lysine biosynthesis	31.02	<0.01	COG0318; COG3320
COG20 Pathway: Cobalamin/B12 biosynthesis	15.51	<0.01	COG1010; COG2243
COG20 Pathway: Pyrimidine salvage; Biotin biosynthesis	10.79	0.02	COG0402; COG2226
COG20 Pathway: Molybdopterin biosynthesis	8.99	0.05	COG0314; COG1977

group of *Acidobacteriota*, GAL08, from hot springs contained a biotin-specific transporter; however, it was not able to synthesize biotin (Ruhl et al., 2022). Although more detailed analysis is needed, the enrichment of vitamin/cofactor biosynthesis genes within the *Tunturibacter* suggests that members of this genus may be able to synthesize vitamins de novo and have increased metabolic capabilities compared with the *Edaphobacter*, *Granulicella*, and *Terriglobus* species.

Acidobacteriota community in Malla tundra heath soils

We examined the distribution of the *Terriglobia* in a set of snow-accumulating and windswept tundra heath soils in Malla Nature Reserve, from which the novel *Tunturibacter* species were isolated. At this site, areas in depressions are sheltered from the winds with high snow accumulation (up to ≥1 m), while windswept areas remain essentially snow-free throughout the winter leading to distinctly different soil temperature profiles and differences in the amplitude of annual temperature variation (Männistö et al., 2024). The bacterial communities were assessed by rRNA operon profiling with the Oxford Nanopore MinION, enabling strain-specific identification of bacterial community members. Overall, rRNA operon reads from the *Acidobacteriota* represented 4.2%–18.4% of the >760 K total bacterial reads from these tundra samples. Specifically, the *Acidobacteriota* reads varied from 1524 to 18,818 reads per sample with an average of 6536 ± 5478 per site. Re-screening of these reads against the augmented *Acidobacteriota* rRNA database, containing the new rRNA operons from this study, indicated that 18%–38% of these *Acidobacteriota* reads have best BLAST matches to *Tunturibacter* and *Granulicella*.

Furthermore, distinct differences in the relative abundance of *Edaphobacter*, *Granulicella*, and *Terriglobus* species/strains could be observed between windswept and snow-accumulating tundra heaths (Figure 5). Reads matching the various *Tunturibacter* strains were generally more dominant in the windswept plots, while the *Granulicella* strain was more abundant in the snow-accumulating plots. These strain and species distinctions correspond to the observed differences in the overall soil microbial communities between windswept and snow-accumulating tundra heaths (Männistö et al., 2024). Snow cover and the linked vegetation shifts and soil C and N dynamics may thus be an important microclimatic driver of bacterial communities. The improved taxonomy of the *Acidobacteriota* combined with the genomic and phenotypic information of cultivated strains will enable an improved understanding of the community response to fluctuating environmental conditions in a changing climate.

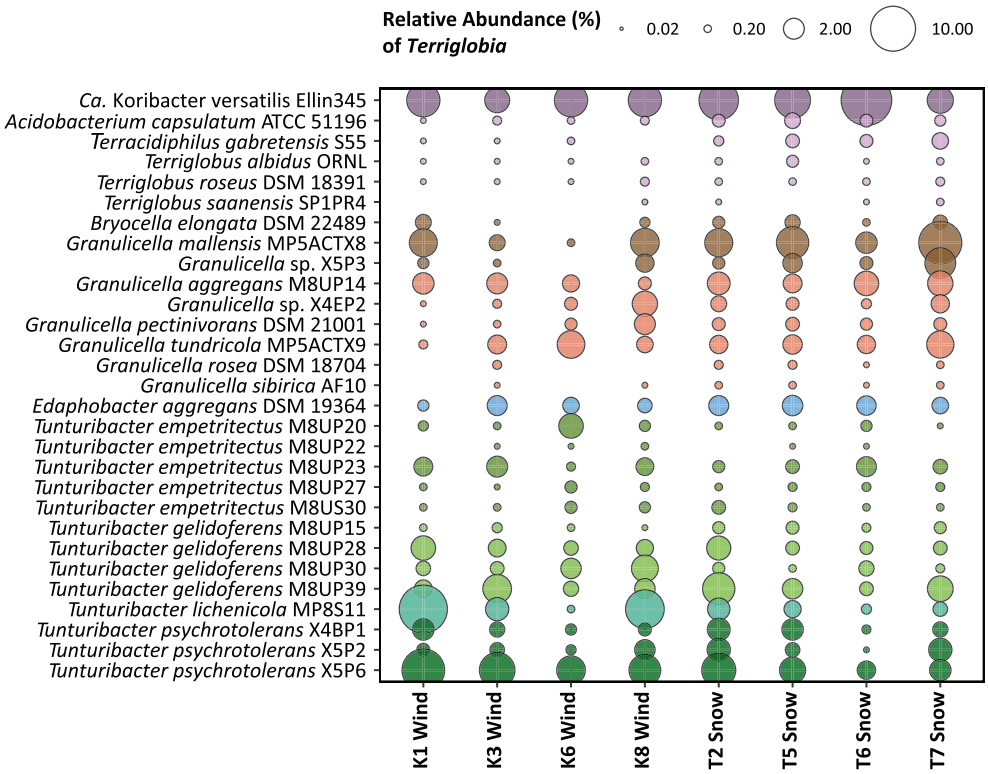


FIGURE 5 *Terriglobia* community in soils of windswept (K1, K3, K6, K8) and snow-accumulating (T2, T5, T6, T7) tundra heath plots of Mt. Pikku Malla. rRNA operon reads from the *Acidobacteriota* represent 4.2%–18.4% of the total bacterial reads.

Ecological context of *Acidobacteriota* in tundra soils

Members of the *Acidobacteriota* are ubiquitous in acidic Arctic tundra and sub-Arctic forest soils. The Kilpisjärvi study site has representative tundra vegetation dominated by dwarf shrub-rich *Empetrum* heaths over acidic soils, or forb- and graminoid-rich *Dryas* heaths over non-acidic soils (Eskelinen et al., 2009; Männistö et al., 2007, 2009, 2013). These soils are organic-rich and well-aerated, harbouring abundant aerobic heterotrophic microbiota where diverse *Acidobacteriota* make up 10%–40% of the total bacterial community (Männistö et al., 2009, 2013). The abundance and composition of the *Acidobacteriota* vary with topography and exposure influence snow accumulation and soil temperatures (Männistö et al., 2013) as well as bedrock material which influences soil pH (Männistö et al., 2007). Different species within the *Acidobacteriota* appear to respond to environmental conditions differently, highlighting the wide functional diversity of these organisms even within the *Terriglobia*. From the tundra heath sites in Kilpisjärvi Finland, several species of *Terriglobus*, *Granulicella*, and *Tunturibacter* have been cultivated (Männistö et al., 2011, 2012, this study). These species appear adapted to the breakdown, utilization, and biosynthesis of diverse polysaccharides, and resilience to fluctuating temperatures and nutrient-deficient conditions.

Increased competition between plants and microbes and within the microbial community can occur due to environmental factors such as the increased presence of woody evergreen shrubs that immobilize nutrients as a consequence of warming-induced 'shrubification' on Arctic soil carbon storage (Stark et al., 2023). Tundra soil carbon and nitrogen cycles are strongly coupled with soil nitrogen availability often decreasing over the growing season, leading to the soil microbial communities becoming increasingly N-limited (Jonasson et al., 1999; Stark & Kytöviita, 2006). Methods to combat low nutrient concentrations include having the functional capacity for nutrient assimilation and transport. *Acidobacteriota* is known to contain genes involved in attaining nitrogen, which include genes essential for ammonia assimilation, for example, glutamine synthetase, and genes for the ammonium channel transporter family (*amtB* gene; Eichorst et al., 2018). In a recent study comparing microbial responses to Arctic greening in Alaskan soils, *Acidobacteriota* most strongly expressed the glutamine synthetase metaprotein, a large component of the proteins involved in ammonia metabolism (Miller et al., 2023). Within our study, glutamine synthetase (COG0174) was annotated mainly within the core genome of the *Tunturibacter* pangenome (Figure 3; Bin 1).

Another adaptation to low nutrient concentrations includes genes for high-affinity transport systems (Eichorst et al., 2018; Kielak et al., 2016). Transporter genes annotated within the *Tunturibacter* pangenome include high-affinity Mn^{2+} porin (COG3659), high-affinity iron transporter (COG4393), and high-affinity nickel/cobalt permease (HoxN; COG3376). *Acidobacteriota* has been shown to contain a broad substrate range of transporters, including the Drug/Metabolite transporter superfamily, the Ammonia Transporter Channel (Amt) Family, and the Metal Ion (Mn^{2+} Iron) Transporter (Nramp; Kielak et al., 2016). This diversity of transporters suggests that *Acidobacteriota* have an advantage in nutrient assimilation in nutrient-poor conditions.

Tundra soil *Acidobacteriota* appears to be oligotrophs with slow growth rates and low population turnover rates that are favoured by the presence of recalcitrant carbon. The genomes of the tundra soil *Acidobacteriota* contain an abundance of conserved genes/gene clusters encoding for modules of the CAZy families, predominately glycoside hydrolases and glycosyltransferases (Figure S5; Eichorst et al., 2018; Rawat et al., 2012). In our study, pangenome glycosyltransferase COGs involved in cell wall biosynthesis (COG0438) and the glycosylation of proteins and lipid IVA (COG1807) were found across all *Acidobacteriota* analysed. Multiple alignments to various CAZy gene families were also found within the *Tunturibacter* indicating a wide ability for utilizing complex carbohydrates. Another interesting feature of the *Acidobacteriota* is their synthesis of hopanoid lipids, which may play a role in regulating membrane stability. Additionally, quorum-sensing associated genes, such as acyl-homoserine lactone (acyl-HSL), were found within several *Tunturibacter* and across *Acidobacteriota* within our pangenome analysis (Parsek et al., 1999). Signalling molecules like acyl-HSLs are known to impact bacterial community dynamics in soils, particularly in response to virulence genes (Parsek et al., 1999; Riaz et al., 2008).

Members of the *Acidobacteriota* are known to play a role in the decomposition of SOM, in particular various biopolymers, and they participate in the global cycling of carbon, iron, and hydrogen. While *Acidobacteriota* constitutes from 5% to 50% of the total bacterial community in organic-rich, low pH, Arctic, and boreal soils based on rRNA gene reads (Männistö et al., 2007, 2009, 2013) they continue to be notoriously difficult to cultivate and are thus woefully under-represented in culture collections. The description of new strains and species provides key phenotypic and genomic information to help us understand why they are so dominant and how they maintain diversity within the group. There is much to learn about their ecosystem functions in soils, their interactions with other microbes, and their adaptations to environmental stress and climate change.

Description of *Tunturibacter* gen. nov.

The results from the multiple lines of analyses presented above indicate that *E. lichenicola* is not a member of the genus *Edaphobacter* and should be reclassified as a species of the proposed new genus *Tunturibacter*, with the proposed name *T. lichenicola* comb. nov. The NCBI BioProject ID for the 10 newly assembled *Tunturibacter* genomes is PRJNA1004338. Accession numbers for all new Tunturibacter 16S rRNA genes and genomes are in Table S6.

Tunturibacter (Tun'tu.ri.bac'ter. tunturi, referring to the Arctic treeless fells in Finland, N.L. masc. n. *bacter*, a short rod; N.L. masc. n. *Tunturibacter* rod-shaped tundra fell bacterium).

Cells are Gram-negative aerobic rods. On agar plates, cells form circular, mucoid colonies. Colony pigment varies from light beige to pink. Produce extracellular polysaccharide-like substances. Sugars are preferred carbon sources and the different strains are capable of hydrolyzing various polysaccharides. The major cellular fatty acids are iso-15:0, iso-13:0, 16:1ω7c, and 16:0. The predominant menaquinone is MK-8. The DNA G + C content is 56%–58%. Strains have been isolated from tundra soil and lichen thalli collected from lichen-dominated forested tundra. The type species is *T. lichenicola* comb. nov.

Emended description of *T. lichenicola* comb. nov.

The description is as given by Belova, Ravin, et al. (2018) and Belova, Suzina, et al. (2018). The type strain is SBC68^T (=DSM 104462^T = VKM B-3208^T).

Description of *Tunturibacter empetritectus* sp. nov.

Tunturibacter empetritectus (em.pet.ri.tectus. *empetri*, referring to the plant *Empetrum nigrum* ssp. *hermaphroditum*; L. adj. *tectus*, covered; L. part. Adj. *empetritectus*, growing under tundra heath dominated by *E. nigrum* ssp. *hermaphroditum*).

Cells are Gram-negative, non-motile, aerobic rods. Colonies are light beige or pink, circular, and smooth when grown on GY agar (Figure S6). Growth occurs at 2–30°C and pH 3.5–6.5. In VL55 mineral medium with 100 mg L^{-1} yeast extract and 5–10 mM carbon source, utilizes cellobiose, xylose, fructose, fucose, glucosamine, glucose, L-glutamic acid (weak), maltose, mannose, *N*-acetyl-glucosamine, salicin and trehalose. Hydrolyzes xylan, pectin, xanthan and gum arabic. The major cellular fatty acids are iso-15:0, iso-13:0, 16:1ω7c, and 16:0. The DNA G + C content determined from the genome sequence of the type strain is 57.82%.

The type strain is M8UP23^T (= DSMZ 117310 = HAMBI 3810) isolated from tundra soil in Malla Nature Reserve, Kilpisjärvi, Finland (69°01′ N, 20°50′ E). NCBI accession numbers for the 16S rRNA gene sequence and the draft genome sequence of the type strain are OR449309 and CP132932-CP132934, respectively.

Description of *T. gelidoferens* sp. nov.

Tunturibacter gelidoferens (ge.li.do.ferens. L. adj. *gelido* cold; L. pres. Part. *Ferens*, to endure; L. part. Adj. *gelidoferens*, cold-enduring).

Cells are Gram-negative, non-motile, aerobic rods. Colonies are pink, circular, and smooth when grown on GY agar (Figure S6). Growth occurs at 2–30°C and pH 3.5–6.5. In VL55 mineral medium with 100 mg L^{-1} yeast extract and 5–10 mM carbon source, utilizes cellobiose, xylose, fructose, fucose, glucosamine, glucose, L-glutamic acid (weak), maltose, mannose, *N*-acetyl-glucosamine, salicin, and trehalose. Hydrolyzes carboxy methyl cellulose (weak), xylan, pectin, lichenin, starch (weak), and gum arabic (weak). The major cellular fatty acids are iso-15:0, iso-13:0, 16:1ω7c, and 16:0. The DNA G + C content determined from the genome sequence of the type strain is 57.42%.

The type strain is M8UP39^T (= DSMZ 117311 = HAMBI 3809) isolated from tundra soil in Malla Nature Reserve, Kilpisjärvi, Finland (69°01′ N, 20°50′ E). NCBI accession numbers for the 16S rRNA gene sequence and the draft genome sequence of the type strain are OR449311 and CP132937–CP132938, respectively.

Description of *T. psychrotolerans* sp. nov.

Tunturibacter psychrotolerans (*psy.chro.to'le.rans*. Gr. Adj. *psychros*, cold; L. pres. Part. *Tolerans*, tolerating; N.L. part. Adj. *psychrotolerans*, cold-tolerating).

Cells are Gram-negative, non-motile, aerobic rods. Colonies are light beige to light pink, circular, and smooth when grown on GY agar (Figure S6). Growth occurs at 2–30°C and pH 3.5–6.5. In VL55 mineral medium with 100 mg L^{-1} yeast extract and 5–10 mM carbon source, utilizes cellobiose, xylose, fructose, fucose, glucosamine (weak), glucose, L-glutamic acid (weak), maltose, mannose, *N*-acetyl-glucosamine (weak), salicin, and trehalose. Hydrolyzes carboxy methyl cellulose (weak), pectin, lichenin, starch, xanthan and gum arabic (weak). The major cellular fatty acids are iso-15:0, iso-13:0, 16:1ω7c, and 16:0. The DNA G + C content determined from the genome sequence of the type strain is 56.72%.

The type strain is X5P6^T (= DSMZ 117309 = HAMBI 3811) isolated from tundra soil in Malla Nature Reserve, Kilpisjärvi, Finland (69°01′ N, 20°50′ E). NCBI accession numbers for the 16S rRNA gene sequence and the draft genome sequence of the type strain are OR449310 and CP132942–CP132943, respectively.

AUTHOR CONTRIBUTIONS

Adriana Messyasz: Writing—original draft; formal analysis; investigation; writing—review and editing; visualization; data curation; methodology. **Minna K. Männistö:** Investigation; writing—review and editing; funding acquisition; conceptualization; methodology. **Lee J. Kerkhof:** Writing—review and editing; supervision; funding acquisition; resources; methodology; investigation. **Max M. Häggblom:** Supervision; writing—review and editing; funding acquisition; conceptualization; project administration; methodology; investigation; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The NCBI BioProject ID for the newly assembled *Tunturibacter* genomes is PRJNA1004338: https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1004338. Accession numbers for 16S rRNA genes are OR449309–OR449318. Accession numbers for genomes are CP132926-CP132945. The rRNA operon reads from Malla Nature Reserve soil samples are available in BioProject ID PRJNA1093128: https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1093128.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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