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TAXONOMIC DESCRIPTION
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Capillibacterium thermochitinicola gen. nov., sp. nov., a novel anaerobic thermophilic chitinolytic bacterium from compost

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Abstract

A novel Gram-negative, spore forming, obligately anaerobic, thermophilic, chitin-degrading bacterium, designated UUS1-1^T, was isolated from compost on Ishigaki Island, Japan by enrichment culturing using chitin powder as the carbon source. The strain has unique, long, hair-like rod morphological features and exhibits strong degradation activity toward crystalline chitin under thermophilic conditions. Growth of the novel strain was observed at 45–65 °C (optimum, 55 °C) and pH 6.5–7.5 (optimum, pH 7.0). In addition to chitin, the strain utilized several other carbon sources, including *N*-acetylglucosamine, glucose, galactose, mannose, maltose, cellobiose, fructose and sucrose. The end products of chitin degradation were acetate, lactate, H_2 and CO_2. Phylogenetic tree analysis based on 16S rRNA gene sequences revealed a clear affiliation of the proposed bacterium to the phylum *Firmicutes*; the most closely related species were *Hydrogenispora ethanolica* LX-B^T and *Desulfotomaculum thermobenzoicum* DSM6193^T with similarities of 90.4 and 87.8%, respectively. The G+C content of the genomic DNA was 52.1 mol%. The average nucleotide identity and digital DNA–DNA hybridization values between the genomes of UUS1-1^T and *H. ethanolica* LX-B^T were 65.5 and 21.0%, respectively. The cellular fatty acid composition of the strain was $C_{16:0}$, anteiso-$C_{15:0}$, $C_{14:0}$, $C_{12:0}$ 3-OH and dimethyl acetal-$C_{13:0}$. Based on phenotypic, chemotaxonomic and genotypic analysis, strain UUS1-1^T represents a novel genus and species, for which the name *Capillibacterium thermochitinicola* gen. nov., sp. nov. is proposed. The type strain is UUS1-1^T (=JCM 33882^T=DSM 111537^T).

Chitin is a crystalline polymer of β−1,4 *N*-acetylglucosamine (GlcNAc) and is the second-most abundant biopolymer in nature after cellulose with approximately 10 billion tons produced yearly [1]. The structure of chitin exists in the exoskeletons of arthropods and is often linked to protein polymers. Chitin can be transformed into valuable products such as GlcNAc and chitin oligosaccharides, which are used widely in agriculture, food and pharmaceutical industries [2]. The degradation of recalcitrant crystalline chitin requires the cooperation of multiple enzymes. Chitinases (EC 3.2.1.14), enzymes that hydrolyse chitin, are synthesized by various microbes, including archaea, bacteria and fungi, and by insects, higher plants and animals [1–3]. Bacterial chitinases hold promise for use in several commercial applications. Thus, screening and studying the properties of thermophilic enzymes, and elucidating the function of chitinases are important related research areas; however, there remains a paucity of information about chitin degradation systems from anaerobic thermophilic bacteria [3]. In this paper, we report the classification and taxonomy of a novel anaerobic, thermophilic, chitinolytic bacterium strain UUS1-1^T belonging to the second candidate in the uncultured taxonomic OPB54 cluster at the order- or class-level of the phylum *Firmicutes*.

ISOLATION AND ECOLOGY

Strain UUS1-1^T was originally isolated from compost collected at Ishigaki Island (Ishigaki Taihi Centre, Ishigaki city, Japan; 24° 23′ 09.9″ N 124° 11′ 28.1″ E) in May 2015. The compost included sugarcane bagasse, rice husk and

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Keywords: chitin degradation; anaerobe; thermophilic; *Firmicutes*; OPB54; *Hydrogenispora*; *Capillibacterium*.
Abbreviations: ANI, average nucleotide identity; dDDH, digital DNA–DNA hybridization; GlcNAc, *N*-acetyl-D-glucosamine.
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Japan Collection of Microorganisms: JCM 33882^T. German Collection of Microorganisms and Cell Cultures GmbH: DSM 111537^T. The GenBank accession numbers for the genome and 16S rRNA gene sequences of *Capillibacterium thermochitinicola* are JAAKDE00000000 and MN602556, respectively.
Three supplementary tables are available with the online version of this article.

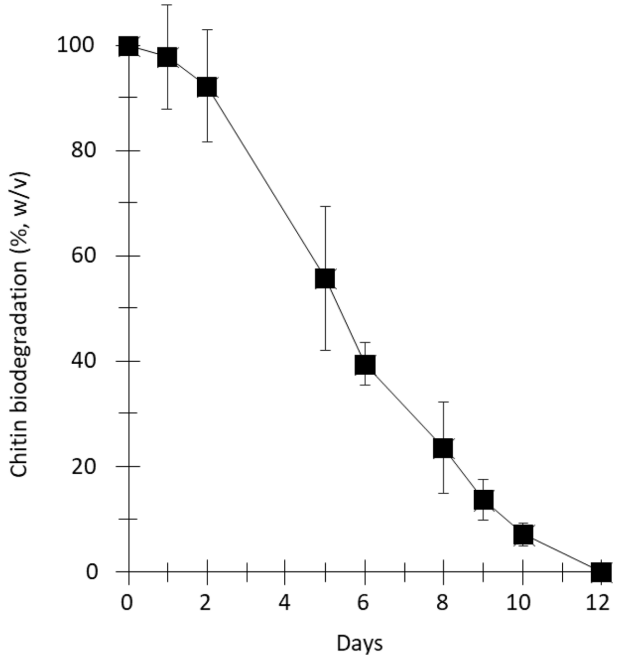

Fig. 1. Biodegradation activity of strain UUS1-1^T toward chitin. The calculated percentage of crystalline chitin (i.e. residual) relative to the original weight is presented. Error bars represent standard deviations (*n*=3).

bovine faeces. The samples were collected 10 to 20 cm below the surface at temperatures between 60 and 75 °C and placed in oxygen-starved Ziploc bags (Johnson) [4, 5]. The samples were stored at −80 °C until initiating the enrichment culture required for species isolation. The Hungate technique [6] for enrichment culturing was used to isolate chitinolytic anaerobic microbes. The basal medium (BM7CO) was composed of (per litre): 1.5 g KH_2PO_4, 2.9 g K_2HPO_4, 2.1 g urea, 3.0 g yeast extract, 4.0 g Na_2CO_3, 0.01 g $CaCl_2{\cdot}2H_2O$, 0.5 g L-cysteine-HCl, 0.5 mg resazurin and 200 µl mineral solution (25.0 g l^{-1} $MgCl_2{\cdot}6H_2O$, 0.312 g l^{-1} $FeSO_4{\cdot}7H_2O$ and 37.5 g l^{-1} $CaCl_2{\cdot}2H_2O$). The BM7CO (pH 7.0) with 0.5% (w/v) crystalline chitin was bubbled under CO_2 and autoclaved. All chemicals were purchased from Fujifilm Wako Pure Chemical Corporation. The initial culture was incubated at 60 °C with static culturing. After culturing for 5 days, cultures displaying chitin degradation were inoculated again with BM7CO supplemented with 0.5% (w/v) crystalline chitin and the enrichment culturing procedure was repeated five times. Single colony isolation was carried out to isolate microbes with chitin degradation activity from the enrichment culture by including 1.0% (w/v) colloidal chitin in the medium and using the roll-tube method. Colloidal chitin was prepared from a chitin powder by the Hsu and Lockwood method [7]. Subsequently, to obtain a pure culture, colonies were isolated several times by the roll-tube method using BM7CO containing 1% glucose as the carbon source. This approach successfully isolated a pure culture and was designated as strain UUS1-1^T. Strain UUS1-1^T degraded crystalline chitin completely under anaerobic thermophilic (60 °C) conditions in 12 days (Fig. 1).

16S rRNA GENE PHYLOGENY

Genomic DNA used as a PCR template was prepared from cells of strain UUS1-1^T using the NucleoSpin Microbial DNA kit (TaKaRa Bio). PCR amplification and sequencing of the 16S rRNA gene were carried out as described previously [8]. The PCR primers used for DNA amplification were the bacterial domain universal primer 27F (5′-AGAGTTTGATCCTGGCTCAG-3′) [9, 10] and the prokaryotic universal primer 1492R (5′-GGTTACCTTGTTACGACTT-3′) [9, 10]. The PCR product was sequenced directly on a DNA sequencer (3730xl DNA Analyzer, Applied Biosystems) and sequence assembly was performed by using GENETYX software version 13. The complete 16S rRNA gene sequence of strain UUS1-1^T was deposited in the GenBank under accession number MN602556 and compared with corresponding sequences obtained from the ribosomal sequence database at the National Center for Biotechnology Information (NCBI). Comparative 16S rRNA gene phylogenetic analysis was performed by BLAST, and multiple alignments with sequences of closely related taxa were carried out using the GenBank database and ClustalX version 1.81 [11]. The phylogenetic tree was reconstructed by the neighbour-joining method [12] and the Tamura three-parameter model [13] using MEGA version X version 10.1 [14]. The topology of the tree and distances were confirmed by bootstrap analysis based on 1,000 resamplings [15]. On the basis of 16S rRNA gene sequence analysis, strain UUS1-1^T is found to be closely related to *Hydrogenispora ethanolica* LX-B^T (<90.4%) [16] in the unidentified taxonomy OPB54 of the phylum *Firmicutes*, which belongs to the order- or class-level based on ARB-SILVA analysis (http://arb-silva.de) [17]. Strain UUS1-1^T is the second candidate to be included in the OPB54 group, which was investigated initially from the Obsidian Pool by Hugenholtz and colleagues [18]. In contrast, relatively low similarity levels were observed between strain UUS1-1^T and the genera *Desulfotomaculum* [19, 20], *Pelotomaculum* [21] and *Moorella* [22], with identities below 88.0%. The phylogenetic trees based on these sequences are presented in Fig. 2. Phylogenetic analysis of 16S rRNA gene sequences showed that strain UUS1-1^T clustered within the genus *Hydrogenispora* with the type strain of *H. ethanolica* LX-B^T, rather than the genus *Desulfotomaculum*; however, the phylogenetic tree showed that strain UUS1-1^T formed an independent branch (Fig. 2).

GENOME FEATURES

Whole-genome sequence analysis of strain UUS1-1^T was performed using the Ion GeneStudio S5 system [23]. The genome was assembled *de novo* using CLC Genomics Workbench 20.0.1 (CLC Bio, Qiagen). The assembled genome sequence of strain UUS1-1^T was found to be 2,482,547 bp, had a G+C content of 52.1 mol%, and was composed of 86 contigs with an N50 of 117,588 bp and a maximum size of 238,885 bp [23]. The whole-genome sequence was deposited

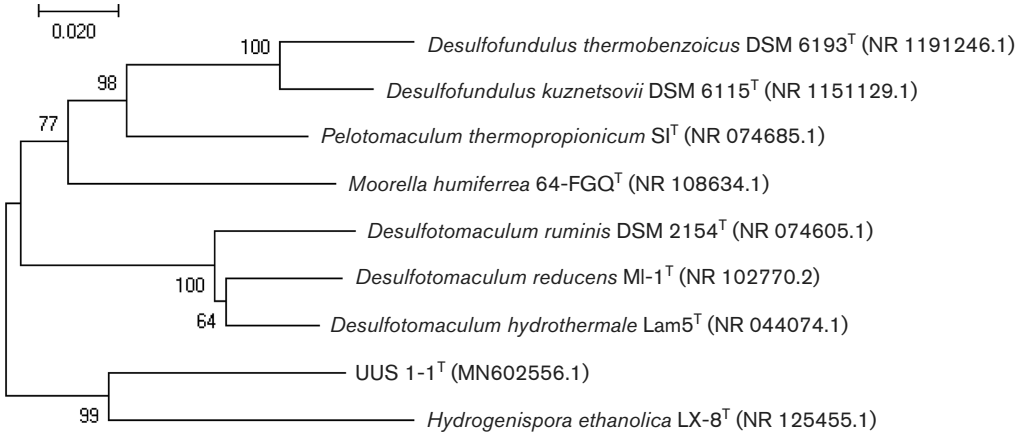

Fig. 2. Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences showing the relationship between strain UUS1-1^T and closely related type strains of species from genera *Hydrogenispora*, *Desulfotomaculum*, *Pelotomaculum* and *Moorella* within the phylum *Firmicutes*. The tree was reconstructed based on a distance-matrix analysis of 16S rRNA sequences. Accession numbers for 16S rRNA gene sequences are given in parentheses for each strain. Bootstrap percentages were obtained from 1,000 resamplings. The bar represents 0.020 nucleotide changes per sequence position.

in the GenBank under accession number JAAKDE00000000 [23]. The most closely related strain in this genus, *H. ethanolica* strain LX-B^T, was nearly identical in its G+C content but 2.4 times larger in size (5,983,461 bp, with a G+C content of 54.2mol%). The average nucleotide identity (ANI) values, the digital DNA–DNA hybridization (dDDH) values and the average amino acid sequence identity (AAI) were calculated using the ANI calculator (www.ezbiocloud.net/tools/ani) [24], the Genome-to-Genome Distance Calculator (GGDC; http://ggdc.dsmz.de/distcalc2.php) [25], and the AAI calculator (http://enve-omics.ce.gatech.edu/aai) [26], respectively. The ANI and the dDDH values based on the genomic sequences between strain UUS1-1^T and the most closely related strain, *H. ethanolica* strain LX-B^T (accession no. SLUN00000000) and *Hydrogenispora* sp. isolate (accession no. DUQQ01000000), which was identified by comprehensive genome-resolved metagenomics, gave ANI values of 65.5 and 82.9%, and dDDH values of 21.0 and 26.0%, respectively, which are well below the defined thresholds for species delineation of 95–96% for ANI and 70% for GGDC [27, 28]. In addition, the AAI values based on the protein sequences in the genomes between strain UUS1-1^T and related strains, including *Desulfofundulus* species, *Desulfotomaculum* species, *H. ethanolica*, *Pelotomaculum thermopropionicum* and *Moorella humiferrea*, revealed AAI values of <50.0%, which are clearly distinguishable for genus delineation of 60–80% AAI [29], except for *Hydrogenispora* sp. (84.8%) (Table S1, available in the online version of this article). Based on these data, strain UUS1-1^T represents a novel species in a new genus of the unidentified taxonomy OPB54 in the phylum *Firmicutes*. Genome annotation was carried out by the NCBI Prokaryotic Genome Annotation Pipeline [30]. Strain UUS1-1^T possessed 2,337 total predicted genes, 2,235 protein-coding sequences, four rRNA genes (encoding two 5S rRNAs, one 16S rRNA and one 23S rRNA), 47 tRNA genes and four CRISPR repeats. The predicted protein-coding sequences were assigned putative functions using the 25 clusters of orthologous groups under Genome ID 2882933831 [23]. The presence of predicted enzymes associated with chitin metabolism [31] in strain UUS1-1^T was confirmed by BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi) and included chitinase (EC 3.2.1.14), *N*-acetylglucosaminidase (EC 3.2.1.52/EC 3.2.1.30/EC 3.2.1.96), chitin deacetylase (EC 3.5.1.41)/*N*-acetylglucosamine deacetylase (EC 3.5.1.33), glucosidase (EC 3.2.1.10/EC 3.2.1.20/EC 3.2.1.21/EC 3.2.1.86), glucokinase (EC 2.7.1.12), glutamine-fructose-6-phosphate aminotransferase (EC 2.6.1.16), phospho-glucosamine mutase (EC 5.4.2.10), glucosamine-6-phosphate deaminase (EC 3.5.99.6) and glucosamine-1-phosphate *N*-acetyltransferase/UDP-*N*-acetylglucosamine pyrophosphorylase (EC 2.3.1.157/EC 2.7.7.23). Meanwhile, the number of predicted chitinase, *N*-acetylglucosaminidase and glucosamine-fructose-6-phosphate aminotransferase was different between strain UUS1-1^T, *H. ethanolica* strain LX-B^T and *Hydrogenispora* sp. (Table S2). The predicted chitinases and chitin deacetylases may play an important role in the efficient degradation of crystalline chitin by strain UUS1-1^T.

PHYSIOLOGY AND CHEMOTAXONOMY

Cells of strain UUS1-1^T were observed by scanning electron microscopy (JSM-6320F, JEOL) and transmission electron microscopy (H-7600, Hitachi) [8]. The cell length was calculated using ImageJ software [32]. Gram staining was performed using the Gram stain kit S (BD Difco). Strain UUS1-1^T has unique, long, hair-like rod morphologies with a length of 15.0–80.0 µm and a width of 0.15–0.40 µm (Fig. 3a). Spores were located terminally and formed a bulged sporangium and were similar to those observed for *H. ethanolica* LX-B^T (Fig. 3a). We could not recognize the presence of flagellar in the SEM images because of the long hair-like rod morphology; however, strain UUS1-1^T may be

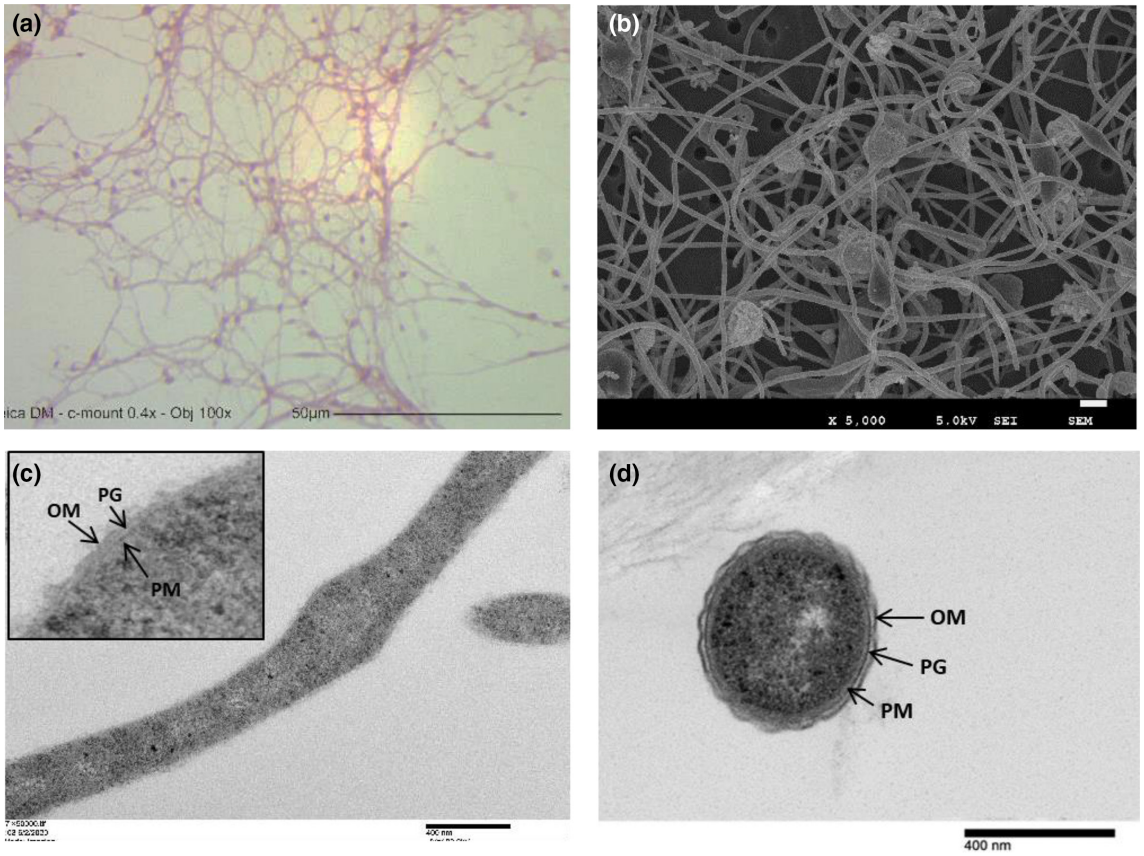

Fig. 3. Morphology of cells from the UUS1-1^T strain grown on medium with colloidal chitin. (a) A phase-contrast microscope photograph of strain UUS1-1^T after Gram staining. Bar, 50 µm. (b) A scanning electron microscope image of strain UUS1-1^T. Bar, 1 µm. (c) Transmission electron microscope (TEM) images of a thin section of strain UUS1-1^T and the cell wall ultrastructure with the outer membrane (OM), the peptidoglycan layer (PG) and plasma membrane (PM) indicated in the inset. Bar, 0.4 µm. (d) TEM image of a longitudinal cross section of a cell. The cell wall ultrastructure also shows the OM, PG and PM, as indicated by the arrows. Bar, 0.4 µm.

mobile due to the presence of genes encoding for proteins that assemble flagellar in the genome sequence (Table S3) [23]. Strain UUS1-1^T possessed properties of a Gram-negative type cell, i.e. the periplasmic space contains no cellular material, and the peptidoglycan layer, outer membrane and plasma membrane were observed (Fig. 3c, d) [33]. Gram staining was demonstrated to be negative.

Physiological characteristics of UUS1-1^T were examined under various growth temperatures and pH values in medium containing 1% (w/v) glucose and GlcNAc (Table 1). Cell growth was examined between 45 and 70 °C. The pH range examined was pH 6.0–9.0 and the pH was adjusted by adding 1 N HCl and NaOH after autoclaving the medium. NaCl tolerance was assessed over the range of 0–5.0% (w/v) at 60 °C. Cell growth was evaluated by determining the OD at 600 nm using a spectrophotometer (UV-mini 1240, Shimadzu) after 7 days of incubation. The optimal conditions for growth of strain UUS1-1^T were 55 °C and pH 7.0, and the cells could survive in 2.0% (w/v) NaCl. The growth of strain UUS1-1^T required anaerobic conditions. Growth of strain UUS1-1^T was observed in media containing the following carbon sources (1% w/v): chitin, starch, galactan, β-glucan, cellobiose, fructose, galactose, GlcNAc, glucose, mannose, maltose and sucrose. Strain UUS1-1^T did not grow in the presence of cellulose, xylan, chitosan, arabinose and xylose as sole carbon sources. Yeast extract was required for vigorous growth of UUS1-1^T. Acetate, lactate, H_2 and CO_2 as end products from chitin, GlcNAc and glucose grown cultures were detected by HPLC (LC-20AD, Shimadzu) using a Shim-pack SCR-102H column with an electric conductivity monitor (CDD-10Avp) and by gas chromatography (GC-2014, Shimadzu) equipped with a thermal conductivity detector and a ShinCarbon ST column (50/80 mesh; GL Science).

Cellular fatty acids were extracted according to the standard protocol of the MIDI Sherlock Microbial Identification System (MIS; MIDI, Sherlock version 6.1). Fatty acids and their methyl esters were identified by using the MIS and the Anaerobic Bacteria Library (MOORE6) for peak identification. The cellular fatty acid composition of strain UUS1-1^T was $C_{10:0}$ 3-OH (6.43%), summed feature A ($C_{12:0}$ 3-OH and/or dimethyl acetal-$C_{13:0}$; 12.49%), iso-$C_{14:0}$ (2.33%), $C_{14:0}$

Table 1. Comparative characteristics of strain UUS1-1^T and its closest phylogenetic relatives

Strains: 1, UUS1-1^T; 2, *Hydrogenispora ethanolica* LX-B^T; 3, *Desulfotomaculum thermobenzoicum* TSB^T; 4, *Pelotomaculum thermopropionicum* SI^T; 5, *Desulfotomaculum hydrothermale* Lam5^T; 6, *Moorella humiferrea* 64-FGQ^T. –, Negative; +, positive; ND, not detected.

Characteristic	1	2	3	4	5	6
16S rRNA similarity (%)	100	<90.4	<87.6	<87.3	<87.1	<86.9
Cultivated environment	Compost	Anaerobic sludge treating herbicide wastewater	Kraft pulp sludge reactor	Methanogenic granular sludge	Hot spring in northeast Tunisia	Terrestrial hydrothermal spring
Cell morphology	Hair-like, long rod	Rod	Spindle rod	Sausage rod	Rod	Rod
Cell size (μm)	0.15–0.40× 15.0–80.0	0.3–0.5×3.0–18.0	1.5–2.0×5.0–8.0	0.7–0.8×1.7–2.8	0.5×2.0–5.0	0.3–0.5×2.0–5.0
Motility	ND	–	+	–	+	+
Spore location	+/Terminal and subterminal	+/Terminal	+/ND	+/Centre	+/Terminal and subterminal	+/Terminal
Gram identification	–	+	+	+	+	+
Temperature optimum/range for growth (°C)	55/45–65	37–45/20–50	62/40–70	55/45–65	50/40–60	65/46–70
pH optimum/range for growth	7.0/6.5–7.5	6.0–7.7/5.0–8.0	7.2/6.0–8.0	7.0/6.7–7.5	7.1/5.8–8.2	6.8–7.0/5.5–8.5
NaCl tolerance (%, w/v)	0–2.0	0–2.5	ND	0–0.4	0–1.5	0–1.5
DNA G+C content (mol%)	52.1	56.1	52.8	52.8	46.8	51.0
References	This study	[16]	[20]	[21]	[19]	[22]

(8.21%), iso-$C_{15:0}$ (8.12%), anteiso-$C_{15:0}$ (20.87%), iso-$C_{16:0}$ (5.82%) and $C_{16:0}$ (24.10%). The fatty acid compositions of strain UUS1-1^T and the reference strains are compared in Table 2. The fatty acid profile of UUS1-1^T was quite different from strains *H. ethanolica* LX-B^T and *D. thermobenzoicum* TSB^T, which contained predominantly anteiso-$C_{15:0}$ and iso-$C_{15:0}$, respectively, and did not contain $C_{10:0}$ 3-OH and summed feature A.

Table 2. Major cellular fatty acids (%) of strain UUS1-1^T and closest phylogenetic relatives

Strains: 1, UUS1-1^T; 2, *Hydrogenispora ethanolica* LX-B^T; 3, *Desulfotomaculum thermobenzoicum* TSB^T; 4, *Pelotomaculum thermopropionicum* SI^T; 5, *Desulfotomaculum hydrothermale* Lam5^T; 6, *Moorella humiferrea* 64-FGQ^T. Cellular fatty acids were analysed by using strain UUS1-1^T grown on BM7CO medium (pH7.0) containing 1% (w/v) glucose at 60 °C under anaerobic conditions. –, Not detected.

Fatty acid	1*	2	3	4	5	6
$C_{10:0}$ 3-OH	6.4	–	–	–	–	–
Summed feature A*	12.5	–	–	–	–	–
iso-$C_{14:0}$	2.3	11.1	–	–	–	1.2
$C_{14:0}$	8.2	4.2	2.0	3.2	14.0	1.0
iso-$C_{15:0}$	8.1	4.3	79.4	76.4	14.6	20.6
anteiso-$C_{15:0}$	20.9	58.6	–	–	14.7	–
iso-$C_{16:0}$	5.8	6.9	–	–	15.6	–
$C_{16:0}$	24.1	9.6	7.4	10.7	16.0	21.7
Reference	This study	[16]	[20]	[21]	[19]	[22]

*Summed feature A contained one or more of the following fatty acids: $C_{12:0}$ 3-OH and/or dimethyl acetal $C_{13:0}$.

On the basis of the phylogenetic, physiological, chemotaxonomic and genotypic features, strain UUS1-1^T likely represents a novel species of a new genus in the phylum *Firmicutes*, for which the name *Capillibacterium thermochitinicola* sp. nov. is proposed.

DESCRIPTION OF *CAPILLIBACTERIUM* GEN. NOV.

Capillibacterium (Ca.pil.li.bac.te'ri.um. L. masc. n. *capillus* hair; N.L. neut. n. *bacterium* a small rod; N.L. neut. n. *Capillibacterium* a hair-like rod).

Cells are Gram-stain-negative. Flagella. Strict anaerobe. Thermophilic and fermentative metabolism. Long hair-shaped. Produces terminal, spherical spores. Chitin is fermented to acetate, lactate, H_2 and CO_2.

DESCRIPTION OF *CAPILLIBACTERIUM THERMOCHITINICOLA* SP. NOV.

Capillibacterium thermochitinicola [ther.mo.chi.ti.ni'co.la. Gr. masc. adj. *thermos* hot; N.L. neut. n. *chitinum* chitin; L. masc. suff. *–cola* (from L. n. *incola*) a dweller, inhabitant; N.L. n. *thermochitinicola* dweller that can live in a hot and anaerobic environment with chitin-degrading activity].

The bacterium displays the following characteristics in addition to those given for the genus description. Cells are rod-shaped, 0.15–0.40 µm in diameter and 15.0–80.0 µm long. Grows at 45–65 °C (optimum, 55 °C), at pH 6.5–7.5 (optimum, pH 7.0) and with 0–2.0% NaCl (w/v). The bacterium uses the carbon substrates chitin, starch, galactan, β-glucan, cellobiose, fructose, galactose, GlcNAc, glucose, mannose, maltose and sucrose. Fatty acid composition is $C_{10:0}$ 3-OH, summed feature A ($C_{12:0}$ 3-OH and/or dimethyl acetal-$C_{13:0}$), iso-$C_{14:0}$, $C_{14:0}$, iso-$C_{15:0}$, anteiso-$C_{15:0}$, iso-$C_{16:0}$ and $C_{16:0}$. The genome of the type strain exhibits 52.1 mol% DNA G+C content. The 16S rRNA gene and genome sequences of the type strain were deposited in the Genbank under accession number MN602556.

The type strain is JCM 33882^T=DSM 111537^T, which was isolated from manure compost on Ishikagi Island (Japan) with crystalline chitin as a carbon source.

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Author contributions
U. U. and S. B. isolated and identified UUS1-1^T. U. U. and A. K. designed the experiments. U. U. and S. B. performed the experiments. A. U. and U. U. designed and performed genome analysis using NGS. A. U., U. U., S. B. and A. K. analysed the data. U. U. and A. K. wrote the paper.

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

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