Reclassification of Angiococcus disciformis, Cystobacter minus and Cystobacter violaceus as Archangium disciforme comb. nov., Archangium minus comb. nov. and Archangium violaceum comb. nov., unification of the families Archangiaceae and Cystobacteraceae, and emended descriptions of the families Myxococcaceae and Archangiaceae

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The species Archangium gephyra, Angiococcus disciformis, Cystobacter minus and Cystobacter violaceus are currently classified in three different genera of the order Myxococcales. The 16S rRNA gene sequences of the respective type strains show a similarity higher than 98.4 % and form a tight phylogenetic group. A dendrogram calculating the similarity of MALDI-TOF spectra confirmed the close relatedness of the four species that grouped in a monophyletic cluster in the neighbourhood of other species of the genus Cystobacter. The type strains shared similar fatty acid patterns of high complexity with iso-C₁₅ : 0, C₁₈ : 0ω5c and iso-C₁₄ : 0 3-OH as the major components. The vegetative cells of these species are uniformly long needle-shaped rods, and the myxospores are short rods, ovoid or irregularly spherical thus differing from the myxospores of species related to Cystobacter fuscus, the type species of this genus. Some enzymic and hydrolysing reactions of the type strains are described. As a result of the high relatedness and similarity of the four species, it is proposed to place them into one genus, and due to phylogenetic and morphological distinctness, the species should be classified in a genus distinct from the genus Cystobacter as Archangium gephyra (type strain M18T=DSM 2261T=ATCC 25201T=NBRC 100087T), Archangium disciforme comb. nov. (type strain CMU 1T=DSM 52716T=ATCC 33172T), Archangium minus comb. nov. (proposed neotype strain Cb m2=DSM 14751T=JCM 12627) and Archangium violaceum comb. nov. (type strain Cb vi61T=DSM 14727T=CIP 109131T=JCM 12629T). Since the family Archangiaceae Jahn 1924 AL has priority over the family Cystobacteraceae McCurdy 1970 AL, it is proposed to assign the genera Archangium, Anaeromyxobacter, Cystobacter, Hyalangium, Melittangium and Stigmatella to the family Archangiaceae. Emended descriptions of the families Myxococcaceae and Archangiaceae are also provided.

At times when morphology was the most important feature in the taxonomy of myxobacteria, four species had been assigned to three different genera. Archangium gephyra, Angiococcus disciformis (listed as Myxococcus disciformis, see below for details) and Cystobacter minus are listed in the Approved Lists of Bacterial Names (AL) (Skerman et al., 1980) and Cystobacter violaceus was described in.
Reichenbach (2005). A historical survey indicates that three of the species experienced reclassification in different genera over time, sometimes repeatedly (Table S1, available in the online Supplementary Material). This fact illustrates that there was no clear rationale to assign these species to the one or the other genus, and that the classification systems rather depended on the importance that the author allocated to specific morphological features. In particular, recognition of members of the genus Archangium is described as problematic: ‘The borderline between Archangium and the genera with sporangioles is markedly fluid’ (Reichenbach, 2005).

When the first almost-comprehensive description of the phylogenetic relationships of myxobacteria based on 16S rRNA gene sequences appeared, the type strain of Archangium gephyra formed a branch distinct from other type strains, confirming the existence of the species on a molecular basis (Spröer et al., 1999). However, two non-type strains morphologically classified as Angiococcus disciformis grouped phylogenetically with the type strain of Archangium gephyra, demonstrating the high relationship of these species. The (type) strains assigned to the four species Archangium gephyra, Angiococcus disciformis, Cystobacter minus and Cystobacter violaceus form one monophyletic branch (Garcia et al., 2010). The aim of the present study was to compare the morphological and physiological characters of these species in order to evaluate their assignment to one common genus. One reason for the reassessment of the taxonomic position of these species is their production of secondary metabolites with perspectives in pharmaceutical application (Reichenbach & Höfte, 1993; Schäberle et al., 2014).

The type strain of C. minus has been lost, and for that reason, strain Cb m2 (DSM 14751) was proposed as neotype strain (Lang & Reichenbach, 2013) and is included as the representative of this species in this study. It will be established as neotype strain in November 2015, two years after the publication of its proposal [Rule 18c of the Bacteriological Code (Lapage et al., 1992)].

All strains used were from Leibniz Institute DSMZ – German Collection of Microorganisms and Cell Cultures, and were maintained on VY/2 agar composed of (per litre): 1.36 g CaCl₂ . 2H₂O, 5 g baker's yeast, 15 g agar, 0.5 mg vitamin B₁₂; pH was adjusted to 7.2 with sterile KOH after autoclaving. All incubations were carried out at 28 °C. The 16S rRNA gene sequences of the strains of the four studied species were retrieved from the European Nucleotide Archive (http://www.ebi.ac.uk/ena/) (Table 1). Pairwise similarities of the 16S rRNA gene sequence of Archangium gephyra DSM 2261T to those of Angiococcus disciformis DSM 52716T, C. minus DSM 14751 and C. violaceus DSM 14727T were 98.6 %, 98.4 % and 98.6 %, respectively (http://www.ezbiocloud.net/eztaxon; Kim et al., 2012). The 16S rRNA gene sequence similarity of Angiococcus disciformis DSM 52716T versus C. minus DSM 14751 and C. violaceus DSM 14727T were 98.8 %

### Table 1. Species and type strains used in this study, and selected differential characteristics

<table>
<thead>
<tr>
<th>Species</th>
<th>Type strain</th>
<th>Isolation Source</th>
<th>Isolation Location</th>
<th>16S rRNA gene sequence</th>
<th>Weak decomposition</th>
<th>Decomposition of:</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. violaceus</em></td>
<td>DSM 14751</td>
<td>Soil</td>
<td>Soil with plant residues</td>
<td>M94374, HE582768-HE582771*</td>
<td>+ + +</td>
<td>+ + +</td>
</tr>
<tr>
<td><em>C. minus</em></td>
<td>DSM 14727T</td>
<td>Soil</td>
<td>Soil</td>
<td>M94374, HE582768-HE582771*</td>
<td>+ + +</td>
<td>+ + +</td>
</tr>
<tr>
<td><em>C. disciformis</em></td>
<td>DSM 2261T</td>
<td>Soil</td>
<td>Soil</td>
<td>M94374, HE582768-HE582771*</td>
<td>+ + +</td>
<td>+ + +</td>
</tr>
</tbody>
</table>

*Sequences of different clones.

**Description from Reichenbach** (2005). The type strain of *C. violaceus* no longer produces fruiting bodies under the conditions applied.
and 98.7 %, respectively, and the similarity between those of C. minus DSM 14751 and C. violaceus DSM 14727<sup>T</sup> was 99.5 % (Table S2). Such high similarity values are generally expected among strains belonging to one genus or even one species (Meier-Kolthoff et al., 2013). The 16S rRNA gene sequence similarities of these four species towards the four Cystobacter species sensu stricto, Cystobacter fuscus, Cystobacter ferrugineus, Cystobacter badius and Cystobacter velatus, were lower than 98.2 %. The Cystobacter species sensu stricto are nearly indistinguishable from each other by their 16S rRNA gene sequences. Phylogenetically, the four species studied here form a branch separate from that including the Cystobacter species sensu stricto (Garcia et al., 2010; Spröer et al., 1999).

The close phylogenetic relatedness and morphological similarity of C. minus and C. violaceus prompted us to determine whether the type strains belong to one species by applying DNA–DNA hybridization. Cells were disrupted by using a Constant Systems TS 0.75 kW (IUL Instruments) and the DNA in the crude lysate was purified by chromatography on hydroxyapatite as described by Cashion et al. (1977). DNA–DNA hybridization was carried out as described by De Ley et al. (1970) under consideration of the modifications described by Huss et al. (1983) using a model Cary 100 Bio UV/VIS-spectrophotometer equipped with a Peltier-thermostatted 6 × 6 multi-cell changer and a temperature controller with in situ temperature probe (Varian). The DNA–DNA relatedness value (9.6 %) was far below the threshold of 70 % given for membership within one species (Wayne et al., 1987).

Biomass for whole-cell fatty acid analyses and matrix-assisted laser desorption/ionization time-of-flight (MALDI-TOF) mass spectra was cultivated on CY agar (3.0 g casitone, 1.36 g CaCl<sub>2</sub> . 2H<sub>2</sub>O, 1.0 g yeast extract and 14 g agar per litre; pH 7.2) for approximately 2 days. Cells were harvested as soon as enough biomass with as few myxospores or fruiting bodies as possible became available. These plates had been inoculated with a suspension of cells freshly grown on VY/2 agar. Sample preparation for MALDI-TOF mass spectrometry was carried out according to Protocol 3 in Schumann & Maier (2014). Instrumental conditions for the measurement were used as described by Tóth et al. (2008). The comparison of MALDI-TOF mass spectra confirmed the close relatedness of the four species. In a score-oriented dendrogram (average linkage, distance measure: correlation), calculated from the spectra of the type strains of the four species and related organisms by using the Biotype software (Bruker Daltonics; version 3.1), Archangium gephyra DSM 2261<sup>T</sup>, Angiococcus disciformis DSM 52716<sup>T</sup>, C. violaceus DSM 14727<sup>T</sup> and C. minus DSM 14751 grouped together in a monophyletic cluster in the neighbourhood of other species of the genus Cystobacter (Fig. 1). The type strain of Archangium gephyra was the most distant strain among the four strains studied.
Fatty acid methyl esters were obtained as described previously (Kämpfer & Kroppenstedt, 1996) and separated by using a gas chromatograph (model 5898A; Hewlett Packard). Peaks were automatically computed and assigned using the Microbial Identification software package (MIDI), TSBA40 method, Sherlock version 4.5. The fatty acid patterns of the four strains were dominated by iso-C15 : 0, iso-C14 : 0 3-OH and C16 : 1 ω5c, and contained low amounts of C14 : 0, C15 : 0, iso-C16 : 0, C16 : 0, iso-C17 : 0, substances with equivalent chain-lengths (ECLs) of 13.565, 14.959, 15.687 and 17.875, and summed feature 4 (including anteiso-C17 : 1 B/iI), accompanied by trace amounts (<1 %) of other compounds (Table 2). The culture age and most possibly intracellular prearrangements accompanying myxospore and fruiting body formation may affect the fatty acid composition. Taking into account that these conditions cannot be adjusted (consistently) among these strains, the fatty acid compositions of the four strains were highly similar. The composition of Angiococcus disciformis displayed the highest complexity as already stated by Garcia et al. (2011). Since the fatty acid pattern of the type strain of C. fuscus also showed a high similarity, fatty acid pattern determination seems not to be a suitable tool for the discrimination of the studied species from those of the core Cystobacter group. We did not confirm the exceptionally high amount of C18 : 0 in Archangium gephrya which was detected by Garcia et al. (2011). Possibly the different growth conditions (liquid media versus agar plates, different media composition) chosen in the two studies resulted in the different outcomes.

Morphology of the spores and colour of the fruiting bodies were observed in VY/2 cultures or in cultures grown on streaks of dead or living cells of Escherichia coli as food bacteria on WAT agar (per litre: 1.0 g CaCl2 .2 H2O and 15 g agar). The vegetative cells of all four species are uniformly described as long slender, needle-shaped rods (Table S3). The myxospores of the cultures studied were ovoid or irregularly spherical (Angiococcus disciformis) or short stout rods with rounded ends, often a mixture of both. The spores of Archangium gephrya DSM 2261T and C. violaceus DSM 14727T were bean-shaped in part. None of the four taxa developed the bent rods with pointed ends characteristic for the Cystobacter species sensu stricto. These are demonstrated in Fig. 2 for a typical strain of C. fuscus (see also Table S3).

The designated type strains for Archangium gephrya and C. fuscus had been maintained in laboratories for decades and did not develop fruiting bodies in our laboratory. However, Archangium gephrya DSM 2261T formed small heaps, uniformly distributed over the surface of agar VY/2, similar to the distribution of fruiting bodies of Corallococcus strains. These heaps contained cells transformed to myxospores (Fig. 2). The yellow fruiting bodies of C. minus DSM 14751 aggregated irregularly on the surface, were piled up or were built on the tips of slime masses rising up from the agar.

### Table 2. Cellular fatty acid compositions (%) of strains used in this study and the type strain C. fuscus (type species of genus)

<table>
<thead>
<tr>
<th>Fatty acid</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>C10 : 0</td>
<td>0.2</td>
<td>0.4</td>
<td>0.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>iso-C11 : 0</td>
<td>0.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C12 : 0</td>
<td></td>
<td></td>
<td></td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>iso-C13 : 0</td>
<td>0.3</td>
<td>0.4</td>
<td>0.4</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>iso-C14 : 0</td>
<td>12.6</td>
<td>16.1</td>
<td>8.4</td>
<td>10.1</td>
<td>7.2</td>
</tr>
<tr>
<td>iso-C16 : 0</td>
<td>1.0</td>
<td>3.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>iso-C17 : 0</td>
<td>0.5</td>
<td>0.7</td>
<td>0.6</td>
<td>0.5</td>
<td>0.8</td>
</tr>
<tr>
<td>iso-C18 : 0</td>
<td>0.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>iso-C19 : 0</td>
<td>0.5</td>
<td>0.4</td>
<td>0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>iso-C24 : 0</td>
<td>0.5</td>
<td>0.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>iso-C25 : 0</td>
<td>0.5</td>
<td>0.5</td>
<td>0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>iso-C26 : 0</td>
<td>0.5</td>
<td>0.5</td>
<td>0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>iso-C27 : 0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>iso-C28 : 0</td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

+Unknown fatty acid or alcohol with an equivalent chain-length (ECL) of 13565.

†Summed features are groups of two or three fatty acids that are treated together for the purpose of evaluation in the MIDI system, and include both peaks with discrete ECLs as well as those where the ECLs are not reported separately [see Montero-Calasanz et al. (2014)]. Summed feature 1 contained iso-C15 : 1 and/or C13 : 0 3-OH; summed feature 2 contained iso-C16 : 0 and/or C14 : 0 3-OH; summed feature 4 contained anteiso-C17 : 1 B/i I.

The sporangioles of the type strain of *Angiococcus disciformis* appearing on streaks of *E. coli* were composed of sporangioles clearly enclosed by opaque envelopes and sitting singly on the agar surface in clusters, thus resembling those of members of the genus *Melittangium*. The oblate form of the sporangioles described earlier (Thaxter 1904; Hook et al., 1980) was not clearly noticeable (Fig. 3a). The larger, dark

(Fig. 3b, c, d). The sporangioles of the type strain of *Angiococcus disciformis* appearing on streaks of *E. coli* were composed of sporangioles clearly enclosed by opaque envelopes and sitting singly on the agar surface in clusters, thus resembling those of members of the genus *Melittangium*. The oblate form of the sporangioles described earlier (Thaxter 1904; Hook et al., 1980) was not clearly noticeable (Fig. 3a). The larger, dark
sporangioles of *C. violaceus* DSM 14727\textsuperscript{T} produced meandering curves and lines on top of the agar surface. These resembled most closely the fruiting bodies of the core species of the genus *Cystobacter* (Fig. 3).

Starch, xylan and aesculin hydrolysis, NaCl tolerance and enzyme activities (API ZYM strips; bioMérieux) were tested as described previously (Lang & Stackebrandt, 2009). Briefly, overlay agar plates containing 2 g potato

**Fig. 3.** Fruiting bodies of *Angiococcus disciformis* DSM 52716\textsuperscript{T} (a), *Cystobacter minus* DSM 14751 [b, c, d (side view)] and *Cystobacter violaceus* DSM 14727\textsuperscript{T} (e). Bars, 100 μm (a, c), 200 μm (b, d, e).
starch or 5 g oat spelt xylan or 5 g colloidal chitin (Hsu & Lockwood, 1975) per litre, respectively, were inoculated at one spot and incubated for 4 or 5 days. Starch and xylan degradation were detected after covering with Lugol’s solution. Clear halos larger than the swarm diameter were scored positive. Aesculin hydrolysis was evaluated after growth for up to 8 days on agar slants containing CY agar plus aesculin, citrate and ferric citrate. Salt tolerance was measured on CY agar plates containing 1.5% NaCl. All strains hydrolysed starch and xylan. Chitin was decomposed by the strains assigned to the genus Cystobacter but not by those of Archangium gephyra or Angiococcus disciformis (Table 1). Aesculin was hydrolysed weakly by the strains of C. minus and C. violaceus. Enzymic properties were tested using the API ZYM strips displaying an individual enzyme pattern for each of the strains. The strains of C. violaceus and C. fuscus were the most active, while Angiococcus disciformis DSM 527161 was the least active strain showing only alkaline and acid phosphatases, esterase, esterase-lipase and naphthol-AS-BI-phosphohydrolase activities; these enzymes were expressed in all strains (Table S4).

In the ‘Key to the species’ of the genus Cystobacter in Bergey’s Manual, two groups of species of the genus Cystobacter are distinguished. One group, including the type species C. fuscus, forming ‘...myxospores relatively slender rods of moderate length and with more or less tapering ends’, and another group comprising the species C. minus, ‘Cystobacter disciformis’ (sic), C. violaceus and Cystobacter gracilis, and forming ‘...myxospores very short fat rods to almost spherical...’ (Reichenbach, 2005). While C. gracilis groups with members of the genera Stigmatella and Hyalangium in the 16S rRNA gene sequence tree (Garcia et al., 2010), the species C. minus, Angiococcus/Cystobacter disciformis and C. violaceus cluster with Archangium gephyra. Thus, the phylogenetic relatedness of these three species correlates with their morphological distinction.

The four type strains presently assigned to three different genera displayed high similarities regarding cell and myxospore morphology, fatty acid pattern, 16S rRNA gene sequence and MALDI-TOF mass spectra. Moreover, strains of Archangium gephyra and C. violaceus produce chemically similar polyketides, named archazolids, and strains of Angiococcus disciformis and Archangium gephyra produce peptides, called tubulysins (Chai et al., 2010; Horstmann et al., 2011). In conclusion, we propose to assign the four related species in one genus distinct from the genus Cystobacter. This measure will, based on a molecular basis, abandon an over-subdivision of these taxa that was established at a time when the enthusiasm about morphological diversity and the developmental capacities of the myxobacteria was culminating.

It is proposed to assign the four species to the genus Archangium, as Archangium gephyra, Archangium disciforme comb. nov., Archangium minus comb. nov. and Archangium violaceum comb. nov. for the following reasons: Rule 44 of the Bacteriological Code (Lapage et al., 1992) reads: ‘If two or more species of different genera are brought together to form a genus, and if these species include the type species of one or more genera, the name of the genus is that associated with the type species having the earliest legitimate generic name’. The genera names Angiococcus and Archangium were described in the same year, 1924, by Jahn (Tables S1 and S3). However, only the genus name Archangium is listed on the AL (Skerman et al., 1980) while the genus name Angiococcus Jahn 1924 is not included. Although not proposed as such, Angiococcus is a revived name (Rule 28a) and should be cited as Angiococcus (ex Jahn 1924) Hook et al. 1980. Similarly, the species name Angiococcus disciformis (Thaxter 1904) Jahn 1924 did not appear on the AL, but an emended description was provided and a neotype strain was designated by Hook et al. in 1980 on pages 135–142 of the Int J Syst Bacteriol (Hook et al. 1980). However, on closer inspection of the strain history, the type strain (CMU-1T=ATCC 33172T) of Angiococcus disciformis, as given by Hook et al. (1980), is listed under the name Myxococcus disciformis Thaxter 1904 on the AL. Thus the species combination Angiococcus disciformis is both a homotypic synonym of Myxococcus disciformis Thaxter 1904 AL, as well as a revival of a combination originally proposed by Jahn (1924), based on the species name proposed by Thaxter (1904). Consequently, the species combination should be cited as Angiococcus disciformis (Thaxter 1904) Hook et al. 1980. This would be then consistent with the view that the genus and species names are validly published as defined by Rules 23a and 24a (Lapage et al., 1992). Based on these arguments, the genus name Angiococcus, which does not appear on the AL must be attributed to Hook et al. (1980) as a revived name. It therefore follows that the genus name Archangium Jahn 1924 AL has priority over the genus name Angiococcus (ex Jahn 1924) Hook et al. 1980.

The different species had been assigned to three different families, Angiococcus disciformis to the family Myxococcaceae by Jahn (1924) and Hook et al. (1980), Archangium gephyra to the family Archangiaceae by Jahn (1924), and C. minus and C. violaceus to the family Cystobacteraceae by Reichenbach (2005). The unification of the species in one genus demands the re-evaluation of the question in which family the genus is allocated correctly. Based on Rules 23b and 24b, the priority of family names placed on the AL is determined by the date of effective publication prior to the AL. Since both family names Cystobacteraceae and Archangiaceae were included in the AL, the family name Archangiaceae Jahn 1924 has priority over the family name Cystobacteraceae McCurdy 1970.

In recognizing that Angiococcus disciformis should be placed in the genus Archangium as Archangium disciforme Thaxter 1904 comb. nov., this species is also placed in the family Archangiaceae - de facto removing the genus Angiococcus (ex Jahn 1924) Hook et al. 1980 (treated here as a heterotypic synonym of Archangium Jahn 1924 AL), and the species Angiococcus disciformis (ex Jahn 1924) Hook et al. 1980 [treated here as a homotypic synonym of Myxococcus
disciformis (Thaxter 1904)], from the family Myxococaceae Jahn 1924 AL. Phylogenetic studies (Garcia et al., 2010) clearly exclude the classification of this species in the family Myxococaceae and support the inclusion in the family Archangiaceae.

McCurdy (1970) treats the genera Archangium Jahn 1924 and Cystobacter Schroeter 1886 as belonging to the families Archangiaceae Jahn 1924 and Cystobacteraceae McCurdy 1970, respectively. It is therefore appropriate to provide emended descriptions of the families Archangiaceae Jahn 1924 and Myxococaceae Jahn 1924.

Currently, the genera Anaeromyxobacter, Hyalangium and Stigmatella are assigned to the family Cystobacteraceae McCurdy 1970. Following the statement of the priority of the genus name Archangiaceae, these species are grouped correctly under the latter family name. However, phylogenetic analysis suggests that these three genera do not form one branch with the other genera assigned to the family Archangiaceae, namely Archangium, Cystobacter and Melittangium. Instead, members of the genera Hyalangium and Stigmatella and the species Cystobacter gracilis phylogenetically group with members of the family Myxococaceae (Garcia et al., 2010). Members of the genus Anaeromyxobacter are the only known myxobacteria having a facultatively anaerobic lifestyle, using a wide range of unusual electron acceptors (Sanford et al., 2002). This extraordinary metabolism comes together with a deep-branching point in the phylogenetic tree, at the suborder level. These facts demand a re-evaluation of the taxonomic positions of these genera in the future.

Emended description of the family Myxococaceae Jahn 1924 AL

Herewith contains currently the genera Myxococcus, Aggregococcus, Coralloccocus and Pyxidicoccus.

The characters of the family are described by Jahn (1924) and Reichenbach (2005). 'The rods contract to build round spores in the fruiting bodies. During sporulation, the spores elongate to rods without dropping an envelope’ [translated from German, Jahn 1924].

Vegetative cells are slender rods with tapering ends, 0.7–0.8 μm × 3–8 μm. Myxospores have a thick capsule, are spherical or ellipsoidal, sometimes slightly deformed, 1.2–2.5 μm in diameter, optically refractile when fully developed. Nutrition is proteolytic–bacteriolytic (Reichenbach, 2005).

The type genus is Myxococcus Thaxter 1892.

Emended description of the family Archangiaceae Jahn 1924 AL

Contains currently the genera Archangium Jahn 1924 AL, Anaeromyxobacter Sanford et al. 2002 VL, Cystobacter Schroeter 1886 AL, Hyalangium Reichenbach 2007 VL, Melittangium Jahn 1924 AL and Stigmatella Berkeley and Curtis 1875 AL.

The family members may have the characters described by Jahn (1924) for the family Archangiaceae ‘The swarms build irregularly bulging or sided fruiting bodies or columnist or finger-like extensions, mostly without clearly discernable membrane’ [translated from German by E. Lang]; and/or those described by McCurdy (1970) for the family Cystobacteraceae ‘Vegetative cells tapered flexible rods which are converted to refractile or phase-dense, rod-shaped microcysts enclosed in sporangia of definite shape. The sporangia may be sessile, occurring singly or in groups and enclosed in a slime membrane or envelope; or borne on stalks (sporangiphores) which may be simple or branched. The sporangia may be solitary or in clusters at the tips of the stalks. The vegetative colonies do not etch or erode agar. Congo red is adsorbed by the vegetative slime. All of the species examined grow well in media containing enzymatically hydrolyzed protein, starch and salts’; or those characters described for the genus Anaeromyxobacter by Sanford et al. (2002) ‘...myxobacterial species that are capable of facultative anaerobic growth using terminal electron acceptors such as nitrate, fumarate, and chlorophenolic compounds. Sulfur compounds are not reduced. Oxygen is used but only at low concentrations. The morphological description of this genus is the same as that of the type[...and only species...] and for the species Anaeromyxobacter dehalogenans ‘Cells are narrow rods 4 to 8 μm long and 0.25 μm wide that exhibit gliding motility. Terminal ends of cells have pilus structures and form blebs periodically[...Cysts are visible in older cultures’.

The type genus is Archangium Jahn 1924.

Emended description of the genus Archangium Jahn 1924 AL

The descriptions of the genus by McCurdy (1974), and of the species included - Angiococcus disciformis by Thaxter (1904), Jahn (1924), McCurdy (1974) and Hook et al. (1980); Cystobacter minus by Krzemieniewska & Krzemieniewski (1926) and McCurdy (1970); and Cystobacter violaceus by Kühlein & Gallwitz (1958), Kühlein & Reichenbach (1964) and Reichenbach (2005) - can be summarized and emended as follows: Gram-negative, gliding bacteria, undergoing development upon starving conditions. Vegetative cells are long slender rods with tapered ends. The swarms form tough slime sheets with radial veins. Does not engrave the agar. Congo red is adsorbed. Myxospores are irregularly coccoid, oval or short rods with blunt but never tapered ends, optically refractile when fully developed. The fruiting bodies containing the myxospores consist either of distinct oval to spherical sporangioles, somewhat oblate for one species, which are gathered in plaques, knobs, cones or ridges, sometimes forming fingers, attached directly to the agar surface or occasionally formed on a short slime cushion, or the fruiting bodies consist of contorted interlaced strings, sometimes subdivided by constrictions often resembling undetached sporangioles. Decomposes starch and xylan. May or may not decompose aesculin or chitin. Whole-cell fatty acids are
dominated by iso-C_{15:0}, iso-C_{14:0}, 3-OH and C_{16:1}ω5c, and contain low amounts of C_{14:0}, C_{15:0}, iso-C_{16:0}, C_{16:0}, iso-C_{17:0}, substances with an ECL of 13.565, 14.959, 15.687 and 17.875, and summed feature 4 (including anteiso-C_{17:1} B/II), accompanied by trace amounts of other compounds. The G+C content of the DNA of two species is concurrently 68 mol%.

The type species is Archangium gephyra Jahn 1924.

Emended description of Archangium gephyra Jahn 1924 AL


The characters of the species are described by Jahn (1924), McDonald (1965, 1967), McCurdy (1974), Galván et al. (1992) and Reichenbach (2005). Vegetative cells are slender rods, 0.4–0.8 × 6–15 μm. Swarm colonies are thin with radiating ridges and concentric folds, can be cut easily. Myxospores are short fat rods with rounded ends, often slightly bean-shaped, up to almost spherical, 1–2 × 1.5–2.8 μm. Fruiting bodies consist of irregular bulges or sidled ridges, up to 1 mm, reddish, without envelope; inside contorted interlooped strings, 40–60 μm wide, sometimes subdivided by irregular constrictions. The fatty acid pattern may be dominated by C_{14:0}, iso-C_{15:0}, iso-C_{14:0} 3-OH, C_{16:0} and C_{16:1}ω5c (this study) or iso-C_{15:0}, C_{16:0}, C_{16:1}ω5c, iso-C_{17:0} 2-OH and C_{18:0} (Garcia et al., 2011), respectively.

The type strain is M18^T (=DSM 2261^T=ATCC 25201^T=NBRC 100087^T). The GenBank accession no. of the 16S rRNA gene of the type strain is DQ768106.

Description of Archangium disciforme (Hook et al. 1980) comb. nov.

Archangium disciforme (dis.ci.for’me. Gr. masc. n. diskos disk; L. fem. n. forma form, shape; N.L. neut. adj. disciforme disk-shaped).

Basonym: △ Myxococcus disciformis Thaxter 1904 AL.

Other synonym: Angiococcus disciformis (Thaxter 1904) Hook et al. 1980, comb. nov. VP.

Shows the properties described by Thaxter (1904), Hook et al. (1980) and (under the name ‘Cystobacter disciformis’) Reichenbach (2005). Vegetative cells are slender, needle-like rods, 0.5–0.7 × 2–10 μm. Myxospores are ellipsoidal or irregularly spherical, enclosed in a tenacious matrix, 1–1.9 μm in diameter, optically refractile. Fruiting bodies consist of irregular bulges or sidled ridges, 6–15 μm, optically refractile. Fruiting bodies consist of irregular bulges or sidled ridges, 10–15 μm wide, encased in a tenacious matrix, 1.8–4.0 μm thick, embedded in a colourless translucent slime. Flat sori may cover surfaces up to 0.5 mm, or sori may sometimes pile up forming finger- or tree-like structures. Formation of secondary sporangioles within primary ones is observed. Major whole-cell fatty acids may be iso-C_{15:0}, iso-C_{14:0}, 3-OH, C_{16:1}ω5c, iso-C_{17:0} and an unknown compound with an ECL of 17.875 (this study), or iso-C_{15:0}, C_{16:0}, C_{16:1}ω5c, iso-C_{17:0} and iso-C_{17:0} 2-OH (Garcia et al., 2011).

The proposed neotype strain is Cb m2 (=DSM 14751=JCM 12627). The GenBank accession no. of the 16S rRNA gene of the proposed neotype strain is AJ233903.

Description of Archangium violaceum (Reichenbach 2007) comb. nov.

Archangium violaceum (vi.o.la’ce.um. L. neut, adj. violaceum violet-coloured).

Basonym: Cystobacter violaceus (ex Kühlwein and Gallwitz 1958) Reichenbach 2007 VL.


The species is as described by Kühlwein & Gallwitz (1958), Kühlwein & Reichenbach (1964) and Reichenbach (2005). Vegetative cells are slender rods with tapering ends, 0.5–0.7 × 8–12 μm. Myxospores are short rods with rounded ends, 0.8–1.8 × 1.8–4.0 μm. Sporangioles are spherical to oval, large, 95–130 × 128–185 μm, single or in groups, and dull brown to deep violet. Major
fatty acids are C\textsubscript{14}:0, iso-C\textsubscript{15}:0, iso-C\textsubscript{14}:0 3-OH, C\textsubscript{16}:1\textit{t} 5c, iso-C\textsubscript{17}:0 and an unknown compound with an ECL of 17.875 (this study) or iso-C\textsubscript{15}:0, C\textsubscript{16}:1\textit{t} 5c and iso-C\textsubscript{17}:0 2-OH (Garcia et al., 2011).

The type strain is strain Cb vi61\textsuperscript{T} (=DSM 14727\textsuperscript{T}=CIP 109131\textsuperscript{T}=JCM 12629\textsuperscript{T}). The GenBank accession no. for the 16S rRNA gene sequence of the type strain is DQ768114.

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**References**


