Transfer of *Streptosporangium viridogriseum* (Okuda et al. 1966), *Streptosporangium viridogriseum* subsp. *kofuense* (Nonomura and Ohara 1969), and *Streptosporangium albidum* (Furumai et al. 1968) to *Kutzneria* gen. nov. as *Kutzneria viridogrisea* comb. nov., *Kutzneria kofuensis* comb. nov., and *Kutzneria albida* comb. nov., Respectively, and Emendation of the Genus *Streptosporangium*

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A chemotaxonomic analysis of 14 *Streptosporangium* species revealed the phenotypic heterogeneity of this genus. The type species, *Streptosporangium roseum*, and 11 other species share similar isoprenoid quinones, fatty acids, and polar lipids. Two species, *Streptosporangium albidum* and *Streptosporangium viridogriseum*, including *S. viridogriseum* subsp. *viridogriseum* and *S. viridogriseum* subsp. *kofuense*, were characterized by a pattern of chemotaxonomic properties that was clearly distinct from the pattern obtained for the authentic *Streptosporangium* species. The results of a previous phylogenetic analysis of 16S ribosomal DNA and 5S rRNA indicated that the type species and its relatives are distantly related to members of the genus *Streptomyces*, whereas a member of the other group was found to be phylogenetically related to, but clearly distinct from, members of the family *Pseudonocardiaceae*. On the basis of these phenotypic and genomic differences, we propose the name *Kutzneria* gen. nov. for a new genus containing the previously misclassified *Streptosporangium* species and describe *Kutzneria viridogrisea* comb. nov., *Kutzneria albida* comb. nov., and *Kutzneria kofuensis* comb. nov. The type species of the new genus is *Kutzneria viridogrisea*, and the type strain is DSM 43850 (= ATCC 25242).

The actinomycete family *Streptosporangiaceae* (3) presently contains the genera *Streptosporangium*, *Microbispora*, *Microtetraspora* (including the former *Actinomadura pusilla* group), *Planomonospora*, and *Planobispora*, as well as the recently described genus *Herbidospora* (11) and, tentatively, the genus *Spirillospora*. Given the presence of a phylogenetic branching pattern, a combination of properties such as wall chemotype, peptidoglycan type, whole-cell sugars, fatty acid and phospholipid profiles, and menaquinones (2, 8) facilitates the delineation of actinomycete genera from neighboring taxa. Unfortunately, the paucity of distinctive chemotaxonomic properties of *Streptosporangium* species has led workers to believe that this genus is a phylogenetically, morphologically, and chemotaxonomically homogeneous taxon, and consequently only the type species of the genus *Streptosporangium*, *Streptosporangium roseum*, was included in previous phylogenetic studies of sporoactinomycetes (24, 25). However, the results of a recent analysis of morphological properties of spores and spore vesicles detected by scanning electron microscopy (18), an analysis of the electrophoretic mobility of ribosomal protein AT-L30 (20), and an analysis of 16S ribosomal DNA (rDNA) (5) and 5S rRNA (11) indicated that the members of this genus are heterogeneous phenotypically and genomically. In this paper we describe the chemotaxonomic properties of members of the genus *Streptosporangium*, and, on the basis of the results of a polyphasic approach to bacterial classification, we propose

creation of the genus *Kutzneria* gen. nov. and the species *Kutzneria viridogrisea* comb. nov., *Kutzneria kofuensis* comb. nov., and *Kutzneria albida* comb. nov.

MATERIALS AND METHODS

Strains and culture conditions. The *Streptosporangium* strains investigated are listed in Table 1. Cells were grown on solidified DSM medium 65 (1) at 28°C for 2 to 3 days.

Analysis of cell wall amino acids and sugars. For amino acid and sugar analyses of whole-cell hydrolysates we used previously described procedures (26).

Extraction and analysis of isoprenoid quinones and polar lipids. Isoprenoid quinones were extracted and purified by using the small-scale integrated procedure of Minnikin et al. (17). Dried preparations were dissolved in 200 µl of isopropanol, and 1- to 10-µl portions were injected into high-performance liquid chromatography (HPLC) column without further purification. Menaquinones were separated with a Lichrosorb RP-18 column (4 by 250 mm) kept at 40°C by using acetonitrile-isopropanol (65:35, vol/vol) as the solvent (10). A silver-loaded ion exchanger was used to separate positional isomers of the isoprene side chains of the menaquinones (9). Polar lipids were extracted, examined by two-dimensional thin-layer chromatography, and identified by using previously described procedures (17).

Extraction and analysis of fatty acids. Fatty acid methyl esters were obtained from freeze-dried biomass (approximately 10 mg) by saponification, methylation, and extraction, using minor modifications (12) of the method of Miller (16). The fatty acid methyl ester mixtures were separated by using a

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TABLE 1. Strains investigated and phospholipids in members of the genera *Streptosporangium* and *Kutzneria*

Species	PE ^a	OH-PE	NPG	DPG	PI
<i>Streptosporangium album</i> DSM 43023 ^{Tb}	+	+	+	+	+
<i>Streptosporangium amethystogenes</i> DSM 43179 ^T	+	+	+	+	+
<i>Streptosporangium fragile</i> DSM 43847 ^T	+	+	+	+	+
<i>Streptosporangium longisporum</i> DSM 43180 ^T	+	+	+	+	+
<i>Streptosporangium nondiastaticum</i> DSM 43848 ^T	ND ^c	ND	ND	ND	ND
<i>Streptosporangium pseudovulgare</i> DSM 43181 ^T	+	+	+	+	+
<i>Streptosporangium roseum</i> DSM 43021 ^T	+	+	+	+	+
<i>Streptosporangium violaceochromogenes</i> DSM 43849 ^T	ND	ND	ND	ND	ND
<i>Streptosporangium viridialbum</i> DSM 43801 ^T	+	+	+	+	+
<i>Streptosporangium vulgare</i> DSM 43802 ^T	+	+	+	+	+
<i>Streptosporangium carneum</i> NRRL 18437 ^{Td}	+	—	—	+	+
<i>Streptosporangium corrugatum</i> DSM 43316 ^T	+	+	—	+	+
<i>Kutzneria viridogrisea</i> DSM 43850 ^T	+	+	—	+	+
<i>Kutzneria kofuensis</i> DSM 43851 ^T	+	+	—	+	+
<i>Kutzneria albida</i> DSM 43870 ^T	+	+	—	+	+

^a PE, phosphatidylethanolamine; OH-PE, hydroxyphosphatidylethanolamine; NPG, ninhydrin-positive and sugar-positive phospholipids; DPG, disphosphatidylglycerol; PI, phosphatidylinositol.

^b T = type strain.

^c ND, not determined.

^d Data from reference 14.

model 5898A microbial identification system (Microbial ID, Inc., Newark, Del.), which consisted of a Hewlett-Packard model 3392 gas chromatograph fitted with a 5% phenylmethyl silicone capillary column (0.2 mm by 25 m), a flame ionization detector, a Hewlett-Packard model 3392 integrator, a Hewlett-Packard model 7673A automatic sampler, and a Hewlett-Packard model 900/300 computer (Hewlett-Packard Co., Palo

Alto, Calif.). Peaks were automatically integrated, and fatty acid names and percentages were determined by using the Microbial ID system. The gas chromatographic parameters were as follows: carrier gas, ultra-high-purity hydrogen; column head pressure, 60 kPa; injection volume, 2 µl; column split ratio, 100:1; septum purge rate, 5 ml/min; column temperatures, 170 to 270°C (increased at a rate of 5°C/min); injection port temperature, 250°C; and detector temperature, 300°C.

Determination of the DNA G+C content. DNA was isolated by using previously described procedures (28). Approximately 20 µg of DNA was hydrolyzed and dephosphorylated as described previously (15). Nucleosides were separated by reverse-phase HPLC. The apparatus used consisted of an LKB model 2150 high-pressure pump equipped with an LKB model 2151 UV detector (270 nm) connected to a Shimadzu model CR-3A integrator. The analytical column was a NUCLEOSIL 100-5C18 column (240 by 4 mm) equipped with a NUCLEOSIL 100-5C18 precolumn (20 by 4 mm); the solvent system used was the solvent system of Tamaoka and Komagata (27). The retention times of the nucleosides were determined with synthetic compounds. Nonmethylated lambda phage DNA with a G+C content of 49.858 mol% (22) was used as a calibration reference. The G+C contents were calculated automatically with the Shimadzu integrator.

RESULTS AND DISCUSSION

Chemotaxonomic properties have been found to be important contributors to the polyphasic approach to bacterial systematics, especially for the circumscription of phylogenetically coherent actinomycete taxa (2, 7). As a result of studies described previously (5, 11, 18, 20) and in this paper, we believe that certain species should not be retained in the genus *Streptosporangium*. The genus name *Kutzneria* is proposed below for these species; Tables 1 to 3 show chemotaxonomic properties of these organisms.

In contrast to the results of morphological studies (18) and an analysis of ribosomal protein components (20), which indicated that there are three *Streptosporangium* species clusters (represented by *S. roseum*, *Streptosporangium corrugatum*, and *Streptosporangium viridigriseum*), in this study only two

TABLE 2. Whole-cell sugars and menaquinone compositions of members of the genera *Streptosporangium* and *Kutzneria*

Species	Whole-cell sugars			Menaquinone composition (%) ^a						
	Galactose	Madurose	Rhamnose	Mk-8 (H ₄)	Mk-9 (H ₀)	Mk-9 (H ₂)	Mk-9 (III,VIII-H ₄)	Mk-9 (II,III-H ₄)	Mk-9 (H ₆)	Mk-10 (H ₄)
<i>Streptosporangium album</i>	+	tr	—							
<i>Streptosporangium amethystogenes</i>	—	+	—		10.1	49.4	33.5			
<i>Streptosporangium fragile</i>	—	—	—			15.0	60.0		25.0	
<i>Streptosporangium longisporum</i>	—	+	—		12.7	35.1	45.0		7.2	
<i>Streptosporangium nondiastaticum</i>	—	—	—		2.0	55.0	40.0		3.0	
<i>Streptosporangium pseudovulgare</i>	—	+	—		11.6	60.4	28.0			
<i>Streptosporangium roseum</i>	+	+	—		5.0	37.8	56.5		0.7	
<i>Streptosporangium violaceochromogenes</i>	—	—	—		19.0	50.0	31.0			
<i>Streptosporangium viridialbum</i>	—	+	—		35.3	42.8	21.9			
<i>Streptosporangium vulgare</i>	—	+	—		38.2	46.7	15.1			
<i>Streptosporangium carneum</i> ^b	—	+	—			++	+++			
<i>Streptosporangium corrugatum</i>	+	tr	—		12.9	52.3	32.4		3.4	
<i>Kutzneria viridogrisea</i>	+	—	+	1.0		3.0		90.0	4.0	2.0
<i>Kutzneria albida</i>	—	—	—					100.0		
<i>Kutzneria kofuensis</i>	+	—	—	1.0				97.0		2.0

^a The designations indicate the number of isoprenyl groups in the side chain and the number of hydrogenated double bonds.

^b Data from reference 14 (no qualitative data available).

TABLE 3. Fatty acid patterns of the genera *Streptosporangium*, *Kutzneria*, and *Saccharothrix*^a

Fatty acid	Mean % in:		
	<i>Streptosporangium</i> (9 strains)	<i>Kutzneria</i> (4 strains)	<i>Saccharothrix</i> (10 strains)
13:0	0.69		
iso-14:0	4.84		2.52
14:0	1.79		
iso-15:0	3.66	2.71	12.73
anteiso-15:0	1.98		3.16
15:1			0.53
15:0	5.12	1.61	0.90
iso-16:1		0.56	5.54
iso-16:0	12.27	30.28	37.01
cis9-16:1	3.51	3.80	1.49
2-OH-iso-15:0			1.20
16:0	10.07	6.16	1.74
Unknown ECL 16.048			2.51
9-methyl-16:0			4.46
10-methyl-16:0	3.97	8.58	
iso-17:0	1.45	6.19	3.48
anteiso-17:0	1.14	7.45	6.48
cis9-17:1	10.90	2.71	4.40
2-OH-iso-16:0	1.17	11.67	4.03
17:0	10.00	4.26	1.58
2-OH-16:0	0.82		
10-methyl-17:0	15.00	5.87	1.28
iso-18:0	0.77	0.86	0.55
cis9-18:1	2.99	0.83	0.67
2-OH-anteiso-17:0		4.48	0.78
18:0	2.20		
10-methyl-18:0	2.73	1.49	

^a Data from reference 4.

main clusters emerged (represented by *S. roseum* and *S. viridogriseum*). The members of each of these clusters are characterized by high levels of similarity in whole-cell sugars, menaquinones, fatty acid patterns, and phospholipid patterns; however, there are significant differences between the characteristics of the two species clusters. All *Streptosporangium* species defined previously (2) have in common wall chemotype III (i.e., meso-diaminopimelic acid [13]), fatty acid pattern 3c (i.e., saturated, unsaturated, iso and anteiso, and 10-methyl branched fatty acids [6], as well as 2-hydroxy fatty acids [7]), a DNA base composition between 69 and 71 mol% (as determined by the thermal denaturation method), and a lack of diagnostic sugars. In contrast to the description of the genus (18), madurose was not found in all species. The majority of species, including type species *S. roseum* but also *S. corrugatum*, are defined by the following combination of characteristics: the principal menaquinones are MK-9(H₂) and MK-9(II,VIII-H₄), MK-9, and/or MK-9(H₆) and the phospholipid type is type IV. The other cluster is composed of the two subspecies of *S. viridogriseum* and *Streptosporangium albidum*. These organisms are characterized by principal isoprenoids of the MK-9(II, III-H₄) type and by phospholipid type II; the DNA G+C contents of these organisms range between 70.3 and 70.7 mol% (this study).

The clustering of species based on morphological and chemotaxonomic properties is consistent with the results of a phylogenetic analysis of representatives of the two clusters. A 16S rDNA analysis (5) revealed that type species *S. roseum*, *Streptosporangium nondiasticum*, and *Streptosporangium pseudovulgare* were closely related (similarity level, 97.3 to 99.4%). These three species exhibited a close relationship to *S.*

corrugatum (similarity levels, 94.4 to 94.7%). These four species were moderately closely related to members of the genus *Streptomyces* (similarity levels, 91.1 to 91.8%). The results of a recent 5S rRNA analysis confirmed this conclusion; members of the family *Streptosporangiaceae* were found to be phylogenetic neighbors of members of the family *Streptomycetaceae* (11). On the other hand, the results of both analyses indicated that *S. viridogriseum* subsp. *viridogriseum* was clearly less closely related to the other *Streptosporangium* species (16S rDNA similarity levels, 90.8 to 91.7%) and clustered with members of the family *Pseudonocardiaceae* (16S rDNA similarity levels, 92.5 to 94.9%) particularly *Saccharothrix australiensis* (16S rDNA similarity level, 94.9%) (5).

The results of investigations described above clearly show that two species of the genus *Streptosporangium*, *S. albidum* and *S. viridogriseum*, including *S. viridogriseum* subsp. *viridogriseum* and *S. viridogriseum* subsp. *kofuense*, should not be retained in the genus *Streptosporangium*. The differences in the primary structures of both 5SrRNA and 16S rRNA, as well as in chemotaxonomic properties and in the electrophoretic mobility of a ribosomal protein, between members of the two clusters are greater than the differences that separate genera belonging to the family *Streptosporangiaceae*. The genus *Streptosporangium* should be restricted to the type species, *S. roseum*, and its relatives. Although there are substantial differences in the primary structure of 16S rRNA between *S. roseum* and *S. corrugatum* (5) and apparently in the amino acid sequence of the AT-L30 protein (20), the differences observed in the chemotaxonomic properties investigated so far are too small to consider *S. corrugatum* a representative of a novel genus. However, workers should be prepared to describe a new genus for *S. corrugatum* when differences in other phenotypic characteristics that have taxonomic value are discovered.

The phylogenetic position of *S. viridogriseum* and its relatives is within the confines of the family *Pseudonocardiaceae*, adjacent to *Saccharothrix australiensis* (5). No obvious exclusive chemotaxonomic features are shared by these organisms and the misclassified *Streptosporangium* species. The phylogenetic distance between *Saccharothrix australiensis* and the misclassified *Streptosporangium* species and the differences in morphology and in the fatty acid and menaquinone patterns, are significant enough to justify the description of a new genus, for which the name *Kutzneria* is proposed. Table 4 shows the key characteristics which differentiate the genera *Kutzneria* and *Streptosporangium* and phenotypically and genomically related genera. Below we also emend the descriptions of the species *K. viridogriseum* and *K. albidum*. The unpublished results of DNA similarity studies (1b) indicate that the two subspecies of *S. viridogriseum* exhibit less than 15% DNA similarity, whereas *S. viridogriseum* subsp. *viridogriseum* and *S. albidum* exhibit more than 30% DNA similarity. This relationship is also reflected by similarities in the fatty acid patterns (Fig. 1). Therefore, we propose that *S. viridogriseum* subsp. *kofuense* should be elevated to species status as *Kutzneria kofuensis*. The type species of the genus *Kutzneria* is *K. viridogrisea* because the original description of *S. viridogriseum* (21) has priority over *S. albidum* (1a) and *S. viridogriseum* subsp. *kofuensis* (19). The species description is the same as the original description except that it is emended to include chemotaxonomic data.

Description of the genus *Kutzneria*. *Kutzneria* (Kutz.ne'ri.a. M.L. fem. n. *Kutzneria*, named after Hans-Jürgen Kutzner, a German microbiologist). The description of morphological characteristics below is taken from the descriptions of the genus *Streptosporangium* and group 1 streptosporangia (18). Stable, branched, cottony aerial mycelium. Globose sporangia are large (diameter, 10 to 48 µm). Sporangial walls are thick

TABLE 4. Comparison of the genus *Kutzneria* with phenotypically and phylogenetically related genera of actinomycetes

Genus	Morphology			Chemotaxonomy			
	Aerial mycelium	Sporangium	Motile spores	Whole-cell sugar type	Phospholipid type	Fatty acid type (>10% of total)	Major menaquinone(s)
<i>Kutzneria</i>	+	+	—	E	II	3c	MK-9(II,III-H ₄)
<i>Saccharothrix</i>	+	—	—	C	II	3f	MK-9(II,III-H ₄), MK-10(II,III-H ₄)
<i>Kibdelosporangium</i>	+	+ ^a	—	A	II	3c	ND ^b
<i>Streptosporangium</i>	+	+	—	B or C	IV	3c	MK-9(H ₀), MK-9(H ₂), MK-9(III, VIII-H ₄)
<i>Planomonospora</i>	+	+	+	B	IV	3c	MK-9(H ₀), MK-9(H ₂), MK-9(III, VIII-H ₄)
<i>Microtetraspora</i>	+	—	—	B or C	IV	3c	MK-9(H ₀), MK-9(H ₂), MK-9(III, VIII-H ₄)
<i>Microbispora</i>	+	—	—	B	IV	3c	MK-9(H ₂), MK-9(III, VIII-H ₄)
<i>Herbidospira</i>	—	—	—	B	IV	3c	MK-10(III,IX-H ₄), MK-10(H ₆), MK-10(H ₂)
<i>Actinomadura</i>	+	—	—	B	I	3a	MK-9(H ₆), MK-9(H ₈)
<i>Spirillospora</i>	+	+	+	B	I or II	3a	MK-9(H ₄), MK-9(H ₆)

^a Sporangium-like structures do not contain spores but germinate directly (23).^b ND, not determined.

and strong. Long sporangiophores more than 50 µm long are formed by septation of coiled, unbranched hyphae within the sporangiophores. The spores are spherical, rod shaped, or oval and nonmotile. Aerobic. Mesophilic. Some species are thermotolerant. Chemoorganotrophic. Gram positive. Cell walls contain N-acetylated muramic acid, *meso*-diaminopimelic acid, and no common characteristic sugars. MK-9(II, III-H₄) is the major isoprenolog. The major phospholipids usually include phosphatidylethanolamine, hydroxyphosphatidylethanolamine, phosphatidylinositol, and diphosphatidylglycerol. Iso-16:0, 2-OH-iso-16:0, 10-methyl-16:0, anteiso-17:0, and 2-OH-anteiso-17:0 fatty acids are major fatty acids. No 13:0, iso-14:0, and 14:0 fatty acids are present. Natural habitat: soil. The G+C content of the DNA is 70.3 to 70.7 mol% (as

determined by HPLC). Phylogenetically related to *Saccharothrix australiensis*.

The type species is *Kutzneria viridogrisea*.

Description of *Kutzneria viridogrisea* (Okuda, Furumai, Watanabe, Okugawa, and Kimura 1966) comb. nov. (Approved Lists 1980). *Kutzneria viridogrisea* (vi.ri.do.gri' se.a. L. adj. *viridis*, green; L. adj. *griseus*, gray; M.L. fem. adj. *viridogrisea*, greenish gray). Descriptions of this taxon have been published previously by Okuda et al. (21) and Nonomura (18). The whole-cell sugars are galactose and rhamnose. The DNA G+C content is 70.3 mol%. Type strain: DSM 43850 (= ATCC 25242).

Description of *Kutzneria albida* (Furumai, Ogawa, and Okuda 1968) comb. nov. (Approved Lists 1980). *Kutzneria albida* (al'bi.da. L. fem. adj. *albidum*, white). Descriptions of this taxon have been published previously by Furumai et al. (1a) and Nonomura (18). The whole-cell sugar is rhamnose. The DNA G+C content is 70.7 mol%. Type strain: DSM 43870 (= ATCC 25243).

Description of *Kutzneria kofuensis* (Nonomura and Ohara 1969) comb. nov. (Approved Lists 1980). *Kutzneria kofuensis* (ko.fu.en'sis. M.L. adj. *kofuensis*, belonging to Kofu, a district in Japan, where the organism was isolated). Descriptions of this taxon have been published previously by Nonomura and Ohara (19) and Nonomura (18). The whole-cell sugars are rhamnose and galactose. The DNA G+C content is 70.6 mol%. Type strain: DSM 43851 (= ATCC 27102).

The exclusion of species from the genus *Streptosporangium* and the chemotaxonomic properties justify emendation of the description of this genus.

Description of the genus *Streptosporangium* Couch 1955, 148^{AL} emend. Stackebrandt et al. 1994. The description below is based on the characteristics given by Nonomura (18). Stable branched mycelium produces globose sporangia up to 10 µm in diameter on the aerial mycelium. The sporangiophores are short (up to 10 µm long). The sporangiospores are spherical-oval or rod shaped (0.2 to 1.3 by 0.2 to 1.5 µm) and nonmotile and are formed by septation of a coiled, unbranched hypha within the sporangium. Cell walls contain N-acetylated muramic acid and *meso*-diaminopimelic acid, but no characteristic sugar occurs in whole-cell hydrolysates. Madurose may be present. The major phospholipids include phosphatidylethanolamine, hydroxyphosphatidylethanolamine, phosphatidylinositol, diphosphatidylglyc-

FIG. 1. Cluster analysis of fatty acid profiles of *Streptosporangium* and *Kutzneria* species. The branching pattern was constructed from Euclidian distance coefficients by the unweighted pair group method with arithmetic averages. The analysis was performed by using the standard MIS software (Microbial ID).

erol, and an *N*-acetylglucosamine-containing phospholipid but no phosphatidylcholine. The predominant menaquinones are MK-9(H₂) and MK-9(II,VIII-H₄), MK-9, and/or MK-9(H₆). The characteristic fatty acids are 13:0, iso-14:0, 14:0, 15:0, iso-16:0, *cis*-9-16:1, 16:0, 10-methyl-16:0, *cis*-9-17:1, 17:0, 10-methyl-17:0, and 18:0 fatty acids. 2-OH-iso-16:0 fatty acid is present. No 2-OH-anteiso-17:0 fatty acid is present. Gram positive. Aerobic. Mesophilic. Chemoorganotrophic. Some species require vitamin B for growth. Natural habitat: soil. The G+C content of the DNA is 69 to 71 mol% (as determined by the thermal denaturation method). Type species: *Streptosporangium roseum* Couch 1955, 151.

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