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# *Moorella caeni* sp. nov., isolated from thermophilic anaerobic sludge from a methanol-fed reactor

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**Abstract**

Strain AMP$^T$ has been previously suggested as a strain of the species *Moorella thermoacetica* Jiang *et al*. 2009 (based on the high 16S rRNA gene identity, 98.3%). However, genome-based phylogenetic analysis of strain AMP$^T$ reveals that this bacterium is in fact a novel species of the genus *Moorella*. Genome relatedness indices between strain AMP$^T$ and *Moorella thermoacetica* DSM 521$^T$ were below the minimum threshold values required to consider them members of the same species (digital DNA–DNA hybridization, 52.2% (<70%); average nucleotide identity, 93.2% (<95%)). Based on phylogenetic and phenotypic results we recommend that strain AMP$^T$ (DSM 21394$^T$=JCM 35360$^T$) should be classified as representing new species, for which we propose the name *Moorella caeni* sp. nov.

## INTRODUCTION

There are currently five species in the genus *Moorella* with validly published names: *M. thermoacetica* (type strains, DSM 521$^T$ and DSM 2955$^T$), *M. glycerini* (type strain, DSM 11254$^T$), *M. mulderi* (type strain, DSM 14911$^T$), *M. humiferrea* (type strain, DSM 23265$^T$) and *M. stamsii* (type strain, DSM 26217$^T$), all with publicly available genomes (https://img.jgi.doe.gov). The first representative of the genus *Moorella*, strain DSM 521$^T$, formerly *Clostridium thermoaceticum*, was isolated in 1943 by Fontaine *et al*. from horse faeces [1] and was used as model organism for the elucidation of the Wood–Ljungdahl pathway [2–5]. In 1983, another representative of this strain was re-isolated from a dried spore stock by Kerby and Zeikus [6] and deposited at DSMZ under number DSM 2955$^T$; these authors also showed that this acetogen could grow autotrophically on CO or $CO_2/H_2$. The genus *Moorella* was created in 1994, after a reorganization of the genus *Clostridium* [7]. *Moorella* sp. strain AMP$^T$ (DSM 21394$^T$) was isolated from a high-temperature methanogenic bioreactor fed with methanol, and its physiology was described by Jiang *et al*. [8]. In that study, strain AMP$^T$ was phylogenetically assigned as a new strain of *M. thermoacetica*, based on 16S rRNA gene identity (98.3%) and an empirical DNA–DNA hybridization (DDH) of 75.2±4.7%. In a more recent genomic comparison of *Moorella* strains, it was suggested [9] that strain AMP$^T$ is yet another *Moorella* species; based on average nucleotide identity (ANI) analysis on a MUMmer alignment, strain AMP$^T$ has an ANIm of 94% with *M. thermoacetica*, which is below the threshold for the species boundary. Here, we provide the genomic and physiological evidence that strain AMP$^T$ represents a novel species of the genus *Moorella*, for which we propose the name *Moorella caeni* sp. nov. (DSM 21394$^T$=JCM 35360$^T$).

## ENRICHMENT AND ISOLATION

Isolation of strain AMP$^T$ from a methanol-fed hight-temperature methanogenic bioreactor has been previously reported by Jiang *et al*. [8]. Here, we give an overview of the isolation procedure. Enrichment cultures were inoculated with granular sludge from a high-temperature (55 °C) lab reactor fed with methanol (for 130 days) [10, 11]. The source of original sludge was a pilot plant upflow anaerobic sludge bed (UASB) reactor treating paper mill wastewater at 55 °C (Paques Biosystems BV, Baulk, The Netherlands) that had been inoculated with mesophilic granular sludge from a UASB reactor treating paper mill wastewater at

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**Keywords:** *Moorella*; *Moorella caeni* sp. nov.; acetogen; methanol; carbon monoxide.
**Abbreviations:** ANIb, average nucleotide identity based on BLAST; dDDH, digital DNA–DNA hybridization; MLSA, multilocus sequence analysis; UASB, upflow anaerobic sludge bed.
The whole-genome assembly accession number for *Moorella caeni* strain AMP$^T$ (=DSM 21394$^T$=JCM 35360$^T$) is GCA_001875325.1. The GenBank/EMBL/DDBJ/PIR accession number for the 16S rRNA gene sequence of *Moorella caenii strain* AMP$^T$ is AY884087.
Three supplementary tables are available with the online version of this article.

40 °C [10]. Granules were crushed under anaerobic conditions, previous to inoculation in 120 ml serum bottles containing 50 ml sterile bicarbonate-buffered anaerobic medium prepared as described by Stams *et al.* [12]. Medium was supplemented with trace elements and vitamins, but was cobalt-deprived [13]. Headspace of the bottles was filled with $N_2$:$CO_2$ (80:20%, v/v at 1.7 atm). Enrichments were incubated at 55 °C in the dark without shaking. Cultures were successively transferred to fresh medium upon methanol consumption. Initially (first seven transfers) methanol was added at a final concentration of 28 mM [13], and subsequently to a concentration of 40 mM [8]. After enrichment, the culture was dominated by a spore-forming bacterium and a rod-shaped methanogen [8]. Isolation of the spore-forming bacterium was achieved by repeated serial dilutions in methanol-containing medium (with addition of $CoCl_2$) using an autoclaved (121 °C for 1 h) culture as inoculum, as detailed by Jiang *et al.* [8]. Purification of strain AMP$^T$ was done by picking colonies from soft-agar surface and further dilution in liquid medium containing the methanogenesis inhibitor bromoethanesulfonate (10 mM) [8]. The pure culture of strain AMP$^T$ was deposited at DSMZ in 2003 (DSM 21394$^T$). In 2022 we deposited the strain also at the Japan Collection of Microorganisms (JCM 35360$^T$).

## GENOME FEATURES AND PHYLOGENY

The genomes of strain AMP$^T$ and of other type strains of *Moorella* species are available in GenBank [14]; assembly accession numbers and general properties of the genomes used here for digital DNA–DNA hybridization (dDDH) and ANI analyses are summarized in Table 1. Besides the two *M. thermoacetica* type strains (DSM 521$^T$ and DSM 2955$^T$) we also included *M. thermoacetica* ATCC 39073 in the comparison, as the physiology of this strain has been well studied.

dDDH calculations were done using the Type (Strain) Genome Server (TYGS), a free bioinformatics platform available at https://tygs.dsmz.de, for a whole genome-based taxonomic analysis [15, 16]. All pairwise comparisons among the set of genomes were conducted using genome BLAST distance phylogeny approach and accurate intergenomic distances inferred under the algorithm 'trimming' and distance formula d5 [17]. Digital DDH values and confidence intervals were calculated using the recommended settings of the Genome-to-Genome Distance Calculator 3.0 [16, 17]. The dDDH values between strain AMP$^T$ and other *Morella* species (Table 1) were well below the typical 70% cut-off value for species delineation [18], indicating that strain AMP$^T$ represents a novel species of the genus *Moorella*.

ANI values were calculated with scripts from the enveomics package [19] using BLASTp (ANIb) [20, 21]. Calculated ANIb between strain AMP$^T$ and *M. thermoacetica* type strains (Table 1) were the below 95% ANI (used as the minimum threshold for definition of same species [22, 23]), once more indicating that strain AMP$^T$ is a novel species of the genus *Moorella*.

**Table 1.** General genome features and pairwise dDDH and ANI comparisons of strain AMP vs. type strain genomes of the genus *Moorella*

Results obtained from the comparison with the closest relative *M. thermoacetica* (type strains DSM 521$^T$ and DSM 2955$^T$ and with *M. thermoacetica* ATTC 39073) are highlighted in grey. All values shown are in %; C.I., confidence interval. dDDH values and G+C content difference obtained with TYGS [15, 16]; results with formula d4 are shown according to recommendation for comparison of incomplete genomes [17]. ANIb values obtained with enveomics package [19, 24].

| | Genome features | | | Genome comparison (with strain AMP as query strain) | | |
|---|---|---|---|---|---|---|
| | **Assembly accession nr.** | **Genome size (MB)** | **G+C content (mol%)** | **dDDH (d4) [C.I]** | **ANIb** | **G+C content difference** |
| Strain AMP | GCA_001875325 | 2.6 | 57.3 | | | |
| *M. thermoacetica* DSM 521$^T$ | GCA_001267405 | 2.5 | 55.5 | 52.2 [49.5–54.8] | 93.20 | 1.06 |
| *M. thermoacetica* DSM 2955$^T$ | GCA_001267435 | 2.6 | 55.8 | 52.3 [49.6–55.0] | 93.22 | 1.20 |
| *M. thermoacetica* ATCC 39073 | GCA_006228565 | 2.6 | 55.8 | 52.4 [49.7–55.0] | 93.20 | 1.20 |
| *M. mulderi* DSM 14980$^T$ | GCA_001594015 | 3.3 | 53.6 | 23.2 [20.9–25.7] | 80.88 | 2.46 |
| *M. stamsii* DSM 26217$^T$ | GCA_002995805 | 3.3 | 57.3 | 23.1 [20.8–25.6] | 81.20 | 3.20 |
| *M. glycerini* DSM 11254$^T$ | GCA_009735625 | 3.6 | 54.5 | 23.6 [21.3–26.1] | 81.01 | 2.27 |
| *M. humiferrea* DSM 23265$^T$ | GCA_002995755 | 2.6 | 53.5 | 21.3 [19.1–23.7] | 79.76 | 3.49 |

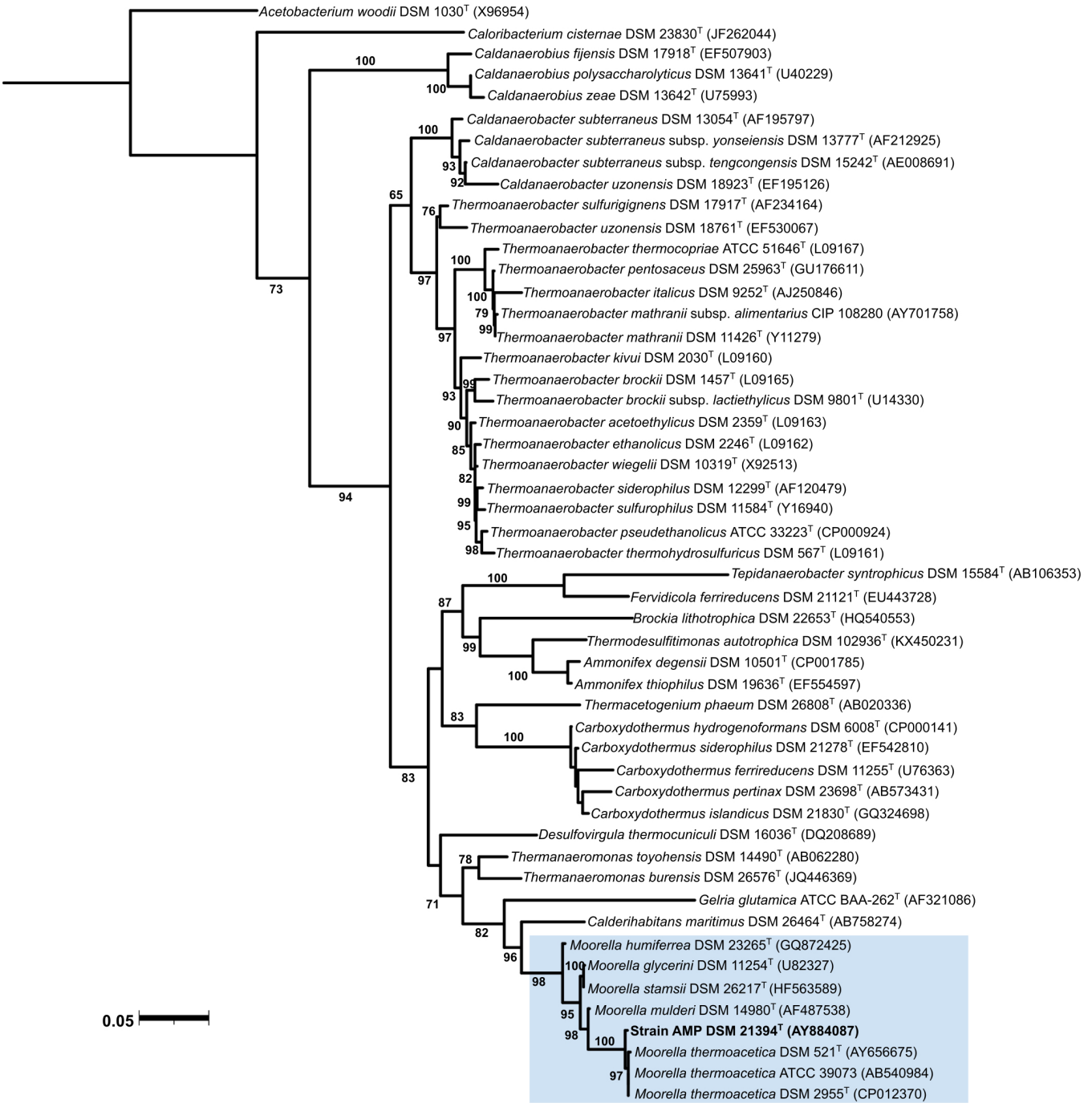


**Fig. 1.** 16S rRNA gene-based phylogenetic tree of several strains (50) belonging to the family Thermoanaerobacteraceae. *Acetobacterium woodii*, a member of the family Eubacteriaceae, was used as outgroup to root the tree. The blue shaded box shows strain AMP$^T$ and repesentatives of the genus *Moorella*. 16S rRNA gene sequences were aligned using MUSCLE [26]. The most suitable substitution model for the alignment was determined using ModelFinder [27] in IQ-TREE 1.6.12 [28, 29]. Phylogenetic analyses were performed with maximum likelihood and ultrafast bootstrap with 10.000 replicates [33]. The obtained maximum-likelihood tree was edited using iTOL 6.5.8 [34] and only nodes supported by ultrafast bootstrap values >0.95 were considered robust.

16S rRNA genes were used to predict the phylogenetic placement of strain AMP$^T$ (Fig. 1). In addition, a genome phylogenetic comparison using the complete set of core genes of all type strains of *Moorella* species and strain AMP$^T$ (Fig. 2a) and a multilocus sequence analysis (MLSA) on the respiratory complex 1 (11 genes, *nuo*A-D and *nuo*H-N; Fig. 2b) were also performed. From these comparisons a clear separation of strain AMP$^T$ from other *Moorella* species is inferred, further supporting its classification

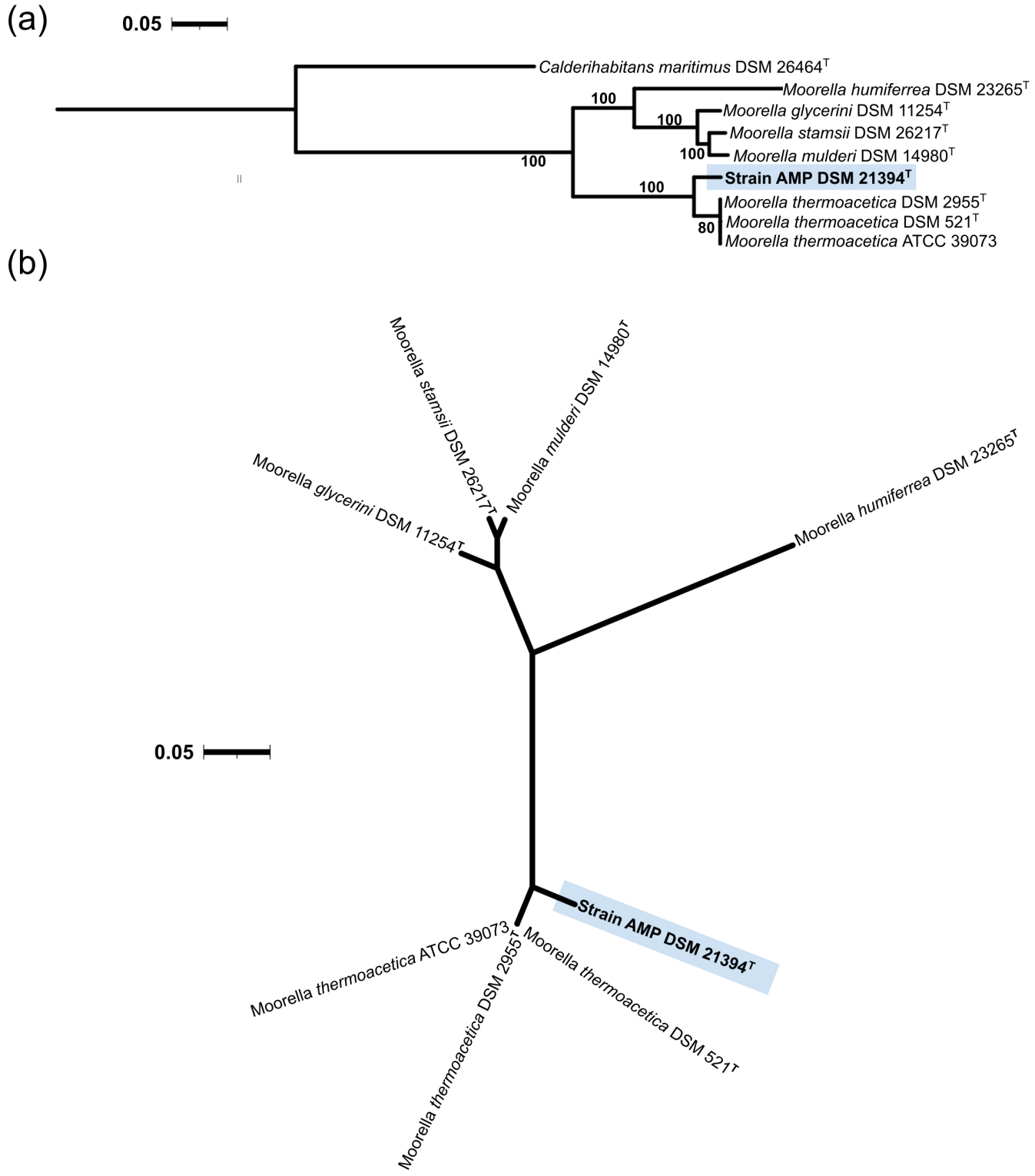


**Fig. 2.** Phylogenetic trees based on (a) core genome and (b) respiratory complex one genes (11 genes, *nuo*A-D and *nuo*H-N). The blue shaded box shows strain AMP$^T$. Alignment of core genes was done using the Roary pan genome pipeline [24], which uses MAFFT version 7 [25]. Alignment of respiratory complex I was done using MUSCLE [26]. The most suitable substitution model for the alignment was determined using ModelFinder [27] in IQ-TREE 1.6.12 [28, 29]. Phylogenetic analyses were performed with maximum likelihood and ultrafast bootstrap with 10.000 replicates. The obtained maximum-likelihood tree was edited using iTOL 6.5.8 [34] and only nodes supported by ultrafast bootstrap values >0.95 were considered robust. The tree was rooted on *Calderihabitans maritimus* GenBank assembly accession number GCA_002207765. The GenBank assembly accession numbers for strain AMP$^T$ and other *Moorella* strains can be found in Table 1.

**Table 2.** Morphological and physiological characteristics of *Moorella* species closely related to strain AMP$^T$

Strains: 1, AMP$^T$ [8]; 2, *M. thermoacetica* DSM 521$^T$/DSM 2955$^T$ [1, 2, 4, 9, 39, 43, 48]; 3, *M. mulderi* DSM 14980$^T$ [49]; 4, *M. stamsii* DSM 26217$^T$ [38]; 5, *M. glycerini* DSM 11254$^T$ [50]; 6, *M. humiferrea* DSM 23265$^T$ [51]. +, Positive; –, negative; ±, variable; NR, not reported; AQDS, 9,10-anthraquinone-2,6-disulphonate.

| Characteristic | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Source | Anaerobic pilot reactor treating paper mill wastewater | Horse faeces | High-temperature sulphate-reducing bioreactor | Anaerobic suspended sludge of a thermophilic municipal solid waste digester | Sediment-water sample of hot spring | Hydrothermal sediment from a freshwater hot spring |
| Cell shape and dimensions | Rod 0.4–1.2×5–14 µm | Rod 0.4×2.8 µm | Rod 0.4–0.6×2–8 µm | Rod 0.6–1.0×2–3 µm | Rod 0.4–0.6×3.0–60.5 µm | Rod 0.3–0.5×2–5 µm |
| Gram stain | Positive | Positive | Positive | Variable | Positive | Positive |
| Temperature (°C) range/optimum for growth | 42–75/60–65 | 45–65/55–60 | 40–70/65 | 50–70/65 | 43–65/58 | 46–70/65 |
| pH range/optimum for growth | 5.0–8.5/6.9 | 6.9 | 5.5–8.5/7.0 | 5.7–8.0/7.5 | 5.9–7.8/6.3–6.5 | 5.5–8.5/7.0 |
| Salinity (NaCl; g l$^{-1}$) range/optimum for growth | 0.6–23/<12 | NR | 0–4/10 | NR | 0–20 | 0–15/0 |
| Substrates: | | | | | | |
| $H_2/CO_2$ | – | – | + | – | – | – |
| Methanol | + | – | + | – | – | – |
| CO | + (to $H_2$) | +* (to acetate) | – | + (to $H_2$) | + (to acetate) | – |
| Formate | +* | – | + | – | – | – |
| Pyruvate | + | + | + | + | + | + |
| Lactate | + | – | + | – | + | +† |
| Mannose | + | + | NR | + | + | – |
| Fructose | + | + | + | + | + | + |
| Glucose | – | + | + | + | + | – |
| Acetate | – | NR | – | – | – | – |
| Ethanol | – | NR | – | – | – | – |
| Glycerol | – | – | – | – | + | +† |
| Arabinose | – | + | – | NR | – | – |
| Xylose | – | + | – | + | – | – |
| Starch | – | – | – | NR | – | – |
| Sucrose | – | – | NR | + | – | + |

Continued

**Table 2.** Continued

| Characteristic | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Benzoate | – | NR | – | – | – | – |
| Vanillin | + | + | NR | NR | NR | NR |
| Vanillate | + | + | NR | NR | NR | NR |
| Electron acceptors: | | | | | | |
| Thiosulphate | + | + | + | – | + | + |
| Nitrate | – | + | – | + | – | + |
| Sulphate | – | + | + | – | – | – |
| Fumarate | – | – | – | NR | + | – |
| Perchlorate | – | ± | + | + | + | + |

*Growth reported only with the addition of thiosulphate as electron acceptor or in syntrophy with a methanogen.
†Growth observed when AQDS or humic acid was added as electron acceptor.

**Table 3.** Cellular fatty acid composition (%) of strain AMP$^T$ (this study) in comparison with other *Moorella* species (data from Alves *et al.* [38])

Strains were grown in bicarbonate-buffered medium supplemented with fructose (20 mM) and yeast extract (0.2 g $l^{-1}$). ND, not detected/no data.

| Fatty acids | Strain AMP$^T$ | *M. stamsii* DSM 26217$^T$ | *M. glycerini* DSM 11254$^T$ | *M. humiferrea* DSM 23265$^T$ |
|---|---|---|---|---|
| $C_{14:0}$ | 2.71 | 0.71 | 2.07 | 0.97 |
| iso- $C_{15:0}$ | 47.36 | 26.18 | 37.62 | 20.58 |
| anteiso- $C_{15:0}$ | ND | 2.23 | ND | ND |
| $C_{15:0}$ | ND | 1.86 | ND | ND |
| iso- $C_{15:0}$ DMA* | 20.27 | 15.11 | 18.15 | 1.60 |
| iso- $C_{16:0}$ | ND | 5.39 | ND | ND |
| $C_{16:0}$ | 9.10 | 7.11 | 10.56 | 21.65 |
| $C_{16:0}$ DMA* | 1.66 | 3.35 | 2.50 | 3.29 |
| iso- $C_{17:0}$ | 5.45 | 6.52 | 11.30 | 21.85 |
| antesio-$C_{17:0}$ | ND | 2.15 | ND | ND |
| antesio-$C_{17:0}$ DMA* | ND | 2.27 | ND | ND |
| $C_{17:0}$ DMA | 5.79 | ND | 1.15 | 2.99 |
| $C_{17:0}$ cyclopropane | 3.04 | ND | ND | 2.21 |
| $C_{18:0}$ DMA* | ND | ND | ND | 1.12 |
| $C_{18:0}$ | 1.76 | 1.38 | 1,79 | 13.49 |
| $C_{18:1}$ ω9*c* | ND | ND | ND | 0.90 |
| $C_{19:0}$ cyclo 11–12 DMA* | ND | ND | 1.44 | ND |

*DMA, dimethylacetal.

as a new species of the genus *Moorella*. The core genome tree was based on the Roary pan genome pipeline [24] using 70% blastp identity cutoff and uses the alignment tool MAFFT version 7 [25]. The 16S rRNA gene and MLSA sequences were aligned with MUSCLE [26]. The most suitable substitution models for the alignments were determined using ModelFinder [27] in IQ-TREE 1.6.12 [28, 29]. The phylogenetic 16S rRNA gene and MLSA analyses were done using a transition model (AC=CG, AT=GT and unequal base frequencies) with empirical base frequencies and rate heterogeneity across sites (Model: TIM3 +F+G4) [30, 31]. The core genome phylogenetic analysis was done with a general time reversible model (unequal rates and unequal base frequencies) with empirical base frequencies and rate heterogeneity across sites (Model: GTR+F+I+G4) [30–32]. Phylogenetic trees were inferred with maximum-likelihood and ultrafast bootstrap with 10000 replicates [33]. The obtained maximum-likelihood tree was edited using iTOL 6.5.8 [34] and only nodes supported by ultrafast bootstrap values >0.95 were considered robust.

## PHYSIOLOGICAL AND MORPHOLOGICAL CHARACTERIZATION

Growth tests with strain AMP$^T$ were described by Jiang *et al.* [8]. Growth on the different substrates was tested in bicarbonate-buffered media (prepared as described by Stams *et al.* [12]). Tests were monitored by measuring increase in medium turbidity and analyses of substrate consumption/product production. Optimal growth conditions were tested with methanol (40 mM) as substrate. Morphology of AMP$^T$ cells was observed by microscopic examination, using cells grown on methanol. A summary of the physiological characteristics of strain AMP$^T$, in comparison with those of other *Moorella* type strains, is shown in Table 2. When applicable, gene prediction, functional annotation and comparison were performed using the tools on the Integrated Microbial Genomes system [35, 36].

Strain AMP$^T$ is a rod-shaped bacterium that can form terminal endospores. When grown on methanol, cells have variable size from 0.4 to 1.2 µm wide and 1–14 µm long. Cells of strain AMP$^T$ stained Gram-positive. The genome of strain AMP$^T$ does not contain any of the typical marker genes for outer membrane components of Gram-negative cells, specifically the genes *Bam*A, *Lpx*A-D, *Kds*A-D and *Lpt*ACFG [37], supporting cells are monoderm.

The optimal temperature range for growth of strain AMP$^T$ is 60–65 °C, but it can grow in a wider range from 42–75 °C. It grows within a pH range of 5.0–8.5, with an optimum at pH 6.9.

Strain AMP$^T$ grows on methanol and on some other one-carbon compounds, such as CO and formate (growth with formate was only observed with thiosulphate as electron acceptor), but not on $CO_2/H_2$. When growing on CO, strain AMP$^T$ produced mainly $H_2$. This hydrogenogenic behaviour is also observed in *M. stamsii* DSM 26217$^T$, and contrasts with the acetogenic behaviour of all the other *Moorella* strains able to grow on CO [38]. In the work by Jiang *et al.* [8] it is reported that strain AMP$^T$ could grow on formate in syntrophy with the methanogen *Methanothermobacter thermoautrophicus* strain NJ1. We were not able to reproduce these results when growing strain AMP$^T$ with *Methanothermobacter thermoautotrophicus* strain ΔH (sharing 99.5% 16S rRNA gene identity with strain NJ1). Unfortunately, strain NJ1 was lost, and thus tests with the original syntrophic partner of strain AMP$^T$ are no longer possible.

Growth of strain AMP$^T$ on vanillin and vanillate was also tested and positive, similarly to what has been observed for *M. thermoacetica* ATCC 39073 [39–43]. These methoxylated compounds are important intermediates in lignin degradation. In *M. thermoacetica*, vanillin is suggested to be degraded *via* vanillate [42]; further, the conversion of vanillate involves the *O*-demethylation-transfer of the methyl group to the Wood–Ljungdahl pathway [44]. Protocatechuate was one of the main products from vanillin degradation by *M. thermoacetica* (besides acetate), as reported by Lux *et al.* [43]; when CO was supplemented, cultures of *M. thermoacetica* seemed to decarboxylate protocatechuate to catechol. We performed a genome search for *O*-demethylase system in all *Moorella* species, specifically the genes *mtv*A, *mtv*B and *mtv*C (methyltransferase for vanillate system (Mtv) characterized by Naidu and Ragsdale [44]). MtvB catalyses methyl transfer from vanillate to the cobalt centre of MtvC, and MtvA catalyses transmethylation from MtvC to tetrahydrofolate, forming methyltetrahydrofolate. At least one copy of each of these genes is present in all analysed *Moorella* species (Table S1, available in the online version of this article), indicating conversion of vanillin/vanillate is likely a common feature of these acetogens.

Analysis of fatty acid profile of strain AMP$^T$ was carried out at the Identification Service, Leibniz Institut DSMZ – Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany. The cellular fatty acid profile revealed that the most abundant fatty acids in strain AMP$^T$ are iso-$C_{15:0}$ (47.36%), iso-$C_{15:0}$ DMA (20.27%) and $C_{16:0}$ (9.10%). The differences observed in the fatty acid profile of strain AMP$^T$ when compared with *M. stamsii*, *M. glycerini* and *M. humiferrea*, are shown in Table 3; the predominant fatty acid in all the four *Moorella* species is iso-$C_{15:0}$. The second most abundant fatty acid, iso-$C_{15:0}$ DMA, is also abundant in *M. stamsii* (15.11%) and in *M. glycerini* (18.15%). *M. humiferrea* presents substantially more abundant $C_{16:0}$, iso- $C_{17:0}$ and $C_{18:0}$ fatty acid profile than in strain AMP$^T$, *M. glycerini* and *M. humiferrea*.

*M. thermoacetica* is known to contain menaquinone and b-type cytochromes [45], though their role in metabolism is not yet understood [46]. Strain AMP$^T$ has analogues to genes in *M. thermoacetica* for the synthesis of menaquinone (*mqnACE*) (Table S2). In fact, these genes are found in all the other *Moorella* strains suggesting menaquinones are intrinsic to this genus. Cytochrome bd oxidase genes are also present in all representatives of the genus *Moorella* (Table S3). In *M. thermoacetica* cytochrome bd oxidase has been implicated in protection against oxidative stress [47], but the involvement of b-type cytochromes in electron transfer to Wood–Ljungdahl pathway enzymes is also hypothesized by some [46].

## DESCRIPTION OF *MOORELLA CAENI* SP. NOV.

*Moorella caeni* (cae'ni. L. gen. n. caeni, of sludge).

The physiological and morphological description is largely based on the work by Jiang *et al.* [8]. Isolated from thermophilic methanogenic sludge from a bioreactor fed with methanol. Cells are Gram-positive, long-rod shaped measuring 0.4–1.2×5–14 µm and can form swollen endospores. It is a strict anaerobic bacterium. Optimal temperature for growth is between 60–65 °C (grows at 42–75 °C), and optimal pH 6.9 (grows at 5.0–8.5). Growth rates remained unchanged when NaCl concentrations were below 12 g $l^{-1}$, and no growth occurred at a NaCl concentration higher than 23 g $l^{-1}$. It can utilize methanol, pyruvate, lactate, mannose, vanillate and vanillin, forming acetate as the main reduced end product. It grows hydrogenogenically on 100% CO. Weak growth on fructose was observed. It uses thiosulphate, but not nitrate, sulphate or fumarate as electron acceptor. It does not grow (in the absence of thiosulphate) on $H_2/CO_2$, formate, glucose, acetate, ethanol, n-propanol, glycerol, melibiose, raffinose, rhamnose, trehalose, arabinose, cellobiose, cellulose, galactose, lactose, maltose, xylose, mannitol, melezitose, ribose, sorbitol, starch, sucrose and benzoate. G+C content of genomic DNA is 57.3 mol%. The major fatty acids are iso-$C_{15:0}$, iso-$C_{15:0}$ DMA, $C_{16:0}$.

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

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