Taxonomic rearrangements of the genera *Thiocapsa* and *Amoebobacter* on the basis of 16S rDNA sequence analyses, and description of *Thiolamprovum* gen. nov.

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Complete nucleotide sequences of the 16S rDNAs were determined from *Thiocapsa* and *Amoebobacter* species, including all available type strains and some additional isolates. The distance-matrix analysis and the dendrogram for estimating the genetic relationships revealed that the investigated strains were found in two major clusters within the *Chromatiaceae*. One cluster comprises all *Amoebobacter* species, *Thiocapsa roseopersicina* and several isolates related to *Thiocapsa roseopersicina*. Representatives of the species *Amoebobacter roseus*, *Amoebobacter pendens* and *Thiocapsa roseopersicina*, the so called 'Thiocapsa roseopersicina group', are very closely related, justifying their inclusion into one genus, *Thiocapsa*, for which an emended description is presented. *Amoebobacter purpureus* and *Amoebobacter pedioformis* formed two separate lines of descent with less than 93\% (89.6-92.9\%) similarity to strains of the 'Thiocapsa roseopersicina group'. Therefore, they will be considered as two separate genera. As a consequence, an emended description is presented for the genus *Amoebobacter*, with *Amoebobacter purpureus* as the new type species and *A. pedioformis* is transferred to *Thiolamprovum pedioforme* gen. nov., comb. nov. Two species, *Thiocapsa pfennigii* and *Thiocapsa halophila*, which have been classified with the genus *Thiocapsa* because of their morphological properties, were found within another major cluster of the *Chromatiaceae* and are only distantly phylogenetically related to the first cluster with 88.4-90.6\% and 90.4-92.2\% sequence similarity, respectively.

**Keywords:** *Thiocapsa*, *Amoebobacter*, *Thiolamprovum*, *Chromatiaceae*, 16S rDNA sequences, genetic relationships, taxonomy

INTRODUCTION

Classification of *Chromatiaceae* (Bavendamm 1924, emend. Imhoff 1984) has been inherited from the morphological studies of Winogradsky (1888) and is still principally based on phenotypic characteristics. The first studies to establish genetic relationships of *Chromatiaceae* species were carried out on the basis of 16S rRNA oligonucleotide cataloguing (Fowler et al., 1984). They demonstrated that these bacteria are moderately related but form a coherent phylogenetic group for which the family name *Chromatiaceae* is justified. They also revealed strong discrepancies between phylogenetic relatedness and the taxonomic system of the family, based on phenotypic traits. Their study demanded more detailed investigations on the phylogenetic relationships within this family to establish a proper basis for a phylogenetically oriented taxonomy.

The first complete 16S rDNA sequences among the *Chromatiaceae* were obtained for *Chromatium vinosum* (De Weerd et al., 1990) and *Chromatium tepidum* (Wahlund et al., 1991). Recently, with the description...
of the new genera and species *Rhabdochromatium marinum* (Dilling et al., 1995), *Chromatium glycolicum* (Caumette et al., 1997) and *Thiorhodococcus minus* (Guyoneaud et al., 1997), more 16S rDNA sequences became available, which confirmed the non-phylogenetic nature of the phenotypic classification of the *Chromatiaceae* (Guyoneaud et al., 1997).

The genera *Thiocapsa* and *Amoebobacter* comprise the spherical and non-motile representatives of the *Chromatiaceae*. The differentiation between the two genera is based on the presence or absence of gas vesicles. In the case of *Ectothiorhodospiraceae* (Imhoff & Siling, 1996) and green sulfur bacteria (Overmann & Tuscheck, 1997), the possession of gas vesicles is not considered to be of taxonomic relevance at the genus level. Moreover, the study based on 16S rRNA oligonucleotide cataloguing (Fowler et al., 1984) had already revealed that some species of these two genera (*Thiocapsa roseopersicina*, *Amoebobacter pendens* and *Amoebobacter roseus*) are very closely related (S values > 0.93) and may actually comprise species of a single genus. Since this work, several new species have been described for both genera: *Amoebobacter pedioformis* (Eichler & Pfennig, 1986), *Amoebobacter purpureus* (Eichler & Pfennig, 1988) and *Thiocapsa halophila* (Caumette et al., 1991). In addition, strains resembling *Thiocapsa roseopersicina* but containing okenone instead of spirilloxanthin as the major carotenoid were isolated (Caumette et al., 1985). These new isolates were described and classified according to their phenotypic traits. Their genetic relationships have not been investigated so far. We have analysed the 16S rDNA sequences of the known species of the genera *Thiocapsa* and *Amoebobacter* (including all available type strains) and propose a taxonomic rearrangement at the genus level.

### METHODS

**Source and culture of bacterial strains.** All *Thiocapsa* and *Amoebobacter* strains used for this study are listed in Table 1, which shows the previously used and the newly proposed names, the original strain designations, the DSM numbers (where available) and the EMBL accession numbers for their 16S rDNA sequences. Cultures of all strains are now maintained in our laboratories (see Table 1).

Strains were cultivated in a synthetic medium prepared anaerobically according to Pfennig & Trüper (1992). The medium contained: 0.03% KH2PO4; 0.05% NH4Cl; 0.005% CaCl2·2H2O; 0.1% MgCl2·6H2O; 0.05% MgSO4·7H2O; 1 ml trace-element solution SL121 (Pfennig & Trüper, 1992); 0.02 mg vitamin B12; 0.15% NaHCO3·0.05% Na2S·9H2O; final pH 7.2. In addition, for some strains, 2% NaCl (strains DSM 5811, DSM 5812, DSM 5813) or 6% NaCl (strain DSM 6210) was added to the medium. Pure cultures were grown and maintained in 50 ml screw-capped bottles filled with synthetic medium.

**PCR amplification and 16S rDNA sequencing and analysis.** DNA for sequencing of 16S rRNA genes was obtained either from 1-2 ml well-grown liquid cultures or from freeze-dried material (*A. pedioformis* DSM 3802, *A. roseus* DSM 235 and *A. pendens* 5813). DNA was extracted and purified by using the QIAGEN genomic DNA buffer set. Recombinant Taq DNA polymerase was used for PCR (Mullis & Faloona, 1987) with the primers: 5'-GTTTGTATCTTGCTCAG-3' and 5'-TACCTTGTAGCATCTCA-3' (positions 11-27 and 1489-1506, respectively; according to the *Escherichia*

<table>
<thead>
<tr>
<th>Previous name</th>
<th>New name</th>
<th>DSM no.</th>
<th>Original designation</th>
<th>EMBL accession no.</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Thiocapsa roseopersicina</em></td>
<td><em>Thiocapsa roseopersicina</em></td>
<td>DSM 217T</td>
<td>1711</td>
<td>Y12364</td>
<td>Pfennig (1989a, b), Pfennig &amp; Trüper (1971a, b)</td>
</tr>
<tr>
<td>'Thiocapsa roseopersicina'</td>
<td><em>Thiocapsa sp.</em></td>
<td>-</td>
<td>9314</td>
<td>Y12303</td>
<td>Mandel et al. (1971)*</td>
</tr>
<tr>
<td>'Thiocapsa roseopersicina'</td>
<td><em>Thiocapsa sp.</em></td>
<td>-</td>
<td>10511</td>
<td>Y12300</td>
<td>Guyoneaud et al. (1997)†</td>
</tr>
<tr>
<td>'Thiocapsa roseopersicina'</td>
<td><em>Thiocapsa sp.</em></td>
<td>-</td>
<td>CE2209</td>
<td>Y12298</td>
<td>Guyoneaud et al. (1996)</td>
</tr>
<tr>
<td>'Thiocapsa roseopersicina'</td>
<td><em>Thiocapsa sp.</em></td>
<td>DSM 5653</td>
<td>5811</td>
<td>Y12301</td>
<td>Caumette et al. (1985)</td>
</tr>
<tr>
<td>'Thiocapsa roseopersicina'</td>
<td><em>Thiocapsa sp.</em></td>
<td>-</td>
<td>5812</td>
<td>Y12302</td>
<td>Caumette (1986)</td>
</tr>
<tr>
<td><em>Thiocapsa halophila</em></td>
<td>Uncertain affiliation</td>
<td>DSM 6210T</td>
<td>SG3202</td>
<td>AJ002796</td>
<td>Caumette et al. (1991)</td>
</tr>
<tr>
<td><em>Thiocapsa pfennigi</em></td>
<td>Uncertain affiliation</td>
<td>DSM 226</td>
<td>8013</td>
<td>Y12373</td>
<td>Mandel et al. (1971)*</td>
</tr>
<tr>
<td><em>Amoebobacter pendens</em></td>
<td><em>Thiocapsa sp.</em></td>
<td>DSM 5652</td>
<td>5813</td>
<td>Y12396</td>
<td>Caumette et al. (1985)</td>
</tr>
<tr>
<td><em>Amoebobacter pendens</em></td>
<td><em>Thiocapsa pendens</em></td>
<td>DSM 236T</td>
<td>1314</td>
<td>AJ002797</td>
<td>Pfennig (1989a, b), Pfennig &amp; Trüper (1971a, b)</td>
</tr>
<tr>
<td><em>Amoebobacter roseus</em></td>
<td><em>Thiocapsa rosea</em></td>
<td>DSM 235T</td>
<td>6611</td>
<td>AJ002798</td>
<td>Pfennig (1989a, b), Pfennig &amp; Trüper (1971a, b)</td>
</tr>
<tr>
<td><em>Amoebobacter purpureus</em></td>
<td><em>Amoebobacter purpureus</em></td>
<td>DSM 4197T</td>
<td>ThSchl2</td>
<td>Y12366</td>
<td>Eichler &amp; Pfennig (1988)</td>
</tr>
<tr>
<td><em>Amoebobacter pedioformis</em></td>
<td><em>Thiolamprovum pedioforme</em></td>
<td>DSM 3802T</td>
<td>CML2</td>
<td>Y12297</td>
<td>Eichler &amp; Pfennig (1986)</td>
</tr>
</tbody>
</table>

* These strains have not been described phenotypically in the literature.  
† Reference for 16S rDNA sequence.  
‡ Tentatively designated as *Thiocapsa roseopersicina forma specialis* by Caumette et al. (1985).
RESULTS AND DISCUSSION

Sequences of 16S rDNA from a number of strains of *Thiocapsa* and *Amoebobacter* species were determined, aligned and compared to those of other *Chromatiaceae*, *Ectothiorhodospiridae*, and *Halorhodospiridae* coli, which were available from the EMBL database. Sequence similarity and evolutionary distances ($K_{uew}$ values) are presented in Table 2; a dendrogram calculated on the basis of these values is shown in Fig. 1. The 16S rDNA gene sequence analysis confirmed that the representatives of the genera *Thiocapsa* and *Amoebobacter* are true members of the *Chromatiaceae*, placed within the gamma-Proteobacteria. Within the radiation of the family *Chromatiaceae*, the strains investigated were found in two clusters. Most of the strains formed one distinct cluster, which was not distinctly affiliated with one of the available reference organisms from this family (see Fig. 1). This cluster comprises all *Amoebobacter* species, *Thiocapsa roseopersicina* and strains related to this latter species. The analysis suggests a common ancestor of all of these strains and of *Chromatium vinosum* and related species. Two species were found within a second cluster, which includes ‘Thiocapsa pfennigii’ and ‘Thiocapsa halophila’ as well as *Rhabdocchromatium marina* and other marine *Chromatiaceae*.

Within the first cluster, *Thiocapsa roseopersicina*, *A. roseus* and *A. pendens* formed a closely related group (in the following referred to as the ‘Thiocapsa roseopersicina group’) with a minimum of 93.9% sequence similarity between the strains included in this study. These results are in agreement with the previous studies on 16S rRNA oligonucleotide cataloging (Fowler et al., 1984), which already recognized the close relationship of these species ($S_{AB}$ value of 0.93). *Amoebobacter purpureus* and *A. pedioformis*, however, formed two different lineages separated from the representatives of the ‘Thiocapsa roseopersicina group’. The sequence similarity between *A. purpureus*, *A. pedioformis* and all the other strains of this cluster was 89.6–91.9 and 88.9–92.9%, respectively. Moreover, the sequence similarity between *A. purpureus* and *A. pedioformis* was 88.9%, suggesting that these two species belong to two separate genera. First of all, these results demonstrate a large phylogenetic distance between presently recognized species.

### Table 2. Levels of 16S rDNA sequence similarity and evolutionary distances of presently recognized *Thiocapsa* and *Amoebobacter* species with other phototrophic purple sulfur bacteria and *Escherichia coli* as reference species.

<table>
<thead>
<tr>
<th>Organism</th>
<th>Sequence similarity (%)</th>
<th>evolutionary distance ($K_{uew}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 <em>Thiocapsa penguinii</em> DSM 2267</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>2 <em>Thiocapsa halophila</em> DSM 62105</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>3 <em>Rhabdocchromatium marinae</em> DSM 2617</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>4 <em>Chromatium gracile</em> DSM 203</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>5 <em>Chromatium minutum</em> DSM 1806</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>6 <em>Thiocapsa roseopersicina</em> DSM 217</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>7 <em>Thiocapsa roseopersicina</em> DSM 314</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>8 <em>Amoebobacter pendens</em> DSM 2367</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>9 <em>Amoebobacter pendens</em> DSM 5652</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>10 <em>Amoebobacter roseus</em> DSM 253</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>11 <em>Thiocapsa roseopersicina</em> DSM 3653</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>12 <em>Amoebobacter pedoformis</em> DSM 3802</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>13 <em>Thiocapsa roseopersicina</em> DSM 10511</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>14 <em>Thiocapsa roseopersicina</em> DSM 2209</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>15 <em>Amoebobacter purpureus</em> DSM 4197</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>16 <em>Amoebobacter pedoformis</em> DSM 3802</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>17 <em>Thiocapsa violacea</em> DSM 2042</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>18 <em>Thiocapsa roseopersicina</em> DSM 2437</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>19 <em>Amoebobacter pendens</em> DSM 2367</td>
<td>90.3</td>
<td>10.0</td>
</tr>
<tr>
<td>20 <em>Escherichia coli</em></td>
<td>90.3</td>
<td>10.0</td>
</tr>
</tbody>
</table>

Alignment length was 1400 positions including gaps (bases 29–1381, according to *Escherichia coli* numbering). All strains were fitted to that size except for ‘Thiocapsa roseopersicina’, DSM 217 (positions 69–1363 according to *Escherichia coli* numbering) and *A. roseus*, DSM 235 (positions 71–1374 according to *Escherichia coli* numbering). The values on the upper right are the uncorrected percentages of sequence similarity; the values on the lower left are $K_{uew}$ values corrected for multiple base change by the method of Jukes & Cantor (1969).

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**col** 16S rRNA numbering of the International Union of Biochemistry). The PCR products were purified by using the QIAquick PCR purification kit. Sequences were obtained by cycle sequencing with the SequiTherm sequencing kit (Pharmacia). Sequences were aligned using the CLUSTAL W program (Thompson et al., 1994). The alignment was from position 29–1381 according to the Escherichia coli numbering (including gaps, approx. 1400 positions). The distance matrix was calculated on the basis of the algorithm according to Jukes & Cantor (1969) with the DNADIST program within the PHYLIP package (Felsenstein, 1989). The FITCH program within the PHYLIP package fitted a tree to the evolutionary distances.

**Table 2.** Levels of 16S rRNA sequence similarity and evolutionary distances of presently recognized *Thiocapsa* and *Amoebobacter* species with other phototrophic purple sulfur bacteria and *Escherichia coli* as reference species.
Fig. 1. Phylogenetic tree showing the relationships on the basis of 16S rDNA sequence similarity of strains belonging to the genera *Thiocapsa* and *Amoebobacter* together with other purple sulfur bacteria and *Escherichia coli* as reference organisms. Strain numbers and deposition numbers of the 16S rDNA sequences (in brackets) of reference strains not included in Table 1 are as follows: *Thiocapsa roseopersicina* DSM 217T (M59151), *Halorhodospira halophila* DSM 244T (M26630), *Escherichia coli* (K02555).

**Table 3.** Differential phenotypic traits of the genera *Thiocapsa*, *Amoebobacter* and *Thiolampro vum*

Data from references cited in Table 1. Bchl, bacteriochlorophyll; sp, spirilloxanthin; ok, okenone. Substrates used by all strains (+), some strains (+ / -) or not used (-).

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Thiocapsa</th>
<th>Amoebobacter</th>
<th>Thiolamprovum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural habitat</td>
<td>Water/mud from freshwater to marine environments</td>
<td>Stratified lakes</td>
<td>Wastewater ponds</td>
</tr>
<tr>
<td>Aggregate pattern</td>
<td>Tetrads, small irregular aggregates</td>
<td>Clumps of up to 40 cells</td>
<td>Platelets</td>
</tr>
<tr>
<td>Cell morphology</td>
<td>Spherical</td>
<td>Spherical/oval</td>
<td>Spherical/oval</td>
</tr>
<tr>
<td>Cell size (µm)</td>
<td>1.0-3.0</td>
<td>1.9-3.8 x 2.0-4.5</td>
<td>2.0 x 2.0-3.0</td>
</tr>
<tr>
<td>Gas vesicles</td>
<td>[+/-]</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Bchl/carotenoid</td>
<td>Bchl a/sp, ok</td>
<td>Bchl a/ok</td>
<td>Bchl a/sp</td>
</tr>
<tr>
<td>Internal membranes</td>
<td>Vesicular</td>
<td>Vesicular</td>
<td>Vesicular</td>
</tr>
<tr>
<td>G + C content (mol%)</td>
<td>63.3-66.3</td>
<td>63.4-64.1</td>
<td>64.5-66.5</td>
</tr>
<tr>
<td>Substrates used:</td>
<td>Sulfide</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Thiosulfate</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Propionate</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Pyruvate</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Malate</td>
<td>+</td>
<td>-</td>
</tr>
</tbody>
</table>
of the genus *Thiocapsa*; *Thiocapsa roseopersicina* (the type species), *Thiocapsa pfennigii* and *Thiocapsa halophila*, which have been classified into the genus *Thiocapsa* on the basis of morphological properties (non-motile cocci with internal sulfur globules). The sequence differences, however, do not merit the grouping of these species within one genus. Therefore, *Thiocapsa pfennigii* and *Thiocapsa halophila* have to be removed from the genus *Thiocapsa*, the name of which will stay with the type species, *Thiocapsa roseopersicina*. A formal taxonomic transfer will not be proposed at this stage, because the exact relationship of these two bacteria with other members of the Chromatiaceae is presently not established.

The second major consequence of our results is the close phylogenetic relationships between *Thiocapsa roseopersicina* and *A. roseus* as well as other Amoebobacter species. *Thiocapsa roseopersicina* may have evolved from an ancestor containing gas vesicles by loss of this property; some strains may still contain genes for the production of gas vesicles and may even be able to form such vesicles under certain, so far unrecognized, conditions. Nonetheless, it is obvious that the formation of gas vesicles is not of taxonomic relevance at the genus level. Other phenotypic features have to be considered to separate *A. purpureus*, *A. pedioformis* and representatives of the 'Thiocapsa roseopersicina group'. Morphological traits such as cell morphology, aggregate patterns and the presence or absence of a strong slime capsule (Table 3) may be considered for characterizing the species. Therefore, on the basis of genetic and phenotypic properties, we propose to maintain the genus *Amoebobacter*, with *A. purpureus* as the new type species and to transfer *A. pedioformis* to Thiolarnprovurn pedioformae gen. nov., comb. nov.

The 'Thiocapsa roseopersicina group' is represented by three species: *Thiocapsa roseopersicina*, *A. pendens* and *A. roseus*. The strains studied do form two sub-groups, corresponding to the three type strains of the species and a second group of isolates tentatively assigned to *Thiocapsa roseopersicina* and *A. pendens*, respectively (Table 1, Fig. 1).

Apart from the formation of gas vesicles, which could be of taxonomic importance at the species level, some physiological features such as substrate utilization and chemolithoautotrophic growth capacities separate the three existing species (Table 4). All strains of *Thiocapsa roseopersicina* characteristically use hydrogen, glycerol, fructose, succinate, fumarate and malate as substrates. *A. pendens* and *A. roseus* do not use hydrogen, glycerol, succinate or fumarate (Table 4). In addition, *A. roseus* does not use malate, whereas *A.

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**Table 4. Differential phenotypic traits of the type strains of the recognized species of the genus *Thiocapsa***

Data from references given in Table 1 and this study. See Table 3 legend for symbols and abbreviations.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th><em>Thiocapsa roseopersicina</em> (DSM 217T)</th>
<th><em>Thiocapsa pendens</em> (DSM 236T)</th>
<th><em>Thiocapsa rosea</em> (DSM 235T)</th>
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</thead>
<tbody>
<tr>
<td>Cell morphology</td>
<td>Spherical</td>
<td>Spherical</td>
<td>Spherical</td>
</tr>
<tr>
<td>Cell size (µm)</td>
<td>1.0–3.0</td>
<td>1.5–2.0</td>
<td>2.0–3.0</td>
</tr>
<tr>
<td>Gas vesicles</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Bchl/carotenoid</td>
<td>Bchl a/sp</td>
<td>Bchl a/sp</td>
<td>Bchl a/sp</td>
</tr>
<tr>
<td>G+C content (mol%)</td>
<td>65.3</td>
<td>65.3</td>
<td>64.3</td>
</tr>
<tr>
<td>SO₄²⁻-assimilation</td>
<td>+</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Chemotrophic growth</td>
<td>+</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Substrates used:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydrogen</td>
<td>+</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Sulfide</td>
<td>+</td>
<td>+</td>
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<tr>
<td>Thiosulfate</td>
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<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Formate</td>
<td>–</td>
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<tr>
<td>Acetate</td>
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</tr>
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<td>Propionate</td>
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</tr>
<tr>
<td>Pyruvate</td>
<td>+</td>
<td>+</td>
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</tr>
<tr>
<td>Malate</td>
<td>+</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>Succinate</td>
<td>+</td>
<td>–</td>
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<tr>
<td>Fumarate</td>
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<td>Glucose</td>
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<td>Fructose</td>
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<td>Glycerol</td>
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pendens is the only species able to use glucose but not fructose. *Thiocapsa roseopersicina* and *A. roseus* can grow chemolithoautotrophically with oxygen in the dark (De Wit & van Gemerden, 1987; Kampf & Pfennig, 1980; Overmann & Pfennig, 1992). The two strains classified as *A. pendens* exhibited differences with regard to chemotrophic growth. *A. pendens* DSM 236T is unable to grow chemotrophically (Kampf & Pfennig, 1980) whereas ‘Amoebobacter pendens’ DSM 5652 grows chemolithoautotrophically (Overmann & Pfennig, 1992). This strain had been originally and tentatively identified as a *Thiocapsa roseopersicina* (Caumette et al., 1985), but was later reclassified as *A. pendens* (Eichler & Pfennig, 1986), although it was different from the type strain of this species with regard to chemotrophic growth and gas vesicles were not always present.

Because ‘it is the presence or absence of phenotypic coherency among strains that should be the deciding factor’ (Stackebrandt & Goebel, 1994), we propose to maintain these three existing species and to consider them as members of the genus *Thiocapsa*, with *Thiocapsa roseopersicina* as the type species. Therefore, we propose to transfer *A. pendens* to *Thiocapsa pendens* comb. nov. and *A. roseus* to *Thiocapsa rosea* comb. nov.

Within this genus, strains 5811 (DSM 5653) and 5812 were mentioned as *Thiocapsa roseopersicina forma specialis* (Caumette et al., 1985), because they contain okenone as the major carotenoid, while the other phenotypic traits were identical to those of *Thiocapsa roseopersicina* (Table 4). They are closely related genetically (Table 2), and could probably be described as a new species within the genus *Thiocapsa* on the basis of genetic relationship and pigment composition. Nevertheless, they both are closely related to the *Thiocapsa* sp. strain 10511 (97-4 and 97-3% sequence similarity, respectively), which contains spirilloxanthin as the main carotenoid. A decision at the species level would require DNA–DNA reassociation studies and is therefore not proposed at the present level of our knowledge. A similar uncertainty that could possibly be resolved by hybridization studies is the exact species assignment of other strains, which have been tentatively identified as belonging to *Thiocapsa roseopersicina* (CE2209, 9314, 10511) and *A. pendens* (DSM 5652). However, knowledge of genetic relationships and phenotypic features undoubtedly permit an assignment of these strains to the genus *Thiocapsa*.

Emended descriptions of the genera *Thiocapsa* and *Amoebobacter* are given, and the following taxonomic changes are proposed: transfer of *Amoebobacter roseus* (the former type species of the genus *Amoebobacter*) to the genus *Thiocapsa* and description as a new combination, *Thiocapsa rosea* comb. nov.; transfer of *Amoebobacter pendens* to the genus *Thiocapsa* and description as a new combination, *Thiocapsa pendens* comb. nov.; definition of *Amoebobacter purpureus* as the new type species of the genus *Amoebobacter*; removal of *Thiocapsa pfennigii* and *Thiocapsa halophila* from the genus *Thiocapsa*; and transfer of *Amoebobacter pedioformis* to the new genus *Thiolamprovum* gen. nov. as *Thiolamprovum pedioforme* comb. nov.

Emended description of the genus *Thiocapsa* Winogradsky 1888, 84A

*Thiocapsa* (Thi.o.cap'sa. Gr. n. thios sulfur; L. n. capsa box; M.L. fem. n. Thiocapsa sulfur box).

Cells are spherical, 1-0-3 µm in diameter, diplococci before multiplication by binary fission and are non-motile. Tetrads may be formed after consecutive division in two perpendicular planes. Individual cells are surrounded by a strong slime capsule. May contain gas vesicles. Gram-negative. Internal photosynthetic membrane system of vesicular type containing the photosynthetic pigments bacteriochlorophyll a and carotenoids. Phototrophic under anoxic conditions in the light, may be chemoautotrophic or mixotrophic under micro-oxic to oxic conditions in the dark. Capable of photolithoautotrophic growth with sulfide, thiosulfate and sulfur as electron donor. Elemental sulfur globules are transiently stored inside the cells, final oxidation product is sulfate. May require vitamin B12. The G+C content of the DNA is 63-3-66-3 mol% (Bd). Type species is *Thiocapsa roseopersicina*.

Description of *Thiocapsa rosea* comb. nov. *(Amoebobacter roseus* Winogradsky 1888, 77A)

*Thiocapsa rosea* (ro'se.a. L. adj. rosea rosy, rose-coloured, pink).

The description is the same as that given by Winogradsky (1888) and Pfennig (1989b). Neotype strain is DSM 235 (= strain 6611, Davis).

Description of *Thiocapsa pendens* comb. nov. *(Amoebobacter pendens* Pfennig and Trüper 1971, 13A; *Rhodothece pendens* Molisch 1906, 230)

*Thiocapsa pendens* (pen'dens. L. part. adj. pendens hanging).

The description is the same as that given by Pfennig, (1989b) and Pfennig & Trüper (1971a). Neotype strain is DSM 236 (= strain 1314, Klein-Kalden).

Emended description of the genus *Amoebobacter* Winogradsky 1888, 71A

*Amoebobacter* (A.moe.bo.bac'ter. Gr. n. amoebe change, transformation; M.L. n. bacter a rod; M.L. masc. n. Amoebobacter changeable rod).

Cells are nearly spherical to oval, 1-9-3-8 x 2-0-4-5 µm in size, may occur in irregular aggregates of up to 40 cells, multiplication by binary fission, non-motile, Gram-negative. Internal photosynthetic membrane system of vesicular type containing the photosynthetic
pigmens bacteriochlorophyll a and carotenoids. Phototrophic under anoxic conditions in the light, may be chemoaotrophic or mixotrophic under micro-oxic conditions in the dark. Capable of photolithoautotrophic growth with sulfide, thiosulfate and elemental sulfur as electron donor, elemental sulfur globules are transiently stored inside the cells, final oxidation product is sulfate. Assimilatory sulfur reduction lacking. The G+C content of the DNA is 63.4–64.1 mol% (Bd). Type species is Amoebobacter purpureus.

Description of *Amoebobacter purpureus* Eichler and Pfennig 1988

*Amoebobacter purpureus* (pur.pur'e.us. L. masc. adj. purpureus purple or purple-red).
The description is the same as that given by Eichler & Pfennig (1988). Type strain is DSM 4197T (=strain ThSchl2T, =SchleinseeT).

Description of *Thiolamprovum* gen. nov.

*Thiolamprovum* (Thi.o.lam.pro'vum. Gr. n. thios sulfur; Gr. n. lampros bright, brilliant; L. n. ovum egg; M.L. masc. n. Thiolamprovum bright egg with sulfur).

Cells nearly spherical to oval, 2 x 2–3 μm in size, may occur in regular platelets of 4–16 cells, multiplication by binary fission, non-motile, Gram-negative. Internal photosynthetic membrane system of vesicular type containing the photosynthetic pigments bacteriochlorophyll a and carotenoids. Phototrophic under anoxic conditions, may be chemoaotrophic or mixotrophic under micro-oxic conditions in the dark. Capable of photolithoautotrophic growth with sulfide, thiosulfate and elemental sulfur as electron donor, elemental sulfur globules are transiently stored inside the cells, final oxidation product is sulfate. Assimilatory sulfate reduction lacking. The G+C content of the DNA is 64.5–66.5 mol% (Bd). Type species is Thiolamprovum pedioforme.

Description of *Thiolamprovum pedioforme* comb. nov. (*Amoebobacter pedioformis* Eichler and Pfennig 1986)

*Thiolamprovum pedioforme* (pe.di.o.for'me. Gr. n. pedion a plain, a flat area; L. n. forma shape; M.L. neut. adj. pedioforme flat-shaped).
The description is the same as that given by Eichler & Pfennig (1986). Type strain is DSM 3802T (=strain CML2T, =TaichungT).

REFERENCES


