A pink-pigmented, facultatively methylotrophic bacterium, designated strain JT1T, was isolated from a thallus of the liverwort Marchantia polymorpha L. and was analysed by using a polyphasic approach. Comparative 16S rRNA gene sequence analysis placed the strain in a clade with Methylobacterium adhaesivum AR27T, Methylobacterium fujisawaense DSM 5686T, Methylobacterium radiotolerans JCM 2831T and Methylobacterium jeotgali S2R03-9T, with which it showed sequence similarities of 97.8, 97.7, 97.2 and 97.4 %, respectively. However, levels of DNA–DNA relatedness between strain JT1T and these and the type strains of other closely related species were lower than 70 %. Cells of JT1T stained Gram-negative and were motile, rod-shaped and characterized by numerous fimbriae-like appendages on the outer surface of their wall (density up to 200 μm−2). Major fatty acids were C18:1ω7c and C16:0. Based on the morphological, physiological and biochemical data presented, strain JT1T is considered to represent a novel species of the genus Methylobacterium, for which the name Methylobacterium marchantiae sp. nov. is proposed. The type strain is JT1T (=DSM 21328T = CCUG 56108T).

Micro-organisms of the genus Methylobacterium are known to inhabit the surfaces of stems, leaves, flowers and roots of various lower and higher plants (bryophytes, ferns, gymnosperms and angiosperms) (Holland, 1997; Lindow & Brandl, 2003; Kutschera, 2007; Schauer & Kutschera, 2008; Delmotte et al., 2009). These common prokaryotic epiphytes are classified within the Alphaproteobacteria and are capable of growing on C1 compounds, such as methanol, as well as on many other organic substrates (Green, 2006). Owing to their characteristic pink pigmentation, which is caused by the presence of carotenoids, these plant-associated bacteria are also referred to as pink-pigmented facultative methylotrophs. Note, however, that the type strains of Methylobacterium nodulans and Methylobacterium jootgali are unpigmented.

A number of studies have shown that methylotrophic bacteria consume methanol that is released as a by-product of cell-wall metabolism in rapidly growing plant organs and is emitted via the stomatal pores of the epidermis (Nemecek-Marshall et al., 1995; Hüve et al., 2007). As epiphytic methylotrophic bacteria produce and secrete growth-promoting hormones such as auxins (Ivanova et al., 2001) and cytokinins (Ivanova et al., 2000; Koenig et al., 2002), these methanol-consuming microbes have been described as phytosymbionts of lower plants such as liverworts and mosses (Kutschera & Koopmann, 2005; Hornschuh et al., 2002, 2006; Kutschera, 2007).

At the time of writing, the genus Methylobacterium comprised 34 recognized species (http://www.bacterio.cict.fr/m/methylobacterium.html). The type species of the genus, Methylobacterium organophilium, was isolated as a facultative methanotroph by Patt et al. (1974, 1976). However, the type strain of this species later lost the ability to assimilate methane (Green & Bousfield, 1983). Kato et al. (2008) proposed emended descriptions of Methylobacterium extorquens and Methylobacterium rhodesianum, with the effect of reclassifying strains of Methylobacterium chloromethanicum and Methylobacterium dichloromethanicum to M. extorquens and strains of Methylobacterium lusitanum to M. rhodesianum. In addition, ‘Methylobacterium goessingense’ (Idris et al., 2006) and ‘Methylobacterium dankookense’ (Lee et al., 2009) have been described, but their names have not been validly published.
In October 2003, we collected fragments of the common liverwort Marchantia polymorpha L. along moist areas of a stream in the mountains around Kassel, Germany (Bergpark Wilhelmshöhe, about 500 m above sea level, 51° 19’ N 9° 24’ E), with the aim of isolating epiphytic, pink-pigmented, facultatively methylotrophic bacteria and analysing their growth-promoting effect on sterile fragments of lower plants (Kutscher et al., 2007). The liverwort samples were stored under aseptic conditions and analysed in the laboratory. Following isolation of a number of strains, we focused our attention on a pink-pigmented isolate designated in our laboratory as strain JT1T. When maintained in liquid medium supplemented with methanol, the organism formed clusters of several hundred cells (Kutscher et al., 2007). This ‘crowding-effect’ was not detected in control populations of Methylobacterium mesophilicum DSM 1708T (Austin & Goodfellow, 1979; Green & Bousfield, 1983).

Based on cytological, biochemical, physiological and molecular data, as well as diagnostic phenotypic features, we suggest that strain JT1T represents a novel Methylobacterium species.

Cellular morphology and motility were determined microscopically (Photomikroskop III; Carl Zeiss) with cells grown to exponential phase in R2A broth. Flagellation was analysed according to the method of Heimbrook et al. (1989). Motility was also tested on 1/10-strength R2A broth supplemented with 0.2 % agar (Weon et al., 2008).

For scanning electron microscopy, bacterial strains were maintained for several days in glycerol-peptone (GP) broth under agitation (150 r.p.m.). In the next step, samples were incubated for 12 h on sterile acetone-cleaned coverslips. Fixation for electron microscopy was as described by Hornschuh et al. (2002).

Gram-staining was performed with a commercial kit (Sigma Diagnostics). Hydrolysis of CM-cellulose and starch was assayed on R2A agar medium by using standard protocols. Staining of sudanophilic inclusions was performed according to the method of Burdon (1946), by using cells from stationary-phase cultures in mineral salts broth supplemented with 5 mM succinate. Production of catalase and oxidase was assayed with ID Colour Catalase and Oxidase Reagent, respectively (both from bioMérieux), according to the manufacturer’s instructions. Indole formation, hydrolysis of gelatin and production of urease, β-galactosidase and β-glucosidase were determined with API 20 NE test strips (bioMérieux). Because of the slow growth of Methylobacterium strains, the results were recorded after 7 days of incubation.

For various physiological tests, bacteria were grown in the minimal salts medium developed by Choi et al. (1989) with 20 ml medium in 100 ml glass beakers maintained at room temperature under constant agitation at 150 r.p.m., according to the protocol of Green & Bousfield (1982). Utilization of different nitrogen sources was determined in the same way, with succinate (5 mM) as carbon source.

Growth in R2A broth at 4, 10, 25, 28, 30, 32, 35 and 37 °C and initial pH 4.0, 5.0, 6.0, 7.0, 7.2, 8.0 and 10.0 was monitored for 14 and 3 days, respectively, by measuring the OD600 with a Uvikon 931 spectrophotometer (Kontron Instruments). Salt tolerance was assayed in R2A broth supplemented with 0, 0.5, 1.0, 2.0, 3.0 and 4.0 % (w/v) NaCl over a period of 3 days.

Pigments were extracted with 80 % (v/v) methanol. The resulting suspension was centrifuged for 5 min at 14 000 r.p.m. to remove the insoluble cell debris. Thereafter, the supernatant was examined at wavelengths of 300–900 nm against 80 % methanol as a reference.

Genomic DNA for sequencing of the 16S rRNA gene and the gene encoding the β-subunit of methanol dehydrogenase (mxaF) was extracted by using a commercially available kit (DNeasy Blood & Tissue kit; Qiagen) according to the manufacturer’s instructions for Gram-positive bacteria. A nearly full-length 16S rRNA gene sequence (1421 nt) was amplified with the universal eubacterial 16S rRNA gene primers FGS6 and FGS1509 (Sy et al., 2001). A partial sequence (516 nt) of the mxaF gene was amplified by using primers 1003f and 1561r (McDonald et al., 1995).

PCR amplification was performed with a Biometra T-Gradient 96 thermocycler in a total volume of 40 μl reaction mixture containing approximately 50 ng genomic DNA, each dNTP (0.2 mM), primers (0.4 μM each), 0.5 U Taq DNA polymerase (Qiagen) and the buffer supplied with the enzyme (containing 1.5 mM MgCl2). PCRs consisted of 30 cycles (30 s at 92 °C, 30 s annealing at 58 °C and 60 s at 72 °C) with an initial denaturation of 5 min at 94 °C and a final elongation step of 5 min at 72 °C. PCR products were purified with the QIAquick PCR purification system (Qiagen) and were sequenced directly with the ABI Prism Dye Terminator sequence kit (Applied Biosystems). Sequencing products were purified with a purification kit and analysed on an Applied Biosystems model 310 DNA sequencer. Results were compared with available sequences from GenBank by using the program BLAST (http://blast.ncbi.nlm.nih.gov/Blast.cgi) to determine an approximate phylogenetic affiliation, and sequences were aligned by using BioEdit version 7.0.9.0 (Hall, 1999) and the CLUSTAL W program (Thompson et al., 1994).

Levels of gene sequence similarity were calculated by determining the evolutionary divergence (p-distance) of the aligned sequences in MEGA4 (Tamura et al., 2007), by using the pairwise deletion option.

Phylogenetic trees were constructed by the neighbour-joining method (Saitou & Nei, 1987) with the program package MEGA4 (Tamura et al., 2007). Evolutionary distances were computed by using the Jukes–Cantor method (Jukes & Cantor, 1969). All positions containing alignment gaps were eliminated from the dataset. A bootstrap confidence analysis was performed on 10 000 replicates to determine the reliability of the tree topology obtained (Felsenstein, 1985). Additional phylogenetic trees
were constructed by using the maximum-parsimony and maximum-likelihood methods, with similar results.

DNA–DNA hybridization experiments were performed by using two different methods. In the first approach, genomic DNA was isolated according to the method of Pitcher et al. (1989) and DNA–DNA hybridization was performed according to Ziemke et al. (1998) with a hybridization temperature of 73.4 °C. A second series of experiments was performed at the DSMZ. Genomic DNA was isolated by using a French pressure cell (Thermo Spectronic) and purification was by chromatography on hydroxyapatite as described by Cashion et al. (1977). DNA–DNA hybridization was carried out as described by De Ley et al. (1970), taking into account the modifications described by Huß et al. (1983), by using a model Cary 100 Bio UV/Vis spectrophotometer equipped with a Peltier-thermostatted 6 × 6 multicell changer and a temperature controller with in situ temperature probe (Varian).

Whole-cell fatty acid analysis was carried out by using the MIDI protocol as described by Kämpfer & Kroppenstedt (1996), except that cells were grown on trypticase soy agar at 28 °C prior to fatty acid extraction.

Cells of strain JT1T were Gram-negative, aerobic, motile rods (1.0–1.3 × 1.9–3.9 μm) that occurred singly or in pairs (in R2A broth grown for 48 h at 28 °C), but formed large aggregates (rosettes) when incubated in mineral salts medium supplemented with methanol (1.0 %) as sole carbon and energy source. Note that the deposited type strain lost this ability during cultivation on R2A agar plates, but the laboratory strain maintained at the University of Kassel still displays this behaviour. The cell surface of strain JT1T was covered with numerous appendages that were up to 300 nm long and 25–40 nm wide, usually described as fimbriae (Ottow, 1975). The density of these structures reached 200 μm–² (Fig. 1). Sudanophilic inclusions were detected. Cells were motile by means of a single polar flagellum in exponentially growing R2A broth cultures, but were non-motile on semi-solid 1/10-strength R2A supplemented with 0.2 % agar. Colonies of strain JT1T were circular, smooth, shiny, red and 1.0–2.0 mm in diameter when grown on R2A agar for at least 7 days (see Supplementary Fig. S1 in IJSEM Online).

Strain JT1T was able to grow on R2A agar, nutrient agar (NA), GP agar or mineral salts medium supplemented with methanol (0.1–1 %, v/v). The optimum pH for growth in R2A broth was pH 7.2, but growth occurred from pH 6.0 to 9.0. The optimum temperature range was 25–30 °C, but cell growth was recorded from 4 to 32 °C. In the presence of 0.5 % NaCl, the growth rate of the cells was inhibited by approximately 50 %. No growth occurred in the presence of 2.0 % NaCl or higher salt concentrations. Catalase, urease and oxidase activities were present. Pigments extracted with methanol showed absorption peaks at 465, 490 and 520 nm. In addition, a peak at 360 nm was detected for methanolic cell extracts. In some cultures, a peak at 770 nm, which is indicative for bacteriochlorophyll a (Sato, 1978; Yurkov & Beatty, 1998), was found. Other morphological and physiological features of strain JT1T are summarized in the species description, and selective characteristics are compared with those of related type strains in Table 1. Strain JT1T could be distinguished from its closest phylogenetic relatives based on the utilization of tartrate, the presence of numerous cell appendages and the (non-)motility on semi-solid 1/10-strength R2A agar. The predominant fatty acids were C18:1ω7c, C16:0 and C18:0, as is typical for members of the genus Methylobacterium (Table 2).

Fig. 1. Scanning electron micrographs that document the phenotypic variability of single cells of strain JT1T. The bacteria were attached to a glass plate before the samples were prepared for microscopy. Bars, 1 μm.
A nearly full-length 16S rRNA gene sequence (1421 nt) for strain JT1T and partial mxaF gene sequences for strain JT1T and the type strains of related species (516 nt) were ascertained. Levels of 16S rRNA gene sequence similarity between strain JT1T and the type strains of all recognized Methylobacterium species were in the range 94.1–97.9 %; its closest phylogenetic relative was ‘M. goesingense’ iEII3 (97.9 % sequence similarity). Its closest recognized relative was Methylobacterium adhaesivum AR27T (97.8 % sequence similarity). Other type strains showing more than 97 % 16S rRNA gene sequence similarity were Methylobacterium fujisawaense DSM 5686T (97.7 %), M. jeotgali S2R03-9T (97.4 %), M. oryzae CBMB20T (97.3 %), M. tardum RB677T (97.3 %) and M. radiotolerans DSM 1819T.

### Table 1. Differential phenotypic characteristics between strain JT1T and the type strains of species of the genus Methylobacterium

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cells occur:</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>In pairs</td>
<td>Rarely</td>
<td>Rarely</td>
<td>Rarely</td>
<td>Rarely</td>
<td>Rarely</td>
<td>+</td>
<td>Rarely</td>
<td>Rarely</td>
</tr>
<tr>
<td>As aggregates/rosettes</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>Rarely</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Cell length (μm)</td>
<td>1.9–3.9</td>
<td>1.6–4.0</td>
<td>1.3–3.2</td>
<td>1.8–3.8</td>
<td>1.8–3.5</td>
<td>2.1–2.8</td>
<td>2.0–5.1</td>
<td>1.9–3.4</td>
</tr>
<tr>
<td>Cell width (μm)</td>
<td>1.0–1.3</td>
<td>1.1–1.5</td>
<td>1.0–1.4</td>
<td>1.0–1.6</td>
<td>0.8–1.2</td>
<td>0.6–0.8</td>
<td>1.3–2.1</td>
<td>1.0–1.4</td>
</tr>
<tr>
<td>Fimbriae</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>ND</td>
<td>–</td>
</tr>
<tr>
<td>Motility on semi-solid agar</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>ND</td>
<td>–</td>
<td>ND</td>
</tr>
<tr>
<td>Oxidase</td>
<td>w</td>
<td>w</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<tr>
<td>Urease</td>
<td>w</td>
<td>w</td>
<td>+</td>
<td>+</td>
<td>w</td>
<td>–</td>
<td>ND</td>
<td>+</td>
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<tr>
<td>Growth on:</td>
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<tr>
<td>D-Glucose</td>
<td>–</td>
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<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>D-Xylose</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>L-Arabinose</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>–</td>
<td>W</td>
</tr>
<tr>
<td>D-Fructose</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Citrate</td>
<td>w</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Acetate</td>
<td>+</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>+</td>
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<tr>
<td>Betaine</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Tartrate</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>ND</td>
<td>–</td>
</tr>
</tbody>
</table>

A nearly full-length 16S rRNA gene sequence (1421 nt) for strain JT1T and partial mxaF gene sequences for strain JT1T and the type strains of related species (516 nt) were ascertained. Levels of 16S rRNA gene sequence similarity between strain JT1T and the type strains of all recognized Methylobacterium species were in the range 94.1–97.9 %; its closest phylogenetic relative was ‘M. goesingense’ iEII3 (97.9 % sequence similarity). Its closest recognized relative was Methylobacterium adhaesivum AR27T (97.8 % sequence similarity). Other type strains showing more than 97 % 16S rRNA gene sequence similarity were Methylobacterium fujisawaense DSM 5686T (97.7 %), M. jeotgali S2R03-9T (97.4 %), M. oryzae CBMB20T (97.3 %), M. tardum RB677T (97.3 %) and M. radiotolerans DSM 1819T.

### Table 2. Major fatty acids of strain JT1T and the type strains of related species of the genus Methylobacterium

<table>
<thead>
<tr>
<th>Fatty acid</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
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<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
</tr>
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<tbody>
<tr>
<td>Saturated</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C16:0</td>
<td>2.6</td>
<td>5.5</td>
<td>3.4</td>
<td>4.7</td>
<td>4.5</td>
<td>3.0</td>
<td>–</td>
<td>4.8</td>
<td>5.5</td>
</tr>
<tr>
<td>C17:0</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.6</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>C18:0</td>
<td>2.3</td>
<td>2.9</td>
<td>2.4</td>
<td>5.8</td>
<td>7.1</td>
<td>4.6</td>
<td>11.8</td>
<td>5.4</td>
<td>4.6</td>
</tr>
<tr>
<td>Unsaturated</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>C17:1ω7c</td>
<td>2.9</td>
<td>0.9</td>
<td>–</td>
<td>0.5</td>
<td>1.7</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1.7</td>
</tr>
<tr>
<td>C18:1ω7c</td>
<td>83.5</td>
<td>83.5</td>
<td>86.8</td>
<td>85.5</td>
<td>83.4</td>
<td>88.2</td>
<td>77.9</td>
<td>88.4</td>
<td>86.2</td>
</tr>
<tr>
<td>Summed feature 3*</td>
<td>8.7</td>
<td>4.7</td>
<td>6.5</td>
<td>1.8</td>
<td>3.2</td>
<td>1.8</td>
<td>–</td>
<td>1.5</td>
<td>2.0</td>
</tr>
<tr>
<td>Unknown ECL</td>
<td>14.959†</td>
<td>–</td>
<td>1.3</td>
<td>–</td>
<td>0.5</td>
<td>–</td>
<td>0.4</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

*Summed features are groups of two or three fatty acids that cannot be separated by GLC with the MIDI system. Summed feature 3 comprised C16:1ω7c and/or iso-C15:0 2-OH.
†Unknown fatty acids have no name listed in the peak library file of the MIDI system and therefore cannot be identified. ECL, Equivalent chain length.
(97.2%). Levels of mxaF gene sequence similarity between strain JT1<sup>T</sup> and the type strains of recognized Methylobacterium species were in the range 89.2–94.8% (M. adhaesivum DSM 17169<sup>T</sup> was its closest relative). Phylogenetic analysis revealed that JT1<sup>T</sup> is a member of the genus Methylobacterium related most closely to ‘M. goesingense’ iEII3 and M. adhaesivum AR27<sup>T</sup> (Fig. 2 and Supplementary Fig. S2).

DNA–DNA hybridization experiments to confirm the species status of the novel isolate revealed relatedness levels of <70% to its closest phylogenetic neighbours. Strain JT1<sup>T</sup> displayed the following levels of DNA–DNA relatedness to members of the genus Methylobacterium: ‘M. goesingense’ iEII3, 54.4%; M. jeotgalii S2R03–9<sup>T</sup>, 30.4% (reciprocal 12.9%); M. fujisawaense DSM 5686<sup>T</sup>, 40.2% (32.0%); M. adhaesivum DSM 17169<sup>T</sup>, 46.2%; M. radiotolerans DSM 1819<sup>T</sup>, 24.0% (41.4%); M. mesophilicum DSM 1708<sup>T</sup>, 33.2% (48.1%). Some of the DNA–DNA hybridization experiments resulted in very high values, which were interpreted as artefacts due to insufficient purification of bacterial DNA. For this reason, additional DNA–DNA hybridization experiments were carried out with strain JT1<sup>T</sup> and ‘M. goesingense’ iEII3 and M. adhaesivum DSM 17169<sup>T</sup>, by using the method established at the DSMZ. Strain JT1<sup>T</sup> showed relatively low levels of DNA–DNA relatedness to ‘M. goesingense’ iEII3 (13.7%, reciprocal 17.9%) and M. adhaesivum DSM 17169<sup>T</sup> (14.7%, reciprocal 16.9%), indicating that strain JT1<sup>T</sup> represents a novel species.

M. oryzae CBMB20<sup>T</sup> and M. tardum RB677<sup>T</sup>, strains that shared >97% 16S rRNA gene sequence similarity with strain JT1<sup>T</sup> but were not included in our DNA–DNA hybridization experiments, could be differentiated clearly from strain JT1<sup>T</sup> based on utilization of L-arabinose and their inability to grow on media that contain tartrate or D-fructose as sole carbon source.

On the basis of the data summarized above, strain JT1<sup>T</sup> could be differentiated clearly from its closest relatives based on several morphological, physiological and biochemical characteristics. Therefore, strain JT1<sup>T</sup> is considered to represent a novel species of the genus Methylobacterium, for which we propose the name Methylobacterium marchantiae sp. nov.

**Description of Methylobacterium marchantiae sp. nov.**

Methylobacterium marchantiae (mar.chan’ti.ae. N.L. gen. n. marchantiae of Marchantia, referring to the isolation of the type strain from a free-living thallus of the liverwort *Marchantia polymorpha* L.).

Cells are aerobic, Gram-stain-negative rods, 1.0–1.3 μm in diameter and 1.9–3.9 μm long, that are motile by means of a single polar flagellum. Cells are non-motile on semi-solid 1/10-strength R2A agar. Cells occur singly or in pairs in exponentially growing R2A broth cultures. Grows slowly, with a growth rate (μ) of approximately 0.1 h<sup>−1</sup>. Growth occurs on R2A agar, NA, GP agar, peptone-yeast-extract-glucose agar, plate count agar and mineral salts agar supplemented with 0.1–1.0% (v/v) methanol. Colonies are red, smooth, shiny, circular and convex with entire margins and a diameter of 1.0–2.0 mm on R2A agar after 7 days of incubation at 28 °C. Pigments are water-insoluble and have absorption maxima in 80% (v/v) methanol at 360, 465, 490, 520 and 770 nm. Positive for oxidase, catalase and urease. Growth occurs at 4–32 °C (optimum 25–30 °C) and at pH 6.0–9.0 (optimum pH 7.2). Does not grow in the presence of 2% NaCl or higher salt concentrations. Cells do not hydrolyse gelatin, CM-cellulose or starch. Sudanophilic inclusions are produced. Negative for indole production, β-glucosidase and β-galactosidase. Utilizes methanol, ethanol, acetate, citrate, glycerol, D-fructose, tartrate, succinate, formate, L-aspartate, L-glutamate and L-glutamate as sole carbon sources and is therefore chemo-organotrophic and facultatively methylotrophic. Does not utilize D-glucose, D-xylose, L-arabinose, mannose, sucrose or betaine as sole carbon sources. Potassium nitrate, ammonium sulphate, ammonium chloride, L-aspartate and L-glutamate are utilized as...
sole nitrogen sources. Major fatty acids are C\textsubscript{18}:1\textomega7c, C\textsubscript{16}:0 and C\textsubscript{18}:0.

The type strain, JTI\textsuperscript{T} (=DSM 21328\textsuperscript{T} =CCUG 56108\textsuperscript{T}), was isolated from the thallus of the liverwort Marchantia polymorpha L.

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References


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