Phylogenetic analysis of the genus *Actinoplanes* and transfer of *Actinoplanes minutisporangius* Ruan *et al.* 1986 and '*Actinoplanes aurantiacus*' to *Cryptosporangium minutisporangium* comb. nov. and *Cryptosporangium aurantiacum* sp. nov.

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The phylogenetic structure of the genus *Actinoplanes* was determined by comparative 16S rDNA sequence analysis of the type strains of all validly described *Actinoplanes* species and other strains of *Actinoplanes*. *Actinoplanes minutisporangius* IFO 15962^T and '*Actinoplanes aurantiacus*' IFO 13967 were placed outside the family *Micromonosporaceae* and appeared to be closely related to the genus *Cryptosporangium*. On the basis of their morphological and chemotaxonomic characteristics and phylogenetic analysis, these strains were reclassified into the genus *Cryptosporangium*. DNA–DNA hybridization revealed that these strains differed from the species previously described in this genus. Therefore, the transfer is proposed of *Actinoplanes minutisporangius* Ruan *et al.* 1986 and '*Actinoplanes aurantiacus*' IFO 13967 to the genus *Cryptosporangium* as *Cryptosporangium minutisporangium* comb. nov. and *Cryptosporangium aurantiacum* sp. nov.

Keywords: *Actinoplanes*, family *Micromonosporaceae*, *Cryptosporangium minutisporangium*, *Cryptosporangium aurantiacum*, 16S rRNA

Introduction

The genus *Actinoplanes* (Couch 1950) emend. Stackebrandt and Kroppenstedt 1987 is a member of the family *Micromonosporaceae* (Krassil'nikov 1938) emend. Stackebrandt *et al.* 1997. Organisms placed in the genus *Actinoplanes* are characterized by the presence of spherical, cylindrical, digitate, lobate, bottle- or flask-shaped or very irregular sporangia. Sporangiospores are motile by tufts of polar flagella. Aerial hyphae are scant. The peptidoglycan contains *meso*-diaminopimelic acid, which may be replaced by hydroxydiaminopimelic acid. Xylose is the diagnostic sugar of whole-cell hydrolysates and small amounts of galactose and/or arabinose are also frequently found. Phosphatidylethanolamine is the diagnostic phospho-

lipid. Iso-/anteiso-branched and monounsaturated fatty acids and/or *cis*-9,10-octadecanoic acid (oleic acid) are predominant. The predominant isoprenoid quinone is MK-9(H₄). The G+C content of DNA ranges from 72.1 to 72.6 mol%. The type species is *Actinoplanes philippinensis* Couch 1950 and more than 20 species have been validly described.

Stackebrandt & Kroppenstedt (1987) proposed the union of the genera *Actinoplanes*, *Amorphosporangium* Couch 1963 and *Ampullariella* Couch 1964 on the basis of chemotaxonomic properties, DNA pairing experiments, rRNA cistron similarity studies and a 16S rRNA oligonucleotide catalogue. *Actinoplanes campanulatus*, *Actinoplanes digitatis*, *Actinoplanes lobatus* and *Actinoplanes regularis* were formerly members of the genus *Ampullariella* and *Actinoplanes auranticolor* and *Actinoplanes globisporus* were formerly members of the genus *Amorphosporangium*. *Actinoplanes armeniacus* (Kalakoutskii & Kusnetsov,

The DDBJ/GenBank/EMBL accession numbers for the 16S rRNA gene sequences determined in this study are shown in Figs 1 and 2.

Fig. 1. Phylogenetic tree, based on neighbour-joining (Saitou & Nei, 1987), derived from 16S rRNA sequences of valid species of the genus *Actinoplanes* and other members of the family *Micromonosporaceae*. *Streptomyces ambofaciens* ATCC 23877^T (M27245) was used as the root organism. Bar, 0.01 K_{nuc} in nucleotide sequences. The numbers on the branches are confidence limits (expressed as percentages) estimated from a bootstrap analysis with 1000 replicates (only values above 50 % are indicated).

Fig. 2. Phylogenetic tree, based on neighbour-joining (Saitou & Nei, 1987), derived from 16S rDNA sequences of the members of the suborder Frankineae. *Streptomyces ambofaciens* ATCC 23877^T (M27245) was used as the root organism. Bar, 0.01 K_{nuc} in nucleotide sequences. The numbers on the branches are confidence limits (expressed as percentages) estimated from a bootstrap analysis with 1000 replicates (only values above 50 % are indicated).

1964) was transferred to the genus *Streptomyces* as *Streptomyces armeniacus* (Wellington & Williams, 1981) on the basis of its morphology, cell wall chemotype and phage susceptibility. *Actinoplanes caeruleus* (Horan & Brodsky, 1986) was transferred to the genus *Couchioplanes* as *Couchioplanes caeruleus* (Tamura *et al.*, 1994) on the basis of its morphology, chemotaxonomy and phylogeny. Goodfellow *et al.* (1990) determined the chemotaxonomic and phenotypic characteristics of species of *Actinoplanes* and reported that the chemical and numerical taxonomic data supported the integrity of the genus. Koch *et al.* (1996) analysed a 500 nt stretch of 16S rDNA from 17 valid species of the genus *Actinoplanes* and reported that two major phylogenetic groups were detected. One contained *Actinoplanes philippinensis* and *Actinoplanes brasiliensis* and the other contained *Actinoplanes cyaneus* and *Actinoplanes regularis*.

In order to provide a basis for determining the phylogenetic relationships among the species of the genus *Actinoplanes*, we analysed the 16S rDNAs of all validly described species as well as some invalid species belonging to the genus.

METHODS

Micro-organisms and culture conditions. The strains investigated in this study were 21 type strains of validly described *Actinoplanes* species and 28 other strains of *Actinoplanes* (Figs 1 and 2). All strains were cultivated at 28 °C for 5 d in yeast extract/glucose broth (containing 10 g yeast extract and 10 g D-glucose in 1000 ml distilled water, pH 7.0) on a rotary shaker.

PCR amplification and sequencing of 16S rDNA. 16S rDNA was amplified by PCR (Saiki *et al.*, 1988) using protocols described previously (Tamura *et al.*, 1998). The 1.5 kb amplified 16S rDNA was subjected to cycle sequencing by using a BigDye Terminator cycle sequencing kit in conjunction with Amplitaq FS (PE Applied Biosystems) and a Gene Amp PCR System 9700 (Perkin Elmer) according to the manufacturer's protocol with the following primers: 9F, 515F (5'-GTGCCAGCAGCCGCGGT-3', positions 515–

531), 785F (5'-GGATTAGATACCCTGGTAGTC-3', 785–805), 1099F (5'-GCAACGAGCGCAACCC-3', 1099–1114), 536R (5'-GTATTACCGCGGCTGCTG-3', 536–519), 802R (5'-TACCAGGGTATCTAATCC-3', 802–785), 1115R (5'-AGGGTTGCGCTCGTTG-3', 1115–1100) and 1541R. The conditions for thermal cycling were 25 cycles of denaturation at 96 °C for 10 s, primer annealing at 50 °C for 5 s and primer extension at 60 °C for 4 min. The products were purified as recommended by PE Applied Biosystems and were analysed with a model ABI PRISM 310 Genetic Analyzer (PE Applied Biosystems) according to the manufacturer's protocol.

Phylogenetic analysis. 16S rDNA sequences of the strains under investigation and reference organisms were aligned against that of *Streptomyces ambofaciens* (Pernodet *et al.*, 1989). CLUSTAL W version 1.7 (Thompson *et al.*, 1994) was used to generate evolutionary distances (the K_{nuc} value of Kimura, 1980), similarity values, neighbour-joining analysis (Saitou & Nei, 1987) from K_{nuc} values and the bootstrap resampling method of Felsenstein (1985) with 1000 replicates for evaluation of the topology of the phylogenetic tree. NJplot (Perrière & Gouy, 1996) was used to plot the phylogenetic tree.

The nucleotide sequence data reported in this paper will appear in the DDBJ, EMBL and GenBank nucleotide sequence databases with the accession numbers listed in Figs 1 and 2.

Analyses of chemotaxonomic characteristics. Analyses of whole-cell sugar composition, amino acid composition of cell wall, menaquinone composition, cellular fatty acid composition, isomers of diaminopimelic acid, acyl type of peptidoglycan, mycolic acid and DNA base composition were performed as described previously (Tamura *et al.*, 1994).

Cultural, physiological and morphological characteristics. Cultural and physiological characteristics were determined as described previously (Yokota *et al.*, 1993; Gordon *et al.*, 1974). Morphology was observed by scanning electron microscopy as described previously (Tamura *et al.*, 2000).

DNA-DNA hybridization. The microplate-hybridization method developed by Ezaki *et al.* (1988, 1989) was applied with minor modifications to determine DNA similarity (Tamura *et al.*, 1999).

RESULTS AND DISCUSSION

Almost complete 16S rRNA sequences were determined and analysed phylogenetically. Fig. 1 shows the phylogenetic tree derived from the 16S rDNA sequences of 21 type strains of validly described *Actinoplanes* species, 28 other strains of *Actinoplanes* and other members of the family *Micromonosporaceae*. With the exception of *Actinoplanes minutisporangius* IFO 15962^T and '*Actinoplanes aurantiacus*' IFO 13967, the members of the genus *Actinoplanes* belonged phylogenetically to the family *Micromonosporaceae*. However, they did not form a stable cluster within the family; most branches had only low bootstrap values and the clustering might change if the operational taxonomic unit were changed.

On other hand, some strains were phylogenetically related. *Actinoplanes missouriensis* IFO 13243^T and *Actinoplanes auranticolor* IFO 12245^T had 99.8% sequence similarity. However, these species have many differences in physiological characteristics (Goodfellow *et al.*, 1990).

Actinoplanes humidus and *Actinoplanes consettensis*, which were isolated from sediments of the River Derwent in the UK (Goodfellow *et al.*, 1990), had 100% sequence similarity. However, in their physiological characteristics, these species are distinguishable by the reduction of nitrate (Goodfellow *et al.*, 1990). DNA–DNA hybridization studies may be required to confirm that they are phenotypically defined species.

Actinoplanes campanulatus, *Actinoplanes digitatis*, *Actinoplanes lobatus* and *Actinoplanes regularis*, which were members of the former genus *Ampullariella*, did not form a coherent cluster within the genus. The same is true of *Actinoplanes auranticolor* and *Actinoplanes globisporus*, members of the former genus *Amorphosporangium*. *Actinoplanes globisporus* IFO 13912^T has the longest branch among the type strains of validly described *Actinoplanes* species, excluding *Actinoplanes minutisporangius* IFO 15962^T, and its similarity to the

type strains of validly described *Actinoplanes* species ranged from 94.8 to 96.9%. For the type strains of validly described *Actinoplanes* species other than *Actinoplanes minutisporangius* IFO 15962^T and *Actinoplanes globisporus* IFO 13912^T, the levels of 16S rDNA sequence similarity were greater than 95.7%. The chemotaxonomic characteristics of *Actinoplanes globisporus* IFO 13912^T were in good agreement with those of the genus *Actinoplanes* (Table 1), thus confirming its assignment to this genus.

Actinoplanes sp. IFO 14428 and *Actinoplanes auranticolor* IFO 13992 formed a cluster with strains of *Couchioplanes*. In neither strain was the sheath of sporangia observable by scanning electron microscope (data not shown), and this morphological feature is characteristic of strains belonging to the genus *Couchioplanes*. However, both strains had *meso*-diaminopimelic acid as the diamino acid of the peptidoglycan, while the members of the genus *Couchioplanes* have lysine.

Actinoplanes minutisporangius IFO 15962^T and '*Actinoplanes aurantiacus*' IFO 13967 were placed outside the family *Micromonosporaceae* (Fig. 1) and were found to be related to members of the genus *Cryptosporangium* (Tamura *et al.*, 1998) (Fig. 2). *Actinoplanes minutisporangius* IFO 15962^T and '*Actinoplanes aurantiacus*' IFO 13967 had 98.0–99.3% similarity to members of the genus *Cryptosporangium*, but less than 93.7% similarity to other *Actinoplanes* species. *Actinoplanes minutisporangius* was reported to produce spherical and subspherical sporangia above and within agar (Ruan *et al.*, 1985), which is consistent with the morphological characteristics of the genus *Cryptosporangium* (Tamura *et al.*, 1998). The major menaquinone and fatty acid patterns of *Actinoplanes minutisporangius* IFO 15962^T and members of *Cryptosporangium* were also in good agreement (Table 1). Thus, on the basis of morphological, physiological, chemotaxonomic and phylogenetic criteria, *Actinoplanes minutisporangius* IFO 15962^T is considered to

Table 1. Chemotaxonomic characteristics of species of *Actinoplanes* and *Cryptosporangium*

All taxa have glutamic acid, alanine, glycine, 3-hydroxydiaminopimelic acid and *meso*-diaminopimelic acid as cell wall amino acids. Pooled data were taken from Goodfellow *et al.* (1990) (*Actinoplanes*) and Tamura *et al.* (1999) (*Cryptosporangium*).

Characteristic	<i>A. globisporus</i> IFO 13912 ^T	<i>Actinoplanes</i>	<i>A. minutisporangius</i> IFO 15962 ^T and ' <i>A. aurantiacus</i> ' IFO 13967	<i>Cryptosporangium</i>
Major menaquinones	8(H ₄), 9(H ₆), 9(H ₈)	9(H ₄), 9(H ₆), 8(H ₂)	9(H ₂), 9(H ₆), 9(H ₈)	9(H ₆), 9(H ₈), 9(H ₄)
Major cellular fatty acid(s)	iso-C _{16:0}	anteiso-C _{15:0} , C _{17:0} , iso-C _{16:0} , anteiso-C _{17:0} , C _{18:0} , C _{19:0} , iso-C _{15:0} , C _{16:0} , C _{18:1}	iso-C _{16:0} , C _{18:1}	iso-C _{16:0} , C _{18:1} , C _{17:1}
Presence of 2-OH fatty acids	+	+ / –	–	–

Table 2. Differential characteristics of species belonging the genus *Cryptosporangium*

Data not obtained in this study were taken from Ruan *et al.* (1985) (*C. minutisporangium*) and Tamura *et al.* (1998) (*C. arvum* and *C. japonicum*). All of the strains listed gave good growth at 20 and 25 °C and no growth at 45 °C. +, Positive; –, negative; w, weakly positive; d, positive or negative.

Characteristic	<i>C. minutisporangium</i> IFO 15962 ^T	<i>C. aurantiacum</i> IFO 13967 ^T	<i>C. arvum</i> YU629-21 ^T	<i>C. japonicum</i> YU636-3 ^T
Acid production from:				
D(+)-Maltose	+	–	+	+
D(+)-Lactose	+	–	+	+
<i>i</i> -Inositol	–	d	+	+
Methyl α -D-glucoside	+	–	+	–
Utilization of carbohydrates:				
<i>i</i> -Inositol	w	w	+	+
D-Sorbitol	–	w	–	d
D(+)-Raffinose	w	–	+	d
Decomposition of urea	+	–	–	–
Hydrolysis of:				
Starch	+	+	–	–
Urea	+	–	–	–
Gelatin	+	–	–	–
Utilization of organic acids:				
Succinate	+	–	–	–
Oxalate	–	+	–	–
Malate	+	–	–	–
Nitrite from nitrate	+	+	–	–
Decomposition of calcium malate	–	–	+	+
Pigmentation in ISP 7	–	Moderate red	Pale reddish brown	Pale reddish brown
Growth at (°C):*				
10	+	–	–	–
15	+	w	++	+
30	++	++	+	+
37	–	++	–	+

* Growth is scored as: ++, good; +, moderate; w, weak; –, no growth.

belong to the genus *Cryptosporangium* rather than the genus *Actinoplanes*.

The chemotaxonomic characteristics of '*Actinoplanes aurantiacus*' IFO 13967 are also consistent with those of the genus *Cryptosporangium* (Table 1). DNA–DNA hybridization was performed between *Actinoplanes minutisporangius* IFO 15962^T, *Actinoplanes aurantiacus* IFO 13967^T, *Cryptosporangium arvum* YU 629–21^T and *Cryptosporangium japonicum* YU 636–3^T, YU 655–31 and YU 656–31. *Actinoplanes minutisporangius* IFO 15962^T exhibited levels of DNA–DNA relatedness of 14–22 % to other strains. '*Actinoplanes aurantiacus*' IFO 13967 exhibited levels of DNA–DNA relatedness of 15–21 % to other strains. All other species of *Cryptosporangium* developed orange-yellow substrate mycelium on most media, but *Actinoplanes minutisporangius* developed brown to brownish black substrate mycelium (Ruan *et al.*, 1985). *Actinoplanes minutisporangius* also differed from other members of the genus *Cryptosporangium* in the hydrolysis of starch and gelatin and the reduction of nitrate (Table 2).

Similarly, '*Actinoplanes aurantiacus*' IFO 13967 differed from other members of the genus *Cryptosporangium* in the utilization of raffinose, hydrolysis of starch and reduction of nitrate (Table 2). These results indicate that this strain represents a novel species of the genus *Cryptosporangium*. We therefore propose that *Actinoplanes minutisporangius* IFO 15962^T be transferred to the genus *Cryptosporangium* as *Cryptosporangium minutisporangium* comb. nov. and that '*Actinoplanes aurantiacus*' IFO 13967 be accepted as a novel species of the genus *Cryptosporangium*, *Cryptosporangium aurantiacum* sp. nov.

Description of *Cryptosporangium minutisporangium* comb. nov.

Basonym: *Actinoplanes minutisporangius* Ruan *et al.* 1986.

The description is based on the data compiled by Ruan *et al.* (1985) and in this study. Morphological, chemo-

taxonomic and general characteristics are as given previously for the genus (Tamura *et al.*, 1998). Spores are motile. Brown to brownish black substrate mycelium is produced. Hydrolyses casein, hypoxanthine, urea, starch and gelatin. Does not hydrolyse adenine or xanthine. Reduces nitrate to nitrite. Phosphatase is negative. Acetate, malate, pyruvate, succinate and propionate are utilized, but lactate, benzoate, citrate, mucate, oxalate and tartrate are not utilized. Acid is produced from arabinose, cellobiose, fructose, galactose, glucose, glycerol, inositol, lactose, maltose, mannitol, mannose, melibiose, methyl α -D-glucoside, rhamnose, salicin, sucrose, trehalose and xylose, but is not produced from adonitol, dulcitol, erythritol, raffinose, sorbitol or methyl α -D-xyloside. The G+C content of the DNA is 76 mol% (T_m). Habitat: soil.

The type strain is IFO 15962^T (= JCM 9458^T = ATCC 49415^T = LL-A-60^T).

Description of *Cryptosporangium aurantiacum* sp. nov.

Cryptosporangium aurantiacum (au.ran.ti.ac'um. M.L. neut. adj. *aurantiacum* orange-coloured).

Morphological, chemotaxonomic and general characteristics are as given for the genus. Moderate red soluble pigment is produced on tyrosine agar (ISP medium 7). Starch is hydrolysed. Gelatin and aesculin are not hydrolysed. Nitrate is reduced. No growth at 4% NaCl. Acid is produced from mannitol, melibiose, rhamnose, arabinose, galactose, mannose, glucose and xylose, but not from erythritol, adonitol, maltose, lactose, sorbitol, methyl α -D-glucoside, dulcitol or raffinose. Mannitol, melibiose, maltose, rhamnose, lactose, inositol, sorbitol, arabinose, galactose, mannose, glucose, xylose and oxalate are utilized, but erythritol, adonitol, methyl α -D-glucoside, dulcitol, raffinose, succinate, malate and citrate are not. Habitat: cultivated soil.

The type strain is IFO 13967^T (= JCM 3241^T = 71-C38^T).

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