**Ancylobacter sonchi** sp. nov., a novel methylotrophic bacterium from roots of *Sonchus arvensis* L.

Nadezhda V. Agafonova, Elena N. Kaparullina, Yuri A. Trotsenko and Nina V. Doronina

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**Abstract**

An aerobic facultatively methylotrophic bacterium was isolated from roots of *Sonchus arvensis* L. and designated strain Osot\(^T\). The cells of this strain were Gram-stain-negative, asporogenous, motile short rods multiplying by binary fission. They utilized methanol, methylamines and a variety of polycarbon compounds as the carbon and energy sources. Methanol was assimilated after sequential oxidation to formaldehyde and CO\(_2\) via the ribulose bisphosphate pathway. The organism grew optimally at 22–29 °C and pH 7.5–8.0. The dominant phospholipids were phosphatidylethanolamine, phosphatidylincholine, phosphatidylglycerol and diphosphatidylglycerol (cardiolipin). The major cellular fatty acids of strain Osot\(^T\) were C\(_{18:1}\)ω7c (49.0%), C\(_{19:0}\)ω8c cyclo (38.3%) and C\(_{16:0}\) (8.4%). The major ubiquinone was Q-10. The DNA G+C content of strain Osot\(^T\) was 66.1 mol% (\(T_m\)). On the basis of 16S rRNA gene sequence analysis strain Osot\(^T\) is phylogenetically related to the members of genus *Ancylobacter* (97.1–98.8% sequence similarity). Based on 16S rRNA gene sequence analysis and DNA–DNA relatedness (27–29%) with type strains of the genus *Ancylobacter*, the novel isolate is classified as a new species of this genus and named *Ancylobacter sonchi* sp. nov.; the type strain is Osot\(^T\) (=JCM 32039\(^T\)).

In 2005, based on the deep branching observed in 16S rRNA gene sequence phylogenetic analysis, *Xanthobacteraceae* fam. nov. was formed from the family *Hyphomicrobiaceae* [1, and presently, according to the LPSN (http://www.bacterio.net/-classifphyyla.html#xanthobacteraceae), it consists of seven genera: *Xanthobacter* (type genus) [2], *Ancylobacter* [3], *Labrys* [4], *Azorhizobium* [5], *Starkeya* [6], *Pseudolabrys* [7] and *Pseudoxanthobacter* [8]. The members of the genus *Ancylobacter* are chemo-organotrophic bacteria, which occur in several ecological niches, play an important role in oligotrophic methylotrophy and are found mostly in aquatic habitats or river mud and in the several soils. At the time of writing, the genus comprises seven validly published names: *Ancylobacter aquaticus* [3, 9], *A. rudongensis* [10], *A. polymorphus* [11], *A. vacuolatus* [11], *A. oerskovii* [12], *A. dichloromethanicus* [13] and *A. defluvii* [14]. *A. rudongensis* is a facultative methylotroph associated with plants and growing on C\(_1\) compounds. Methanol, formaldehyde, formate, methylated amines, and other C\(_1\) compounds are natural products of plant metabolism [15, 16]. Aerobic methylotrophs actively use these C\(_1\) compounds as growth substrates. It has been shown that the plant phyllosphere is colonized by aerobic methylotrophic bacteria of different taxonomic groups, which are phytohormone synthesizing phytohormones (auxins and cytokinins) and vitamin B\(_{12}\), and also reducing the level of ethylene through the activity of 1-aminoacyclopropane-1-carboxylate desaminase [17, 18]. However, rhizospheric and rhizoplane methylotrophs, in contrast to the phyllospheric ones, have been characterized to a much lesser extent.

Here, we describe a novel species of the genus *Ancylobacter*, *Ancylobacter sonchi* sp. nov., isolated from roots of *Sonchus arvensis* L.

The novel strain was isolated from the root of field sow thistle (*Sonchus arvensis* L.), which was dug out of the soil in the vicinity of Pushchino, Moscow region. The root (1 g) was washed three times with sterile distilled water and placed into an Erlenmeyer flask (750 ml) with 200 ml of sterile medium ‘K’ and 0.5% (v/v) methanol. The ‘K’ medium contained g l\(^{-1}\): KH\(_2\)PO\(_4\) 2.0; (NH\(_4\))\(_2\)SO\(_4\) 2.0; MgSO\(_4\).7H\(_2\)O 0.025; NaCl, 0.5; FeSO\(_4\).7H\(_2\)O, 0.002; pH 7.5. The pH value was adjusted to 7.5 by adding 5 M NaOH. The flask was incubated for 1 week at 28 °C with shaking (180 r.p.m.). In subsequent enrichments, 20 ml of the previous enrichment culture was diluted 1:10 (until the total

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**Keywords:** *Ancylobacter sonchi* sp. nov., facultative methylotroph; ribulose bisphosphate pathway; phytosymbiont.

The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene and maxF gene sequences of the strain Osot are KY492736 and KY496776, respectively.

Three supplementary figures and two supplementary tables are available with the online Supplementary Material.
volume reached 200 ml) with the same medium and was incubated at 28 °C with shaking for 3 days. The enrichment culture suspension was plated onto agarized (2 %; Difco) ‘K’ medium with 0.5 % methanol to obtain single colonies.

Representative species of the genus *Ancylobacter* (A. *defluvii* VKM B, 2789T; A. *dichloromethanicus* VKM B, 2484T; A. *rudongensis* DSM 17131T; A. *aquaticus* DSM 101T; A. *polymorphus* DSM 2457T; A. *vacuolatus* DSM 1277T) were used as the reference strains, as well as the strain *Starkeya novella* IAM 12100T. Cell morphology, Gram staining, motility and flagellation were studied for the new isolate grown on ‘K’ agarized medium.

For electron microscopy, an aliquot of cell suspension was mounted on a Formvar-coated copper grid and stained with 0.2 % (w/v) phosphotungstic acid (pH 7.2). Samples were prefixed with 1.5 % (v/v) glutaraldehyde in 0.05 M cacodylate buffer (pH 7.2). Negatively stained preparations were imaged in a JEOL JEM-100B transmission electron microscope at an operating voltage of 60 kV.

Growth at different temperatures (4–42 °C), pH values (5.0–10.0) and various concentrations of methanol (0.5–5 % v/v) was tested in liquid medium ‘K’. In the case of testing of halotolerance, the strain was grown in liquid mineral medium ‘K’ with various concentrations of NaCl (0–3 %).

Utilization of a wide range of growth substrates was determined after cultivation on liquid ‘K’ medium for 2 weeks with methanol replaced by other carbon compounds (organics acids, sugars, amino acids and alcohols). Carbohydrates, organic acids, amino acids and methylated amines were added at concentrations of 0.05–0.3 % (w/v), while alcohols were added at concentrations of 0.2–0.5 % (v/v). Also API 20E/20NE/50CH strips (bioMérieux) were used according to the manufacturer’s instructions. To test alternative nitrogen sources, (NH₄)₂SO₄ was replaced by other nitrogen compounds (1 %, w/v). Catalase and oxidase activities were determined as described previously [19]. Starch hydrolysis was detected using iodine solution on solid medium ‘K’ containing 0.2 % (w/v) soluble starch after 7 days of incubation. Methane utilization was tested under an atmosphere containing methane and air (1:1, v/v) in flasks (700 ml) containing 100 ml ‘K’ medium and fitted with rubber stoppers. Autotrophic growth with hydrogen as an electron donor was tested by the same procedure but under a H₂/O₂/CO₂ atmosphere (7:2:1, by vol.). Utilization of dichloromethane was tested as described earlier [20]. Vitamin requirements were analysed on a medium containing either thiamin, biotin, folic acid, B₁₂ (50 µg l⁻¹) or a mixture of vitamins (Sigma). The control medium did not contain vitamins. Indole production from 1 mM l-tryptophan was determined on medium ‘K’ in which (NH₄)₂SO₄ was replaced with 0.5 % (w/v) KNO₃ with the Salkowski reagent (0.05 M FeCl₃ in 35 % HClO₄) [21]. The concentration of auxins was determined from the calibration curve constructed using standard indole-3-acetic acid (Sigma) solutions. Analysis of the strain OsotT culture liquid showed that it was able to synthesize indole derivatives at a concentration of 6–9.5 µg ml⁻¹ (OD₆₀₀ of the culture, 1.0).

Sensitivity to antibiotics was examined by placing Difco discs on cells spread on ‘K’ agar plates. The discs contained the following antibiotics (µg): gentamicin (10), neomycin (30), streptomycin (10), ampicillin (10), nalidixic acid (30), lincomycin (2), novobiocin (5), erythromycin (15), penicillin (10), chloramphenicol (30), oxacillin (5), tetracycline (30) and kanamycin (30). The effect of antibiotics on cell growth was assessed after 3 days at 28 °C.

The phosphate-solubilizing activity of strain OsotT was determined in modified medium ‘K’ with insoluble Ca₃(PO₄)₂ (5 g l⁻¹) as the sole phosphorus source as described previously [22]. Insoluble phosphates were solubilized: up to 167.3±6.4 µM phosphorus ions was released in the experiment with Ca₃(PO₄)₂.

The ability to synthesize siderophores was revealed by the universal chemical method on agar medium ‘K’ (without FeCl₃) with Chrome Azurol S (CAS; Sigma Aldrich) [23]. The culture liquid of the strain OsotT was tested for catechol-type siderophores by the method according to Arnow [24].

Cells of the newly isolated strain were Gram-stain-negative, asporogenous, motile oval rods 0.4–0.5 × 1.6–1.8 µm (Fig. 1). Reproduction occurred by binary fission. When grown on solid medium ‘K’ with methanol, colonies were 2 mm in diameter after 3–5 days of growth at 28 °C, opaque, shiny and white, with a convex shape and smooth surface. On R2A agar after 3 days of growth at 28 °C colonies were 1 mm in diameter, translucent, glossy and yellow, with a convex shape.

Strain OsotT was positive for oxidase, catalase, urease, arginine dehydrolase, β-glycosidase, β-galactosidase and

![Image](https://www.microbiologyresearch.org)
acetoain production. It utilized methanol and primary methylated amines (methylamine, dimethylamine, trimethylamine) as growth substrates. Growth occurred on trypticase soy agar (TSA), Luria–Bertani medium, nutrient medium (Difco), glucose, arabinose, mannose, mannitol, potassium gluconate, inositol, sorbitol, sucrose, melibiose, l-rhamnose, acetate, glutamate, succinate, fumarate, xylose, lactose, fructose, galactose, D-gluconic acid, pyruvate and acetamide and in an atmosphere of H₂/O₂/CO₂. H₂S was not produced and gelatin was not liquefied. No growth occurred on dichloromethane or CH₄/O₂ gas mixtures as carbon and energy sources. Ammonia and nitrate were used as the nitrogen sources. Nitrate was not reduced to nitrite.

Growth occurred at temperatures between 10 and 30 °C; the optimum growth temperature was 22–29 °C. Robust growth of the strain was observed in the pH range 6.0–9.0, and optimal growth was observed at pH 7.5 and 8.0. No growth was observed at pH 5.0 and 9.5. Growth was completely inhibited in the presence of NaCl at concentrations above 0.5% (w/v).

Enzyme assays of primary and intermediary pathways of C₁ metabolism essential for taxonomy of methylotrophic bacteria were done as described by Trotsenko et al. [25]. Protein was assayed by the standard Lowry method. Enzyme activities were expressed as nanomoles of transformed substrate, or the product formed, per minute per milligram of protein.

The enzymic profile of methanol-grown cells indicated that strain Osot T oxidized methanol to formaldehyde by classical pyrroloquinoline quinone (PQQ)-linked methanol dehydrogenase (Table S1, available with the online Supplementary Material). NAD⁺-dependent formaldehyde dehydrogenase stimulated by GSH was observed. Also, NAD⁺-linked formate dehydrogenase was detected in the strain. Having ribulose-1,5-bisphosphate carboxylase activity, strain Osot T employs the RuBP pathway for C₅ assimilation. Glucose-6-phosphate and 6-phosphogluconic dehydrogenases were active with NADP⁺. Activity of fructose-1,6-bisphosphate aldolase was found but not KDPG (2-keto-3-deoxy-6-phosphogluconate) aldolase. The tricarboxylic acid cycle was complete as shown by activity of α-ketoglutarate dehydrogenase. Primary ammonia assimilation occurred by means of glutamate dehydrogenase.

Cells of strain Osot T and the reference type strains for chemotaxonomic experiments were harvested from R2A agar at 28 °C after 48 h incubation. Fatty acid extraction from 40–60 mg cells was carried out by the use of whole biomass acid methanalysis in 0.4 ml 1.2 N HCl in methanol by heating to 80 °C for 1 h. Resulting fatty acid methyl esters were extracted twice with 0.2 ml hexane and processed on an Agilent Technologies AT-5850/5973 GC-MS system with a cross-linked methyl silicone capillary column (HP-5ms). The oven temperature was programmed from 140 to 320 °C in increments of 7 °C min⁻¹. Between 1 and 2 µl of derivatized sample was injected into the gas chromatograph at 280 °C. Fatty acids and other lipid components were ionized by electron impact at 70 eV after separation in the GC column and analysed in scan mode. The quadrupole mass spectrometer had a resolution of 0.5 mass units over the whole mass range of 2-950 amu. The sensitivity of the GC-MS system was 0.01 ng of methyl stearate. Each substance was confirmed by its mass spectrum and NIST 14 (http://nistmassspectrumently.com/) mass spectral database library search. Ubiquinones were extracted and purified as described previously [26]. Their analysis was done by using a Finnigan MX-1310 GS-MS system. The cellular fatty acid profile of strain Osot T is shown in Table S2. The obtained data indicate a considerable similarity in the fatty acid composition of our strain and the type cultures of the genus Ancylobacter. The major ubiquinone was Q-10, which is in accordance with the grouping of strain Osot T within the genus Ancylobacter [27].

Polar lipids were extracted from 500 mg cell biomass (exponentially grown cells) with chloroform/methanol (1:2, v/v) by stirring for 1 h in an ice bath, followed by centrifugation at 5000 g for 20 min; two phases separated during this period. The extraction procedure was performed twice and the upper phase was collected and combined. Then, 2 ml chloroform and 2 ml distilled water were added to the supernatant and the resulting mixture was subjected to careful shaking for 15 min in an ice bath. The mixture was then centrifuged and three phases separated. The lowest phase with polar lipids was withdrawn, evaporated at 30 °C and dissolved in 200 µl chloroform. Polar lipids were separated by two-dimensional TLC (Kieselgel 60, 10×10 cm; Merck) by using chloroform/methanol/water (65:25:4, by vol.) in the first direction, followed by chloroform/methanol/acetic acid/water (85:12:15:4, by vol.) in the second direction. Plates were sprayed with various specific reagents for detection of different polar lipids [28]. Phospholipid standards from Sigma were used during comparative analysis. Analysis of the cellular phospholipids of our isolate revealed the presence of phosphatidylethanolamine, phosphatidylcholine, phosphatidylglycerol, diphosphatidylglycerol (cardiolipin) and two unknown phospholipids (Fig. S1).

DNA was isolated and purified as described previously [29]. 16S rRNA gene sequencing was carried out using previously published primers [30]. The PCR-product of the 16S rRNA gene was purified using the Zymoclean Gel DNA Recovery kit (Zymo Research). The 16S rRNA gene sequencing was carried out using the BigDye Terminator v. 3.1 reaction kit followed by the analysis of reaction products in an automated sequencer (3730 DNA Analyzer; Applied Biosystems). Preliminary screening for similarity was done with the BLAST tool (http://www.ncbi.nlm.nih.gov/blast). The 16S rRNA gene sequence of strain Osot T was aligned against those of closely related strains obtained from recent GenBank releases using the CLUSTALW software [31]. Positions of the sequence uncertainties were omitted and a total of 1392 nucleotides were used in the analysis. Phylogenetic trees were reconstructed by maximum parsimony, minimum
The 16S rRNA gene sequence analysis revealed that strain OsotT belonged to the genus *Ancylobacter* and shared the highest pairwise similarity values with *A. rudongensis* AS 1.1761T (98.1 %), *A. defluvii* SK15T (99.0 %) and effectively published but not validated 'Ancylobacter abiegnus' Z-0056 (99.0 %) [33]. On the other hand 'A. abiegnus' Z-0056 showed a high level of 16S rRNA similarity to *A. defluvii* SK15T (99.3 %). The neighbour-joining phylogenetic tree based on 16S rRNA gene sequences showed that the isolate formed a branch with the type strains of genus *Ancylobacter* (Fig. 2). This branching pattern was also supported by the trees reconstructed with various methods (maximum parsimony, maximum likelihood, minimum evolution) implemented in the MEGA5 program.

The mxaF gene encodes the large subunit of the classical pyrroloquinoline quinone (PQQ)-linked methanol dehydrogenase, which catalyses the oxidation of methanol to formaldehyde in the majority of extant Gram-negative methylo trophic bacteria [34]. Using primers f1003 and r1561 and the protocol [35], we were able to amplify an approximately 505 bp mxaF gene fragment from DNA. The mxaF gene amplicon was purified using the Zymoclean Gel DNA Recovery kit (Zymo Research) and it was sequenced as described above. Processing and translation of nucleotide sequence to the amino acid sequence was performed using Gene Runner (version 3.05) (Hastings Software). Then the determined MxaF sequence was aligned using the CLUSTALW software. Trees based on MxaF amino acid sequences showing the phylogenetic position of the new strain OsotT among methylotrophic bacteria were reconstructed by using the maximum likelihood and neighbour-joining methods using the software package MEGA5 [32]. Comparative analysis of amino acid sequences of MxaF protein confirmed these data, showing high levels of similarity between strain OsotT and other *Ancylobacter* species (89.0–92.9 %) (Fig. S2).

For genotypic differences between strain OsotT and the members of the genera *Ancylobacter* and *Starkeya* the RAPD (random amplified polymorphic DNA) fingerprinting technique was performed using 10-base primers OPQ1 and OPQ6, which had been selected from among seven different primers (OPQ1, OPQ2, OPQ6, OPQ10, OPM3, OPM7, OPM10) as described previously [36]. Results of RAPD analysis demonstrated that strain OsotT has a different DNA fingerprint pattern, indicating that it represents a separate species of the genus *Ancylobacter*. Moreover, our strain OsotT exhibited a banding pattern clearly different from that of *S. novella* IAM 12100T (Fig. S3).

The DNA G+C content was determined by thermal denaturation (Tm) as described previously [37]. DNA–DNA hybridization experiments were performed as described previously [38]. The DNA–DNA relatedness of strain OsotT with *A. rudongensis* AS 1.1761T and *A. defluvii* SK15T was 29 and 27 %, respectively. These results have confirmed that strain OsotT does not belong to the genospecies *A. rudongensis* or *A. defluvii*. The DNA G+C content of the novel strain OsotT was 66.1 mol% (Tm).

![Phylogenetic position of the strain OsotT based on the results of comparative analysis of the 16S rRNA gene sequences. The scale corresponds to 2 nucleotide substitutions per 100 nucleotides (evolutionary distances). Phylogenetic analysis was performed with MEGA5 [32]. The maximum likelihood method was used. The root was determined by including the sequence of Escherichia coli O157:H7 (AY513502) as an outgroup.](image-url)
Based on the above results, we concluded that the new isolate represents a separate novel species, for which the name *Ancylobacter sonchi* sp. nov. is proposed.

Characteristics of the type cultures of the genus *Ancylobacter* are summarized in Table 1. Most members of the genus *Ancylobacter* were isolated from water and soil samples, and only *A. rudongensis* was isolated from the rhizosphere. Our isolate uses plant metabolites and, in its turn, synthesizes auxins (indole derivatives) and siderophores, and therefore can positively influence plant growth, i.e. it is a phytosymbiont.

### DESCRIPTION OF *ANCYLOBACTER SONCHI* SP. NOV.

*Ancylobacter sonchi* (son’chi. L. gen. n. sonchi of the plant *Sonchus arvensis*, the source of the rhizosphere from which the type strain was isolated). Gram-negative, motile, asporogenous oval rods that are 0.4–0.5×0.6–1.0 µm in size. Multiplies by binary fission. Colonies on mineral salts/methanol agar are white, opaque, shiny, with a convex shape and smooth surface, 2 mm in diameter after 3–5 days of growth at 28°C. Colonies on R2A agar after 3 days of growth at 28°C are 1 mm in diameter, translucent, glossy, and yellow with a convex shape.

Strictly aerobic, catalase-, oxidase- and urease-positive. Growth occurs at pH 6.0–9.0 and in a temperature range of 10–30°C. Optimal growth at 22–29°C and pH 7.5–8.0 with 0.05% (w/v) NaCl. No growth occurs in liquid mineral medium 'K' in the presence 0.5% (w/v) NaCl. Autotrophic growth occurs on mineral salts medium with a gas mixture of H₂/O₂/CO₂ but not on methane or dichloromethane. Nitrate is not reduced to nitrite. Produces indole from tryptophan on medium with nitrate as a nitrogen source. Acetoin is produced. Synthesizes catechol-type siderophores; solubilizes insoluble phosphates. H₂S is not produced and gelatin is not liquefied. No vitamins or other growth factors are required. Facultative methylotroph that utilizes methanol, methylated amines and a variety of polycarbon compounds. Assimilates C₁ compounds via the RuBP pathway. Ammonia is assimilated by glutamate dehydrogenase.

Table 1. Some differential characteristics of the *Ancylobacter* species

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Nitrates and ammonium salts serve as nitrogen sources. The major fatty acids are C₁₈:1ω7c, cyclo and C₁₆:0. The major ubiquinone is Q-10. The predominant phospholipids are phosphatidylethanolamine, phosphatidylglycerol, phosphatidylcholine and diphosphatidylglycerol (cardiolipins). Strain Osot³ is resistant to neomycin, nalidixic acid, penicillin, chloramphenicol, oxacillin and lincomycin, but sensitive to ampicillin, erythromycin, gentamicin, novobiocin, tetracycline, streptomycin and kanamycin. DNA G+C content is 66.1 mol% (Tm). The type strain Ancylobacter sonchi (=VKM B-3145 =JCM 32039) was isolated from field sow thistle (Sonchus arvensis L.) at Pushchino, Moscow region (Russia).

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

References


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