Taxonomic Status of *Kitasatosporia*, and Proposed Unification with *Streptomyces* on the Basis of Phenotypic and 16S rRNA Analysis and Emendation of *Streptomyces* Waksman and Henrici 1943, 339^{AL}

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Species classified within the genus *Kitasatosporia* share many of the phenotypic characteristics typical of streptomycetes. By using a probabilistic identification scheme, they were identified with *Streptomyces exfoliatus* cluster 5, a species group within *Streptomyces*. The four species studied hybridized with a 16S rRNA genus probe for *Streptomyces* spp., indicating a close relationship between the two genera. The *kitasatosporias* were resistant to selected polyvalent streptomycete phages tested. Quantitative analysis showed that *meso*-diaminopimelic acid varied from 49 to 89% in *Kitasatosporia* species and from 1 to 16% in *Streptomyces* species depending on growth conditions. On the basis of 16S rRNA analysis, it is proposed to reduce *Kitasatosporia* to synonymy with *Streptomyces*. As a result, the new names proposed are *Streptomyces mediocidicus* comb. nov., *Streptomyces phosalacineus* comb. nov., *Streptomyces setae* comb. nov., and *Streptomyces griseolosporus* comb. nov., nom. nov.

The genus *Kitasatosporia* was proposed to include newly isolated actinomycete strains which contained similar amounts of LL and *meso* isomers of diaminopimelic acid (DAP) and also glycine and galactose in their cell walls (9). Further analysis revealed that most of the LL-DAP was in the aerial mycelium, and the *meso*-DAP was in the vegetative mycelium (15). The morphology and physiology of the strains were characteristic of *Streptomyces* spp., but submerged growth resulted in production of sporelike cells which contained LL-DAP, whereas the mycelium contained *meso*-DAP (15). Labeda (5) described a new species, *Kitasatosporia mediocidica*, which contained both LL- and *meso*-DAP and showed traces of glycine in whole-cell hydrolysates. The sugars galactose and rhamnose were also detected. Further species were described but they had more LL- than *meso*-DAP (ratio of 3:1) (7). The cell wall typical of *Streptomyces* spp. contains major amounts of LL-DAP with glycine, wall chemotype 1 (1), although minor amounts of *meso*-DAP can be detected.

The aim of the present study was to clarify the relationship between the genera *Kitasatosporia* and *Streptomyces* and determine if the former should be grouped with members of the family *Streptomycetaceae* on the basis of 16S rRNA, phage susceptibility, chemotype, and phenotype.

MATERIALS AND METHODS

Strains. *K. griseola* NRRL B-16229, *K. mediocidica* NRRL 16109^T, *K. phosalacinea* NRRL B-16230, and *K. setae* NRRL B-16185 (representing the type species) were kindly supplied by D. Labeda and preserved in 10% glycerol at –20°C. Other actinomycetes used for cell wall analysis are listed in Table 2.

Morphology and physiology. Strains were examined by

using the methods of Williams et al. (19), and their phenotypes were compared with those of *Streptomyces* spp. by use of a probabilistic identification scheme for the major species groups (20).

Cell wall analysis. Strains were grown in shake flasks at 30°C for 3 days in tryptone soy broth (Oxoid) (25 ml in 250-ml flasks), harvested by centrifugation, and washed with distilled water and ethanol before being dried. Whole-cell hydrolysates were prepared by using 60 mg of dried cells, and cell wall type was determined by thin-layer chromatography (14). Cells were also harvested from plate cultures grown for 2 days at 30°C on peptone agar containing (weight/volume) peptone, 0.6%; Bacto Casitone, 0.4%; yeast extract, 0.3%; glucose, 0.1%; beef extract, 0.15%; and agar, 2.0%. For high-pressure liquid chromatography (HPLC) analysis, dried hydrolyzed samples were suspended in 10 ml of Milli-Q water and diluted 1:3 before injection into the HPLC. LL- and *meso*-DAP were measured as the fluorescent *o*-phthalaldehyde derivatives (3).

Phage typing. The polyvalent phage DP9, 102, 93, 86, 35, and 34, known to be specific for the *Streptomycetaceae* with cell wall chemotype 1 (17), were tested for lysis on lawns of the four *Kitasatosporia* species by using the methods of Wellington and Williams (17).

Isolation of crude RNA, probe synthesis, and hybridization conditions. Cells grown in shake flasks containing tryptone soy broth (30 ml in 100-ml flasks) were harvested after 12 h by centrifugation. Isolation of crude RNA, labeling of probes, and dot blot hybridization were done as described by Stackebbrandt and Charfreitag (12). Three hundred nanograms of crude RNA from each of the 4 *Kitasatosporia* strains and the 16 streptomycete and nonstreptomycete reference strains was hybridized with 10⁵ cpm of ³²P-labeled probes (depending on the specific activity, between 20 and 50 ng of RNA). The probes were directed against specific stretches of the 16S rRNA. Hybridization was done in 6× SSC (1× SSC is 0.15 M NaCl, 0.015 M trisodium citrate, and 0.001 M EDTA, pH 7)–0.1% sodium dodecyl sulfate (pH 7.2) at 28°C for the eubacterial consensus probe (5' CTACCAG

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TABLE 1. Identification of *Kitasatosporia* species by a probability matrix for *S. exfoliatus* cluster group 5 (20)

Species	Identification score	
	Wilcoxon <i>P</i>	Taxonomic distance $\pm$ s.e. (d)
<i>K. griseola</i> NRRL B-16229	0.99	0.43 + 2.3
<i>K. mediocidica</i> NRRL B-16109	0.97	0.44 + 2.48
<i>K. phosalacinea</i> NRRL B-16230	0.98	0.39 + 1.32
<i>K. setae</i> NRRL B-16185	0.97	0.41 + 1.91

GGTATCTAAT 3', targeting positions 787 to 803 [*Escherichia coli* nomenclature]) and at 38°C for the *Streptomyces*-specific probe (5' GCGTCGAATTAAGCCACA 3', positions 950 to 967). After hybridization, filters were washed with 6× SSC for 2 min at room temperature and then for 15 min under more-stringent conditions to destroy unspecifically reassociated hybrids (see legend to Fig. 1). Autoradiography was for 20 h.

Sequence homology of 16S rRNA. The sequence data for the *Streptomyces* species were from Witt et al. (21, 22), and the basis for homology calculation was a reduced sequence alignment that had eliminated all the absolutely conserved positions.

Sequence data for *Kitasatosporia* species were provided by Martin Embley, Department of Paramedical Sciences, North East London Polytechnic, London, England.

RESULTS

Probabilistic identification. The phenotypes of the four *Kitasatosporia* species, all identified with the *Streptomyces* cluster group 5 of Williams et al. (20) (*Streptomyces exfoliatus*), and the identification scores show a close similarity between all four species and *S. exfoliatus* (Table 1). The results also indicate that there is phenotypic similarity among the *Kitasatosporia* species. The strains had a number of atypical characters; they failed to degrade xanthine or allantoin, and *K. setae* and *K. phosalacinea* were resistant to rifampin (test method of Williams et al. [20] was used). The taxonomic distance scores (Table 1) indicate that the species are not close to the centroid of the group.

Cell wall analysis. Cell wall analysis of submerged growth (3-day culture) by thin-layer chromatography revealed significant amounts of LL-DAP in all *Kitasatosporia* species except *K. mediocidica*. Quantification of the relative amounts of each isomer present in biomass from both liquid and solid cultures was achieved by HPLC analysis (Table 2). By using HPLC, meso-DAP was also detected in *Streptomyces* species at levels between 1 and 16%, depending on the species analyzed. The level of meso-DAP detected in *Kitasatosporia* strains varied from 49 to 89%, where variation was dependent on the amount of sporulation in the cultures, as previously reported for this group (15). Except for *S. griseus*, which can produce sporelike bodies, the *Streptomyces* species did not produce submerged spores. It can be concluded that under any of the conditions tested, the *Kitasatosporia* species always had at least three times more meso-DAP in the cells than *Streptomyces* species had. Within the *Streptomyces* genus, variations in the amounts of meso-DAP were recorded, but no clear correlation was seen with the morphological type of biomass analyzed.

The ratios of meso- to LL-DAP for *Kitasatosporia* species (submerged growth, 3 days) varied from 9:1 to 1:1. Only

TABLE 2. Proportions of LL-DAP and meso-DAP in different actinomycete species

Organism ^a	Collection no.	% DAP	
		LL	meso
<i>Actinoplanes auranticolor</i> (S)	JCM 3038	10	90
<i>Actinoplanes phiippinensis</i> (S)	JCM 3001	14	86
<i>Ampullariella digitata</i> (S)	ATCC 15349	13	87
<i>Faenia rectivirgula</i> (S)	ATCC 33515	5	95
<i>Kineosporia curantiaca</i> (S)	JCM 3230	63	37
<i>Nocardioides albus</i> (S)	ATCC 27980	95	5
<i>Saccharomonospora viridis</i> (S)	IFO 12207	8	92
<i>Sporichthya polymorpha</i> (S)	JCM 3089	100	0
<i>Streptomyces albus</i> (S)	ISP 5313	95	5
<i>Streptomyces albus</i> (L)	ISP 5313	88	12
<i>Streptomyces cyaneus</i> (S)	JCM 4220	91	9
<i>Streptomyces flaveus</i> (S)	A 2001	99	1
<i>Streptomyces griseoruber</i> (S)	JCM 4200	95	5
<i>Streptomyces griseus</i> (S)	ISP 5236	93	7
<i>Streptomyces griseus</i> (L)	ISP 5236	93	7
<i>Streptomyces roseiscleroticus</i> (S)	JCM 3104	85	15
<i>Streptomyces purpureus</i> (S)	JCM 3172	84	16
<i>Kitasatosporia griseola</i> (S)	NRRL B-16229	16	84
<i>Kitasatosporia griseola</i> (L)	NRRL B-16229	21	79
<i>Kitasatosporia mediocidica</i> (S)	NRRL B-16109	37	63
<i>Kitasatosporia mediocidica</i> (L)	NRRL B-16109	11	89
<i>Kitasatosporia phosalacinea</i> (S)	NRRL B-16230	24	76
<i>Kitasatosporia phosalacinea</i> (L)	NRRL B-16230	51	49
<i>Kitasatosporia setae</i> (S)	NRRL B-16185	31	69
<i>Kitasatosporia setae</i> (L)	NRRL B-16185	22	78

^a Cells were harvested from solid (S) or liquid (L) media.

Kitasatosporia strains contained galactose in the hydrolysate.

Phage typing. All species of *Kitasatosporia* tested were resistant to polyvalent *Streptomyces* phage. These phage lyse some members of *S. exfoliatus* cluster 5 and a wide range of *Streptomyces* species, although some species, such as *S. aureofaciens*, were resistant to all phage (17).

rRNA probing. The results of the dot blot hybridization are shown in Fig. 1. The autoradiogram illustrates hybridization between crude RNA of *Kitasatosporia* species, selected streptomycetes, other actinomycetes, and the ³²P-labeled probes. The universal probe (Fig. 1A) was used to show the presence and availability of RNA at each dot. The *Streptomyces* probe (Fig. 1B and C) has been shown to detect all members of the genera *Streptomyces* and *Streptoverticillium* (13) but fails to bind to RNA from all other members of the order *Actinomycetales*. Nonactinomycetes so far investigated also do not bind with the probe. The specificity of the probe is due to a single but highly unique base pair (C at position 955 [*E. coli* numbering]). The washing temperature therefore has to be raised to 52°C (autoradiogram C in Fig. 1), which is only 2°C below the melting temperature of the homologous hybrid. The RNAs from all the *Kitasatosporia* strains, even at the highly stringent washing temperature (Fig. 1C), gave strong hybridization signals with the *Streptomyces* probe. RNAs from *Streptomyces* and *Streptoverticillium* species hybridized with the genus probe. It is evident that the 16S rRNAs from the *Kitasatosporia* strains contain the *Streptomyces*-specific signature nucleotide at position 955.

16S rRNA homologies. The sequence homology between the type species *K. setae*, *S. albus*, and *Streptoverticillium baldacii* (Table 3) shows that there is a high degree of homology between *K. setae* and *S. baldacii*. The latter

FIG. 1. Autoradiogram of dot blot hybridization between 16S rRNAs from strains of *Kitasatosporia* (lane a), *Streptovorticillium* (lane b), *Streptomyces* (lane c), and other actinomycetes (lanes d and e). (A) Eubacterial consensus probe (28°C hybridization temperature [ht], 34°C washing temperature [wt]); (B and C) *Streptomyces* probe. (B) 38°C ht, 48°C wt. (C) Subsequent washing of filter B at 52°C. Organisms: a1, *K. setae*; a2, *K. mediocidica*; a3, *K. phosalacinea*; a4, *K. griseola*; b1, *Streptovorticillium rubroverticillatum*; b2, *Streptovorticillium griseovorticillatum*; b3, *Streptovorticillium morokaense*; b4, *Streptovorticillium abikoense*; c1, *S. exfoliatus*; c2, *S. albus*; c3, *S. kauaiensis*; c4, *S. griseus*; d1, *Actinomadura malachitica*; d2, *Nocardia farcinica*; d3, *Dermatophilus congolense*; d4, *Frankia Mut 15*; e1, *Saccharothrix australiensis*; e2, *Streptosporangium amethystogenes*; e3, *Tsukamurella aurantiaca*; e4, *Thermomonospora mesophila*.

species has a higher degree of homology to *K. setae* than to other streptomycetes such as *S. brasiliensis*. *K. setae* is also closely related to *S. lavendulae*.

DISCUSSION

The taxonomic status of the genus *Kitasatosporia* is uncertain. The data presented here strongly indicate that members of this genus are closely related to members of the genus *Streptomyces*. We have provided definitive evidence that *Kitasatosporia* species can be grouped with *Streptomyces* and *Streptovorticillium* species on the basis of rRNA probe analysis. However, *Kitasatosporia* species identify phenotypically with *Streptomyces* and not with *Streptovorticillium* species. Conversely, streptovorticillia are susceptible to phage used to type the *Streptomyces* genus, but the species of *Kitasatosporia* tested were resistant. This may reflect differences in restriction enzymes or receptors. The cell wall analysis of *Kitasatosporia* species is confused but does indicate more *meso*-DAP than occurs in *Streptomyces* and *Streptovorticillium* species. Takahashi et al. (16) made a detailed study of the distribution of *meso*- and LL-DAP in the different phases of growth. *Streptomyces* species contained only LL-DAP in aerial and vegetative mycelia, whereas *K. setae*, *K. phosalacinea*, and *K. griseola* contained LL-DAP in the aerial mycelium and *meso*-DAP in the vegetative mycelium. Only LL-DAP was detected in submerged and aerial spores. Nakamura et al. (7) reported differences in the ratio of LL- to *meso*-DAP when they analyzed submerged

growth. *K. setae* was found to contain the isomers in a ratio of 1:3, while two new species were described with ratios of 3:1. Other analyses of submerged growth have simply quoted the isomers to be present in equal amounts (5, 9). Obviously, the amounts of *meso*- and LL-DAP are variable and depend on the growth conditions and extent of sporulation. In the current study, *meso*-DAP was detected in significant amounts only by HPLC of extracts from submerged mycelium grown in tryptone soy broth. However, the results were variable and depended on the species examined and the extent of sporulation in the culture, as spores contained LL-DAP but mycelium contained predominantly *meso*-DAP. Differing amounts (1 to 16%) of *meso*-DAP can be detected by HPLC in the whole-cell hydrolysates of mycelia from *Streptomyces* species. This suggests that the relative amounts of *meso*-DAP may not be a good criterion for the delimitation of a genus. *Kitasatosporia* species are also identified by the presence of galactose in whole-cell hydrolysates (9), which appears to be unaffected by the form of growth. This is the only distinguishing feature serving to separate *Kitasatosporia* from *Streptomyces* species. One of the other characteristics cited is the formation of submerged spores, but there have been reports clearly illustrating the formation of spores in submerged cultures of *S. griseus* (2).

Nomenclatural considerations. On the basis of 16S rRNA homology, *K. setae* shows a high degree of homology to *S. lavendulae* and *S. baldaccii*. *Streptovorticillium* has been proposed as a synonym of *Streptomyces* on the basis of chemotaxonomic, biochemical, and phylogenetic similarities (22). Our data support a similar synonymy for *Kitasatosporia*.

The unification of *Kitasatosporia* with *Streptomyces* is proposed, and species transferred to the genus *Streptomyces* are *K. griseola*, *K. mediocidicus*, *K. phosalacinea*, and *K. setae*. The specific epithet for *K. setalba* was in violation of Rule 12a of the *International Code of Nomenclature*, and so the name was revised to *K. setae* (10). New combinations therefore include *S. mediocidicus* (Labeda, 1988) comb. nov., *S. phosalacineus* (Takahashi, Owai and Omura, 1984) comb. nov., and *S. setae* (Omura, Takahashi, Iwai and Tanaka, 1982) comb. nov.

For the *Kitasatosporia* species *K. griseola*, it is necessary to substitute a new specific epithet to produce *S. griseolosporeus*, because there is a senior homonym (see Rules 34a

TABLE 3. Homology of stretches of 16S rRNA (excluding all absolutely conserved positions) of selected *Streptomyces* species and *K. setae*

Organism	Collection no. ^a	% Homology with:			
		<i>K. setae</i>	<i>S. baldaccii</i>	<i>S. lavendulae</i>	<i>S. albus</i>
<i>K. setae</i>	ATCC 33774				
<i>S. baldaccii</i>	DPDU 0819	91.6			
<i>S. lavendulae</i>	ISP 5069	91.0	95.8		
<i>S. albus</i>	ISP 5313	89.3	92.2	93.0	
<i>S. brasiliensis</i>	ATCC 23727	88.2	90.1	91.4	92.8

^a DPDU, Instituto di difesa delle Pianta, Università degli studi di Udine, Udine, Italy.

and 41a, *International Code of Nomenclature of Bacteria* [6]), *S. griseolus*, cited on the *Approved List of Bacterial Names* (11). The species "*K. cystarginea*" (4), "*K. grisea*," and "*K. papulosa*" (7) are not on the *Approved List of Bacterial Names* but are possible candidates for transfer to the genus *Streptomyces*.

Emendation of *Streptomyces* Waksman and Henrici 1943, 339^{AL}. The description of the genus *Streptomyces* (18) together with emendation, including *Streptovorticillium* (22) and adding to the description to include *Kitasatosporia* (10), forms the basis for this emendation. Vegetative hyphae (0.5 to 0.2 μ m in diameter) produce a well-developed branched mycelium that rarely fragments. Reproduction by germination of the aerial, nonmotile spores. In most species, the aerial mycelium forms chains of spores, the surfaces of which are smooth, hairy, spiny, or warty. In other species, the aerial mycelium consists of long straight filaments bearing branches (3 to 6) at regular intervals which are arranged in whorls (verticils). The appearance at ca. $\times 100$ magnification is of barbed wire. Each branch of the verticil produces at its apex an umbel of two or more spore chains, with spores lacking ornaments. A few species produce spores on the substrate mycelium or in liquid culture. Sclerotia, pycnidia, sporangiumlike bodies, and synnemalike structures may be formed. Form discrete and lichenoid, leathery or butyrous colonies. Initially, colonies are smooth surfaced but later develop a weft of aerial mycelium that may appear floccose, cottony, granular, powdery, or velvety.

Produce a wide variety of pigments responsible for the color of the vegetative and aerial mycelia. Colored diffusible pigments may also be formed. Many strains produce one or more antibiotics. Gram positive but not acid fast. Aerobes. Chemoorganotrophic, having an oxidative type of metabolism. Most strains use a wide range of organic compounds as sole sources of carbon for energy and growth, but some can utilize only a limited number of carbon sources. Substrate growth may develop under reduced oxygen tensions or increased carbon dioxide concentrations. Temperature optimum, 25 to 35°C at pH 5.5 to 9.0; some species grow at temperatures within the psychrophilic and thermophilic ranges.

The cell wall peptidoglycan contains major amounts of LL-DAP in spores and hyphae; major amounts of meso-DAP may be detected in the vegetative hyphae. Galactose may be present in the whole-cell hydrolysate. They lack mycolic acids, contain major amounts of saturated, iso-, and anteiso-fatty acids, possess either hexa- or octahydrogenated menaquinones with nine isoprene units as the predominant isoprenolog, and have complex polar lipid patterns that typically contain diphosphatidylethanolamine, phosphatidyl-diglycerol, phosphatidylinositol, and phosphatidylmannosides. They are widely distributed in soil, including compost. A few species are pathogenic for animals and humans; others are phytopathogens. The G+C content of the DNA is 66 to 78 mol% (at melting temperature).

Type species: *S. albus* (Rossi-Doria) Waksman and Henrici 1943, 339.

Description of *S. griseolosporeus* nom. nov. gri'se.o.lo.spo're.us. M.L. adj. *griseolus*, somewhat grey; M.L. n. *spora*, a spore; *griseolosporeus*, somewhat grey spored.

The species has been described as *K. griseola* by Takahashi et al. (16) and by Omura et al. (8). The new name is substituted as a result of homonymy (Rule 34a).

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REFERENCES

1. Becker, B., M. P. Lechevalier, and H. A. Lechevalier. 1965. Chemical composition of cell-wall preparations from strains of various form-genera of aerobic actinomycetes. *Appl. Microbiol.* 13:236-243.
2. Glazebrook, M. A., J. L. Doull, C. Stutard, and L. C. Vining. 1990. Sporulation of *Streptomyces venezuelae* in submerged cultures. *J. Gen. Microbiol.* 136:581-588.
3. Jorgensen, N. O. G. 1987. Free amino acids in lakes: concentration and assimilation rates in relation to phytoplankton and bacterial production. *Limnol. Oceanogr.* 32:97-111.
4. Kusakabe, H., and K. Isono. 1988. Taxonomic studies on *Kitasatosporia cystarginea* sp. nov., which produces a new antifungal antibiotic cystarginea. *J. Antibiot.* 41:1758-1762.
5. Labeda, D. P. 1988. *Kitasatosporia mediocidica* sp. nov. *Int. J. Syst. Bacteriol.* 38:287-290.
6. Lapage, S. P., P. H. A. Sneath, E. F. Lessel, V. B. D. Skerman, H. P. R. Seeliger, and W. A. Clark (ed.). 1975. International code of nomenclature of bacteria, 1975 revision. American Society for Microbiology, Washington, D.C.
7. Nakamura, Y., E. Ono, T. Kohda, and H. Shibai. 1989. Two new carbapenem antibiotic-producing actinomycetes: *Kitasatosporia papulosa* sp. nov. and *Kitasatosporia grisea* sp. nov. *J. Antibiot.* 52:18-29.
8. Omura, S., Y. Takahashi, and Y. Iwai. 1989. Genus *Kitasatosporia*, p. 2594-2598. In S. T. Williams, M. E. Sharpe and J. G. Holt (ed.), *Bergey's manual of systematic bacteriology*, 9th ed. The Williams & Wilkins, Co., Baltimore.
9. Omura, S., Y. Takahashi, Y. Iwai, and H. Tanaka. 1982. *Kitasatosporia*, a new genus of the order *Actinomycetales*. *J. Antibiot.* 35:1013-1019.
10. Omura, S., Y. Takahashi, Y. Iwai, and H. Tanaka. 1985. Revised nomenclature of *Kitasatosporia setalba*. *Int. J. Syst. Bacteriol.* 35:221.
11. Skerman, V. B. D., V. McGowan, and P. H. A. Sneath. 1980. Approved list of bacterial names. *Int. J. Syst. Bacteriol.* 30:225-420.
12. Stackebrandt, E., and O. Charfreitag. 1990. Partial 16S rRNA primary structure of five *Actinomyces* species: phylogenetic implications and development of an *Actinomyces israelii*-specific oligonucleotide probe. *J. Gen. Microbiol.* 136:37-43.
13. Stackebrandt, E., D. Witt, C. Kemmerling, R. Kroppenstedt, and W. Liesack. 1991. Designation of streptomycete 16S and 23S rRNA-based target regions for oligonucleotide probes. *Appl. Environ. Microbiol.* 57:1468-1477.
14. Stanek, J. L., and G. D. Roberts. 1974. Simplified approach to identification of aerobic actinomycetes by thin layer chromatography. *Appl. Microbiol.* 28:226-231.
15. Takahashi, Y., Y. Iwai, and S. Omura. 1983. Relationship between cell morphology and the types of diaminopimelic acid in *Kitasatosporia setalba*. *J. Gen. Appl. Microbiol.* 29:459-465.
16. Takahashi, Y., Y. Iwai, and S. Omura. 1984. Two new species of the genus *Kitasatosporia*, *Kitasatosporia phosalacinea* sp. nov. and *Kitasatosporia griseola* sp. nov. *J. Gen. Appl. Microbiol.* 30:377-387.
17. Wellington, E. M. H., and S. T. Williams. 1981. Host ranges of phage isolated to *Streptomyces* and other genera. *Zentralbl. Bakteriol. Abt. 1* 11(Suppl.):93-98.
18. Williams, S. T., M. Goodfellow, and G. Alderson. 1989. Genus *Streptomyces* Waksman and Henrici 1943, 339^{AL}, p. 2452-2492. In S. T. Williams, M. E. Sharp, and J. G. Holt (ed.), *Bergey's manual of systematic bacteriology*, 9th ed. The Williams & Wilkins Co., Baltimore.
19. Williams, S. T., M. Goodfellow, G. Alderson, E. M. H. Wellington, P. H. A. Sneath, and M. J. Sackin. 1983. Numerical classification of *Streptomyces* and related genera. *J. Gen. Mi-*

- crobiol. **129**:1815–1830.
20. Williams, S. T., M. Goodfellow, E. M. H. Wellington, J. C. Vickers, G. Alderson, P. H. A. Sneath, M. J. Sackin, and A. M. Mortimer. 1983. A probability matrix for identification of some streptomycetes. *J. Gen. Microbiol.* **129**:1815–1830.
21. Witt, D., W. Liesack, and E. Stackebrandt. 1989. Identification of streptomycetes by 16S rRNA sequences and oligonucleotide probes, p. 679–684. *In* T. Hattori, Y. Ishida, Y. Maruyama, R. Morita, and A. Uchida (ed.), Recent advances in microbial ecology. Japan Scientific Society Press, Tokyo, Japan.
22. Witt, D., and E. Stackebrandt. 1990. Unification of the genera *Streptovercillium* and *Streptomyces* and amendment of *Streptomyces* Waksman and Henrici 1943, 339^{AL}. *Syst. Appl. Microbiol.* **13**:361–371.