**Pedobacter psychrophilus** sp. nov., isolated from fragmentary rock

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**Abstract**

Strain P4487A\(^T\) was isolated during investigation of cultivable bacterial populations of environmental materials sampled at James Ross Island, Antarctica. It revealed Gram-stain-negative short rod-shaped cells producing a pink pigment. Phylogenetic analysis based on 16S rRNA gene sequences allocated strain P4487A\(^T\) to the genus *Pedobacter* but showed that the strain represents a distinct intrageneric phylogenetic lineage clearly separated from remaining *Pedobacter* species. Phylogenetically, strain P4487A\(^T\) formed a common branch with the *Pedobacter arcticus* and *Pedobacter ligniformis* cluster while the highest value of 94.4% 16S rRNA gene sequence similarity suggested that *Pedobacter lentus* is the most closely related species. Biochemical and physiological test results enabled the differentiation of strain P4487A\(^T\) from all phylogenetically closely related species. Chemotaxonomic analyses of strain P4487A\(^T\) showed MK-7 as the respiratory menaquinone, sym-homospermidine as the major polyamine, phosphatidylethanolamine and two unidentified lipids as the major fatty acids, all of which corresponded with characteristics of the genus *Pedobacter*. The results showed that strain P4487A\(^T\) represents a novel species within the genus *Pedobacter*, for which the name *Pedobacter psychrophilus* sp. nov. is proposed. The type strain is P4487A\(^T\) (=CCM 8644\(^T\)=LMG 29436\(^T\)).

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The genus *Pedobacter* [1] represents a large group of species inhabiting different environmental, mainly terrestrial and aquatic, habitats worldwide. Members of the genus *Pedobacter* are Gram-stain-negative rod-shaped bacteria producing catalase, oxidase and phosphatase while being negative for the production of nitrate reductase and urease [2]. The presence of MK-7 as the major respiratory menaquinone, homospermidine as the major polyamine, phosphatidylethanolamine as the major polar lipid and presence of sphingolipids is typical for the genus *Pedobacter* [2]. The number of novel *Pedobacter* species with validly published names has increased significantly in recent years. At the time of writing, the genus *Pedobacter* harboured more than 60 recognized species [3]. The present taxonomic study deals with strain P4487A\(^T\) isolated in the framework of a project investigating bacterial populations inhabiting the Antarctic environment. The studied strain was isolated from fragmentary rock sampled at James Ross Island, Antarctica (GPS: 63° 49’ 20.316” S, 57° 50’ 20.5404” W). The sampling site was located at the north-east foot of the Lachman Crags mesa and formed a shallow depression filled by volcanic stones and rock fragments that ranged from 0.3 to 20.0 cm in size. The samples were taken from the south-facing side of an individual monolithic rock exhibiting a heavily fragmented surface caused by frost weathering. Therefore, the sampling site was a typical shaded habitat with a lower surface temperature than sunlit surfaces of the monolith. The sample was suspended in sterile saline solution, and 200 µl of the suspension was spread on R2A agar plates and cultivated at 15 °C for 5–7 days. Individual colonies were picked up, purified and pure cultures were maintained at −70 °C until analysed.

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**Abbreviation:** WGS, whole genome sequencing.

The GenBank/EMBL/DBJ accession number for the 16S rRNA gene sequence of strain CCM 8644\(^T\) (=P4487A\(^T\)) is KX113374. The Whole Genome Shotgun projects have been deposited at DDBJ/EMBL/GenBank under accession LWHJ00000000. The version described in this paper is LWHJ01000000.

Four supplementary figures and one supplementary table are available with the online Supplementary Material.
The analysed strain, designated P4487Aᵀ, was deposited in the Czech Collection of Microorganisms and BCCM/LMG Bacteria Collection under accession numbers CCM 8644ᵀ and LMG 29436ᵀ, respectively. Reference strain Pedobacter arcticus CCTCC AB 2010223ᵀ was obtained from the China Center for Type Culture Collection and Pedobacter lentus KCTC 12875ᵀ was obtained from the Korean Collection for Type Cultures.

DNA for 16S rRNA gene sequence analysis was extracted by using a FastPrep Lysing Matrix type B and FastPrep Homogenizer (MP Biomedicals) and purified via a High Pure PCR Template Preparation Kit (Roche Diagnostics). A fragment of the 16S rRNA gene corresponding to positions 8−1542 used for Escherichia coli was amplified by PCR with FastStart PCR Master (Roche Diagnostics) and conserved primers pA (AGAGTTTGTATCCTGTGCTCAG) and pH (AAGGAGGTGATCCAGCGCA) described by Edwards et al. [4], and purified using a QIAquick PCR Purification Kit (Qiagen). Sequencing was performed using PCR primers and custom primers F1 (GTGGGGACKRAACAGGA TTAG), F2 (CGTCARGTCMTCATGGCCCTT), R1 (A TTACCCGCGCTGTCGGCAC) and R2 (CACATSMGCC MCCRCCTTGT) in the Eurofins MWG Operon sequencing facility. The obtained sequence was identified via the EzTaxon database [5] which showed the type strain of P. lentus (accession no. EF446146) as its closest neighbour with a 16S rRNA gene sequence similarity value of 94.4 %, followed by those of Pedobacter terricola (94.3 %) and Pedobacter daechungensis (94.1 %). To characterize strain P4487Aᵀ in more detail, whole genome sequencing (WGS) was performed. The purified genomic DNA was used for 400 bp sequencing library preparation as described previously [6]. The sample was loaded on a 316v2 chip and sequenced using an Ion PGM Hi-Q sequencing kit (Life Technologies) on an Ion PGM system (Life Technologies). Quality trimming and error correction of the reads were performed with the Ion Torrent Suite Software (v5.0.2). The assembly computation was performed using the plug-in Assembler SPAdes (v5.0.0). The total length of the assembly comprised 3 999 136 bp. Assembled contigs larger than 500 bp were used for subsequent analysis. To estimate the DNA G+C content, the draft genome sequence was used. The DNA G+C content of strain P4487Aᵀ was 46.3 mol%.

The complete 16S rRNA gene sequence extracted from WGS data using the RNAmer 1.2. server [7] showed similarity with that obtained by Sanger sequencing and therefore was used for further phylogenetic comparison with 16S rRNA gene sequences from recognized species of the genus Pedobacter retrieved from the GenBank/EMBL/DDBJ database. Phylogenetic analysis was performed using MEGA v6 software [8]. Genetic distances were corrected using Kimura’s two-parameter model and the evolutionary history was inferred using the maximum-likelihood and neighbour-joining methods. Comparative analysis of the 16S rRNA gene assigned strain P4487Aᵀ to the genus Pedobacter but it was distantly separated from remaining Pedobacter species. The trees reconstructed using the maximum-likelihood (Fig. 1) and neighbour-joining (Fig. S1, available in the online Supplementary Material) clustering methods showed robust clustering (>80 % bootstrap value) of strain P4487Aᵀ with the cluster comprising the type strains of P. arcticus and Pedobacter lignilitoris.

The phenotypic profile of strain P4487Aᵀ was assessed by a set of key tests relevant for Gram-negative rod-shaped bacteria. P. arcticus CCTCC AB 2010223ᵀ and P. lentus KCTC 12875ᵀ were used as reference strains for evaluation of phenotypic test results obtained under the same conditions as for strain P4487Aᵀ. Oxidase (OXItest; Erba-Lachema) and catalase (ID colour Catalase; bioMérieux) activities were determined according to the manufacturers’ instructions. Further tube and plate conventional tests for urease, oxidation-fermentation (OF) test, motility, arginine dihydrolase, ornithine decarboxylase and lysine decarboxylase, hydrolysis of casein, DNA, aesculin, gelatin, lecithin (egg-yolk reaction), ONPG, starch, Tween 80 and tyrosine, acid production from fructose, maltose, mannitol and xylose, nitrate and nitrite reduction, indol production, and Simmon’s citrate, acetamide and sodium malonate utilization tests were done as described previously [9–11]. The temperature range for growth (1, 5, 10, 15, 20, 25, 30 and 35 °C) and NaCl concentration tolerance (0, 1, 2 and 3 %, w/v) were tested on R2A agar (Oxoid) adjusted accordingly. The pH range for growth was tested on R2A agar adjusted to pH 5.0–10.0 (in increments of 1 pH unit) by using the following buffer systems: pH 5.0−8.0, 0.1 M KH₂PO₄/0.1 M NaOH; pH 9.0–10.0, 0.1 M NaHCO₃/0.1 M Na₂CO₃. The pH of the R2A agar was confirmed after autoclaving. Aerobic growth of strain P4487Aᵀ was assessed on brain heart infusion agar, Columbia blood agar, MacConkey agar, nutrient agar, plate count agar, R2A agar and tryptone soya agar (all from Oxoid) and anaerobic growth was tested on R2A agar using the Anaerocolt A system (Merck). Biochemical and growth tests were carried out using cells grown on R2A agar at 20 °C and read daily for up to 7 days with incubation at 20 °C. Cellular morphology was further investigated by transmission electron microscopy using a Morgagni 268D Philips (FEI) electron microscope (Fig. S2). Phenotypic screening showed that strain P4487Aᵀ was Gram-stain-negative, rod-shaped, aerobic, non-fermenting, and oxidase- and catalase-positive. It revealed small pink colonies when cultivated on R2A agar plates at 20 °C. The colonies became dark red–orange after the cultivation was prolonged for more than 1 week. Further extensive phenotypic characterization using the Biolog system with the Gram-negative identification test panel GN2 MicroPlate (Biolog) and API ZYM (bioMérieux) was done according to the manufacturers’ instructions. Screening for flexirubin-type pigment production was done using a 20 % KOH test as described by Bernardet et al. [12]. Gliding motility was assessed by a direct microscopic examination of cell colonies grown on the agar surface as well as using a hanging drop method as suggested by Bernardet et al. [12]. The antibiotic resistance pattern was obtained by the disc diffusion method on R2A agar (Oxoid). Sixteen antibiotic discs (Oxoid) relevant for Gram-
negative rods [13, 14] were tested: ampicillin (10 µg), aztreonam (30 µg), carbenicillin (100 µg), cefixim (5 µg), cefazidim (10 µg), cephaplexin (30 µg), ciprofloxacin (5 µg), gentamicin (10 µg), chloramphenicol (30 µg), imipenem (10 µg), kanamycin (30 µg), cotrimoxazol (25 µg), piperacillin (30 µg), polymyxin B (300 U), streptomycin (10 µg) and tetracycline (30 µg). CLSI/EUCAST standards were followed for cultivation and inhibition zone diameter reading. The biochemical and physiological characteristics and antibiotic susceptibility pattern of strain P4487A are

P. cryoconitis DSM 14825T (AJ438170)
P. hartonius WB 3.3-3T (AM491371)
P. antarcticus 4BYT (HM448033)
P. ginsengisoli Gsoil 104T (AB245371)
P. steynii WB 2.3-45T (AM491372)
P. duraquae WB 2.1-25T (AM491368)
P. trunci THG-DN3.19T (KM035944)
P. heparinus DSM 2366T (AJ438172)
P. panaciterrae Gsoil 042T (AB245368)
P. boryungensis BR-9T (HM640986)
P. insulae DS-139T (EF100697)
P. koreensis WPCB189T (DQ092871)
P. ureilyticus THG-T11T (KF532135)
P. ardleyensis R2-28T (KJ631640)
P. rhizosphaerae 01-96T (AM279214)
P. jejuni THG-DR3T (KC252614)
P. soli 15-51T (AM279215)
P. suwonensis 15-52T (DQ097274)
P. agri PB92T (EF660751)
P. alluvionis NWER-II1T (EU030688)
P. ginsenosidimutans THG 45T (GU138374)
P. glucosidilyticus 1-2T (EUS65748)
P. pituitosus MIC2002T (JX978785)
P. arcticus NRRL B-59457T (HM051286)
P. lignilitoris W-WS13T (KP641351)
P. psychrophilus P4487AT (KX113374)
P. silvilitoris W-WS1T (KM229740)
P. alpinus RSP19T (KP008109)
P. daechungensis Dae 13T (AB267722)
P. rivuli HME8457T (JQ911707)
P. lentus DS-40T (EF446146)
P. terricola DS-45T (EF446147)
P. composti TR6-06T (AB267720)
P. oryzae N7T (EU109726)
P. tourneirensis TF5-37.2-LB10T (GU198945)
F. aquatile DSM 1132T (AM230485)

Fig. 1. Phylogenetic tree based on 16S rRNA gene sequences showing the position of strain P4487AT within the genus Pedobacter. The evolutionary history was inferred by using the maximum-likelihood method based on the Kimura two-parameter model. Bootstrap probability values (percentages of 1000 tree replications) greater than 50% are indicated at branch points. There were a total of 1523 positions in the final dataset. Flavobacterium aquatile DSM 1132T (AM230485) was used as an outgroup. Bar, 0.02 substitutions per nucleotide position.
given in the species description below. The tests distinguishing strain P4487A\(^T\) from phylogenetically closest related *Pedobacter* species are shown in Table 1.

Spectrophotometric characterization of the produced pigment(s) was done from cells grown on R2A agar for 72 h at 20 °C. Cells were washed off and rinsed twice using 0.1 M phosphate buffer (pH 7.2). Harvested cells were suspended in an extraction mixture composed of equal volumes of acetone, ether and ethanol (96 %). Extraction was done in a shaker for 120 min at 4 °C (shaking interval: 120 swings min\(^{-1}\)) and centrifuged at 5000 g at 4 °C for 20 min. The supernatant was evaporated in vacuum at room temperature and the evaporation residue was diluted in hexane. A Cary 100Bio (Agilent) spectrophotometer was used for the measurement of spectra. The extracted pigment showed a whole absorbance spectrum with a typical major peak at 479 nm and less distinct peaks at 450 and 509 nm. Another major peak was observed at 270 nm (Fig. S3). The obtained spectrum resembled that of \(\beta\)-carotene as described by Burns et al. [15].

Analysis of fatty acid methyl esters was performed using an Agilent 7890B gas chromatograph according to the standard protocol of the Sherlock MIDI Identification System (MIDI Sherlock version 6.2, MIDI database RTSBA 6.21). *P. arcticus* CCTCC AB 2010223\(^T\) and *P. lentus* KCTC 12875\(^T\) were used for comparison of fatty acid analysis results of strain P4487A\(^T\) obtained under the same laboratory conditions. The strains were grown on R2A agar (Oxoid) at 20 ±2 °C for 72 h (except *P. lentus* KCTC 12875\(^T\), which was cultivated for 7 days), where the bacterial communities reached the late-exponential stage of growth according to the four quadrants streak method [16]. The predominant fatty acids of strain P4487A\(^T\) were summed feature 3 (C\(_{16:1}\) \(\omega7c/C_{16:1}\) \(\omega6c\)) (21.0 %), iso-C\(_{15:0}\) (15.4 %) and iso-C\(_{17:0}\) 3-OH (11.6 %), which corresponded with those typically found in *P. arcticus* CCTCC AB 2010223\(^T\), *P. lentus* KCTC 12875\(^T\) and *Pedobacter heparinus* DSM 2366\(^T\) (Table S1) as well as in other *Pedobacter* species [2].

Quinones and polar lipids were extracted from freeze-dried biomass grown on R2A agar at 20 °C for 72 h and analysed as described previously [17–20]. The analysis of strain P4487A\(^T\) revealed MK-7 as the respiratory quinone (100 %). The major polar lipid was phosphatidylethanolamine, followed by three unknown polar lipids (L1, L2, and L5) and an unknown aminolipid (AL2). Moderate amounts of five unknown polar lipids (L3, L4, L6–L8), an unknown aminolipid (AL1) and an unknown aminoglycolipid (AGL1) were detected (Fig. S4). The presence of phosphatidylethanolamine and lipid L2 was reported in the close relatives of strain P4487A\(^T\), namely *P. arcticus*, *P. lignilitoris* and *P. lentus* [21, 22]. On the other hand, the presence of aminolipids corresponding chromatographically to AL2 was reported for *P. arcticus* and *P. lignilitoris* but not for *P. lentus*. However, the presence of the unidentified aminoglycolipid AGL1 and lipid L1 in addition to some minor lipids clearly distinguished strain P4487A\(^T\) from its close relatives. Mild alkaline hydrolysis of the total polar lipid extract [23] of strain P4487A\(^T\) revealed the presence of an aminolipid.

### Table 1. Differentiation of strain P4487A\(^T\) from phylogenetically related *Pedobacter* species

| Taxa: 1, strain P4487A\(^T\); 2, *P. alpinus*; 3, *P. arcticus*; 4, *P. daechungensis*; 5, *P. glucosidilyticus*; 6, *P. lentus*; 7, *P. lignilitoris*; 8, *P. rivuli*; 9, *P. silvilitoris*; 10, *P. terricola*. +, Positive; −, negative; v, weakly positive; o, strain-dependent. Data for strain P4487A\(^T\), *P. arcticus* CCTCC AB 2010223\(^T\) and *P. lentus* KCTC 12875\(^T\) were obtained in this study; data for the remaining *Pedobacter* species were retrieved from Yoon et al. [27], An et al. [28], Luo et al. [29], Kang et al. [30], Li et al. [31] and Park et al. [22, 32]. |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Characteristic** | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| Growth at 30 °C | − | − | − | + | + | + | + | + | + | + |
| Enzyme activities: | | | | | | | | | | |
| α-Glucosidase | + | o | + | − | + | + | + | + | + | + |
| β-Galactosidase | + | + | − | + | − | − | − | + | − | + |
| Acid phosphatase | + | + | − | + | − | − | − | + | + | + |
| Naphthol-AS-BI-phosphohydrolase | + | + | − | + | − | − | − | + | + | + |
| Valine arylamidase | + | + | − | − | + | − | − | + | + | + |
| α-Fucosidase | − | − | + | − | + | − | − | − | − | − |
| α-Galactosidase | − | − | − | − | − | − | − | − | − | − |
| β-Glucosidase | − | − | + | − | − | − | − | − | − | − |
| Arginine dihydrolase | − | − | − | − | − | − | − | − | − | − |
| Cystine arylamidase | − | − | − | − | − | − | − | − | − | − |
| Chymotrypsin | − | − | − | − | − | − | − | − | − | − |
| N-Acetyl-β-glucosaminidase | − | + | + | + | + | + | + | + | + | + |

*Opposite results were reported by Zhou et al. [21].†Opposite results were reported by Yoon et al. [27].
that did not stain positive for phosphate. Hence, it is clear that this alkali-stable lipid is not a sphingophospholipid as reported to be present in members of the neighbouring genus Sphingobacterium [24] or more distantly related genera such as Bacteroides and Prevotella [23] but might show a chemical structure similar to sphingosine and dihydroxyphosphosine, which do not contain phosphate. However, this observation does not conflict with the characteristics of other Pedobacter species, which were reported to contain sphingolypid(s), but none of them was reported to contain a sphingophospholipid. Biomass for the detection of polyamines was harvested from cells grown on R2A agar at 20 °C for 72 h (late exponential growth phase). Extraction and analysis was done as described previously [20, 25, 26]. Strain P4487T contained sym-homospermidine as the major polyamine. Both the presence of a quinone system with MK-7 predominating and the major polyamine sym-homospermidine are in line with the characteristics listed in the description of the family Sphingobacteriaceae [1].

The results obtained in this study demonstrated that strain P4487T represents a novel Pedobacter species for which the name Pedobacter psychrophilus sp. nov. is proposed.

DESCRIPTION OF PEDOBACTER PSYCHROPHILUS SP. NOV.

Pedobacter psychrophilus (psy.cró’phi.lus. Gr. adj. psychros cold; Gr. adj. philos liking, loving; N.L. masc. adj. psychrophilus cold-loving).

Cells are Gram-stain-negative, short rods, occurring predominantly in pairs or in irregular clusters, non-motile and non-spore-forming. Colonies on R2A agar are pink, circular, slightly convex, smooth and glistening with whole margins, and reach about 1 mm in diameter when cultivated at 20 °C for 5 days. Produces carotenoid pigment. Flexirubintype pigments are absent. Aerobic; no anaerobic growth on R2A agar is detected. Aerobic but non-fermenting in the oxidative-fermentative (OF) test. Grows at 5–25 °C. Growth does not occur at 1, 30 or 35 °C. Grows in the presence of up to 2 % (w/v) NaCl and at pH 6–9. Most abundant growth is observed on R2A agar without NaCl, at pH 8.0 and at 20 °C. No fluorescein pigment on King B medium. Grows on plate count agar and R2A agar, but not on tryptone soya agar, brain heart infusion agar, MacConkey agar, Columbia blood agar or nutrient agar. Positive for production of catalase, oxidase (weak), DNase, esterase (C4), esterase lipase (C8) (weak), leucine arylamidase, valine arylamidase, naphthal-AS-BI-phosphohydrolase, β-galactosidase, α-glucosidase, alkaline phosphatase and acid phosphatase. Negative for production of urease, arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase, lipase (C14), cystine arylamidase, tryptsin, chymotrypsin, β-glucuronidase, β-glucosidase, α-galactosidase, N-acetyl-β-glucosaminidase, α-mannosidase, α-fucosidase, nitrate reduction and nitrite reduction. Aesculine, ONPG and starch hydrolysis are positive. Negative for indole production, Simmons citrate, sodium malonate, acetamide and hydrolysis of gelatin, Tween 80, tyrosine, caseine and lecithin (egg-yolk reaction). Acid is produced from xylose and maltose, but not from fructose or mannitol. Sensitive to ampicillin, carbenicillin, cetazidim, cephalothin, ciprofloxacin, gentamicin, chloramphenicol, imipenem, kanamycin, cotrimoxazol, pipercillin, polymyxin B, streptomycin and tetracycline, but resistant to aztreonam and cefixim. Carbon source utilization ability via respiration, determined in Biolog GN2 MicroPlate test panels, is positive for α-cyclodextrin, dextrin, glycerogen, N-acetyl-D-glucosamine, cellobiose, gentiobiose, α-D-glucose, lactose, maltose, melibiose, turanose, α-ketobutyric acid, L-glutamic acid and glycolyl L-glutamic acid but negative for Tween 40, Tween 80, N-acetyl-D-galactosamine, adonitol, L-arabinose D-arabitol, erythritol, D-fructose, L-fucose, D-galactose, myo-inositol, lactulose, D-mannitol, D-mannose, methyl β-D-glucoside, D-psicose, raffinose, L-rhamnose, D-sorbitol, sucrose, trehalose, xylitol, pyruvic acid methyl ester, succinic acid monomethyl ester, acetic acid, cis-aconitic acid, citric acid, formic acid, D-galactonic acid lactone, D-galacturonic acid, D-gluconic acid, D-glucosaminic acid, D-glucuronic acid, α-hydroxybutyric acid, β-hydroxybutyric acid, γ-hydroxybutyric acid, p-hydroxyphenylacetic acid, itaconic acid, α-ketogluutaric acid, α-ketovaleric acid, D-lactic acid, malonic acid, propionic acid, quinic acid, D-saccharic acid, sebacic acid, succinic acid, bromosuccinic acid, succinamic acid, gluturonamide, L-alaninamide, D-alanine, L-alanine, L-alanyl glycine, L-asparagine, L-aspartic acid, glycy L-aspartic acid, L-histidine, hydroxy-L-proline, L-leucine, L-ornithine, L-phenylalanine, L-proline, L-prolylglutamic acid, D-serine, L-serine, L-threonine, D,L-carnitine, γ-aminobutyric acid, urocanic acid, inosine, uridine, thymidine, phenylethylamine, putrescine, 2-aminoethanol, 2,3-butanediol, glycerol, D,L-α-glycerol phosphate, α-D-glucose 1-phosphate and D-glucose 6-phosphate. Contains an alkaline stable lipid lacking a phosphate group, MK-7 as the respiratory quinone, sym-homospermidine as the major polyamine and iso-C15:0, iso-C17:0 3-OH and summed feature 3 (C16:1ω7c/C16:1ω6c) as major cellular fatty acids.

The type strain, P4487T (=CCM 8644T=LMG 29436T), was isolated from fragmentary rock sampled at James Ross Island, Antarctica. The genomic DNA G+C content of the type strain is 46.3 mol%.

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

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