Acidianus sulfidivorans sp. nov., an extremely acidophilic, thermophilic archaeon isolated from a solfatara on Lihir Island, Papua New Guinea, and emendation of the genus description

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A novel, extremely thermoacidophilic, obligately chemolithotrophic archaeon (strain JP7T) was isolated from a solfatara on Lihir Island, Papua New Guinea. Cells of this organism were non-motile, Gram-negative staining, irregular-shaped cocci, 0.5–1.5 μm in size, that grew aerobically by oxidation of sulfur, Fe2+ or mineral sulfides. Cells grew anaerobically using Fe3+ as a terminal electron acceptor and H2S as an electron donor but did not oxidize hydrogen with elemental sulfur as electron acceptor. Strain JP7T grew optimally at 74 ± 6°C (temperature range 45–83°C) and pH 0.8–1.4 (pH range 0.35–3.0). On the basis of 16S rRNA gene sequence similarity, strain JP7T was shown to belong to the Sulfolobaceae, being most closely related to the type strains of Acidianus ambivalens (93.7%) and Acidianus infernus (93.6%). Cell-membrane lipid structure, DNA base composition and 16S rRNA gene sequence similarity data support the placement of this strain in the genus Acidianus. Differences in aerobic and anaerobic metabolism, temperature and pH range for growth, and 16S rRNA gene sequence differentiate strain JP7T from recognized species of the genus Acidianus, and an emendation of the description of the genus is proposed. Strain JP7T is considered to represent a novel species of the genus Acidianus, for which the name Acidianus sulfidivorans sp. nov. is proposed. The type strain is JP7T (= DSM 18786T = JCM 13667T).

The genus Acidianus, which was first described by Segerer et al. (1986), is a member of the order Sulfolobales (Stetter, 1989), and comprises three formally recognized species of facultatively aerobic thermoacidophiles isolated from geothermal or hydrothermal systems. The phylogenetically similar species Acidianus infernus and Acidianus ambivalens and the more distantly related and less thermophilic species Acidianus brierleyi (Fuchs et al., 1996), originally named Sulfolobus brierleyi (Brierley & Brierley, 1973; Zillig et al., 1980), grow as facultative aerobes with the ability to oxidize or reduce elemental sulfur depending on the available oxygen supply and are capable of autotrophic growth. Two recently described species, ‘Acidianus tengchongensis’ and ‘Acidianus manzaensis’, have extended the genotypic and phenotypic diversity within the genus (He et al., 2004; Yoshida et al., 2006).

Abbreviation: GDGTs, glycerol dialkyl glycerol tetraethers.
The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain JP7T is AY907891.
with 1% (w/v) chalcopyrite concentrate as the energy source. A pure strain, designated JP7\textsuperscript{T}, was isolated by using serial decimal dilutions to extinction in shake flasks of basal medium at pH 0.8 supplemented with 1% (w/v) chalcopyrite concentrate. Strain JP7\textsuperscript{T} was maintained routinely in shake flasks with this medium and the incubation conditions given above. Unless specified otherwise, strain JP7\textsuperscript{T} was grown in basal medium at pH 0.8. Cell morphology was similar to other members of the order Sulfolobales, with slightly aspherical shape, and occasional planar sides and edges. Cells occurred singly or occasionally in pairs, the latter particularly during the exponential growth phase. On all growth media, cells ranged between 0.5 and 1.5 \( \mu \text{m} \) in diameter and were non-motile. Cells of strain JP7\textsuperscript{T} stained Gram-negative.

Energy sources for growth of strain JP7\textsuperscript{T} were tested in shake flask culture incubated aerobically using the basal medium described above. Chemically defined inorganic substrates tested were elemental sulfur (5 g l\textsuperscript{−1}) and FeSO\textsubscript{4}.7H\textsubscript{2}O (10 g l\textsuperscript{−1}). A stock solution of FeSO\textsubscript{4}.7H\textsubscript{2}O was sterilized by filtration through a 0.2-\( \mu \text{m} \) pore size filter. Elemental sulfur was sterilized by heating at 100°C for 1 h, which was repeated twice on consecutive days. The concentration of Fe\textsuperscript{2+} was determined spectrophotometrically (Wilson, 1960). Growth on elemental sulfur was determined by phase-contrast microscopy and by measuring total solution sulfur concentration by using inductively coupled plasma optical emission spectroscopy. Although specific detection of sulfate was not performed, it was assumed that elemental sulfur was oxidized completely to sulfate as the pH of the medium decreased significantly, presumably because of production of sulfuric acid. Strain JP7\textsuperscript{T} grew successfully using Fe\textsuperscript{2+} or sulfur as an energy source, although to lower cell density than growth on chalcopyrite concentrate. Strain JP7\textsuperscript{T} oxidized Fe\textsuperscript{2+} rapidly compared with uninoculated controls; however, growth using Fe\textsuperscript{2+} as the sole energy source was not sustained in subsequent subcultures without the addition of elemental sulfur or mineral sulfide or other reduced sulfur compounds. Complex mineral sulfides were also tested as energy sources for growth of strain JP7\textsuperscript{T}. These tests were conducted in shake flasks containing basal medium at pH 0.8. Mineral sulfides tested included pyrite (1%, w/v), chalcopyrite and arsenopyrite (1–10%, w/v), which were added as sterilized, finely ground concentrates or finely ground massive sulfides. Growth was monitored with a phase-contrast microscope over three subsequent subcultures where possible. Strain JP7\textsuperscript{T} grew well on all three mineral sulfide substrates and maintained good growth over numerous subcultures on chalcopyrite and arsenopyrite up to a loading of 10% (w/v). Growth was also observed on chalcopyrite and pyrite in basal medium prepared without yeast extract at pH 0.8 over subsequent subcultures, with a cell density of 10\textsuperscript{8} cells ml\textsuperscript{−1} achieved after 5–7 days incubation. A significantly higher growth rate on chalcopyrite was achieved when the growth medium contained yeast extract, with a cell density of 10\textsuperscript{8} cells ml\textsuperscript{−1} achieved after 3 days incubation. These results suggested that strain JP7\textsuperscript{T} is a facultative autotroph, although confirmation of this via uptake of radio-labelled carbon was not performed. Optimal growth was achieved in medium containing NaCl up to a concentration of 0.5% (w/v). No growth occurred in medium containing NaCl at a concentration of 1% (w/v). Strain JP7\textsuperscript{T} was less halotolerant than previously described species of the genus Acidianus, which are able to grow in medium containing up to 4% (w/v) NaCl (Segerer et al., 1986).

Growth of strain JP7\textsuperscript{T} under anaerobic conditions was tested by using H\textsubscript{2} or H\textsubscript{2}S (Na\textsubscript{2}S.9H\textsubscript{2}O added at 2 g l\textsuperscript{−1}) as an electron donor and elemental sulfur or ferric iron [Fe\textsubscript{2}(SO\textsubscript{4})\textsubscript{3} at 10 g l\textsuperscript{−1}] as a terminal electron acceptor. A. infernus DSM 3191\textsuperscript{T}, A. ambivalens DSM 3772\textsuperscript{T} and A. brierleyi DSM 1651\textsuperscript{T} were included as reference strains in anaerobic growth tests. The media and growth conditions used were as described by Segerer et al. (1986) except that no sodium sulfide was added to the anaerobic media. All cultures showing growth were subcultured twice for confirmation of growth. A. infernus DSM 3191\textsuperscript{T} and A. ambivalens DSM 3772\textsuperscript{T} grew by oxidizing H\textsubscript{2} and by reducing elemental sulfur to H\textsubscript{2}S as expected. A. brierleyi DSM 1651\textsuperscript{T} and strain JP7\textsuperscript{T} did not grow by oxidizing H\textsubscript{2} or by reducing elemental sulfur. A. brierleyi has previously been reported to grow by oxidizing H\textsubscript{2} and by reducing elemental sulfur (Segerer et al., 1986), although, as discussed below, interpretation of this result is difficult owing to the addition of sodium sulfide (0.75 g l\textsuperscript{−1}) to the anaerobic growth medium. Strain JP7\textsuperscript{T} and A. brierleyi grew by oxidizing H\textsubscript{2}S and by reducing ferric iron (Fig. 1) both with and without the addition of organic carbon. Strain JP7\textsuperscript{T} and A. brierleyi DSM 1651\textsuperscript{T} grew when sodium sulfide was added at 0.75 g l\textsuperscript{−1}, the concentration used in the anaerobic media prepared by Segerer et al. (1986). This result suggests that the previously reported growth by A. infernus DSM 3191\textsuperscript{T}, A. ambivalens DSM 3772\textsuperscript{T} (squares) in anaerobic medium by oxidation of H\textsubscript{2}S and reduction of ferric iron. Reduction of ferric iron to ferrous iron in an uninoculated control (open circles) is also shown. No cells were detected in the uninoculated control.

**Fig. 1.** Cell densities (solid symbols) and ferrous iron concentration (open symbols) for growth of strain JP7\textsuperscript{T} (triangles) and A. brierleyi DSM 1651\textsuperscript{T} (squares) in anaerobic medium by oxidation of H\textsubscript{2}S and reduction of ferric iron. Reduction of ferric iron to ferrous iron in an uninoculated control (open circles) is also shown. No cells were detected in the uninoculated control.
Aerobic organotrophic growth by strain JP7T was tested by using glucose, sucrose, cellobiose, gelatin, yeast extract, meat extract and tryptone (each at 1 g l\(^{-1}\)), each provided separately as the sole energy source. Cell growth was monitored by phase-contrast microscopy. Basal medium containing 0.1 g yeast extract l\(^{-1}\) at pH 0.8 was used to provide a source of micronutrients, carbon or other growth requirements for testing of organic substrates. Strain JP7T was unable to grow using any of the organic substrates as a sole energy source.

The temperature range for growth of strain JP7T was determined via a temperature gradient incubator (Terratec Asia Pacific) and by application of the Ratkowsky equation (Ratkowsky et al., 1983; Plumb et al., 2002; Franzmann et al., 2005). For this test, strain JP7T was grown in a mineral-sulfide-free medium that enabled non-destructive turbidimetric measurement of growth. The medium contained (per litre) 0.4 g MgSO\(_4\cdot7\text{H}_2\text{O}\), 0.4 g (NH\(_4\))\(_2\)SO\(_4\), 0.4 g KH\(_2\)PO\(_4\), 4.0 g K\(_2\)SO\(_4\cdot6\text{H}_2\text{O}\), 2.0 g FeSO\(_4\cdot7\text{H}_2\text{O}\) and 1.0 g meat extract, with pH adjusted to 0.8 with 18 M H\(_2\)SO\(_4\). The potassium tetraethionate, ferrous sulfate and meat extract were added as filter-sterilized solutions to the basal medium after sterilization by autoclaving at 121 °C for 20 min. Biomass in cultures grown at 24 different temperatures ranging from 40 to 85 °C was quantified by measuring the optical density at 550 nm. The square root of the inverse of the time taken to reach an optical density of 0.25 at each temperature was plotted against temperature and the plot was fitted by using the Ratkowsky equation. Extrapolated minimum, optimum and maximum temperatures for growth were 45.2 ± 1.3, 74.4 ± 0.7 and 82.5 ± 0.8 °C, respectively. At the temperature closest to the extrapolated optimum at which strain JP7T was grown (72.9 °C), the generation time of strain JP7T in this mixotrophic medium was 8.4 h. Strain JP7T was not as thermophilic as A. infernus or A. ambivalens, which grew optimally at 90 and 80 °C, respectively (Segerer et al., 1986; Zillig et al., 1986), but was more thermophilic than A. brierleyi, which grew optimally at 70 °C (Segerer et al., 1986).

The pH range for growth of strain JP7T was determined by using two different approaches. Growth at different pH was tested with either basal medium containing chalcopyrite concentrate (1 %, w/v) or basal medium supplemented with FeSO\(_4\cdot7\text{H}_2\text{O}\) (10 g l\(^{-1}\)). The pH of the medium was adjusted by using concentrated H\(_2\)SO\(_4\). All pH measurements were made at room temperature by using a SenTix HW electrode and a pH 330i meter (WTW). Standard solutions of pH 2.0 and pH 1.0 buffer (Merck) were used for calibration and to test the accuracy of low pH readings. Inoculated and uninoculated control flasks were set up in duplicate. As stated above, strain JP7T required a small amount of sulfur or mineral sulfide in the growth medium in order to maintain successful growth over repeated subcultures; however, the inclusion of sulfur or mineral sulfide causes significant changes in pH of the medium owing either to acid production via sulfur oxidation or to acid consumption via mineral sulfide oxidation, and the resulting change in pH makes assessment of the pH range for growth difficult. In order to minimize changes in pH of the medium due to addition of sulfur or mineral sulfide, the effect of pH on the growth of strain JP7T was tested in basal medium containing Fe\(^{2+}\) as the sole energy source. Inoculum was prepared by growing strain JP7T in basal medium at pH 0.8 or 1.8 with chalcopyrite concentrate (1 %, w/v). All flasks were incubated in a shaker operated at ~72 °C, with shaking at 150 r.p.m. Cultures grown on chalcopyrite were monitored using a Helber counting chamber and phase-contrast microscopy. In cultures grown on ferrous sulfate, oxidation of Fe\(^{2+}\) was monitored by measuring the Fe\(^{2+}\) concentration spectrophotometrically (Wilson, 1960). Strain JP7T grew and oxidized Fe\(^{2+}\) over a broad range of pH. At the extremes of the pH range tested (pH 0.4 and 3.0) strain JP7T oxidized the least Fe\(^{2+}\) (Fig. 2a). Strain JP7T oxidized Fe\(^{2+}\) at a similar rate at pH 0.8, 1.0 and 1.4, although a slight lag prior to achieving the maximum oxidation rate was observed at pH 0.8 and 1.0. Slower rates of Fe\(^{2+}\) oxidation were observed at other test pH values, but rates of Fe\(^{2+}\) oxidation at these pH values were greater than occurred in the uninoculated controls. Growth on chalcopyrite concentrate was observed at all pH values tested up to a pH of 2.2. A comparison of the growth of strain JP7T on chalcopyrite over a range from pH 0.4 to 1.0 was made (Fig. 2b). At such a low pH, acid production or consumption by the mineral sulfide does not change pH effectively. Growth at pH 0.4, 0.6 and 0.8 occurred after an initial lag period; however, the growth rate and maximum cell density achieved at pH 0.8 and 1.0 were almost identical. In another test, cell growth was maintained over numerous subcultures in basal medium with chalcopyrite (1 %, w/v) at pH 0.35. At this extremely low pH, cells remained intact but were
Contiguous sequence (1473 bases) was assembled by using CGGCGGCTG-3. 

25Fa, 530Fa (5-cycle-sequencing kit (Applied Biosystems) and primers sequenced by using the BigDye Terminator version 3.1 kit (MO BIO Laboratories Inc.) and both strands were products were purified with the UltraClean PCR Clean-up kit (MO BIO Laboratories Inc.). The PCR of strain JP7T extended to significantly lower values than for other species of Acidianus. According to Segerer et al. (1986) and Zillig et al. (1986), the lower pH limit for growth of A. infernus, A. ambivalens and A. brierleyi was pH 1.0, with optimal growth occurring between pH 1.5 and 2.0.

The 16S rRNA gene was amplified from cells of strain JP7T by using direct lysis PCR with primers 25Fa (5’-TCYG-GTTGATCCYGCCRG-3’) and 1492R (5’-ACGGITACC-TTGTAGACCTT-3’). A 1 ml sample of culture was centrifuged at 12,000 g for 8 min to pellet the cells. Pelleted cells were resuspended in 1 ml PBS (pH 7.2) and 1 μl of this solution was then used as template for PCR by using the HotstarTaq Master Mix (Qiagen). The PCR products were purified with the UltraClean PCR Clean-up kit (MO BIO Laboratories Inc.) and both strands were sequenced by using the BigDye Terminator version 3.1 cycle-sequencing kit (Applied Biosystems) and primers 25Fa, 530Fa (5’-GTGTCAACGCCCGCCGG-3’), 934Fa (5’-AGGAAATTTGCGGAGGACGAGC-3’), 519R (5’-TTACCG-CGCCGGCTG-3’), 915R (5’-GTGCTCCGCCGCAATT-CCT-3’) and 1492R. A near-complete 16S rRNA gene contiguous sequence (1473 bases) was assembled by using Chromas Pro (Technelysium) and then compared with sequence data in the GenBank database via BLAST (Altschul et al., 1997) available at http://www.ncbi.nlm.nih.gov. The sequence was then aligned against reference sequences of species of Acidianus by using the program ARB (Ludwig et al., 2004). A phylogenetic tree was constructed by using distance matrix calculations and the neighbour-joining method (Saitou & Nei, 1987) available in the ARB program. The stability of tree nodes was evaluated by using bootstrap resampling (Felsenstein, 1985). Construction of a similarity matrix was performed also within ARB by using representative sequences from the Sulfolobales. The 16S rRNA gene sequence of strain JP7T was most closely related to that of ‘A. manzaensis’ NA-1, with a similarity of 97.2%. The 16S rRNA gene sequences of A. ambivalens DSM 3772T, A. infernus DSM 3191T, A. brierleyi DSM 1651T shared similarity of 92.6, 92.3 and 91.2 %, respectively, with that of strain JP7T. On the basis of 16S rRNA gene sequence analysis, there is probably some doubt as to whether A. brierleyi should be included in the genus Acidianus, although it shares many phenotypic similarities with other members of this genus. Similarity of the 16S rRNA gene sequence of strain JP7T to those of the type strains of two other representatives of the Sulfolobaceae, Metallosphaera prunae and Sulfolobus solfataricus, was 90 and 87.7 %, respectively. A phylogenetic tree generated from 16S rRNA gene sequence data from members of the Sulfolobales (Fig. 3) shows strain JP7T clustering with ‘A. manzaensis’. The positioning of strain JP7T with other species of the genus Acidianus was well supported according to bootstrap analysis.

Genomic DNA for the determination of base composition was extracted from a late-exponential phase culture according to the method of Plumb et al. (2001), but without the use of the bead-beating step. The DNA was purified by using the UltraClean PCR Clean-up kit (MO BIO Laboratories Inc.). Agarose gel electrophoresis was used to confirm the extraction of high-molecular-mass genomic DNA. The DNA was hydrolysed with P1 nuclease and the nucleotides were dephosphorylated with bovine alkaline phosphatase (Mesbah et al., 1989). The G+C content was determined by analysing the resultant deoxyribonucleosides by HPLC (Shimadzu Corp.). The column used for analysis was a VYDAC 201SP54 (C18, 5 μm, 250 × 4.6 mm) equipped with a 201GD54H guard column (Vydac). The DNA G + C content of strain JP7T was 31.1 mol%, which is close to that of A. ambivalens (31 mol%), A. infernus (32.7 mol%) and A. brierleyi (31.5 mol%) (Segerer et al., 1986; Zillig et al., 1986).

Freeze-dried biomass collected from cultures of strain JP7T was used to characterize the cell membrane phospholipids. Biomass was placed in a thick-walled test tube along with 3 ml of a mixture containing 10:1:1 methanol/CHCl3/concentrated HCl. The test tube was capped and the mixture was heated overnight at 95 °C in a water bath. After cooling, 1 ml water was added and the reaction mixture was extracted three times with 1.8 ml portions of a 4:1 mixture of n-hexane and CH2Cl2. The extracts were pooled and the

![Fig. 2. Plot showing the relationship between growth and pH for strain JP7T based on oxidation of Fe²⁺ (a) and growth on chalcopyrite concentrate (b).](http://ijs.sgmjournals.org)
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The solvent was removed under a stream of N₂. The ether lipids were stored at −20 °C. Gas chromatographic analysis was carried out by using a Hewlett Packard 5890 gas chromatograph equipped with an on-column auto-injector and a flame-ionization detector that was maintained at 405 °C. The capillary column used was a 2.5-m polyimide-clad SGE HT5, with an internal diameter of 0.25 mm and a film thickness of 0.1 µm (SGE International). Samples were injected with the injector and column at 30 °C. The oven temperature was maintained for 2 min, then increased at 35 °C min⁻¹ to 350 °C and then at 5 °C min⁻¹ to 400 °C. At the end of the run, the oven was cooled at a rate of 30 °C min⁻¹ in order to reduce the likelihood of column damage as a result of rapid temperature change. The carrier gas was helium and the head pressure was 35 kPa. The ether lipids eluted as well-separated peaks. The concentrations of glycerol dialkyl glycerol tetraethers (GDGTs) and glycerol dialkyldialkyl glycerol tetraethers (calditols) were determined. Analysis of the ether lipids in strain JP7T showed an almost 50:50 split between GDGTs and calditols. Cyclized forms of each of these tetraethers with one to eight mid-chain cyclopentyl rings were detected, with the majority of tetraethers containing six rings. Although the distribution of cyclized tetraether lipids varies according to factors such as temperature and pH, this ether lipid profile was consistent with profiles of members of the Sulfolobales grown at high temperature (De Rosa et al., 1983).

The phenotypic and genotypic characteristics described above suggest that strain JP7T is a member of the genus Acidianus. Differences in 16S rRNA gene sequence, aerobic and anaerobic growth, temperature range for growth and pH range for growth justify the conclusion that strain JP7T represents a novel species of the genus Acidianus. The name Acidianus sulfidivorans sp. nov. is proposed for this novel species.

**Emended description of Acidianus Segerer et al. 1986**

Cells are Gram-negative and occur singly or occasionally in pairs during exponential growth; the cells have an irregular coccoid morphology (sometimes lobed or showing sharp bends, and resembling tetrahedrons, pyramids, discs or dishes). Cells are non-motile. Cell width is between 0.5 and 2 µm, depending on culture conditions. A surrounding envelope about 25 nm wide covering the cell membrane is evident in thin section. The envelope is composed of sub-units in a hexagonal array. The cells are facultative aerobes. Lithotrophic growth occurs aerobically by means of S⁰ oxidation, mineral sulfide oxidation or Fe⁡²⁺ oxidation. Anaerobic growth occurs by means of S⁰ reduction with H₂ or H₂S. The cells are autotrophic and may grow organotrophically on yeast extract without S⁰ in the presence of O₂. The organisms are thermoadophilic, thriving between pH 0.35 and 6 and between 45 and 96 °C. They grow in the presence of 0.1 % NaCl and may grow in media containing up to 4 % NaCl. Neither muramic acid nor meso-diaminopimelic acid is present, indicating the absence of murein. Elongation factor 2 is sensitive to adenosine diphosphate ribosylation by diphtheria toxin. Cells contain isoprenyl ether lipids, which consist of GDGTs and calditols, including lipids with mid-chain cyclopentyl rings, and also caldariellaquinone. Members of the genus are resistant to vancomycin, ampicillin and kanamycin (150 µg ml⁻¹ each). DNA-dependent RNA polymerase shows incomplete immunological cross-reactions with antibody against DNA-dependent RNA polymerase from Sulfolobus acidocaldarius DSM 639T. The purified DNA has a G+C content of 31–33 mol%. Members of the genus occur in acidic solfataras and in marine hydrothermal systems. The type species is Acidianus infernus.

**Description of Acidianus sulfidivorans sp. nov.**


Displays the following properties in addition to those given in the emended genus description. Cells are 0.5–1.5 µm in diameter. Growth is obligately chemolithotrophic. Good
growth occurs under aerobic conditions on elemental sulfur, ferrous iron, pyrite and other mineral sulfides. Under anaerobic conditions, ferrous iron or elemental sulfur serve as the terminal electron acceptor for growth via oxidation of H₂S. Cells do not grow using elemental sulfur as a terminal electron acceptor for oxidation of H₂. Cells are facultatively autotrophic, as they grow when provided with CO₂ as the sole source of carbon and heterotrophically using yeast extract or meat extract as a carbon source. Cells do not grow organotrophically. Cells grow over a range of temperatures from 45 to 83 °C, with optimum growth at 74 °C. The pH range for growth is 0.35–3.0, with optimal growth at pH 0.8–1.4. Optimal growth occurs at up to 0.5 % (w/v) NaCl. The DNA G+C content is 31.1 mol%. Cell membrane lipids consist of a mixture of GDGTs and glycerol dialkyl calditol tetraethers, most of which are cyclized tetraethers.

The type strain, JP7T (=DSM 18786T = JCM 13667T), was isolated from the sulfur-rich acidic edge of a solfataric hot spring.

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References


