Caloramator quimbayensis sp. nov., an anaerobic, moderately thermophilic bacterium isolated from a terrestrial hot spring

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An anaerobic, moderately thermophilic, terminal-spore-forming bacterium, designated strain USBA A1T, was isolated from a terrestrial hot spring located at an altitude of 2683 m in the Andean region of Colombia (04° 50’ 14.0” N 75° 32’ 53.4” W). Cells of strain USBA A1T were Gram-stain-positive, straight to slightly curved rods (0.9×2.5 μm), that were arranged singly or in pairs, and were motile by means of flagella. Growth occurred at 37–55 °C and pH 6.0–8.0, with a doubling time of 2 h under the optimal conditions (50 °C and pH 7.0). Glucose fermentation in strain USBA A1T required yeast extract or peptone (each at 0.2 %, w/v). The novel strain fermented sugars, amino acids, Casamino acids, propanol, propionate, starch and dextrin, but no growth was observed on galactose, lactose, xylose, histidine, serine, threonine, benzoate, butyrate, lactate, pyruvate, succinate, methanol, ethanol, glycerol, casein, gelatin or xylan. The end products of glucose fermentation were formate, acetate, ethanol and lactate. Strain USBA A1T did not grow autotrophically (with CO2 as carbon source and H2 as electron donor) and did not reduce thiosulfate, sulfate, elemental sulfur, sulfite, vanadium (V) or Fe (III) citrate. Growth of strain USBA A1T was inhibited by ampicillin, chloramphenicol, kanamycin, penicillin and streptomycin (each at 10 μg ml−1). The predominant fatty acids were iso-C15 : 0, C16 : 0 and iso-C17 : 0 and the genomic DNA G+C content was 32.6 mol%. 16S rRNA gene sequence analysis indicated that strain USBA A1T belonged in the phylum Firmicutes and that its closest relative was Caloramator viterbiensis JW/MS-VS5T (95.0 % sequence similarity). A DNA–DNA relatedness value of only 30 % was recorded in hybridization experiments between strain USBA A1T and Caloramator viterbiensis DSM 13723T. Based on the phenotypic, chemotaxonomic and phylogenetic evidence and the results of the DNA–DNA hybridization experiments, strain USBA A1T represents a novel species of the genus Caloramator, for which the name Caloramator quimbayensis sp. nov. is proposed. The type strain is USBA A1T (=CMPUJ U833T =DSM 22093T).

The genus Caloramator is a member of the order Clostridiales, phylum Firmicutes. The current members of the genus can be placed in two groups based on their optimum growth temperature; C. proteoclasticus, C. coolhaasii, C. viterbiensis and C. mitchellensis, grow optimally at 50–58 °C and are considered to be moderate thermophiles, whereas C. fervidus, C. indicus and C. australicus grow at or above 60 °C and are considered to be thermophiles. The natural habitats of these species include hot springs, non-volcanic but geothermally heated waters, and mesophilic or thermophilic granular sludges. At the time of writing, all members of the genus Caloramator are strict anaerobes and ferment carbohydrate (particularly glucose, fructose, maltose, galactose and sucrose) in the presence of trace amounts of yeast extract. Recently the members of the genus were differentiated into four clusters based on the signature nucleotides of their 16S rRNA genes (Ogg & Patel, 2011a), and the complete genome of C. australicus was also sequenced (Ogg & Patel, 2011b). In this paper, the characteristics of a novel Caloramator-like bacterium that was isolated from a hot spring in the Andes mountains are described.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain USBA A1T is JN648101.

Two supplementary tables and a supplementary figure are available with the online version of this paper.
Water samples were collected from two hot springs, at Jaímana (04° 50' 23.0" N 75° 03' 1.6" W) and Parador de Quimbaya (04° 50' 14.0" N 75° 32' 53.4" W), which are both located at an altitude of 2683 m in the Colombian Andes, in an area where a thermal anomaly causes ground temperatures of >250 °C (Alfaro & Jaramillo, 2002). The water that flows from these springs is meteoric in origin, characterized by low mineralization and heated by underlying magmatic chambers (Alfaro et al., 2002). For the sampling, sterile glass containers were filled to the brim with water from a hot spring, then capped and transported to the laboratory. The temperatures of the waters at the sampling points ranged between 54 °C and 58 °C, while the pH values of the waters ranged between 6.3 and 6.5. The sampled waters contained (l−1) 11 mg sulphate, 1230–1240 mg total dissolved solids, 41 mg magnesium, 279 mg sodium and 345 mg chloride.

Enrichment medium was prepared using filtered spring water supplemented (l−1) with 1 g starch (Sigma), 0.5 g yeast extract (Sigma), 1 ml 0.1 % (w/v) resazurin solution and 1 ml of the trace element solution described by Imhoff-Stuckle & Pfennig (1983). The pH value of the medium was adjusted to 6.5 with 1 M NaOH solution before the medium was boiled and cooled to room temperature under a stream of nitrogen gas, then dispensed into Hungate tubes (5 ml per tube), under oxygen-free nitrogen gas, and sterilized by autoclaving for 20 min (at 121 °C and 15 p.s.i.). Prior to use, 0.05 ml of 2 % (w/v) Na2S.9 H2O or cysteine-HCl. For long-term storage, cells of the novel strain were held at −70 °C in BM supplemented with 20 % (v/v) glycerol.

The morphology of strain USBA A T was determined by phase-contrast microscopy (Eclipse 50; Nikon) and electron microscopy, using the methods described by Patel et al. (1985). Cells of strain USBA-AT were slightly curved to straight rods (0.9 × 2.5 μm) that generally occurred singly or in pairs. They were Gram-staining-positive, motile by means of flagella and were strict anaerobes. Electron micrographs revealed a cell-wall ultrastructure that was typical of Gram-positive bacteria, with a thick peptidoglycan layer (Fig. 1). The presence of terminal spores was confirmed by phase-contrast microscopy. At least some of the cells in cultures that had been incubated at 80 °C for up to 20 min survived and multiplied when subcultured in fresh growth medium at 55 °C.

Characterization studies were performed in BM supplemented with 20 mM D-glucose (Sigma) and 0.2 % (w/v) yeast extract. The pH value of this medium was adjusted to 7.0 with 1 M NaOH solution. The ability of the strain to grow aerobically was tested in the same medium except that the medium was prepared aerobically and without any Na2S.9 H2O or cysteine-HCl. For long-term storage, cells of the novel strain were held at −70 °C in BM supplemented with 20 % (v/v) glycerol.

Pure cultures were isolated by serially diluting the enrichment cultures and incubating each dilution on basal medium supplemented with 0.1 % (w/v) starch and 0.05 % (w/v) yeast extract and solidified with 2.0 % (w/v) Noble agar (Sigma), using the roll-tube technique (Hungate, 1969). After 2 days of incubation at 55 °C, white, irregular and convex colonies (0.2 mm in diameter) with undulate edges developed in the roll tubes. Each of several, single, well-isolated colonies was transferred into a fresh tube of growth medium and the whole procedure was repeated at least twice. The three colonies that were finally selected for further study had similar colony characteristics as described above. The cells from the three colonies were morphologically similar, Gram-staining-positive, strictly anaerobic, thermophilic, motile and possessed terminal spores. The 16S rRNA gene sequences of the three isolates showed 99 % sequence similarity to each other. Only one of the isolates, designated strain USBA-A T, was selected for detailed characterization. This novel strain was isolated from the Parador de Quimbaya hot spring.
Cell growth was monitored in a DR 5000 spectrophotometer (Hache Lange), as absorbance at 580 nm. All tests were performed in duplicate, with the novel strain subcultured at least once under the same experimental conditions before being used as an inoculum. To determine the pH range for growth, the pH of the basal medium was adjusted, to values between 5.0 and 9.0, with anaerobic stock solutions of NaHCO₃ (10 %, w/v), Na₂CO₃ (10 %, w/v) or H₂SO₄ (1 M). Strain USBA AT grew at pH values between 6.0 and 8.0 (optimum pH 7.0), at temperatures between 37 and 55 °C (optimum 50 °C), and with 0.0–0.6 % (w/v) NaCl (optimum no NaCl). Growth of strain USBA AT was tested in BM with 20 mM glucose or without glucose, in the presence of 0.0–0.2 % (w/v) yeast extract and/or 0.0–0.2 % (w/v) peptone.

Growth, monitored by measuring turbidity and by microscopy after incubation for up to 48 h, was observed in the cultures with 20 mM glucose (as a carbon source) and either 0.2 % (w/v) yeast extract or 0.2 % (w/v) peptone. No growth was observed with glucose in the absence of both yeast extract and peptone, indicating that the novel strain required yeast extract or peptone for glucose fermentation. Strain USBA AT grew optimally in BM with 20 mM glucose and 0.2 % (w/v) yeast extract at 50 °C and pH 7.0, and had a generation time of 2.0 h under these conditions. Unless indicated otherwise, all subsequent growth experiments were conducted using these optimal conditions.

Utilization of carbon sources was tested in glucose-free BM with 0.2 % (w/v) yeast extract, at pH 7.0. Sterile anaerobic stock solutions of the soluble substrates to be tested were injected into Hungate tubes containing sterile BM. Insoluble substrates (starch, xylan, cellulose, dextrin, casein and leucine) were weighed directly into empty Hungate tubes before basal medium supplemented with 0.2 % (w/v) yeast extract was dispensed into the tubes and sterilized. The substrates were tested at final concentrations of 20 mM (monosaccharides, disaccharides and alcohols), 10 mM (organic acids and amino acids), 0.2 % (w/v) (starch, xylan, cellulose, dextrin) or 1.0 % (w/v) (peptone, yeast extract, tryptone, casein, Casamino acids and gelatin). As indicated in Table 1 and the species description, strain USBA AT was able to use a range of sugars and amino acids as sole carbon sources.

After 2 weeks of incubation at 55 °C, the end products of glucose fermentation were investigated by HPLC, using a Prominance LC-20AT chromatograph (Shimadzu) equipped with a reverse-phase C18 ultra-aqueous column (150 mm × 4.6 mm, 5 μm ID; Restek), an SPD-M20A diode-array detector (Shimadzu) set at 210 nm, and a mobile phase of 0.5 % (v/v) H₃PO₄ (pH 2.5) with a flux of 0.5 ml min⁻¹. The end products from glucose fermentation were identified as formate, acetate, ethanol and lactate.

Sodium thiosulfate (20 mM), sodium sulfate (20 mM), and elemental sulfur (1 %, w/v), were tested as electron acceptors in BM supplemented with 0.2 % (w/v) yeast extract. The electron donors tested were 20 mM glucose, 20 mM alanine, 20 mM arginine, 1.0 % (w/v) peptone, 1.0 % (w/v) yeast extract and 1.0 % (w/v) Casamino acids. Sulfide production was determined photometrically (Cord-Ruwisch, 1985) after 14 days of incubation at 50 °C, with Na₂S, 9H₂O-free BM used as the negative control. Strain USBA AT did not reduce any of the electron acceptors evaluated. The reduction of soluble ammonium Fe (III) citrate was evaluated, using the ferrozine method (Sørensen, 1982), in BM supplemented with 0.2 % (w/v) yeast extract and a carbon source [glucose (20 mM), peptone (1 %, w/v), Casamino acids (1 %, w/v), alanine (10 mM) or arginine (10 mM)]. The carbon sources were added from sterile, anaerobic stock solutions before the cultures were incubated for 8 days at 50 °C. As negative control, a culture containing BM lacking substrate was used. Strain USBA AT was unable to reduce Fe (III) citrate in the presence any of the carbon sources tested. When the reduction of 2 and 10 mM sodium orthovanadate (Sigma) was similarly evaluated, strain USBA AT did not reduce vanadium (V) in the presence any of the carbon sources tested (i.e. the culture medium never turned green or formed green precipitates).

Strain USBA AT did not grow autotrophically when incubated for 48 h at 50 °C in BM supplemented with 0.2 % (w/v) yeast extract, in an atmosphere of H₂/CO₂ (80 : 20, v/v) at 2 bars.

Antibiotic sensitivity was determined by injecting appropriate aliquots of antibiotics (ampicillin, streptomycin, kanamycin, penicillin and chloramphenicol) from filter-sterilized stock solutions into Hungate tubes containing pre-sterilized growth medium, to give final concentrations of 10 and 100 μg ml⁻¹. Strain USBA AT was completely inhibited by 10 μg ml⁻¹ of each tested antibiotic. Analyses of polar lipids and fatty acids and the evaluation of genomic DNA G+C content were carried out by the Identification Service of the Deutsche Sammlung von Mikroorganismen und Zellkulturen (DSMZ), Braunschweig, Germany. Polar lipids were separated by two-dimensional TLC and then detected by spraying the plates with molybdophosphoric acid and heating at 200 °C for 10 min. The lipids identified were diphasphatidylglycerol (DPG), phosphatidylglycerol (PG), phosphatidylethanolamine (PE), two unidentified aminophospholipids(PN1, PN2), seven unidentified phospholipids (PL1–PL7), two unidentified aminolipids (AL1–AL2), three unidentified glycolipids (GL1–GL3), three unidentified phosphoaminoglycolipids (PGNL1–PNGL3) and another three unidentified lipids (L1–L3) (Fig. S1, available in IJSEM Online). The major cellular fatty acids of strain USBA AT were identified as iso-C₁₄ : 0, C₁₆ : 0, iso-C₁₇ : 0, C₁₄ : 0, iso-C₁₅ : 0, C₁₆ : 1 and C₁₀ : 0 14-0 (Table S1). Genomic DNA was isolated from cells of the novel strain and purified by chromatography on hydroxyapatite before its G+C content (32.6 mol%).
Table 1. Phenotypic traits of strain USBA AT and established members of the genus Caloramator

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Strain 1</th>
<th>Strain 2</th>
<th>Strain 3</th>
<th>Strain 4</th>
<th>Strain 5</th>
<th>Strain 6</th>
<th>Strain 7</th>
<th>Strain 8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isolation source</td>
<td>Hot spring (Colombia)</td>
<td>Geothermal waters (Great Artesian Basin, Australia)</td>
<td>Microbial mat (Great Artesian Basin, Australia)</td>
<td>Hot spring (Italy)</td>
<td>Anaerobic thermophilic granular sludge</td>
<td>Mesophilic granular methanogenic sludge</td>
<td>Non-volcanically heated waters (India)</td>
<td>Hot spring (New Zealand)</td>
</tr>
<tr>
<td>Morphology and size (μm)</td>
<td>Straight to slightly curved rods, 2.5–6.0 × 0.9</td>
<td>Slightly curved rods, 1.5–3.5 × 0.4–0.8</td>
<td>Slightly curved rods, 2.5–4.2 × 0.8–1.0</td>
<td>Straight to slightly curved rods, 2.0–3.0 × 0.4–0.6</td>
<td>Rod-shaped to filamentous, 2.4–4.0 × 0.4</td>
<td>Slightly curved rods, 2.4–4.0 × 0.5–0.7</td>
<td>Rods, 10–20 × 0.6–0.8</td>
<td>Rods, 0.65–2.0 × 2.5–2.5</td>
</tr>
<tr>
<td>DNA G+C content (mol%)</td>
<td>32.6</td>
<td>38</td>
<td>34</td>
<td>32</td>
<td>26.4</td>
<td>31</td>
<td>25.6 ± 0.3</td>
<td>39</td>
</tr>
<tr>
<td>Spore formation</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>Motility</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>Presence of flagella</td>
<td>+</td>
<td>+</td>
<td>++</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>NR</td>
</tr>
<tr>
<td>Optimum temperature (°C)</td>
<td>50</td>
<td>55</td>
<td>60</td>
<td>58</td>
<td>50–55</td>
<td>55</td>
<td>60–65</td>
<td>68</td>
</tr>
<tr>
<td>pH growth range</td>
<td>6.0–8.0</td>
<td>6.0–9.0</td>
<td>6.0–9.0</td>
<td>5.0–7.8</td>
<td>6.0–8.0</td>
<td>6.0–9.5</td>
<td>6.2–9.2</td>
<td>5.5–9.0</td>
</tr>
<tr>
<td>Optimum pH</td>
<td>7.0</td>
<td>7.0</td>
<td>7.0</td>
<td>6.0–6.5</td>
<td>7.0–7.5</td>
<td>7.0–7.5</td>
<td>8.1</td>
<td>7.0–7.5</td>
</tr>
<tr>
<td>Amino acids supporting growth</td>
<td>Ala, Arg, Glu, Val, Arg, Ala, Ile, Val, Met</td>
<td>Val, Arg, Ala, Glu, Ile, Met</td>
<td>Thr Ser, Glu, Thr, Leu, Met, Asp, Ala, Arg, Met</td>
<td>Glu, Asp, Ala, Met, Asp, His, Val</td>
<td>Glu, Met, Arg, His, Thr, Leu, Val, Gly</td>
<td>Acetate, lactate, Ethanol, H₂, CO₂, CO₂, H₂</td>
<td>Ethanol, acetate, Acetate, ethanol, formate, lactate, H₂</td>
<td>Ethanol, acetate, Acetate, i-butyrate, lactate, CO₂, H₂</td>
</tr>
<tr>
<td>End products of glucose fermentation</td>
<td>Formate, acetate, ethanol, lactate</td>
<td>Acetate, ethanol, H₂, CO₂, acetate</td>
<td>Ethanol, acetate</td>
<td>Ethanol, H₂, CO₂, CO₂, H₂</td>
<td>Acetate, lactate, Ethanol, acetate, formate, lactate, H₂</td>
<td>Ethanol, acetate, Acetate, i-butyrate, lactate, CO₂, H₂</td>
<td>Ethanol, acetate, Acetate, i-butyrate, lactate, H₂, CO₂</td>
<td></td>
</tr>
<tr>
<td>Electron acceptors</td>
<td>–</td>
<td>Vanadium (V)</td>
<td>Vanadium (V)</td>
<td>Amorphous Fe (III) oxohydroxide, manganese (IV)</td>
<td>Vanadium (V), soluble Fe (III) citrate</td>
<td>Vanadium (V), soluble Fe (III) oxohydroxide, manganese (IV)</td>
<td>NR</td>
<td>Elemental sulfur</td>
</tr>
</tbody>
</table>
was determined by HPLC, as described Mesbah et al. (1989).

The methods used for 16S rRNA gene amplification and sequencing have been reported previously (Andrews & Patel, 1996). The generated sequences were assembled into a single contig before the consensus sequence, of 1517 nt, was corrected manually for errors within version 5.0.1 of the BioEdit software package (Hall, 1999). The most closely related sequences held in GenBank (version 152) and the Ribosomal Database Project II (release 10) were identified using BLAST (Altschul et al., 1997) and then, aligned and manually adjusted (according to their secondary structure) using BioEdit. Nucleotide ambiguities were omitted. Evolutionary distances were calculated by using the Jukes and Cantor option (Jukes & Cantor, 1969) in TREECON (Van de Peer et al., 1997). Phylogenetic trees were constructed from evolutionary distances using the neighbour-joining method (Saitou & Nei, 1987). The topology of the tree was established by the bootstrap method, with 1000 resamplings (Felsenstein, 1985). The phylogenetic analysis of the 1300 unambiguous nucleotides of the 16S rRNA gene sequence indicated that strain USBA A T was a member of the genus Caloramator, family Clostridiaceae, class Clostridia, phylum Firmicutes (Fig. 2). The most closely related type strain was Caloramator viterbiensis JW/MS-VS5 T (95.0 % sequence similarity) followed by the type strains of the other members of the genus Caloramator (with a mean 16S rRNA gene sequence similarity of 91 %). However, in DNA–DNA hybridization experiments conducted at the DSMZ, strain USBA A T was a member of the genus Caloramator viterbiensis DSM 13723 T showed a DNA–DNA relatedness value of only 30 %.

The current, established members of the genus Caloramator, ‘Caloramator uzoniensis’ and Thermobrachium celere were recently separated into four clusters (I, II, III and IV) on the basis of 14 key signature nucleotides in their 16S rRNA genes (Ogg & Patel, 2011a). In comparisons based on 13 such signature nucleotides, strain USBA A T was found to have nine, five, seven and nine signatures in common with clusters I, II, III and IV, respectively. Interestingly, the 14th key signature (helix 6) was made up of 146 nt in strain USBA A T whereas this signature is represented by 45, 158, 43–45 and 43 nt in clusters I, II, III and IV, respectively. These data suggest that strain USBA A T should be regarded as a member of a new cluster (cluster V).

Strain USBA A T and established members of the genus Caloramator have some characteristics in common: they are all strictly anaerobic and thermophilic, have cell-wall ultrastructures that are typical of Gram-positive bacteria, ferment carbohydrates such as glucose, fructose, maltose, mannose and sucrose (Table S2), amino acids such as alanine, arginine and valine, and glutamate. However, strain USBA A T has some characteristics that distinguish it from all current members of the genus Caloramator: it ferments manitol, isoleucine and propanol but not pyruvate, histidine or gelatin, and it does not utilize any of the electron acceptors [sodium thiosulfate, sodium sulfate, elemental sulfur, vanadium (V) and soluble ammonium Fe (III) citrate] that are used by established species of the genus Caloramator. Marked differences in some phenotypic traits also separate strain USBA A T from its closest relative, C. viterbiensis JW/MS-VS5 T, including the temperature and pH optima and ranges for growth, the presence of readily demonstrable spores, flagella and motility in strain USBA A T and the ability of C. viterbiensis JW/MS-VS5 T, but not strain USBA A T, to utilize lactose, galactose, cellobiose, glycerol glutamine, histidine, leucine, serine and threonine but not arginine, propanol or arabinose (Seyfried et al., 2002). The 16S rRNA sequence similarity and level of DNA–DNA relatedness between strain USBA A T and C. viterbiensis JW/MS-VS5 T also indicate that strain USBA A T represents a novel species, for which the name Caloramator quimbayensis sp. nov. is proposed.

**Fig. 2.** Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences, showing the relationship between strain USBA A T and established members of the genus Caloramator. Escherichia coli ATCC 11775 T was used as an outgroup. Bootstrap values >95 % (based on 1000 resamplings) are shown at branch points. Bar, 0.02 substitution per nucleotide position.
Description of Caloramator quimbayensis sp. nov.

Caloramator quimbayensis (quim.ba.yen’sis. N.L. masc. adj. quimbayensis, of or belonging to the Quimbaya, the Colombian indigenous group that once lived in the geographical region where the type strain was isolated).

Cells are obligately anaerobic and moderately thermophilic, spore-forming, straight to slightly curved rods (2.5 × 0.9 μm) that are usually seen singly or in pairs. They have a cell-wall ultrastructure of the Gram-positive type and are motile by means of flagella. Growth occurs at 37–55 °C (optimum 50 °C) but not at 30 °C or 60 °C, at pH 6.0–8.0 (optimum pH 7.0) but not at pH 5.0 or pH 8.5. Does not require NaCl for growth but tolerates NaCl up to a concentration of 0.6% (w/v). Ferments glucose, fructose, arabinose, maltose, mannitol, mannose, ribose, sucrose, alanine, arginine, glutamate, isoleucine, valine, propanol, peptone, propionate, Casamino acids, starch and dextrin. End products from glucose fermentation are lactate, acetate, ethanol and, presumably, CO2 and H2. Unable to ferment galactose, lactose, xylose, glutamine, histidine, serine, threonine, benzoate, butyrate, lactate, pyruvate, propionate, succinate, ethanol, glycerol, methanol, casein, cellulose, gelatin or xylan. Sodium sulfate, sodium thiosulfate, elemental sulfur, vanadium (V) and Fe (III) citrate are not reduced in the presence of glucose and 0.2% (w/v) yeast extract. Does not grow autotrophically in the presence of CO2 as carbon source and H2 as electron donor. Growth is inhibited by ampicillin, streptomycin, penicillin, chloramphenicol and kanamycin (each at 10 μg ml⁻¹).

The type strain, USBA A² (=CMPUJ U83³ =DSM 22093²), was isolated from a water sample collected from the Parador de Quimbaya terrestrial hot spring in Risaralda, Colombia. The genomic DNA G+C content of the type strain is 32.6 mol%.

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