A numerical classification of the genera *Streptomyces* and *Streptoverticillium* using miniaturized physiological tests

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(Received 26 October 1990; accepted 13 February 1991)

Eight hundred and twenty-one strains of the genera *Streptomyces* and *Streptoverticillium* were physiologically characterized using a total of 329 miniaturized tests. Overall similarities of all strains were determined by numerical taxonomic techniques using the UPGMA algorithm and the S_{SM} and the S_J coefficients as measures of similarity. Test error was within acceptable limits. Comparison of photometric and visual test reading revealed overall differences of 7.45%. A total of 15 major clusters (six or more strains), 34 minor clusters (less than six strains) and 40 single-member clusters were defined at the 81.5% similarity level (S_{SM}). Two clusters containing physiologically, and in some cases morphologically and genetically, different groups could be further subdivided at the 84.0% similarity level (S_{SM}). Generally, similar groupings were obtained with the Jaccard coefficient at similarity levels ranging from 59.6% to 64.6% similarity (S_J), with changes in the definition of clusters and subclusters. The cophenetic correlation coefficients r_{cs} for the UPGMA/ S_J and the UPGMA/ S_{SM} analysis were 0.6929 and 0.8239, respectively. Several phenons showed significant overlap with others, indicating the physiological variability within the species. The phenetic data in most cases confirm the major phenons of the study of Williams *et al.* (1983), *Journal of General Microbiology* 129, 1743–1813 (although the cluster-groups defined in that study could only be detected in part) and the results indicate that the genus *Streptomyces* is still overspeciated. Some of the major groupings obtained were very much in line with chemotaxonomic and genetical data. However, several clusters containing only a few strains should be regarded as preliminary 'species' until further information is available. The majority of *Streptoverticillium* strains presently assigned to different species formed a homogeneous subcluster defined at the 84.0% similarity level (S_{SM}). Thus, on the basis of numerical phenetic and (published) molecular genetic and chemotaxonomic data, our study supports the suggestion that members of the genus *Streptoverticillium* be reclassified into the genus *Streptomyces*.

Introduction

The genera *Streptomyces* and *Streptoverticillium* are classified within the family *Streptomycetaceae* and contain Gram-positive aerobic, sporeforming actinomycetes, producing extensive branching substrate and aerial mycelia with LL-diaminopimelic acid and glycine but no characteristic sugar in the wall (wall type I *sensu* Lechevalier & Lechevalier, 1970a, b). They are widely distributed in nature, play an important role in the turnover of organic matter and are of considerable industrial importance (Kutzner, 1981; Williams *et al.*,

1984; Goodfellow *et al.*, 1984). Studies on the chemotaxonomy of various genera of the *Actinomycetales* have revealed the value of chemical markers as differentiating characters at the genus level and even at higher taxonomic levels (Collins & Jones, 1981; Goodfellow & Cross, 1984; Kroppenstedt, 1985; Lechevalier & Lechevalier, 1970a, b; Lechevalier *et al.*, 1977; Minnikin & Goodfellow, 1980; Minnikin *et al.*, 1977; Stackebrandt, 1986). However, although variation of fatty acid and mycolic acid patterns has been found within the genera *Streptomyces* and *Streptoverticillium*, chemotaxonomic data are only of limited importance for species differentiation (Minnikin *et al.*, 1978; Goodfellow & Schaal, 1979; Goodfellow & Wayne, 1982; Kroppenstedt, 1985).

Studies of rRNA catalogues have shown the *Streptomycetaceae* to be a coherent taxon (Goodfellow & Cross,

Abbreviations: OTU, operational taxonomic unit; p-NA, *p*-nitroanilide; p-NP, *p*-nitrophenyl; RA, *Retinaculiaperti*, RF, *Rectiflexibilis*; SP, *Spirales* (spore chain categories).

1984; Stackebrandt & Woese, 1981; Stackebrandt *et al.*, 1981). Because of the similarity between species in chemotaxonomic characters, numerical taxonomy studies have been very important to the taxonomy of streptomycetes (Alderson *et al.*, 1984). The extensive numerical classification of Williams *et al.* (1983a) using 394 type cultures of *Streptomyces* tested for 139 unit characters was the foundation of an extensive species reduction within the genus *Streptomyces*. In this study 23 major, 20 minor and 25 single-member clusters, containing 219, 46 and 25 validly described species, respectively, were defined at the 77.5% or 81% S_{SM} or 63% S_j similarity levels. This study forms the basis of the classification in *Bergey's Manual of Systematic Bacteriology*, vol. 4 (Williams *et al.*, 1989) and provides an invaluable framework for streptomycete taxonomy, including identification (Williams *et al.*, 1983b; Langham *et al.*, 1989).

The current classification of the genus *Streptoverticillium* (Locci & Schofield, 1989) is also based on a numerical taxonomic study: 111 strains were tested with 185 unit characters (Locci *et al.*, 1981), and were grouped into 10 multi-membered and 14 single-member clusters. Identification of species can also be achieved by numerical procedures (Williams *et al.*, 1985).

Current improvements in streptomycete taxonomy are mainly concerned with the use of chemotaxonomic, molecular genetic and serological data (Fierro *et al.*, 1987; Mordarski *et al.*, 1986; Saddler *et al.*, 1987; O'Donnell, 1988; Ridell *et al.*, 1986; Gladek *et al.*, 1985) to evaluate the species defined by the numerical studies. Chemotaxonomic methods have still to be improved for the analysis of quantitative data (O'Donnell, 1988). Further aims in streptomycete taxonomy and identification are the evaluation of the taxonomic position of 'species' which have not been part of a natural classification ('species' currently classified into species category IV of Williams *et al.*, 1989) and the development of rapid tests for presumptive identification of unknown isolates.

Although miniaturized tests have gained wide acceptance in diagnostic microbiology, these tests have only rarely been applied to members of the *Actinomycetales*. In an initial approach, Goodfellow *et al.* (1987) studied the production of extracellular enzymes by 88 streptomycetes representing 19 numerically defined species of Williams *et al.* (1983a) and found different patterns of enzyme activity within each of the groups.

The aim of our study was to evaluate the species and species-groups defined by Williams *et al.* (1983a) and Locci *et al.* (1981) in an extensive numerical study, and to compare the results with those obtained by other methods. Furthermore, the taxonomic position of many *Streptomyces* strains not included in the study of

Williams *et al.* (1983a) and currently classified in species category IV (Williams *et al.*, 1983a) was evaluated.

Methods

Bacterial strains. A total of 821 strains of the genera *Streptomyces* and *Streptoverticillium* were used in the study. All strains were reference organisms from the Deutsche Sammlung von Mikroorganismen und Zellkulturen (DSMZ), Braunschweig, FRG, from which 420 strains were ISP cultures, and 363 strains were ones used in the study of Williams *et al.* (1983a). Of these cultures, 115 were type strains of validly described species (Williams *et al.*, 1989). They are listed in detail in Table 1. All strains were cultivated on glucose/yeast extract/malt extract agar (GYM) containing the following constituents (g l⁻¹): yeast extract, 4; malt extract, 10; D-glucose, 4; CaCO₃, 2; agar, 15. They were incubated aerobically at 28 °C.

Biochemical tests. Each strain was examined for 329 unit characters, including carbon source utilization tests, sugar fermentation tests and qualitative enzyme tests using chromogenic substrates. Tests were performed in standard microtitration plates (Greiner, Nürtingen, FRG). All tests were read both visually and photometrically.

Carbon source utilization was tested in a mineral medium containing the following constituents (g l⁻¹): K₂HPO₄, 1.74; KH₂PO₄, 1.36; (NH₄)₂SO₄, 5.0; MgSO₄·7H₂O, 0.5; CaCl₂·2H₂O, 0.1; NaCl, 9.0; yeast extract (Oxoid), 0.02; bio-lactysate (bio-Merieux), 0.02; vitamin solution, 5 ml [containing (mg l⁻¹): calcium pantothenate, 0.1; nicotinic acid, 0.1; biotin, 0.005; cyanocobalamin, 0.005; folic acid, 0.1; pyridoxine, 0.1; *p*-aminobenzoic acid, 0.1; thiamin pyrophosphate, 0.1; inositol, 0.1; thiamin, 0.1; riboflavin, 0.1]; trace element solution, 1 ml [containing (mg l⁻¹): H₃BO₃, 0.5; CuSO₄·5H₂O, 0.04; KI, 0.1; FeCl₃·6H₂O, 0.2; MnSO₄·H₂O, 0.2; Na₂MoO₄·2H₂O, 0.2; ZnSO₄·7H₂O, 0.4]. After adding the different carbon sources, at a final concentration of 0.2% (w/v), or 0.05% (w/v) for aromatic compounds, the media were sterilized by filtration. The utilization of 240 compounds was tested (Table 2).

Qualitative enzyme tests were done in filter-sterilized medium (pH 7.2) containing 0.05 M-Tris/HCl buffer and 0.05% (w/v) each of yeast extract (Oxoid) and bio-lactysate (bio-Merieux). Filter-sterilized solutions of chromogenic substrates [*p*-nitrophenyl-(*p*-NP-) linked substrates] were added at final concentrations of 2 mM. For *p*-nitroanilides (*p*-NA), concentrations of 1 mM were used. Hydrolysis of 42 chromogenic substrates was tested (Table 2).

Sugar fermentation tests were done in the medium of Hugh and Leifson (1953). A total of 47 different sugars (1%, w/v) were tested (Table 2).

To obtain homogeneous suspensions for inoculation of the different test wells, all strains were cultivated in liquid GYM medium for 72 h at 28 °C. After growth, the cell agglomerates were mechanically homogenized using a sterile Ultraturrax (Jahnke & Kunkel, Staufen, FRG) for 1 min at 4000 r.p.m. From this homogenate, 100 µl aliquots were transferred to 5 ml of 0.9% (w/v) NaCl and each test well was filled with 50 µl of the bacterial suspension. Test plates were covered with plastic seals (Flow Laboratories) and incubated at 28 °C for 14 d. Test results were read photometrically with a Multiscan MCC340 photometer (Flow Laboratories). A carbon substrate utilization test was considered positive if $A_{414}(\text{test}) - A_{414}(\text{assimilation control}) > 0.05$, and a qualitative enzyme test was considered positive if $A_{414}(\text{test}) - A_{414}(\text{chromogenic substrate control}) > 0.3$. All test results were checked visually.

Coding of data. All of the characters were scored plus (1) or minus (0) and then examined using a cluster program written in FORTRAN. Clustering was achieved with the unweighted average linkage

(UPGMA) algorithm (Sneath & Sokal, 1973) using the simple matching coefficient (S_{SM}) and the Jaccard coefficient (S_J). Overlap of clusters was calculated between all pairs of major and minor clusters using the formulas given in the OVCLUS program (Sneath, 1979). The chosen critical value of overlap V_0 was set at 5%, according to Williams *et al.* (1983a). The cophenetic correlation coefficient (r_{cs}) as a measure of agreement between the similarity values implied by a phenogram and those of the original similarity matrix were calculated for both classifications according to Sneath & Sokal (1973).

Test reproducibility. All tests were performed in triplicate for 20 randomly chosen strains (Table 1), and an estimate of test variance (s_i^2) and the average probability (p_{ti}) of an erroneous result were calculated according to the formulae of Sneath & Johnson (1972).

Computing. All calculations were done on a personal computer (Compaq Deskpro AT 80386).

Results

Test error and final data-matrix

Test error was estimated for visually-read test results by calculation of the pooled variances and the average probability of an erroneous result. For 20 strains grouped into different species or species-groups by Williams *et al.* (1983a), all tests were performed in triplicate (Table 1). The average probability (p_{ti}) of an erroneous result for all tests ($n = 329$) was 3.11%. Within the test groups, significant differences in reproducibility were found. Carbon substrate utilization tests ($n = 240$) gave a p_{ti} of 2.71%, qualitative enzyme tests ($n = 42$) a p_{ti} of 1.14%, and tests for acid formation from various sugars ($n = 47$) a p_{ti} of 7.09%. A comparison of visual and photometric test readings for all strains (821) and all tests (329) gave overall discrepancies of 7.45%. The discrepancies varied from 0% to 66%. The most obvious deviations were found for the substrate utilization tests of the aromatic compounds 3-hydroxyphenylacetate and protocatechuate. Several strains produced a brown colouration of the test media independent of growth. Additionally, the tests for acid formation from different sugars showed high inconsistencies with respect to differences between visual and photometric readings. Small differences were found for the qualitative enzyme tests using chromogenic substrates.

Because of the different growth characteristics of the 20 strains chosen for reproducibility studies, and their great variability in several features (speed and homogeneity of growth, etc.), it was not possible to determine the extent of test variations due to different degrees of uniformity of the test organisms themselves, or to unknown and uncontrolled factors that affect test responses of most or all test organisms. Therefore we did not exclude tests in advance from the final data matrix, which contained 821 strains against 329 unit characters. As in the study of Williams *et al.* (1983a), the data shown

in Tables 2 to 4 should serve as a reference source. Diagnostic properties were selected using computer programs and a probability matrix was constructed for identification purposes. This matrix contained characters of high consistency and stability within the taxa (see the accompanying paper: Kämpfer & Kroppenstedt, 1991). The following sections refer exclusively to the visually checked test results.

Clustering of strains using the UPGMA algorithm with the S_{SM} coefficient and characterization of taxa

A simplified phenogram of the S_{SM} /UPGMA analysis is given in Fig. 1. The classification based on the S_{SM} /UPGMA analysis gave compact clusters in a homogeneous phenogram. The cophenetic correlation coefficient r_{cs} as a measure of correlation between corresponding pairs from the similarity matrix and the cophenetic matrix was 0.8239.

Because of the numerous tests performed, from 1653 possible overlapping clusters and subclusters (single-member clusters were not considered in these calculations), a total of 106 pairs of phena showed overlap at a confidence interval of $P = 90\%$, 122 pairs were found at a confidence interval of $P = 95\%$, and 226 overlapping pairs of phena could be obtained with $P = 99\%$ taking a chosen level of $V_0 = 5\%$ (Williams *et al.*, 1983a).

Fifteen major clusters (containing six or more strains), 34 minor clusters (containing less than six strains) and 40 single-member clusters were obtained. They were numbered consecutively in ascending similarity, independent of the number of strains they contained. The clusters were defined at a similarity level of 81.5% (S_{SM}). In contrast to the analysis of Williams *et al.* (1983a), we did not classify all the different phena into cluster-groups, but two clusters (clusters 1 and 22) could be divided into subclusters at a similarity level of 84.0% (S_{SM}). These subclusters were composed of morphologically and physiologically distinct groups, which could also be differentiated on the basis of genetical and chemotaxonomic data. Several major clusters of the study of Williams *et al.* (1983a) could be recovered, whereas others (in most cases the smaller ones) could not.

The composition of the different clusters is shown in Table 1. In accordance with the study of Williams *et al.* (1983a), phena were named, when possible, after the earliest described 'species' which they contained. The same practice was followed for phena not included in the Approved Lists of Bacterial Names (Skerman *et al.*, 1980). Where more than one type strain was described in the same year, the name was selected alphabetically. In many cases, strains with the same species designations were found in different phena. In these cases, and for clusters which were similar in composition to those of

Fig. 1. Simplified phenogram showing the relationship between the phena recovered in the UPGMA/ S_{SM} analysis. Single-member clusters are not labelled.

Table 1. Designation and source of cultures assigned to clusters and subclusters of the UPGMA/ S_{SM} analysis

A total of 821 strains are listed, including 115 type strains designated by Williams *et al.* (1989), 348 type strains of nomenspecies listed in the Approved Lists of Bacterial Names (Skerman *et al.*, 1980) and 420 ISP cultures (Shirling & Gottlieb, 1968*a, b*, 1969, 1972). Clusters were defined at the 81.5% similarity level (S_{SM}). Clusters 1 and 22 were subdivided into subclusters at a similarity level of 84.0% (S_{SM}).

S_{SM} †	S_J ‡	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
Strains assigned to cluster 1: <i>Streptomyces albidoflavus</i> /S. <i>griseus</i> /S. <i>antibioticus</i>					
Strains assigned to subcluster 1-1: <i>Streptomyces albidoflavus</i> (52)					
1-1	1-1	<i>S. albidoflavus</i>	*DSM 40792 NRRL B-2663		Category I Species no. 01
1-1	1-1	<i>S. albidoflavus</i> #	*DSM 40455 ^T ATCC 25422 ISP 5455	A 1A	Category I Species no. 01
1-1	1-1	<i>S. albidus</i>	DSM 40869		
1-1	1-1	<i>S. albus</i>	*DSM 40890		Category I Species no. 09
1-1	1-1	<i>S. albus</i>	*DSM 40891		Category I Species no. 09
1-1	1-1	<i>S. albus</i>	*DSM 40671		Category I Species no. 09
1-1	1-1	<i>S. alni</i>	DSM 40557 ATCC 27415 ISP 5557	A 08	
1-1	1-1	<i>S. badius</i>	*DSM 40139 ^T ATCC 19888 ISP 5139	C Sm	Category III Species no. 15
1-1	1-1	<i>S. candidus</i>	DSM 40838 ATCC 4838		
1-1	1-1	<i>S. canescens</i>	*DSM 40001 ^(T) ATCC 19736 ISP 5001	A 1A	Category I Species no. 01
1-1	1-1	<i>S. cellulosa</i>	*DSM 40802 ATCC 3313		
1-1	1-1	<i>S. champavatii</i>	*DSM 40841 ^T NRRL B-5682		Category IV Species no. 02 (yellow series)
1-1	1-1	<i>S. citreus</i>	DSM 40364 ATCC 25441 ISP 5364	A 1A	
1-1	1-1	<i>S. coelicolor</i>	*DSM 40233 ^(T) ATCC 23899 ISP 5233	A 1A	Category I Species no. 01
1-1	1-1	<i>S. coelicolor</i>	*DSM 40623		Category I Species no. 01
1-1	1-1	<i>S. coelicolor</i>	*DSM 40624 IMRU 3570		Category I Species no. 01
1-1	1-1	<i>S. coelicolor</i>	*DSM 40675		Category I Species no. 01
1-1	1-1	<i>S. coelicolor</i>	*DSM 40678		Category I Species no. 01
1-1	1-1	<i>S. coelicolor</i>	*DSM 40665		Category I Species no. 01
1-1	1-1	<i>S. coelicolor</i>	*DSM 40679		Category I Species no. 01
1-1	1-1	<i>S. coelicolor</i>	*DSM 40680		Category I Species no. 01
1-1	1-1	<i>S. coelicolor</i>	*DSM 40681		Category I Species no. 01
1-1	1-1	<i>S. coelicolor</i>	*DSM 40682		Category I Species no. 01
1-1	1-1	<i>S. coelicolor</i>	*DSM 40683		Category I Species no. 01
1-1	1-1	<i>S. collinus</i>	*DSM 40909		Category I Species no. 11
1-1	1-1	<i>S. coriofaciens</i>	DSM 40485 ATCC 14155 ISP 5485	A 1A	
1-1	1-1	<i>S. diastaticus</i> #	*DSM 40496 ^T ATCC 3315 ISP 5496	A 19	Category I Species no. 12
1-1	1-1	<i>S. felleus</i>	*DSM 40130 ^(T) ATCC 19752 ISP 5130	A 1A	Category I Species no. 01
1-1	1-1	<i>S. globisporus</i>	*DSM 40991 ATCC 21553		Category I Species no. 02
1-1	1-1	<i>S. globisporus</i> subsp. <i>caucasicus</i>	*DSM 40814 ATCC 19907		Category I Species no. 02
1-1	1-1	<i>S. gougerotii</i>	*DSM 40324 ^(T) ATCC 10975 ISP 5324	A 1A	Category I Species no. 01
1-1	1-1	<i>S. griseus</i>	*DSM 40661		Category I Species no. 02
1-1	1-1	<i>S. griseus</i>	*DSM 40882		Category I Species no. 02
1-1	1-1	<i>S. griseus</i>	*DSM 40931		Category I Species no. 02
1-1	1-1	<i>S. griseus</i>	*DSM 40984		Category I Species no. 02
1-1	1-1	<i>S. griseus</i>	*DSM 40983		Category I Species no. 02
1-1	1-1	<i>S. griseus</i> subsp. <i>solvifaciens</i>	*DSM 40933 NRRL B-1561		Category I Species no. 02
1-1	1-1	<i>S. hominis</i>	DSM 40770 ATCC 3008		
1-1	1-1	<i>S. intermedius</i>	*DSM 40372 ^(T) ATCC 3329 ISP 5372	A 1A	Category I Species no. 01
1-1	1-1	<i>S. krainskii</i>	DSM 40321 ATCC 25465 ISP 5321	A 1A	
1-1	1-1	<i>S. levoris</i>	DSM 40202 ATCC 15876 ISP 5202		
1-1	1-1	<i>S. limosus</i>	*DSM 40131 ^(T) ATCC 19778 ISP 5131	A 1A	Category I Species no. 01
1-1	1-1	<i>S. ochroleucus</i>	DSM 40591 ATCC 3006 ISP 5591		
1-1	1-1	<i>S. odorifer</i>	*DSM 40347 ^(T) ATCC 6246 ISP 5347	A 1A	Category I Species no. 01
1-1	1-1	<i>S. prunicolor</i>	*DSM 40335 ^T ATCC 25487 ISP 5335	A 11	Category III Species no. 01
1-1	1-1	<i>S. rutgersensis</i>	*DSM 40077 ^(T) ATCC 3350 ISP 5077	A 1A	Category I Species no. 01
1-1	1-1	<i>S. sampsonii</i>	*DSM 40394 ^(T) ATCC 25495 ISP 5394	A 1A	Category I Species no. 01
1-1	1-1	<i>S. saprophyticus</i>	DSM 40537 ATCC 3351 ISP 5537	A 1A	
1-1	1-1	<i>S. somaliensis</i>	*DSM 40267 ATCC 19437 ISP 5267		Category IV Species no. 08 (white series)
1-1	1-1	<i>Streptomyces</i> sp.	DSM 40622		
1-1	1-1	<i>Streptomyces</i> sp.	DSM 40872		
1-1	1-1	<i>S. tetanumemus</i>	DSM 40585 ATCC 27471 ISP 5585	A 1A	
Strains assigned to subcluster 1-2: <i>Streptomyces halstedii</i> (6)					
1-2	15	<i>S. flavogriseus</i>	*DSM 40323 ^(T) ATCC 25452 ISP 5323	A 1C	Category I Species no. 03
1-2	15	<i>S. flavidovirens</i>	*DSM 40062 ^(T) ATCC 3320 ISP 5062	A 1C	Category I Species no. 03
1-2	15	<i>S. griseolus</i>	*DSM 40067 ^(T) ATCC 3325 ISP 5067	A 1C	Category I Species no. 03
1-2	15	<i>S. halstedii</i> #	*DSM 40068 ^T ATCC 10897 ISP 5068	A 1C	Category I Species no. 03
1-2	15	<i>S. nigrifaciens</i>	*DSM 40071 ^(T) ATCC 19791 ISP 5071	A 1C	Category I Species no. 03
1-2	15	<i>S. scabies</i>	DSM 40859 IFO 3111		

Table 1 (continued)

$S_{SM}†$	$S_J‡$	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
Strains assigned to subcluster 1-3: <i>Streptomyces griseus</i> (81)					
1-3	1-2	<i>S. acidoresistans</i>	DSM 40540 ATCC 27413 ISP 5540	A 1B	Category IV Species no. 04 (green series)
1-3	10	<i>S. acrimycini</i>	*DSM 40135 ^T ATCC 19885 ISP 5135		
1-3	1-2	<i>S. albidus</i>	DSM 40320 ATCC 25423 ISP 5320		
1-3	1-2	<i>S. albidus</i>	DSM 40793 NRRL B-1672	A 1B	Category I Species no. 02
1-3	8	<i>S. albovinaceus</i>	*DSM 40136 ^(T) ATCC 15823 ISP 5136		
1-3	8	<i>S. albovinaceus</i>	*DSM 40796 ATCC 12951	A 1B	Category I Species no. 02
1-3	1-2	<i>S. albobiridis</i>	*DSM 40326 ^(T) ATCC 25425 ISP 5326		
1-3	1-20	<i>S. aureus</i>	DSM 40862 ATCC 3309	A 1B	Category I Species no. 02
1-3	1-2	<i>S. bacillaris</i>	*DSM 40598 ^(T) ATCC 15855 ISP 5598		
1-3	30	<i>S. californicus</i>	*DSM 40058 ^T ATCC 3312 ISP 5058	A 09	Category II Species no. 02
1-3	1-2	<i>S. californicus</i>	*DSM 40801 ATCC 15436		
1-3	1-2	<i>S. cavourensis</i>	*DSM 40300 ^(T) ATCC 14889 ISP 5300	A 1B	Category II Species no. 02
1-3	1-2	<i>S. chrysomallus</i>	*DSM 40128 ^(T) ATCC 11523 ISP 5128		
1-3	1-2	<i>S. citreofluorescens</i>	*DSM 40265 ^(T) ATCC 15858 ISP 5265	A 1B	Category I Species no. 02
1-3	1-2	<i>S. cretaceus</i>	DSM 40561 ATCC 3005 ISP 5561		
1-3	1-2	<i>S. cyaneofuscatus</i>	*DSM 40148 ^(T) ATCC 23619 ISP 5148	A 1B	Category I Species no. 02
1-3	1-2	<i>S. fimicarius</i>	*DSM 40322 ^(T) ATCC 25449 ISP 5322		
1-3	1-2	<i>S. floridae</i>	*DSM 40938 NCIB 9345	A 1B	Category IV Species no. 04 (yellow series)
1-3	1-2	<i>S. fluorescens</i> #	*DSM 40203 ^(T) ATCC 15860 ISP 5203		
1-3	1-2	<i>S. fradiae</i>	*DSM 40705 NRRL 2599	A 1B	Category II Species no. 18
1-3	1-2	<i>S. fradiae</i>	*DSM 40940		
1-3	1-2	<i>S. fulvissimus</i>	*DSM 40767	A 03	Category I Species no. 02
1-3	1-20	<i>S. fulvoviridis</i>	DSM 40210 ATCC 15863 ISP 5210		
1-3	1-2	<i>S. globisporus</i>	*DSM 40199 ^(T) ATCC 15864 ISP 5199	A 1B	Category I Species no. 02
1-3	1-2	<i>S. globisporus</i>	*DSM 40871		
1-3	1-2	<i>S. griseinus</i>	*DSM 40047 ^(T) ATCC 23915 ISP 5047	A 1B	Category I Species no. 02
1-3	1-2	<i>S. griseobrunneus</i>	*DSM 40066 ^(T) ATCC 19762 ISP 5066		
1-3	1-2	<i>S. griseus</i>	*DSM 40236 ^(T) ATCC 23345 ISP 5236	A 1B	Category I Species no. 02
1-3	1-2	<i>S. griseus</i>	*DSM 40627		
1-3	1-2	<i>S. griseus</i>	*DSM 40653	A 1B	Category I Species no. 02
1-3	1-2	<i>S. griseus</i>	*DSM 40654		
1-3	1-2	<i>S. griseus</i>	*DSM 40656	A 1B	Category I Species no. 02
1-3	1-2	<i>S. griseus</i>	*DSM 40657		
1-3	1-2	<i>S. griseus</i>	*DSM 40658	A 1B	Category I Species no. 02
1-3	1-2	<i>S. griseus</i>	*DSM 40659		
1-3	1-2	<i>S. griseus</i>	*DSM 40660	A 1B	Category I Species no. 02
1-3	1-2	<i>S. griseus</i>	*DSM 40670		
1-3	1-2	<i>S. griseus</i>	*DSM 40695	A 1B	Category I Species no. 02
1-3	1-2	<i>S. griseus</i>	*DSM 40707 NRRL 2764		
1-3	1-2	<i>S. griseus</i>	*DSM 40693	A 1B	Category I Species no. 02
1-3	1-2	<i>S. griseus</i>	*DSM 40757		
1-3	1-2	<i>S. griseus</i>	*DSM 40759 ATCC 15395	A 1B	Category I Species no. 02
1-3	1-2	<i>S. griseus</i>	*DSM 40855 ATCC 10137		
1-3	1-2	<i>S. griseus</i>	*DSM 40817 ATCC 10971	A 1B	Category I Species no. 02
1-3	1-2	<i>S. griseus</i>	*DSM 40878		
1-3	1-2	<i>S. griseus</i>	*DSM 40881 ATCC 13968	A 1B	Category I Species no. 02
1-3	1-2	<i>S. griseus</i>	*DSM 40939		
1-3	1-2	<i>S. griseus</i> subsp. <i>alpha</i>	*DSM 40937 ^(T) NRRL B-2249	A 1B	Category I Species no. 02
1-3	1-2	<i>S. griseus</i> subsp. <i>farinosus</i>	DSM 40932		
1-3	1-2	<i>S. halstedii</i>	*DSM 40863 ATCC 13449	A 1B	Category I Species no. 03
1-3	1-2	<i>S. lavendulae</i>	*DSM 41571 ATCC 13664		
1-3	1-2	<i>S. lavendulae</i>	*DSM 41572 ATCC 13665	A 1B	Category I Species no. 22
1-3	1-2	<i>S. lipmanii</i>	*DSM 40070 ^(T) ATCC 3331 ISP 5070		
1-3	1-20	<i>S. luteolutescens</i>	DSM 40600 ATCC 27445 ISP 5600	A 1B	Category I Species no. 02
1-3	1-2	<i>S. mediocidicus</i>	DSM 40864 ATCC 13278		
1-3	1-2	<i>S. mediocidicus</i>	DSM 40865 ATCC 13279	A 23	Category I Species no. 20
1-3	1-2	<i>S. microflavus</i> #	*DSM 40331 ^T ATCC 13231 ISP 5331		
1-3	1-2	<i>S. oligocarophilus</i>	DSM 40589 ATCC 27453 ISP 5589	A 1B	Category I Species no. 20
1-3	10	<i>S. olivoviridis</i>	*DSM 40211 ^(T) ATCC 15882 ISP 5211		
1-3	1-2	<i>S. ornatus</i>	DSM 40307 ATCC 23265 ISP 5307	A 1B	Category II Species no. 02
1-3	1-2	<i>S. parvus</i>	*DSM 40348 ^(T) ATCC 12433 ISP 5348		
1-3	1-2	<i>S. pluricologrescens</i>	*DSM 40019 ^(T) ATCC 19798 ISP 5019	A 1B	Category I Species no. 02
1-3	1-2	<i>S. praecox</i>	*DSM 40393 ^T ATCC 3374 ISP 5393		
1-3	1-2	<i>S. reticuli</i>	DSM 40776 ATCC 23384	A 1B	Category IV Species no. 08 (yellow series)
1-3	4	<i>S. roseochromogenes</i>	DSM 40463 ATCC 13400 ISP 5463		

Table 1 (continued)

S _{SM} †	S _J ‡	Strain designation§	Strain numbers		Williams group¶	Bergey category and species no.††	
1-3	1-2	<i>S. roseochromogenes</i>	DSM 40856	ATCC 3347			
1-3	10	<i>S. scabies</i>	DSM 40078	ATCC 23962 ISP 5078	A 03		
1-3	1-2	<i>S. setonii</i>	*DSM 40395 ^(T)	ATCC 25497 ISP 5395	A 1B	Category I	Species no. 02
1-3	1-2	<i>S. sindenensis</i>	*DSM 40255 ^(T)	ATCC 23963 ISP 5255	A 1B	Category I	Species no. 02
1-3	1-2	<i>S. sindenensis</i>	*DSM 40993			Category I	Species no. 02
1-3	1-2	<i>Streptomyces</i> sp.	DSM 40920				
1-3	1-2	<i>Streptomyces</i> sp.	DSM 40992				
1-3	1-2	<i>Streptomyces</i> sp.	DSM 40969				
1-3	1-2	<i>Streptomyces</i> sp.	DSM 40977				
1-3	1-2	<i>Streptomyces</i> sp.	DSM 40615				
1-3	1-2	<i>S. streptomycini</i>	DSM 40200	ATCC 15886 ISP 5200			
1-3	1-2	<i>S. vinaceus</i>	*DSM 40257	ATCC 11861 ISP 5257	A 06	Category I	Species no. 05
1-3	47	<i>S. viridochromogenes</i>	*DSM 41585	NRRL B-1792		Category III	Species no. 04
1-3	1-2	<i>S. vulgaris</i>	DSM 40201	ATCC 15895 ISP 5201			
1-3	1-2	<i>S. willmorei</i>	*DSM 40459 ^(T)	ATCC 6867 ISP 5459	A 1B	Category I	Species no. 02
1-3	1-2	<i>S. willmorei</i>	*DSM 40861			Category I	Species no. 02
Strains assigned to subcluster 1-4: <i>Streptomyces olivaceus</i> (6)							
1-4	1-4	<i>S. flavogriseus</i>	*DSM 40990	ATCC 3331		Category I	Species no. 03
1-4	1-4	<i>S. olivaceus</i>	*DSM 41536	ATCC 11626		Category I	Species no. 03
1-4	1-4	<i>S. olivaceus</i>	*DSM 41538	ATCC 21379		Category I	Species no. 03
1-4	1-4	<i>S. olivaceus</i>	*DSM 41539	ATCC 21381		Category I	Species no. 03
1-4	1-4	<i>S. olivaceus</i>	*DSM 41540	ATCC 21382		Category I	Species no. 03
1-4	1-4	<i>S. scabies</i>	DSM 40611	ATCC 3352			
Strains assigned to subcluster 1-5: <i>Streptomyces antibioticus</i> (19)							
1-5	9	<i>S. achromogenes</i>	*DSM 40028 ^(T)	ATCC 12767 ISP 5028	A 19	Category I	Species no. 12
1-5	9	<i>S. antibioticus</i>	*DSM 40715			Category I	Species no. 21
1-5	9	<i>S. antibioticus</i>	*DSM 40725			Category I	Species no. 21
1-5	9	<i>S. antibioticus</i>	*DSM 40868	ATCC 11891		Category I	Species no. 21
1-5	9	<i>S. antibioticus</i>	*DSM 41566	ATCC 14890		Category I	Species no. 21
1-5	9	<i>S. antibioticus</i>	*DSM 41567	ATCC 14975 ISP 5014		Category I	Species no. 21
1-5	9	<i>S. antibioticus</i>	*DSM 41569	ATCC 31771		Category I	Species no. 21
1-5	11	<i>S. argenteolus</i>	*DSM 40226 ^(T)	ATCC 11009 ISP 5226	A 15	Category I	Species no. 08
1-5	11	<i>S. aurantiogriseus</i>	*DSM 40138 ^T	ATCC 19887 ISP 5138	A Sm	Category III	Species no. 09
1-5	9	<i>S. eurythermus</i>	*DSM 40014 ^(T)	ATCC 15848	A 23	Category I	Species no. 20
1-5	11	<i>S. galbus</i>	*DSM 40480	ATCC 14077 ISP 5480		Category I	Species no. 08
1-5	11	<i>S. griseochromogenes</i>	*DSM 40499 ^(T)	ATCC 14511 ISP 5499	A 18	Category I	Species no. 11
1-5	1-16	<i>S. griseoluteus</i>	*DSM 40392 ^T	ATCC 12768 ISP 5392	C 43	Category II	Species no. 11
1-5	1-16	<i>S. lucensis</i>	*DSM 40317 ^(T)	ATCC 17804 ISP 5317	A 31	Category I	Species no. 21
1-5	9	<i>S. nogalater</i>	*DSM 40546 ^T	ATCC 27451 ISP 5546	A 34	Category III	Species no. 06
1-5	59	<i>S. recifensis</i>	*DSM 40115 ^(T)	ATCC 19803 ISP 5115	A 23	Category I	Species no. 20
1-5	9	<i>S. spadici</i>	DSM 40476	ATCC 19017 ISP 5476	A 34		
1-5	1-16	<i>S. violaceusniger</i>	*DSM 41601	NRRL B-5799		Category I	Species no. 16
1-5	9	<i>Sv. lavenduligriseum</i>	*DSM 40487 ^(T)	ATCC 13306 ISP 5487	A 34	Streptov.	Species no. 02
Strains assigned to subcluster 1-6: <i>Streptomyces flaveolus</i> (16)							
1-6	1-31	<i>S. alboniger</i>	*DSM 40043 ^(T)	ATCC 12461 ISP 5043	A 1B	Category I	Species no. 02
1-6	1-14	<i>S. collinus</i>	*DSM 40733			Category I	Species no. 11
1-6	1-10	<i>S. echinatus</i>	*DSM 40013 ^(T)	ATCC 19748 ISP 5013	A 18	Category I	Species no. 11
1-6	1-13	<i>S. flaveolus</i>	*DSM 40061 ^T	ATCC 3319 ISP 5061	A 24	Category II	Species no. 05
1-6	1-16	<i>S. griseofuscus</i>	*DSM 40191 ^(T)	ATCC 23916 ISP 5191	A 12	Category I	Species no. 07
1-6	1-14	<i>S. heimi</i>	DSM 40328	ATCC 25460 ISP 5328			
1-6	1-16	<i>S. hygroscopicus</i>	*DSM 40771	ATCC 10976		Category I	Species no. 16
1-6	1-16	<i>S. lavendulae</i>	*DSM 40708			Category I	Species no. 22
1-6	1-16	<i>S. misionensis</i>	*DSM 40306 ^(T)	ATCC 14991 ISP 5306	A 31	Category I	Species no. 21
1-6	1-16	<i>S. murinus</i>	*DSM 40091 ^(T)	ATCC 19788 ISP 5091	A 17	Category I	Species no. 10
1-6	1-15	<i>S. naganishii</i>	*DSM 40282 ^(T)	ATCC 23939 ISP 5282	A 31	Category I	Species no. 21
1-6	1-16	<i>S. roseoluteus</i>	DSM 40240	ATCC 23975 ISP 5240	A 17		
1-6	1-14	<i>Streptomyces</i> sp.	DSM 40781				
1-6	1-16	<i>S. umbrinus</i>	*DSM 40278 ^(T)	ATCC 19929 ISP 5278	A 05	Category I	Species no. 04
1-6	1-12	<i>S. umbrosus</i>	DSM 40242	ATCC 25504 ISP 5242	A 33		
1-6	1-16	<i>S. violaceusniger</i>	*DSM 40710	NRRL 2834		Category I	Species no. 16
Strains assigned to subcluster 1-7: <i>Streptomyces diastatochromogenes</i> (25)							
1-7	1-19	<i>S. actuosus</i>	DSM 40337	ATCC 25421 ISP 5337			
1-7	1-15	<i>S. antibioticus</i> #	*DSM 40234 ^T	ATCC 8663 ISP 5234	A 31	Category I	Species no. 21
1-7	1-15	<i>S. arenae</i>	*DSM 40734			Category I	Species no. 11
1-7	1-19	<i>S. aureus</i>	DSM 40867	ATCC 15437			

Table 1 (continued)

S _{SM} †	S _J ‡	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
1-7	1-15	<i>S. bobili</i>	*DSM 40056 ^T ATCC 3310 ISP 5056		Category IV Species no. 02 (white series)
1-7	1-15	<i>S. capoamus</i>	*DSM 40494 ^(T) ATCC 19006 ISP 5494	C 45	Category II Species no. 13
1-7	1-15	<i>S. diastatochromogenes</i>	*DSM 40700		Category I Species no. 12
1-7	1-15	<i>S. echinatus</i>	*DSM 40730		
1-7	1-19	<i>S. fumanus</i>	*DSM 40154 ^(T) ATCC 19904 ISP 5154	A 18	Category I Species no. 11
1-7	1-15	<i>S. galilaeus</i>	*DSM 40481 ^(T) ATCC 14969 ISP 5481	A 19	Category I Species no. 12
1-7	1-21	<i>S. ghanaensis</i>	*DSM 40746 ^T ATCC 14672		Category IV Species no. 05 (green series)
1-7	1-15	<i>S. glaucescens</i>	*DSM 40922		Category III Species no. 05
1-7	1-15	<i>S. glaucescens</i>	*DSM 40923		Category III Species no. 05
1-7	1-15	<i>S. glaucescens</i>	*DSM 40924		Category III Species no. 05
1-7	1-15	<i>S. griseoaurantiacus</i>	*DSM 40430 ^(T) ATCC 19840 ISP 5430	A 12	Category I Species no. 07
1-7	1-14	<i>S. griseoflavus</i>	*DSM 40698 NRRL 2717		Category I Species no. 17
1-7	1-19	<i>S. griseosporus</i>	*DSM 40562 ATCC 27435 ISP 5562	A 23	Category I Species no. 20
1-7	1-14	<i>S. lavendulae</i>	*DSM 40713 NRRL 2856		Category I Species no. 21
1-7	1-19	<i>S. mirabilis</i>	*DSM 40553 ^(T) ATCC 27447 ISP 5553	A 19	Category I Species no. 12
1-7	1-19	<i>S. olivaceus</i>	*DSM 41542 ATCC 21549		Category I Species no. 03
1-7	1-15	<i>S. rishiriensis</i>	*DSM 40489 ^(T) ATCC 14812 ISP 5489	A 19	Category I Species no. 12
1-7	1-15	<i>Streptomyces</i> sp.	DSM 40981		
1-7	1-19	<i>Streptomyces</i> sp.	DSM 40836		
1-7	1-15	<i>S. thermoflavus</i>	DSM 40574 ATCC 27473 ISP 5574	A 36	
1-7	1-15	<i>S. versipellis</i>	DSM 40491 ATCC 27475 ISP 5491	A Sm	
Strain assigned to subcluster 1-8: <i>Streptoverticillium luteoreticuli</i> (1)					
1-8	1-17	<i>Sv. luteoreticuli</i>	DSM 40509 ATCC 27446 ISP 5509		Streptov. Species no. 07
Strains assigned to cluster 2: <i>Streptomyces exfoliatus</i> (30)					
2	1-7	<i>S. albocinereus</i>	DSM 40794 NRRL 3419		
2	1-7	<i>S. avellaneus</i>	*DSM 40554 ^(T) ATCC 23730 ISP 5554		Category II Species no. 17
2	1-7	<i>S. candidus</i>	DSM 40141 ATCC 19891 ISP 5141	A 03	
2	38	<i>S. cinereoruber</i>	*DSM 40012 ^(T) ATCC 19740 ISP 5012	A 05	Category I Species no. 04
2	1-7	<i>S. cremeus</i>	*DSM 40147 ^(T) ATCC 19897 ISP 5147	A 1B	Category I Species no. 02
2	1-7	<i>S. exfoliatus</i> #	*DSM 40060 ^T ATCC 12627 ISP 5060	A 05	Category I Species no. 04
2	1-7	<i>S. felleus</i>	*DSM 40976		Category I Species no. 01
2	1-7	<i>S. filamentosus</i>	*DSM 40022 ^(T) ATCC 19753 ISP 5022	A 05	Category I Species no. 04
2	1-7	<i>S. flavochromogenes</i>	DSM 40541 ATCC 14841 ISP 5541	A 05	
2	1-7	<i>S. gardneri</i>	*DSM 40064 ^(T) ATCC 9604 ISP 5064	A 04	Category I Species no. 04
2	1-7	<i>S. griseofaciens</i>	DSM 40816 ATCC 13180		
2	1-7	<i>S. hydrogenans</i>	*DSM 40586 ^(T) ATCC 19631 ISP 5586	A 05	Category I Species no. 04
2	1-7	<i>S. litmocidini</i>	*DSM 40164 ^(T) ATCC 19914 ISP 5164	A 05	Category I Species no. 04
2	1-7	<i>S. narbonensis</i>	*DSM 40016 ^(T) ATCC 19790 ISP 5016	A 04	Category I Species no. 04
2	1-7	<i>S. nashuillensis</i>	*DSM 40314 ^(T) ATCC 25476 ISP 5314	A 05	Category I Species no. 04
2	1-7	<i>S. olivaceus</i>	*DSM 40702		Category I Species no. 03
2	1-7	<i>S. omiyaensis</i>	*DSM 40552 ^(T) ATCC 27454 ISP 5552	A 05	Category I Species no. 04
2	1-7	<i>S. roseofulvus</i>	*DSM 40172 ^(T) ATCC 19921 ISP 5172	A 14	Category II Species no. 04
2	1-7	<i>S. roseolus</i>	*DSM 40174 ^(T) ATCC 23210 ISP 5174	A 05	Category I Species no. 04
2	1-7	<i>S. roseosporus</i>	*DSM 40122 ^(T) ATCC 23958 ISP 5122	A 05	Category I Species no. 04
2	1-7	<i>S. roseus</i>	DSM 40076 ATCC 19808 ISP 5076	A 07	
2	1-7	<i>S. scabies</i>	DSM 40996		
2	1-7	<i>Streptomyces</i> sp.	DSM 40887		
2	1-7	<i>S. spiroverticillatus</i>	*DSM 40036 ^(T) ATCC 19811 ISP 5036	A 06	Category I Species no. 05
2	1-7	<i>S. tanashiensis</i>	*DSM 40195 ^T ATCC 23967 ISP 5195		Category IV Species no. 30 (grey series)
2	1-7	<i>S. venezuelae</i>	*DSM 40230 ^(T) ATCC 10712 ISP 5230	A 06	Category I Species no. 05
2	1-7	<i>S. venezuelae</i>	*DSM 40634 ATCC 10595		Category I Species no. 05
2	1-7	<i>S. violaceorectus</i>	*DSM 40279 ^(T) ATCC 25514 ISP 5279	A 05	Category I Species no. 04
2	1-7	<i>S. violascens</i>	*DSM 40183 ^(T) ATCC 23968 ISP 5183	A 06	Category I Species no. 05
2	1-7	<i>S. zaomyceticus</i>	*DSM 40196 ^(T) ATCC 27482 ISP 5196	A 05	Category I Species no. 04
Strains assigned to cluster 3: <i>Streptomyces gelaticus</i> (3)					
3	1-3	<i>S. gelaticus</i>	*DSM 40065 ^T ATCC 3323 ISP 5065	A Sm	Category III Species no. 11
3	1-3	<i>S. naraensis</i>	DSM 40508 ATCC 13788 ISP 5508	A 1C	
3	1-3	<i>S. niveus</i>	*DSM 40613		Category I Species no. 02
Strains assigned to cluster 4: <i>Streptomyces graminofaciens</i> (6)					
4	1-23	<i>S. diastaticus</i>	*DSM 40650		Category I Species no. 12
4	1-23	<i>S. graminofaciens</i>	*DSM 40559 ^T ATCC 12705 ISP 5559	A 26	Category III Species no. 03
4	6	<i>S. novaecaesareae</i>	*DSM 40358 ^T ATCC 27452 ISP 5358	J Sm	Category III Species no. 25
4	1-23	<i>S. olivaceus</i>	*DSM 41537 ATCC 12019		Category I Species no. 03
4	1-23	<i>S. pristinaespiralis</i>	DSM 40338 ATCC 25486 ISP 5338	A 26	
4	6	<i>S. thermoviolaceus</i>	*DSM 40443 ^(T) ATCC 19283 ISP 5443	C 45	Category II Species no. 13

Table 1 (continued)

<i>S</i> _{SM} †	<i>S</i> _J ‡	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
Strains assigned to cluster 5: <i>Streptomyces parvus</i> (5)					
5	10	<i>S. longisporoflavus</i>	*DSM 40165 ^T ATCC 19915 ISP 5165	A 39	Category II Species no. 10
5	29	<i>S. michiganensis</i>	*DSM 40015 ^(T) ATCC 14970 ISP 5015	A 06	Category I Species no. 05
5	29	<i>S. parvus</i>	*DSM 40829 ATCC 12320		Category I Species no. 02
5	29	<i>S. puniceus</i>	*DSM 40083 ^(T) ATCC 19801 ISP 5083	A 09	Category II Species no. 02
5	29	<i>S. xanthochromogenes</i>	*DSM 40111 ^T ATCC 19818 ISP 5111	F 63	Category II Species no. 15
Strains assigned to cluster 6: <i>Streptomyces rochei</i> (79)					
6	1-10	<i>S. albaduncus</i>	*DSM 40478 ^T ATCC 14698 ISP 5478		Category IV Species no. 02 (grey series)
6	10	<i>S. albogriseolus</i>	*DSM 40712 NRRL 2835		Category I Species no. 07
6	1-18	<i>S. albogriseolus</i>	*DSM 40003 ^(T) ATCC 23875 ISP 5003	A 12	Category I Species no. 07
6	1-18	<i>S. althoticus</i>	*DSM 40092 ^(T) ATCC 19724 ISP 5092	A 12	Category I Species no. 07
6	1-18	<i>S. ambofaciens</i>	*DSM 40697 NRRL 2531		Category I Species no. 20
6	1-18	<i>S. ambofaciens</i>	*DSM 40053 ^(T) ATCC 23877 ISP 5053	A 23	Category I Species no. 20
6	1-18	<i>S. arabicus</i>	*DSM 40252 ^(T) ATCC 23881 ISP 5225	A 12	Category I Species no. 07
6	10	<i>S. atroolivaceus</i>	*DSM 40137 ^T ATCC 19725 ISP 5137	A 03	Category II Species no. 20
6	1-18	<i>S. aureofaciens</i>	*DSM 40731		Category II Species no. 04
6	1-2	<i>S. baarnensis</i>	*DSM 40232 ^(T) ATCC 23885 ISP 5232	A 1B	Category I Species no. 02
6	1-18	<i>S. caesi</i>	DSM 40419 ATCC 19828 ISP 5419	A 21	
6	1-18	<i>S. calvus</i>	*DSM 40010 ^(T) ATCC 13382 ISP 5010	A 12	Category I Species no. 07
6	1-18	<i>S. carnosus</i>	DSM 40294 ATCC 25437 ISP 5294	A 15	
6	1-18	<i>S. cellulosa</i>	*DSM 40362 ^T ATCC 25439 ISP 5362	A 13	Category II Species no. 03
6	1-18	<i>S. chromofuscus</i> #	*DSM 40273 ^T ATCC 23896 ISP 5273	A 15	Category I Species no. 08
6	1-18	<i>S. cinereoruber</i> subsp. fructofermentans	DSM 40692 ^(T) NRRL 2588		Category I Species no. 04
6	1-18	<i>S. coelestis</i>	*DSM 40421 ^(T) ATCC 19830 ISP 5421	A 21	Category I Species no. 14
6	1-18	<i>S. cyanocolor</i>	DSM 40245	A 21	
6	1-18	<i>S. cyanocolor</i>	DSM 40425 ATCC 19835 ISP 5425	A 21	
6	1-18	<i>S. cyanogenus</i>	DSM 40426 ATCC 19836 ISP 5426		
6	10	<i>S. daghestonicus</i>	*DSM 40149 ^(T) ATCC 23620 ISP 5149	A 17	Category I Species no. 10
6	1-18	<i>S. diastaticus</i>	*DSM 40934		Category I Species no. 12
6	1-18	<i>S. fimbriatus</i>	*DSM 40942 ^T ATCC 15051		Category IV Species no. 16 (grey series)
6	1-10	<i>S. flavoviridis</i>	DSM 40153 ATCC 19903 ISP 5153	A 28	
6	1-18	<i>S. fradiae</i>	*DSM 40696 NRRL 2598		Category II Species no. 18
6	1-18	<i>S. fradiae</i>	*DSM 40711 NRRL 2765		Category II Species no. 18
6	1-10	<i>S. galbus</i>	*DSM 40089 ^(T) ATCC 23910 ISP 5089	A 15	Category I Species no. 08
6	1-18	<i>S. gancidicus</i>	*DSM 40935 ^T NRRL B-1872		Category IV Species no. 17 (grey series)
6	1-18	<i>S. geysiriensis</i>	*DSM 40742 ^T ATCC 15303		Category IV Species no. 18 (grey series)
6	1-10	<i>S. glaucescens</i>	*DSM 40155 ^T ATCC 23622 ISP 5155	A 28	Category III Species no. 05
6	1-18	<i>S. griseoflavus</i>	*DSM 40456 ^T ATCC 25456 ISP 5456	A 37	Category I Species no. 17
6	1-18	<i>S. griseoflavus</i>	*DSM 40709 NRRL 2833		Category I Species no. 17
6	1-18	<i>S. griseoincarnatus</i>	*DSM 40274 ^(T) ATCC 23623 ISP 5274	A 13	Category II Species no. 03
6	1-10	<i>S. griseomycini</i>	*DSM 40159 ^(T) ATCC 23625 ISP 5159	A 12	Category I Species no. 07
6	10	<i>S. griseoroseus</i>	DSM 40768 ATCC 12125		
6	1-18	<i>S. griseorubens</i>	*DSM 40160 ^(T) ATCC 19909 ISP 5160	A 12	Category I Species no. 07
6	1-10	<i>S. griseostramineus</i>	*DSM 40161 ^T ATCC 23628 ISP 5161	F 60	Category IV Species no. 06 (green series)
6	10	<i>S. griseoviridis</i> #	*DSM 40229 ^T ATCC 23920 ISP 5229	A 17	Category I Species no. 10
6	1-18	<i>S. lividans</i>	DSM 40434 ATCC 19844 ISP 5434	A 21	
6	1-18	<i>S. lusitanus</i>	*DSM 40568 ^(T) ATCC 15842 ISP 5568	C 44	Category II Species no. 12
6	10	<i>S. macrosporeus</i>	DSM 40096 ATCC 19783 ISP 5096	A 38	
6	1-18	<i>S. malachitofuscus</i>	DSM 40332 ATCC 25471 ISP 5332		
6	1-18	<i>S. malachitorectus</i>	DSM 40333 ATCC 25472 ISP 5333		
6	1-18	<i>S. matensis</i>	*DSM 40188 ^(T) ATCC 23935 ISP 5188	A 12	Category I Species no. 07
6	1-18	<i>S. minutiscleroticus</i>	DSM 40301 ^(T) ATCC 17757 ISP 5301	A 15	Category I Species no. 08
6	1-18	<i>S. mutabilis</i>	*DSM 40169 ^(T) ATCC 19919 ISP 5169	A 12	Category I Species no. 07
6	1-11	<i>S. nodosus</i>	*DSM 40109 ^(T) ATCC 14899 ISP 5109	A 35	Category II Species no. 08
6	1-18	<i>S. parvulus</i>	*DSM 40728		Category I Species no. 07
6	1-18	<i>S. parvulus</i>	*DSM 40048 ^(T) ATCC 12434 ISP 5048	A 12	
6	1-10	<i>S. pilosus</i>	*DSM 40097 ^(T) ATCC 19797 ISP 5097	A 37	Category I Species no. 17
6	1-18	<i>S. pilosus</i>	*DSM 40714 NRRL 2857		Category I Species no. 17
6	1-18	<i>S. plicatus</i>	*DSM 40319 ^(T) ATCC 25483 ISP 5319	A 12	Category I Species no. 07
6	1-18	<i>S. pseudogriseolus</i>	*DSM 40026 ^(T) ATCC 12770 ISP 5026	A 12	Category I Species no. 07
6	1-18	<i>S. pulcher</i>	DSM 40566 ATCC 13849 ISP 5566	A 12	
6	1-18	<i>S. rochei</i> #	*DSM 40231 ^T ATCC 10739 ISP 5231	A 12	Category I Species no. 07
6	10	<i>S. rosa</i>	DSM 40533 ATCC 27462 ISP 5533	A 17	
6	1-2	<i>S. rubiginosohelvolus</i>	*DSM 40176 ^T ATCC 19926 ISP 5176		Category IV Species no. 12 (red series)
6	1-18	<i>S. rubiginosus</i>	*DSM 40177 ^(T) ATCC 19927 ISP 5177	A 12	Category I Species no. 07

Table 1 (continued)

S _{SM} †	S _J ‡	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††	
6	1-18	<i>S. scabies</i>	DSM 40960			
6	1-18	<i>Streptomyces</i> sp.	DSM 40916			
6	1-18	<i>Streptomyces</i> sp.	DSM 40975			
6	1-18	<i>Streptomyces</i> sp. (<i>lazureus</i>)	DSM 40433	ATCC 19843 ISP 5433		
6	1-18	<i>Streptomyces</i> sp. (<i>mitakaensis</i>)	DSM 40972			
6	1-18	<i>Streptomyces</i> sp. (<i>mitakaensis</i>)	DSM 40973			
6	1-18	<i>S. tendae</i>	*DSM 40101 ^(T)	ATCC 19812 ISP 5101	A 12	Category I Species no. 07
6	1-18	<i>S. tendae</i>	*DSM 40729			Category I Species no. 07
6	1-18	<i>S. thermodiastaticus</i>	*DSM 40573 ^(T)	ATCC 27472 ISP 5573	A 1C	Category I Species no. 03
6	1-18	<i>S. thermophilus</i>	DSM 40365	ATCC 19282 ISP 5365	A 15	
6	1-18	<i>S. tuirus</i>	*DSM 40505		A 21	Category I Species no. 14
6	1-18	<i>S. variabilis</i>	*DSM 40179 ^(T)	ATCC 19930 ISP 5179	A 12	Category I Species no. 07
6	1-18	<i>S. vinaceodruppus</i>	*DSM 40470 ^(T)	ATCC 25511 ISP 5470	A 12	Category I Species no. 07
6	1-18	<i>S. violaceolatus</i>	*DSM 40438 ^(T)	ATCC 19847 ISP 5438	A 21	Category I Species no. 14
6	1-18	<i>S. violaceoruber</i>	*DSM 40687			Category IV Species no. 34 (grey series)
6	1-18	<i>S. violaceoruber</i>	*DSM 40783			Category IV Species no. 34 (grey series)
6	1-18	<i>S. viridiviolaceus</i>	*DSM 40280 ^T	ATCC 27478 ISP 5280		Category IV Species no. 35 (grey series)
6	1-18	<i>S. viridodiastaticus</i>	*DSM 40249 ^T	ATCC 25518 ISP 5249		Category IV Species no. 36 (grey series)
6	1-4	<i>S. viridogenes</i>	DSM 40454	ATCC 3372 ISP 5454	A 03	
6	1-18	<i>S. viridosporus</i>	*DSM 40243 ^(T)	ATCC 27479 ISP 5243	A 15	Category I Species no. 08
6	1-18	<i>S. werraensis</i>	*DSM 40486 ^(T)	ATCC 14424 ISP 5486	A 12	Category I Species no. 07
Strains assigned to cluster 7: <i>Streptomyces prasinopilosus</i> (7)						
7	3	<i>S. albocyanus</i>	DSM 40197	ATCC 15845 ISP 5197	A Sm	
7	3	<i>S. cellostaticus</i>	*DSM 40189 ^(T)	ATCC 23894 ISP 5189	A 06	Category I Species no. 05
7	3	<i>S. cyanoalbus</i>	*DSM 40198 ^(T)	ATCC 15859 ISP 5198	A 37	Category I Species no. 17
7	3	<i>S. prasinopilosus</i>	*DSM 40098 ^(T)	ATCC 19799 ISP 5098	A 37	Category I Species no. 17
7	3	<i>S. prasinus</i>	*DSM 40099 ^(T)	ATCC 19800 ISP 5099	A 37	Category I Species no. 17
7	3	<i>S. prasinus</i>	*DSM 40688			Category I Species no. 17
7	3	<i>Streptomyces</i> sp.	DSM 40985			
Strains assigned to cluster 8: <i>Streptomyces</i> sp. (4)						
8	20	<i>S. hygrosopicus</i>	*DSM 41531	ATCC 31039		Category I Species no. 16
8	19	<i>S. scabies</i>	DSM 40999			
8	19	<i>S. scabies</i>	DSM 40995			
8	19	<i>Streptomyces</i> sp.	DSM 40750	ATCC 21619		
Strains assigned to cluster 9: <i>Streptomyces violaceus</i> (118)						
9	1-19	<i>S. afghaniensis</i>	*DSM 40228 ^(T)	ATCC 23871 ISP 5228	A 18	Category I Species no. 11
9	1-19	<i>S. alanosinicus</i>	*DSM 40606 ^T	ATCC 15710 ISP 5606		Category IV Species no. 01 (grey series)
9	1-19	<i>S. antibioticus</i>	*DSM 40723	NRRL 3207		Category I Species no. 21
9	1-19	<i>S. arenae</i>	*DSM 40737			Category I Species no. 11
9	1-19	<i>S. arenae</i>	*DSM 40293 ^(T)	ATCC 25428 ISP 5293	A 18	Category I Species no. 11
9	1-9	<i>S. atrofaciens</i>	DSM 40475	ATCC 27418 ISP 5475	A 33	
9	1-19	<i>S. azureus</i>	*DSM 40106 ^(T)	ATCC 14921 ISP 5106	A 18	Category I Species no. 11
9	1-19	<i>S. bicolor</i>	DSM 40140	ATCC 23614 ISP 5140	A 18	
9	1-19	<i>S. bottropensis</i>	*DSM 40262 ^(T)	ATCC 25435 ISP 5262	A 19	Category I Species no. 12
9	1-19	<i>S. caelestis</i>	*DSM 40084 ^(T)	ATCC 15084 ISP 5084	A 18	Category I Species no. 11
9	1-19	<i>S. canarius</i>	*DSM 40528 ^(T)	ATCC 27423 ISP 5528	A 20	Category I Species no. 13
9	1-19	<i>S. canus</i>	*DSM 40017 ^T	ATCC 12237 ISP 5017	A 25	Category III Species no. 02
9	1-19	<i>S. chartreusis</i>	*DSM 40085 ^(T)	ATCC 14922 ISP 5085	A 18	Category I Species no. 11
9	1-19	<i>S. chartreusis</i>	*DSM 41592	NRRL B-2199		Category I Species no. 11
9	1-19	<i>S. chartreusis</i>	*DSM 41593	NRRL B-8150		Category I Species no. 11
9	1-19	<i>S. chartreusis</i>	*DSM 41594	NRRL B-8151		Category I Species no. 11
9	1-19	<i>S. chartreusis</i>	*DSM 41595	NRRL B-8152		Category I Species no. 11
9	1-19	<i>S. chartreusis</i>	*DSM 41596	ATCC 21901		Category I Species no. 11
9	1-19	<i>S. chartreusis</i>	*DSM 41597	NRRL B-16268		Category I Species no. 11
9	1-19	<i>S. chibaensis</i>	*DSM 40220 ^(T)	ATCC 23895 ISP 5220	A 24	Category II Species no. 05
9	1-19	<i>S. cinnabarinus</i>	*DSM 40467 ^(T)	ATCC 23617 ISP 5467	A 18	Category I Species no. 11
9	1-19	<i>S. coeliatus</i>	DSM 40422	ATCC 19833 ISP 5422		
9	1-19	<i>S. coerulatus</i>	DSM 40424	ATCC 19834 ISP 5424		
9	1-19	<i>S. coeruleofuscus</i>	*DSM 40144 ^(T)	ATCC 23618 ISP 5144	A 18	Category I Species no. 11
9	1-19	<i>S. coeruleorubidus</i>	*DSM 40145 ^(T)	ATCC 13740 ISP 5145	A 18	Category I Species no. 11
9	1-19	<i>S. coerulescens</i>	*DSM 40146 ^(T)	ATCC 19896 ISP 5146	A 18	Category I Species no. 11
9	1-19	<i>S. collinus</i>	*DSM 40129 ^(T)	ATCC 19743 ISP 5129	A 18	Category I Species no. 11
9	1-19	<i>S. collinus</i>	*DSM 40726			Category I Species no. 11
9	1-19	<i>S. coralus</i>	DSM 40256 ^(T)	ATCC 23901 ISP 5256	A 19	

Table 1 (continued)

<i>S</i> _{SM} †	<i>S</i> _I ‡	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
9	1-19	<i>S. corchorusii</i>	*DSM 40340 ^(T) ATCC 25444 ISP 5340	A 20	Category I Species no. 13
9	1-9	<i>S. crystallinus</i>	*DSM 40945		Category IV Species no. 03 (red series)
9	19	<i>S. curacoi</i>	DSM 40107 ATCC 13385 ISP 5107	A 18	Category I Species no. 11
9	1-19	<i>S. cyaneus</i> #	*DSM 40108 ^T ATCC 14923 ISP 5108	A 18	Category I Species no. 11
9	1-19	<i>S. diastatochromogenes</i>	*DSM 40449 ^(T) ATCC 12309 ISP 5449	A 19	Category I Species no. 12
9	1-19	<i>S. diastatochromogenes</i>	*DSM 40608 ATCC 23862		Category I Species no. 12
9	1-19	<i>S. durhamensis</i>	*DSM 40539 ^(T) ATCC 23194 ISP 5539	A 30	Category II Species no. 06
9	1-19	<i>S. filipinensis</i>	*DSM 40112 ^T ATCC 23905 ISP 5112	A 30	Category II Species no. 06
9	1-19	<i>S. flaveolus</i>	*DSM 40719		Category II Species no. 05
9	1-19	<i>S. flavochromogenes</i>	DSM 40651		
9	1-19	<i>S. fradiae</i>	*DSM 41544 ATCC 15861		Category II Species no. 18
9	1-19	<i>S. griseoruber</i>	*DSM 40275 ^(T) ATCC 23626 ISP 5275	A 21	Category I Species no. 14
9	1-19	<i>S. griseorubiginosus</i>	*DSM 40469 ^(T) ATCC 23627 ISP 5469	A 18	Category I Species no. 11
9	1-19	<i>S. hawaiiensis</i>	*DSM 40042 ^(T) ATCC 12236 ISP 5042	A 18	Category I Species no. 11
9	1-19	<i>S. humidus</i>	*DSM 40263 ^(T) ATCC 12760 ISP 5263	A 19	Category I Species no. 12
9	1-19	<i>S. hygroscopicus</i> subsp. <i>ossamyceticus</i>	DSM 40824 ^(T) ATCC 15420		Category I Species no. 16
9	1-19	<i>S. iakyrus</i>	*DSM 40482 ATCC 15375 ISP 5482	A 18	Category I Species no. 11
9	1-19	<i>S. indigocolor</i>	DSM 40432 ATCC 19842 ISP 5432	A 18	
9	1-19	<i>S. ipomoeae</i>	*DSM 40818 ATCC 11747		Category IV Species no. 02 (blue series)
9	1-19	<i>S. janthinus</i>	*DSM 40206 ^(T) ATCC 15870 ISP 5206	A 18	Category I Species no. 11
9	20	<i>S. lavendulae</i>	*DSM 41580 ATCC 21138		Category I Species no. 22
9	1-19	<i>S. lavendulae</i>	*DSM 41577 ATCC 15873		Category I Species no. 22
9	1-19	<i>S. lavendulae</i>	*DSM 41579 ATCC 19008		Category I Species no. 22
9	1-19	<i>S. lincolnensis</i>	*DSM 40355 ^(T) ATCC 25466 ISP 5355	A 19	Category I Species no. 12
9	1-19	<i>S. lomondensis</i>	*DSM 41428		Category IV Species no. 03 (blue series)
9	1-19	<i>S. longisporus</i>	*DSM 40166 ^(T) ATCC 23931 ISP 5166	A 18	Category I Species no. 11
9	1-19	<i>S. longisporus</i>	*DSM 40910		Category I Species no. 11
9	1-19	<i>S. luteogriseus</i>	*DSM 40483 ^(T) ATCC 15072 ISP 5483	A 18	Category I Species no. 11
9	1-9	<i>S. melanogenes</i>	DSM 40192 ATCC 23937 ISP 5192	A 33	Category II Species no. 07
9	1-19	<i>S. minoensis</i>	DSM 40031 ATCC 19787 ISP 5031	A 19	
9	1-19	<i>S. neyagawaensis</i>	*DSM 40588 ^(T) ATCC 27449 ISP 5588	A 18	Category I Species no. 11
9	1-9	<i>S. noboritoensis</i>	*DSM 40223 ^T ATCC 25477 ISP 5223	A 33	Category II Species no. 07
9	1-19	<i>S. olivaceoviridis</i>	*DSM 40334 ^T ATCC 23630 ISP 5334	A 20	Category I Species no. 13
9	1-19	<i>S. olivochromogenes</i>	*DSM 40451 ^(T) ATCC 3336 ISP 5451	A 19	Category I Species no. 12
9	1-19	<i>S. olivochromogenes</i> subsp. <i>cytovirinus</i>	DSM 40828 ATCC 12791		Category I Species no. 12
9	1-19	<i>S. peruviansis</i>	DSM 40592 ATCC 27459 ISP 5592	A 18	
9	19	<i>S. phaeochromogenes</i>	*DSM 40073 ^T ATCC 3338 ISP 5073	A 40	Category I Species no. 18
9	1-19	<i>S. phaeopurpureus</i>	*DSM 40125 ^(T) ATCC 23946 ISP 5125	A 09	Category II Species no. 02
9	1-19	<i>S. phaeoviridis</i>	*DSM 40285 ^(T) ATCC 23947 ISP 5285	A 19	Category I Species no. 12
9	1-19	<i>S. pseudovenezuelae</i>	*DSM 40212 ^(T) ATCC 23951 ISP 5212	A 18	Category I Species no. 11
9	1-19	<i>S. purpurascens</i>	*DSM 40310 ^(T) ATCC 25489 ISP 5310	A 18	Category I Species no. 11
9	1-19	<i>S. purpurascens</i>	*DSM 40747 NRRL B-1480		Category I Species no. 11
9	1-19	<i>S. regalis</i>	DSM 40532 ATCC 27460 ISP 5532		
9	1-19	<i>S. regensis</i>	*DSM 40551 ^(T) ATCC 27461 ISP 5551	A 20	Category I Species no. 13
9	1-19	<i>S. resistomycificus</i>	*DSM 40133 ^(T) ATCC 19804 ISP 5133	A 18	Category I Species no. 11
9	1-19	<i>S. roseogriseus</i>	DSM 40488 ATCC 12414 ISP 5488		
9	1-19	<i>S. roseoviolaceus</i>	*DSM 40277 ^(T) ATCC 25493 ISP 5277	A 18	Category I Species no. 11
9	1-19	<i>S. scabies</i>	DSM 40997		
9	1-19	<i>S. scabies</i>	DSM 41000		
9	1-19	<i>S. scabies</i>	DSM 40998		
9	1-19	<i>Streptomyces</i> sp.	DSM 40718		
9	1-19	<i>Streptomyces</i> sp.	DSM 40970		
9	1-19	<i>Streptomyces</i> sp. (<i>gannmycicus</i>)	DSM 40572 ATCC 27434 ISP 5572	A 30	
9	1-19	<i>S. steffisburgensis</i>	DSM 40547 ATCC 27466 ISP 5547	A 38	
9	1-19	<i>S. tendae</i>	*DSM 40732		Category I Species no. 07
9	1-19	<i>S. thermotolerans</i>	DSM 40227 ATCC 11416 ISP 5227	A 18	
9	1-19	<i>S. torulosus</i>	*DSM 40894 ^T NRRL B-3889		Category IV Species no. 31 (grey series)
9	1-19	<i>S. violaceochromogenes</i>	*DSM 40181 ^T ATCC 19932 ISP 5181		Category IV Species no. 33 (grey series)
9	19	<i>S. violaceus</i> #	*DSM 40082 ^T ATCC 15888 ISP 5082	A 06	Category I Species no. 05
9	1-19	<i>S. violaceus</i>	*DSM 40753		Category I Species no. 05
9	20	<i>S. violaceusniger</i>	*DSM 40182		Category I Species no. 16
9	1-19	<i>S. violarus</i>	*DSM 40205 ^(T) ATCC 15891 ISP 5205	A 18	Category I Species no. 11
9	1-19	<i>S. violochromogenes</i>	DSM 40207 ATCC 15893 ISP 5207	A 18	
9	1-19	<i>S. viridis</i>	DSM 40381 ATCC 15732 ISP 5381	A 27	

Table 1 (continued)

<i>S</i> _{SM} †	<i>S</i> _J ‡	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
9	9	<i>S. viridochromogenes</i>	*DSM 41586 NRRL B-2310		Category III Species no. 04
9	20	<i>S. viridochromogenes</i>	*DSM 41521 ATCC 13759		Category III Species no. 04
9	20	<i>S. viridochromogenes</i>	*DSM 41584 NRRL B-1656		Category III Species no. 04
9	20	<i>S. viridochromogenes</i>	*DSM 41588 NRRL B-3063		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 40110 ^T ATCC 14920 ISP 5110	A 27	Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 40666		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 40736		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 40721 NRRL B-2860		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 40784		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 40110d ^(T)		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 41514		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 41516		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 41520		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 40666d		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 40513 ATCC 3356		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 41517		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 41518		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 41519		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 41522 ATCC 21240		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 41523 ATCC 21724		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 41587 NRRL B-3027		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 41590 NRRL B-3607		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 41591 NRRL B-12033		Category III Species no. 04
9	1-19	<i>S. viridochromogenes</i>	*DSM 41589 NRRL B-3263		Category III Species no. 04
9	1-19	<i>S. yokosukanensis</i>	*DSM 40224 ^(T) ATCC 25520 ISP 5224	A 30	Category II Species no. 06
Strains assigned to cluster 10: <i>Streptomyces sparsogenes</i> (2)					
10	1-29	<i>S. hygroscopicus</i>	*DSM 41532 ATCC 31050		Category I Species no. 16
10	1-29	<i>S. sparsogenes</i>	*DSM 40356 ^(T) ATCC 25498 ISP 5356	A 32	Category I Species no. 16
Strains assigned to cluster 11: <i>Streptomyces psammoticus</i> (5)					
11	1-20	<i>S. aureomonopodiales</i>	DSM 40914		
11	1-20	<i>S. parvulus</i>	*DSM 40912		
11	1-21	<i>S. psammoticus</i>	*DSM 40341 ^T ATCC 25488 ISP 5341	F 67	Category II Species no. 17
11	1-20	<i>S. rochei</i>	*DSM 40913		Category I Species no. 07
11	1-20	<i>S. viridochromogenes</i>	*DSM 41515		Category III Species no. 04
Strains assigned to cluster 12: <i>Streptomyces aurantiacus</i> (2)					
12	19	<i>S. aurantiacus</i>	*DSM 40412 ^T ATCC 19822 ISP 5412	C 45	Category II Species no. 13
12	19	<i>S. tauricus</i>	DSM 40560 ATCC 27470 ISP 5560	A 19	
Strains assigned to cluster 13: <i>Streptomyces niveoruber</i> (9)					
13	1-19	<i>S. albospinus</i>	*DSM 41422		Category IV Species no. 03 (grey series)
13	1-19	<i>S. cyanoglomerus</i> subsp. <i>cellulosae</i>	*DSM 40427 ATCC 19837 ISP 5427		
13	1-19	<i>S. ederensis</i>	*DSM 40741 ^T ATCC 15304		Category IV Species no. 14 (grey series)
13	1-19	<i>S. griseoruber</i>	*DSM 40769		Category I Species no. 14
13	1-18	<i>S. hygroscopicus</i>	*DSM 40632 NRRL B-1503		
13	1-19	<i>S. niveoruber</i>	*DSM 40638 ^T ATCC 14971		Category IV Species no. 08 (red series)
13	1-19	<i>S. scabies</i>	DSM 40994		
13	1-19	<i>Streptomyces</i> sp.	DSM 40989		
13	1-19	<i>S. toyocaensis</i>	DSM 40030 ATCC 19814 ISP 5030	A 29	
Strains assigned to cluster 14: <i>Streptomyces</i> sp. (2)					
14	21	<i>S. albus</i>	*DSM 40832 NRRL 2490		Category I Species no. 09
14	21	<i>S. scabies</i>	DSM 40962		
Strain assigned to cluster 15: <i>Streptomyces massasporeus</i> (1)					
15	1-19	<i>S. massasporeus</i>	*DSM 40035 ^T ATCC 19785 ISP 5035	D SM	Category III Species no. 19
Strain assigned to cluster 16: <i>Streptomyces lanatus</i> (1)					
16	1-19	<i>S. lanatus</i>	*DSM 40090 ^(T) ATCC 19775 ISP 5090	A 18	Category I Species no. 11
Strains assigned to cluster 17: <i>Streptomyces griseoalbus</i> (2)					
17	7	<i>S. flaviscleroticus</i>	*DSM 40270 ^(T)		Category I Species no. 08
17	7	<i>S. griseoalbus</i>	*DSM 40468 ^T ATCC 23624 ISP 5468		Category IV Species no. 05 (yellow series)
Strain assigned to cluster 18: <i>Streptomyces griseoruber</i> (1)					
18	23	<i>S. griseoruber</i> #	*DSM 40281 ^T ATCC 23919 ISP 5281	A 21	Category I Species no. 14

Table 1 (continued)

<i>S</i> _{SM} †	<i>S</i> _J ‡	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
Strain assigned to cluster 19: <i>Streptomyces cyaneogriseus</i> (1)					
19	23	<i>S. cyaneogriseus</i>	DSM 40534	ISP 5534 H Sm	
Strains assigned to cluster 20: <i>Streptomyces chrysomallus</i> (6)					
20	32	<i>S. albidoflavus</i>	*DSM 40880		Category I Species no. 01
20	1-20	<i>S. canadiensis</i>	DSM 40837	ATCC 17776	
20	32	<i>S. cellulotholus</i>	*DSM 40839 ^T	ATCC 29806	Category IV Species no. 01 (yellow series)
20	32	<i>S. chromogenes</i>	DSM 40765		
20	32	<i>S. chrysomallus</i>	*DSM 40870		
20	1-8	<i>S. griseobrunneus</i>	*DSM 40915		Category I Species no. 02
Strains assigned to cluster 21: <i>Streptomyces thermovulgaris</i> (5)					
21	1-5	<i>S. anandii</i>	*DSM 40535 ^(T)	ATCC 19388 ISP 5535	B 42 Category I Species no. 19
21	1-5	<i>Streptomyces</i> sp.	DSM 40980		
21	2	<i>S. thermotritificans</i>	*DSM 40579 ^(T)	ATCC 23385 ISP 5579	A 36 Category II Species no. 09
21	2	<i>S. thermovulgaris</i>	*DSM 40444 ^(T)	ATCC 19284 ISP 5444	A 36 Category II Species no. 09
21	2	<i>S. thermovulgaris</i>	*DSM 40787		Category II Species no. 09
Strains assigned to cluster 22: <i>Streptovorticillium</i> sp./ <i>Streptomyces lavendulae</i> / <i>Streptomyces fradiae</i>					
Strains assigned to subcluster 22-1: <i>Streptovorticillium griseocarneum</i> (51)					
22-1	40	<i>Sv. flavopersicum</i>	*DSM 40093 ^(T)	ATCC 19756 ISP 5093	F 56 Streptov. Species no. 01
22-1	40	<i>Sv. griseovorticillatum</i>	*DSM 40507 ^(T)		F 58 Streptov. Species no. 01
22-1	40	<i>Sv. mediocidicus</i>	DSM 40021	ATCC 23936 ISP 5021	F Sm Streptov. Species no. 02
22-1	40	<i>Sv. aridum</i>	*DSM 40527 ^(T)	ATCC 27417 ISP 5527	Streptov. Species no. 03
22-1	40	<i>Sv. aspergilloides</i>	DSM 40565	ATCC 14808 ISP 5565	F 59 Streptov. Species no. 08
22-1	40	<i>Sv. aureoversales</i>	*DSM 40387 ^(T)	ATCC 15853 ISP 5387	Streptov. Species no. 05
22-1	40	<i>Sv. baldacii</i>	*DSM 40845 ^T	ATCC 23654	Streptov. Species no. 01
22-1	40	<i>Sv. bivorticillatum</i>	*DSM 40272 ^(T)	ATCC 23615 ISP 5272	Streptov. Species no. 01
22-1	40	<i>Sv. blastmyceticum</i>	*DSM 40029 ^(T)	ATCC 19731 ISP 5029	F 58 Streptov. Species no. 02
22-1	40	<i>Sv. caespitosum</i>	DSM 40603	ATCC 27442 ISP 5603	Streptov.
22-1	40	<i>Sv. cinnamoneum</i> subsp. <i>alboporum</i>	*DSM 40897 ^(T)	ATCC 25186	Streptov. Species no. 02
22-1	40	<i>Sv. cinnamoneum</i>	*DSM 40005 ^T	ATCC 11874 ISP 5005	F 55 Streptov. Species no. 02
22-1	40	<i>Sv. cinnamoneum</i> subsp. <i>azocolutum</i>	DSM 40646	ATCC 12686	Streptov. Species no. 03
22-1	40	<i>Sv. cinnamoneum</i> subsp. <i>lanosum</i>	*DSM 40898 ^(T)	ATCC 25187	Streptov. Species no. 02
22-1	40	<i>Sv. cinnamoneum</i> subsp. <i>sparsum</i>	*DSM 40899 ^(T)	ATCC 25185	Streptov. Species no. 02
22-1	40	<i>Sv. distallicum</i>	*DSM 40846 ^(T)	NCIB 8936	Streptov. Species no. 01
22-1	40	<i>Sv. ehimensense</i>	*DSM 40253 ^(T)	ATCC 23903 ISP 5253	Streptov. Species no. 09
22-1	40	<i>Sv. eurocidicum</i>	*DSM 40604 ^(T)	ATCC 27428 ISP 5604	F 56 Streptov. Species no. 02
22-1	40	<i>Sv. fervens</i> subsp. <i>fervens</i>	*DSM 40086 ^(T)	ATCC 27429 ISP 5086	Streptov. Species no. 01
22-1	40	<i>Sv. fervens</i> subsp. <i>melrosporus</i>	*DSM 40905 ^(T)	NRRL 3117	Streptov. Species no. 01
22-1	40	<i>Sv. griseocarneum</i>	*DSM 40004 ^T	ATCC 12628 ISP 5004	F 55 Streptov. Species no. 03
22-1	40	<i>Sv. hachijoense</i>	*DSM 40114 ^T	ATCC 19769 ISP 5114	F 55 Streptov. Species no. 04
22-1	40	<i>Sv. hiroshimensense</i>	*DSM 40037 ^(T)	ATCC 19772 ISP 5037	F 57 Streptov. Species no. 01
22-1	40	<i>Sv. kentuckense</i>	*DSM 40052 ^(T)	ATCC 12691 ISP 5052	F SM Streptov. Species no. 11
22-1	40	<i>Sv. kishiwadense</i>	*DSM 40397 ^T	ATCC 25464 ISP 5397	Streptov. Species no. 15
22-1	40	<i>Sv. lilacinum</i>	*DSM 40254 ^T	ATCC 23930 ISP 5254	Streptov. Species no. 16
22-1	40	<i>Sv. luteovorticillatum</i>	*DSM 40038 ^(T)	ATCC 23933 ISP 5038	F 55 Streptov. Species no. 03
22-1	40	<i>Sv. mashuense</i>	*DSM 40221 ^(T)	ATCC 23934 ISP 5221	F 55 Streptov. Species no. 03
22-1	40	<i>Sv. mashuense</i>	*DSM 40896 ^(T)		Streptov. Species no. 03
22-1	40	<i>Sv. mobaraense</i>	*DSM 40847 ^T	ATCC 29032	Streptov. Species no. 07
22-1	40	<i>Sv. morookaensis</i>	DSM 40503 ^T	ATCC 19166 ISP 5503	F 59 Streptov. Species no. 08
22-1	40	<i>Sv. netropsis</i>	*DSM 40259 ^(T)	ATCC 23940 ISP 5259	F 56 Streptov. Species no. 01
22-1	40	<i>Sv. orinoci</i>	*DSM 40571 ^T	ATCC 23202 ISP 5571	F 58 Streptov. Species no. 17
22-1	40	<i>Sv. parvisporogenum</i>	*DSM 40473 ^(T)	ATCC 12568 ISP 5473	Streptov. Species no. 02
22-1	40	<i>Sv. paucisporogenum</i>	DSM 40315	ATCC 12596 ISP 5315	F 55 Streptov. Species no. 02
22-1	40	<i>Sv. pentaticum</i> subsp. <i>jenense</i>	DSM 40848		Streptov. Species no. 03
22-1	40	<i>Sv. rectivorticillatum</i>	*DSM 40436 ^T	ATCC 19845 ISP 5436	F 57 Streptov. Species no. 18
22-1	40	<i>Sv. reticulum</i>	DSM 40893	ATCC 25607	Streptov. Species no. 19
22-1	40	<i>Sv. reticulum</i> subsp. <i>protomycicum</i>	DSM 40849 ^T		Streptov. Species no. 19
22-1	40	<i>Sv. roseovorticillatum</i>	*DSM 40039 ^(T)	ATCC 19807 ISP 5039	Streptov. Species no. 01
22-1	40	<i>Sv. roseovorticillatum</i> subsp. <i>alboporum</i>	DSM 40900	ATCC 25189	Streptov. Species no. 01
22-1	40	<i>Sv. rubrovorticillatum</i>	DSM 40851		Streptov. Species no. 01
22-1	40	<i>Sv. salmonis</i>	*DSM 40895 ^(T)	NRRL B-1472	Streptov. Species no. 05

Table 1 (continued)

S _{SM} †	S _J ‡	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
22-1	40	<i>Sv. septatum</i>	*DSM 40577 ^(T) ATCC 27464 ISP 5577	F 55	Streptov. Species no. 02
22-1	40	<i>Sv. sporiferum</i>	DSM 40901 ATCC 25188		Streptov. Species no. 02
22-1	40	<i>Sv. takataensis</i>	DSM 40576 ATCC 27469 ISP 5576		Streptov. Species no. 09
22-1	40	<i>Sv. thioluteum</i>	*DSM 40027 ^T ATCC 12310 ISP 5027	F Sm	Streptov. Species no. 21
22-1	40	<i>Sv. tropicalensis</i>	DSM 40520 ATCC 17963 ISP 5520	F 55	Streptov. Species no. 03
22-1	40	<i>Sv. verticillium</i>	DSM 40903 ATCC 15003		Streptov. Species no. 06
22-1	40	<i>Sv. viridoflavum</i>	*DSM 40237 ^(T) ATCC 12631 ISP 5237	J 70	Streptov. Species no. 24
22-1	40	<i>Sv. waksmanii</i>	DSM 40464		Streptov. Species no. 09
Strains assigned to subcluster 22-2: <i>Streptomyces roseoviridis</i> (5)					
22-2	37	<i>S. olivaceus</i>	*DSM 40694 NRRL 2716		Category I Species no. 03
22-2	1-15	<i>S. prasinosporus</i>	*DSM 40506 ^T ATCC 17918 ISP 5506	A 38	Category III Species no. 07
22-2	37	<i>S. roseoviridis</i>	*DSM 40175 ^(T) ATCC 23959 ISP 5175	A 05	Category I Species no. 04
22-2	37	<i>S. showdoensis</i>	*DSM 40504 ^(T) ATCC 15105 ISP 5504	A 06	Category I Species no. 05
22-2	37	<i>S. termittum</i>	*DSM 40329 ^(T) ATCC 25499 ISP 5329	A 05	Category I Species no. 04
Strains assigned to subcluster 22-3: <i>Streptomyces lavendulae</i> (43)					
22-3	43	<i>S. aburaviensis</i>	*DSM 40033 ^T ATCC 23869 ISP 5033	A 02	Category II Species no. 01
22-3	42	<i>S. acidomyceticus</i>	DSM 40798 ATCC 11611		
22-3	1-8	<i>S. albohervatus</i>	DSM 40410 ATCC 19820 ISP 5410		
22-3	1-8	<i>S. chryseus</i>	*DSM 40420 ^(T) ATCC 19829 ISP 5420	A 17	Category I Species no. 10
22-3	42	<i>S. cinnamomensis</i>	*DSM 40803 ^T ATCC 12308		Category IV Species no. 02 (red series)
22-3	42	<i>S. cirratus</i>	*DSM 40479 ^(T) ATCC 14699 ISP 5479	F 62	Category II Species no. 14
22-3	42	<i>S. colombiensis</i>	*DSM 40558 ^(T) ATCC 27425 ISP 5558	F 61	Category I Species no. 22
22-3	1-7	<i>S. felleus</i>	*DSM 40647 NRRL 2251		Category I Species no. 01
22-3	1-8	<i>S. flavescens</i>	DSM 40428 ATCC 19838 ISP 5428		
22-3	42	<i>S. flavotricini</i>	*DSM 40152 ^(T) ATCC 23621 ISP 5152	F 61	Category I Species no. 22
22-3	1-8	<i>S. fradiae</i>	*DSM 40809 ATCC 14443		Category II Species no. 18
22-3	42	<i>S. globosus</i>	*DSM 40815 ^T ATCC 14979		Category IV Species no. 19 (grey series)
22-3	42	<i>S. goshikiensis</i>	*DSM 40190 ^(T) ATCC 23914 ISP 5190	F 61	Category I Species no. 22
22-3	42	<i>S. griseolavendus</i>	DSM 40385 ATCC 25457 ISP 5385		
22-3	43	<i>S. helveticus</i>	*DSM 40431 ^(T) ATCC 19841 ISP 5431	F 62	Category II Species no. 14
22-3	42	<i>S. katrae</i>	*DSM 40550 ATCC 27440 ISP 5550	F 61	Category I Species no. 22
22-3	1-8	<i>S. lateritius</i>	*DSM 40163 ^T ATCC 19913 ISP 5163	H Sm	Category III Species no. 23
22-3	1-8	<i>S. lavendofoliae</i>	*DSM 40217 ^T ATCC 15872 ISP 5217		Category IV Species no. 07 (red series)
22-3	42	<i>S. lavendulae</i> #	*DSM 40069 ^T ATCC 8664 ISP 5069	F 61	Category I Species no. 22
22-3	42	<i>S. lavendulae</i>	*DSM 40625		Category I Species no. 22
22-3	42	<i>S. lavendulae</i>	*DSM 40748 ATCC 14159		Category I Species no. 22
22-3	42	<i>S. lavendulae</i>	*DSM 41573 ATCC 14158		Category I Species no. 22
22-3	42	<i>S. lavendulae</i>	*DSM 41574 ATCC 14160		Category I Species no. 22
22-3	42	<i>S. lavendulae</i>	*DSM 41576 ATCC 14162		Category I Species no. 22
22-3	42	<i>S. lavendulae</i>	*DSM 41570 ATCC 11924		Category I Species no. 22
22-3	42	<i>S. lavendulae</i>	*DSM 41575 ATCC 14161		Category I Species no. 22
22-3	42	<i>S. lavendulae</i>	*DSM 41582 ATCC 31336		Category I Species no. 22
22-3	42	<i>S. lavendulae</i>	*DSM 41581 ATCC 25233		Category I Species no. 22
22-3	1-8	<i>S. lavendulae</i>	*DSM 41578 ATCC 15874		Category I Species no. 22
22-3	1-8	<i>S. lavendulocolor</i>	*DSM 40216 ^(T) ATCC 15871 ISP 5216	F 61	Category I Species no. 22
22-3	1-8	<i>S. luridus</i>	*DSM 40081 ^T ATCC 19782 ISP 5081	F 62	Category II Species no. 14
22-3	42	<i>S. polychromogenes</i>	*DSM 40316 ^(T) ATCC 12595 ISP 5316	F 61	Category I Species no. 22
22-3	42	<i>S. pseudolavendulae</i>	DSM 40213		Category I Species no. 11
22-3	43	<i>S. purpeofuscus</i>	*DSM 40283 ^T ATCC 23952 ISP 5283		Category IV Species no. 26 (grey series)
22-3	1-5	<i>S. purpureus</i> #	*DSM 43362 ^(T)		Category I Species no. 23
22-3	42	<i>S. racemochromogenes</i>	*DSM 40194 ^(T) ATCC 23954 ISP 5194	F 61	Category I Species no. 22
22-3	42	<i>S. roseochromogenes</i>	DSM 40879 IFO 3363		
22-3	1-8	<i>Streptomyces</i> sp.	DSM 40766		
22-3	1-9	<i>Streptomyces</i> sp. (<i>natalensis</i>)	DSM 40357 ATCC 27448 ISP 5357	A 29	
22-3	42	<i>S. subrutilus</i>	*DSM 40445 ^(T) ATCC 27467 ISP 5445	F 61	Category I Species no. 22
22-3	42	<i>S. toxytricini</i>	*DSM 40178 ^(T) ATCC 19813 ISP 5178	F 61	Category I Species no. 22
22-3	42	<i>S. vinaceus</i>	*DSM 40515 ^(T) ATCC 27476 ISP 5515	A 06	Category I Species no. 05
22-3	42	<i>S. virginiae</i>	*DSM 40094 ^(T) ATCC 19817 ISP 5094	F 61	Category I Species no. 22
Strains assigned to subcluster 22-4: <i>Streptomyces misakiensis</i> (17)					
22-4	43	<i>S. albolongus</i>	*DSM 40570 ^(T) ATCC 27414 ISP 5570	F 63	Category II Species no. 15
22-4	43	<i>S. aureofaciens</i>	*DSM 40127 ^T ATCC 10762 ISP 5127	A 14	Category II Species no. 04
22-4	43	<i>S. aureofaciens</i>	*DSM 40631 ATCC 13304		Category II Species no. 04
22-4	43	<i>S. aureofaciens</i>	*DSM 40642 ATCC 13303		Category II Species no. 04
22-4	43	<i>S. aureofaciens</i>	*DSM 40703		
22-4	1-7	<i>S. bikiniensis</i>	*DSM 40581 ^T ATCC 11062 ISP 5581	F 64	Category III Species no. 21

Table 1 (continued)

S _{SM} †	S _J ‡	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
22-4	1-6	<i>S. cuspidosporus</i>	*DSM 41424		Category IV Species no. 11 (grey series)
22-4	43	<i>S. finlayi</i>	*DSM 40218 ^T ATCC 23340 ISP 5218	I Sm	Category III Species no. 24
22-4	43	<i>S. fradiae</i>	*DSM 40810 ATCC 15438		Category II Species no. 18
22-4	43	<i>S. herbaricolor</i>	*DSM 40123 ^(T) ATCC 23922 ISP 5123	A 02	Category II Species no. 01
22-4	35	<i>S. karnatakensis</i>	DSM 40345 ATCC 25463 ISP 5345	C 44	
22-4	43	<i>S. misakiensis</i>	*DSM 40222 ^T ATCC 23938 ISP 5222	F 66	Category II Species no. 16
22-4	35	<i>S. pactum</i>	*DSM 40530 ^T ATCC 27456 ISP 5530	C 44	Category II Species no. 12
22-4	62	' <i>S. pyridomyceticus</i> '	DSM 40024 ATCC 23953 ISP 5024		
22-4	1-7	<i>S. venezuelae</i>	*DSM 40755		Category I Species no. 05
22-4	43	<i>S. viridifaciens</i>	DSM 40239 ATCC 11989 ISP 5239	F 66	
22-4	43	<i>S. xanthocidicus</i>	*DSM 40575 ^(T) ATCC 27480 ISP 5575	F 66	Category II Species no. 16
Strains assigned to subcluster 22-5: <i>Streptomyces fradiae</i> (17)					
22-5	39	<i>S. albus</i>	*DSM 40950		Category I Species no. 09
22-5	39	<i>S. clavuligerus</i>	*DSM 40751 ^T ATCC 27064		Category IV Species no. 10 (grey series)
22-5	39	<i>S. fradiae</i>	*DSM 40063 ^T ATCC 10745 ISP 5063	G 68	Category II Species no. 18
22-5	39	<i>S. fradiae</i>	*DSM 40877		Category II Species no. 18
22-5	39	<i>S. fradiae</i>	*DSM 40953		Category II Species no. 18
22-5	39	<i>S. fradiae</i>	*DSM 40955		Category II Species no. 18
22-5	39	<i>S. fradiae</i>	*DSM 40956		Category II Species no. 18
22-5	39	<i>S. fradiae</i>	*DSM 40952		Category II Species no. 18
22-5	39	<i>S. fradiae</i>	*DSM 40954		Category II Species no. 18
22-5	39	<i>S. fradiae</i>	*DSM 40957		Category II Species no. 18
22-5	39	<i>S. fradiae</i>	*DSM 40958		Category II Species no. 18
22-5	39	<i>S. fradiae</i>	*DSM 41543 ATCC 11903		Category II Species no. 18
22-5	39	<i>S. fradiae</i>	*DSM 41551 ATCC 21896		Category II Species no. 18
22-5	39	<i>S. fradiae</i>	*DSM 41545 ATCC 19063		Category II Species no. 18
22-5	39	<i>S. fradiae</i>	*DSM 41550 ATCC 21401		Category II Species no. 18
22-5	1-5	<i>S. roseoflavus</i>	*DSM 40536 ATCC 13167 ISP 5536		Category IV Species no. 10 (red series)
22-5	39	<i>S. roseolilacinus</i>	*DSM 40173 ^(T) ATCC 19922 ISP 5173	G 68	Category II Species no. 18
Strains assigned to cluster 23: <i>Streptomyces griseolus</i> (2)					
23	4	<i>Sv. avidinii</i>	*DSM 40526 ^(T) ATCC 27419 ISP 5526	F 56	Streptov. Species incertae sedis
23	4	<i>S. griseolus</i>	*DSM 40854 ATCC 11796		Category I Species no. 03
Strains assigned to cluster 24: <i>Streptomyces fungicidicus</i> (4)					
24	5	<i>S. fungicidicus</i>	DSM 40811 ATCC 13853		
24	56	<i>S. hygroscopicus</i>	*DSM 41527 ATCC 21705		Category I Species no. 16
24	56	<i>S. hygroscopicus</i>	*DSM 41604 NRRL B-16256		Category I Species no. 16
24	57	<i>Streptomyces</i> sp.	DSM 40987		
Strains assigned to cluster 25: <i>Streptomyces lydicus</i> (17)					
25	1-9	<i>S. albulus</i>	*DSM 40492 ^(T) ATCC 12757 ISP 5492	A 29	Category I Species no. 15
25	5	<i>S. bottropensis</i>	*DSM 40800 ATCC 13854		Category I Species no. 12
25	5	<i>S. fasciculatus</i>	DSM 40054 ATCC 19751 ISP 5054	A 29	
25	5	<i>S. hygroscopicus</i>	*DSM 40823		Category I Species no. 16
25	5	<i>S. hygroscopicus</i>	*DSM 41525 ATCC 15869		Category I Species no. 16
25	5	<i>S. hygroscopicus</i>	*DSM 41526 ATCC 21582		Category I Species no. 16
25	5	<i>S. hygroscopicus</i>	*DSM 41528 ATCC 21722		Category I Species no. 16
25	1-15	<i>S. kurssanovii</i>	DSM 40162 ^T ATCC 15824 ISP 5162	F 60	Category IV Species no. 20 (grey series)
25	5	<i>S. libani</i>	*DSM 40555 ^(T) ATCC 23732 ISP 5555	A 29	Category I Species no. 15
25	5	<i>S. lydicus</i> #	*DSM 40461 ^T ATCC 25470 ISP 5461	A 29	Category I Species no. 15
25	5	<i>S. nigrescens</i>	*DSM 40276 ^(T) ATCC 23941 ISP 5276	A 29	Category I Species no. 15
25	1-9	<i>S. noursei</i>	*DSM 40635 ^T ATCC 11455		Category IV Species no. 23 (grey series)
25	1-23	<i>S. ostreogriseus</i>	DSM 40511 ATCC 27455 ISP 5511	A 25	
25	5	<i>S. platensis</i>	*DSM 40041 ^(T) ATCC 13865 ISP 5041	A 29	Category I Species no. 15
25	5	<i>S. sioyaensis</i>	*DSM 40032 ^(T) ATCC 13989 ISP 5032	A 29	Category I Species no. 15
25	1-9	<i>Streptomyces</i> sp. (<i>chromogenus</i>)	DSM 40384 ATCC 27424 ISP 5284	A 33	
25	5	<i>S. tubercidicus</i>	*DSM 40261 ^T ATCC 25502 ISP 5261	C 47	Category III Species no. 14
Strains assigned to cluster 26: <i>Streptomyces flavidovirens</i> (2)					
26	33	<i>S. flavidovirens</i>	*DSM 40150 ^T ATCC 19900 ISP 5150		Category IV Species no. 03 (yellow series)
26	27	<i>S. tenebrarius</i>	DSM 40477 ATCC 17920 ISP 5477		
Strains assigned to cluster 27: <i>Streptomyces fradiae</i> (2)					
27	31	<i>S. fradiae</i>	*DSM 41549 ATCC 21098		Category II Species no. 18
27	31	<i>S. fradiae</i>	*DSM 41548 ATCC 21097		Category II Species no. 18

Table 1 (continued)

<i>S</i> _{SM} †	<i>S</i> _J ‡	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
Strains assigned to cluster 28: <i>Streptomyces prasinus</i> (2)					
28	9	<i>S. achromogenes</i> subsp. <i>rubradiris</i>	*DSM 40789 ^(T) NRRL 3061		Category I Species no. 12
28	9	<i>S. prasinus</i>	*DSM 40774 ATCC 15825		Category I Species no. 17
Strain assigned to cluster 29: <i>Streptomyces loidensis</i> (1)					
29	1-32	<i>S. loidensis</i>	DSM 40825 ATCC 11415		
Strains assigned to cluster 30: <i>Streptomyces albus</i> (17)					
30	1-34	<i>S. albus</i>	*DSM 40763 IMRU 3888		Category I Species no. 09
30	1-34	<i>S. albus</i>	*DSM 40965		Category I Species no. 09
30	1-34	<i>S. albus</i>	*DSM 40951		Category I Species no. 09
30	1-34	<i>S. albus</i>	*DSM 40964		Category I Species no. 09
30	1-34	<i>S. albus</i>	*DSM 40946		Category I Species no. 09
30	1-34	<i>S. albus</i>	*DSM 40947		Category I Species no. 09
30	1-34	<i>S. albus</i>	*DSM 40948		Category I Species no. 09
30	1-34	<i>S. albus</i>	*DSM 40949		Category I Species no. 09
30	1-34	<i>S. albus</i>	*DSM 40963		Category I Species no. 09
30	1-34	<i>S. albus</i>	*DSM 40652		Category I Species no. 09
30	1-34	<i>S. almquistii</i>	*DSM 40447 ^(T) ATCC 618 ISP 5447	A 16	Category I Species no. 09
30	1-34	<i>S. antibioticus</i>	*DSM 40764 ATCC 10382		Category I Species no. 21
30	1-34	<i>S. flocculus</i>	*DSM 40327 ^(T) ATCC 25453 ISP 5327	A 16	Category I Species no. 09
30	1-34	<i>S. flocculus</i>	*DSM 40808 ATCC 13257		Category I Species no. 09
30	1-34	<i>S. gibsonii</i>	*DSM 40959		Category IV Species no. 05 (white series)
30	1-34	<i>S. rangoon</i>	*DSM 40452 ^T ATCC 6860 ISP 5452		Category IV Species no. 07 (white series)
30	1-34	<i>S. rimosus</i>	*DSM 41560 ATCC 19655		Category I Species no. 19
Strains assigned to cluster 31: <i>Streptomyces cacaoi</i> (3)					
31	1-34	<i>S. aminophilus</i>	*DSM 40186 ^(T) ATCC 14961 ISP 5186	A 16	Category I Species no. 09
31	46	<i>S. antibioticus</i>	*DSM 41568 ATCC 15849		Category I Species no. 21
31	1-34	<i>S. cacaoi</i>	*DSM 40057 ^(T) ATCC 3082 ISP 5057	A 16	Category I Species no. 09
Strain assigned to cluster 32: <i>Streptomyces albus</i> (1)					
32	27	<i>S. albus</i>	*DSM 40313 ^T ATCC 3004 ISP 5313	A 16	Category I Species no. 09
Strains assigned to cluster 33: <i>Streptomyces alboflavus</i> (19)					
33	1-33	<i>S. alboflavus</i>	*DSM 40045 ^T ATCC 12626 ISP 5045	E 54	Category III Species no. 20
33	1-33	<i>S. aureocirculatus</i>	*DSM 40386 ^(T) ATCC 19823 ISP 5386	A 03	Category II Species no. 20
33	1-33	<i>S. aureofasciculus</i>	DSM 40414 ATCC 19824 ISP 5414	E 54	
33	1-33	<i>S. aureomonopodiales</i>	DSM 40416 ATCC 19825 ISP 5416		
33	1-33	<i>S. aureovercillatus</i>	*DSM 40080 ^(T) ATCC 15854 ISP 5080	A 10	Category I Species no. 06
33	1-33	<i>S. cinnamomensis</i>	*DSM 40804 ATCC 15413		Category IV Species no. 02 (red series)
33	1-33	<i>S. flavofungini</i>	DSM 40366 ATCC 27430 ISP 5366	B 42	
33	1-33	<i>S. kanamyceticus</i>	*DSM 41555 ATCC 21268		Category I Species no. 19
33	1-33	<i>S. kanamyceticus</i>	*DSM 41552 ATCC 21259		Category I Species no. 19
33	1-33	<i>S. kanamyceticus</i>	*DSM 41554 ATCC 21261		Category I Species no. 19
33	1-33	<i>S. kanamyceticus</i>	*DSM 41556 ATCC 21486		Category I Species no. 19
33	1-33	<i>S. kanamyceticus</i>	*DSM 41553 ATCC 21260		Category I Species no. 19
33	1-33	<i>S. longispororuber</i>	*DSM 40749 ATCC 13931		Category I Species no. 06
33	1-33	<i>S. longispororuber</i>	*DSM 40599 ^(T) ATCC 27443 ISP 5599	A 10	Category I Species no. 06
33	1-33	<i>S. longissimus</i>	DSM 40435 ATCC 19850 ISP 5435	E 54	
33	1-33	<i>S. moderatus</i>	DSM 40529 ATCC 23443 ISP 5529	A Sm	
33	1-33	<i>S. nobilis</i>	DSM 40441 ATCC 19251 ISP 5441	A 10	
33	1-33	<i>S. paraguayensis</i>	DSM 40567 ATCC 27458 ISP 5567	C 46	
33	1-33	<i>S. venezuelae</i>	*DSM 40727		Category I Species no. 05
Strain assigned to cluster 34: <i>Streptomyces fulvissimus</i> (1)					
34	1-33	<i>S. fulvissimus</i>	*DSM 40593 ^T ATCC 27431 ISP 5593	A 10	Category I Species no. 06
Strains assigned to cluster 35: <i>Streptomyces rimosus</i> (24)					
35	1-33	<i>S. albofaciens</i>	*DSM 40268 ^(T) ATCC 25184 ISP 5268	B 42	Category I Species no. 19
35	1-33	<i>S. alboflavus</i>	*DSM 40761 NCIB 9453		Category III Species no. 20
35	1-33	<i>S. capuensis</i>	DSM 40402 ATCC 25436 ISP 5402	B 42	
35	41	<i>S. catenulae</i>	*DSM 40258 ^(T) ATCC 12476 ISP 5258	C 43	Category II Species no. 11
35	1-33	<i>S. chrestomyceticus</i>	*DSM 40545 ^(T) ATCC 14947 ISP 5545	B 42	Category I Species no. 19

Table 1 (continued)

<i>S</i> _{SM} †	<i>S</i> _J ‡	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
35	1-33	<i>S. djakartensis</i>	*DSM 40743 ^T ATCC 13441		Category IV Species no. 12 (grey series)
35	1-33	<i>S. erumpens</i>	*DSM 40941 ^T ATCC 23266		Category IV Species no. 15 (grey series)
35	1-33	<i>S. fungicidicus</i>	DSM 40020 ATCC 27432 ISP 5020	A 16	
35	1-33	<i>S. humifer</i>	DSM 40602 ATCC 13748 ISP 5602	A 1C	
35	1-33	<i>S. hygroscopicus</i>	*DSM 40821 ATCC 13810		
35	1-33	<i>S. krestomyceticus</i>	DSM 40820		
35	1-33	<i>S. mauvecolor</i>	*DSM 40827		Category IV Species no. 08 (violet series)
35	1-33	<i>S. peucetius</i>	*DSM 40754 NCIB 10972		Category IV Species no. 09 (red series)
35	41	<i>S. ramulosus</i>	*DSM 40100 ^T ATCC 19802 ISP 5100	C Sm	Category III Species no. 16
35	1-33	<i>S. rimosus</i> #	*DSM 40260 ^T ATCC 10970 ISP 5260	B 42	Category I Species no. 19
35	1-33	<i>S. rimosus</i>	*DSM 40673		Category I Species no. 19
35	1-33	<i>S. rimosus</i>	*DSM 41557 ATCC 13224		Category I Species no. 19
35	1-33	<i>S. rimosus</i>	*DSM 41559 ATCC 14673		Category I Species no. 19
35	1-33	<i>S. rimosus</i>	*DSM 41562 ATCC 23307		Category I Species no. 19
35	1-33	<i>S. rimosus</i>	*DSM 41563 ATCC 33022		Category I Species no. 19
35	1-33	<i>S. rimosus</i>	*DSM 41558 ATCC 14500		Category I Species no. 19
35	1-33	<i>S. rimosus</i>	*DSM 41561 ATCC 19656		Category I Species no. 19
35	1-33	<i>S. somaliensis</i>	*DSM 40760 ATCC 14817		
35	1-33	<i>S. vendargensis</i>	DSM 40379 ATCC 25507 ISP 5379		
Strains assigned to cluster 36: <i>Streptomyces rimosus</i> (2)					
36	45	<i>S. rimosus</i>	*DSM 41565 ATCC 33024		Category I Species no. 19
36	45	<i>S. rimosus</i>	*DSM 41564 ATCC 33023		Category I Species no. 19
Strain assigned to cluster 37: <i>Streptomyces varsoviensis</i> (1)					
37	028	<i>S. varsoviensis</i>	*DSM 40346 ^T ATCC 25505 ISP 5346	C 46	Category III Species no. 13
Strain assigned to cluster 38: <i>Actinomadura luteofluorescens</i> (1)					
38	025	<i>A. luteofluorescens</i>	*DSM 40398 ^(T) ATCC 25469 ISP 5398		
Strain assigned to cluster 39: <i>Streptomyces caelicus</i> (1)					
39	1-28	<i>S. caelicus</i>	DSM 40835 NRRL 2957		
Strain assigned to cluster 40: <i>Streptomyces spheroides</i> (1)					
40	48	<i>S. spheroides</i>	*DSM 40292 ^(T) ATCC 23965 ISP 5292	A 1B	Category I Species no. 02
Strains assigned to cluster 41: <i>Streptomyces endus</i> (2)					
41	12	<i>S. endus</i>	*DSM 40187 ^(T) ATCC 23904 ISP 5187	A 32	Category I Species no. 16
41	12	<i>S. violaceusniger</i>	*DSM 40699		Category I Species no. 16
Strain assigned to cluster 42: <i>Streptomyces olivaceus</i> (1)					
42	14	<i>S. olivaceus</i>	*DSM 40072 ^(T) ATCC 3335 ISP 5072	A 1C	Category I Species no. 03
Strain assigned to cluster 43: <i>Streptomyces niveus</i> (1)					
43	13	<i>S. niveus</i>	*DSM 40088 ^(T) ATCC 19793 ISP 5088	A 1B	Category I Species no. 02
Strains assigned to cluster 44: <i>Streptomyces</i> sp. (2)					
44	1-24	<i>Streptomyces</i> sp.	DSM 40974		
44	1-24	<i>Streptomyces</i> sp.	DSM 40982		
Strain assigned to cluster 45: <i>Streptomyces scabies</i> (1)					
45	1-24	<i>S. scabies</i>	*DSM 40961		
Strain assigned to cluster 46: <i>Streptomyces pallidus</i> (1)					
46	1-19	<i>S. pallidus</i>	DSM 40531 ATCC 27457 ISP 5531	A 18	
Strain assigned to cluster 47: <i>Streptomyces anulatus</i> (1)					
47	1-35	<i>S. anulatus</i> #	*DSM 40361 ^T ATCC 27416 ISP 5361	A 1B	Category I Species no. 02
Strain assigned to cluster 48: <i>Streptomyces parvulus</i> (1)					
48	26	<i>S. parvulus</i>	*DSM 40722		Category I Species no. 07
Strains assigned to cluster 49: <i>Streptomyces roseiscleroticus</i> (2)					
49	22	<i>S. roseiscleroticus</i>	*DSM 40303 ^(T) ATCC 17755 ISP 5303		Category II Species no. 19
49	22	<i>S. ruber</i>	*DSM 40304 ^(T)		Category IV Species no. 11 (red series)

Table 1 (continued)

S _{SM} †	S _J ‡	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
Strains assigned to cluster 50: <i>Streptomyces violatus</i> (2)					
50	19	<i>S. saraceticus</i>	DSM 40241 ATCC 25496 ISP 5241	A 29	
50	19	<i>S. violatus</i>	*DSM 40209 ^(T) ATCC 15892 ISP 5209	A 18	Category I Species no. 11
Strains assigned to cluster 51: <i>Streptomyces violaceusniger</i> (5)					
51	18	<i>S. antimycoticus</i>	*DSM 40284 ^T ATCC 23880 ISP 5284		Category IV Species no. 05 (grey series)
51	1-30	<i>S. capreolus</i> subsp. <i>capreolus</i>	*DSM 40225 ^(T) ATCC 23892 ISP 5225	J Sm	
51	18	<i>S. melanosporofaciens</i>	*DSM 40318 ^(T) ATCC 25473 ISP 5318	A 32	Category I Species no. 16
51	18	<i>Streptomyces</i> sp.	DSM 40967		
51	18	<i>S. violaceusniger</i> #	*DSM 40563 ^T ATCC 27477 ISP 5563	A 32	Category I Species no. 16
Strain assigned to cluster 52: <i>Streptomyces bluensis</i> (1)					
52	17	<i>S. bluensis</i>	*DSM 40564 ^(T) ATCC 27420 ISP 5564	A 39	Category II Species no. 10
Strains assigned to cluster 53: <i>Streptomyces violaceusniger</i> (3)					
53	18	<i>S. hygroscopicus</i>	*DSM 41534 ATCC 31955		Category I Species no. 16
53	18	<i>S. violaceusniger</i>	*DSM 41599 NRRL B-1477		Category I Species no. 16
53	18	<i>S. violaceusniger</i>	*DSM 41600 NRRL B-1478		Category I Species no. 16
Strains assigned to cluster 54: <i>Streptomyces violaceusniger</i> (5)					
54	18	<i>S. hygroscopicus</i>	*DSM 41524 ATCC 15166		Category I Species no. 16
54	18	<i>S. hygroscopicus</i>	*DSM 41530 ATCC 29253		Category I Species no. 16
54	18	<i>S. hygroscopicus</i>	*DSM 41603 NRRL B-1865		Category I Species no. 16
54	18	<i>S. violaceusniger</i>	*DSM 41602 NRRL B-16257		Category I Species no. 16
54	18	<i>S. violaceusniger</i>	*DSM 41598 NRRL B-1356		Category I Species no. 16
Strains assigned to cluster 55: <i>Streptomyces hygroscopicus</i> (2)					
55	18	<i>S. hygroscopicus</i>	*DSM 41535 ATCC 39150		Category I Species no. 16
55	18	<i>S. rutgersensis</i> subsp. <i>castelarensis</i>	*DSM 40830 ATCC 15191		Category I Species no. 01
Strain assigned to cluster 56: <i>Streptomyces hygroscopicus</i> (1)					
56	16	<i>S. hygroscopicus</i> subsp. <i>ascomyceticus</i>	DSM 40822 ATCC 14891		
Strains assigned to cluster 57: <i>Streptomyces hygroscopicus</i> (2)					
57	52	<i>S. hygroscopicus</i>	*DSM 41533 ATCC 31080		Category I Species no. 16
57	53	<i>S. hygroscopicus</i>	*DSM 41529 ATCC 21840		Category I Species no. 16
Strain assigned to cluster 58: <i>Streptomyces caeruleus</i> (1)					
58	50	<i>S. caeruleus</i>	*DSM 40103 ^T ATCC 27421 ISP 5103		Category IV Species no. 07 (grey series)
Strain assigned to cluster 59: <i>Streptomyces</i> sp. (1)					
59	54	<i>Streptomyces</i> sp.	DSM 40966		
Strain assigned to cluster 60: <i>Streptomyces malachiticus</i> (1)					
60	51	<i>S. malachiticus</i>	DSM 40167 ATCC 19918 ISP 5167	A 12	
Strain assigned to cluster 61: <i>Streptomyces bellus</i> (1)					
61	1-22	<i>S. bellus</i>	*DSM 40185 ^(T) ATCC 14925 ISP 5185	A 18	Category I Species no. 11
Strain assigned to cluster 62: <i>Streptomyces xantholiticus</i> (1)					
62	24	<i>S. xantholiticus</i>	*DSM 40244 ^(T) ATCC 27481 ISP 5244	C 24	Category II Species no. 05
Strain assigned to cluster 63: <i>Streptomyces albosporeus</i> (1)					
63	49	<i>S. albosporeus</i>	*DSM 40795 ^T ATCC 15394		Category IV Species no. 01 (red series)
Strains assigned to cluster 64: ' <i>Streptomyces longissimus</i> ' (3)					
64	1-30	<i>S. eburosoreus</i>	DSM 40944		
64	1-30	' <i>S. longissimus</i> '	DSM 40826 ATCC 14562		
64	1-30	<i>Amycolatopsis mediterranei</i>	*DSM 40773		
Strains assigned to cluster 65: <i>Streptomyces</i> sp. (2)					
65	1-29	<i>Streptomyces</i> sp.	DSM 40988		
65	1-29	<i>Streptomyces</i> sp.	DSM 40986		
Strains assigned to cluster 66: <i>Streptomyces flocculus</i> (3)					
66	34	<i>S. alborubidus</i> #	DSM 40465 ATCC 23612 ISP 5465	A 12	
66	34	<i>S. albus</i>	*DSM 40785		Category I Species no. 09
66	34	<i>S. flocculus</i>	*DSM 40936		Category I Species no. 09

Table 1 (continued)

<i>S</i> _{SM} †	<i>S</i> _J ‡	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
Strain assigned to cluster 67: <i>Nocardia</i> sp. (1)					
67	34	<i>Nocardia</i> sp. (<i>S. listeri</i>)	DSM 40297		
Strains assigned to cluster 68: <i>Streptomyces sulphureus</i> (2)					
68	2	<i>Streptomyces</i> sp.	DSM 40968		
68	2	<i>S. sulphureus</i>	*DSM 40104 ^T ATCC 27468 ISP 5104	C Sm	Category III Species no. 17
Strains assigned to cluster 69: <i>Streptomyces ochraceiscleroticus</i> (10)					
69	1-26	<i>S. niger</i>	*DSM 40302 ^(T)	A 40	Category I Species no. 18
69	1-26	<i>S. ochraceiscleroticus</i>	DSM 40594		Category III Species no. 08
69	1-26	<i>S. ochraceiscleroticus</i>	*DSM 43155 ^(T)		Category III Species no. 08
69	1-26	<i>S. olivaceiscleroticus</i>	*DSM 40595 ^T ATCC 15722 ISP 5595		Category IV Species no. 24 (grey series)
69	1-26	<i>S. purpureogeniscleroticus</i>	*DSM 40271 ^(T)	A 40	Category I Species no. 18
69	1-26	<i>S. sclerotialus</i>	*DSM 40269 ^(T)		Category I Species no. 18
69	1-26	<i>Streptomyces</i> sp.	DSM 40156		
69	1-26	<i>S. verne</i>	DSM 40079 ATCC 3353 ISP 5079	A 40	
69	1-26	<i>S. violaceoruber</i>	*DSM 40049 ^T ATCC 14980 ISP 5049		Category IV Species no. 34 (grey series)
69	1-26	<i>S. violens</i>	*DSM 40597 ^(T) ATCC 15898 ISP 5597	A 40	Category I Species no. 18
Strain assigned to cluster 70: <i>Streptomyces fradiae</i> (1)					
70	1-26	<i>S. fradiae</i>	*DSM 40943		Category II Species no. 18
Strain assigned to cluster 71: <i>Streptomyces poonensis</i> (1)					
71	1-19	<i>S. poonensis</i>	*DSM 40596 ^(T) ATCC 15723 ISP 5596	A 22	Category II Species no. 19
Strain assigned to cluster 72: <i>Streptomyces</i> sp. (1)					
72	1-26	<i>Streptomyces</i> sp.	DSM 40857 ATCC 11862		
Strain assigned to cluster 73: <i>Streptomyces olivaceus</i> (1)					
73	1-26	<i>S. olivaceus</i>	*DSM 40756 ATCC 11071		Category I Species no. 03
Strain assigned to cluster 74: <i>Streptomyces erythrogriseus</i> (1)					
74	1-27	<i>S. erythrogriseus</i>	*DSM 40116 ^T ATCC 27427 ISP 5116		Category IV Species no. 04 (red series)
Strain assigned to cluster 75: <i>Streptomyces bambergiensis</i> (1)					
75	1-25	<i>S. bambergiensis</i>	*DSM 40590 ^T ATCC 13879 ISP 5590	A Sm	Category III Species no. 10
Strains assigned to cluster 76: <i>Streptomyces</i> sp./ <i>Streptoverticillium</i> sp./ <i>Nocardia</i> sp. (9)					
76	73	<i>N. carneus</i>	DSM 40840		
76	72	<i>N. coroniformis</i>	DSM 40806		
76	69	<i>S. cinerocrocatus</i>	DSM 40876		
76	69	<i>S. galtieri</i> (<i>N. galtieri</i>)	DSM 40350 ATCC 27433		
76	71	<i>S. phaeochromogenes</i>	*DSM 40788 NRRL B-1266		Category I Species no. 18
76	71	<i>S. rubescens</i>	DSM 40777 NRRL B-1519		
76	70	<i>Nocardia salmonicida</i>	DSM 40472	I 69	
76	69	<i>S. viridis</i>	DSM 40637		
76	69	<i>Sv. albireticuli</i>	*DSM 40051 ^T ATCC 19721 ISP 5051	F SM	Streptov. Species no. 11
Strain assigned to cluster 77: <i>Streptomyces ipomoeae</i> (1)					
77	74	<i>S. ipomoeae</i>	*DSM 40383 ^T ATCC 25462 ISP 5383		Category IV Species no. 02 (blue series)
Strains assigned to cluster 78: <i>Streptomyces fragilis</i> (2)					
78	58	<i>S. fragilis</i>	*DSM 40044 ^T ATCC 23908 ISP 5044	G SM	Category III Species no. 22
78	60	<i>S. griseoplanus</i>	*DSM 40009 ^(T) ATCC 19766 ISP 5009	A 29	Category I Species no. 15
Strains assigned to cluster 79: <i>Streptomyces lipmanii</i> (3)					
79	63	<i>S. amakusaensis</i>	*DSM 40219 ^T ATCC 23876 ISP 5219	B Sm	Category III Species no. 12
79	61	<i>S. lipmanii</i>	*DSM 40752 ATCC 27357		Category I Species no. 02
79	44	<i>S. olivaceus</i>	*DSM 41541 ATCC 21542		Category I Species no. 03
Strains assigned to cluster 80: <i>Streptomyces</i> sp. (3)					
80	65	<i>S. fradiae</i>	*DSM 41547 ATCC 21096		Category II Species no. 18
80	64	<i>S. glaucescens</i>	*DSM 40510		Category III Species no. 05
80	66	<i>S. verevaensis</i>	*DSM 43167 ^T		Category III Species no. 18
Strain assigned to cluster 81: <i>Streptomyces exfoliatus</i> (1)					
81	55	<i>S. exfoliatus</i>	*DSM 40735		Category I Species no. 04
Strains assigned to cluster 82: <i>Streptomyces</i> sp. (2)					
82	77	<i>S. chrysomallus</i>	*DSM 40685		
82	78	<i>Streptomyces</i> sp.	DSM 40889		

Table 1 (continued)

$S_{SM}^{\dagger}$	$S_j^{\ddagger}$	Strain designation§	Strain numbers	Williams group¶	Bergey category and species no.††
83	76	<i>S. aureofaciens</i>	Strain assigned to cluster 83: <i>Streptomyces aureofaciens</i> (1) *DSM 40643 ATCC 13305	Category II	Species no. 04
84	67	<i>S. xanthophaeus</i>	Strain assigned to cluster 84: <i>Streptomyces xanthophaeus</i> (1) *DSM 40134 ^(T) ATCC 19819 ISP 5134 F 61	Category I	Species no. 22
85	12	<i>S. hygroscopicus</i>	Strain assigned to cluster 85: <i>Streptomyces hygroscopicus</i> (1) *DSM 40578 ^(T) ATCC 27438 ISP 5578 A 32	Category I	Species no. 16
86	75	<i>S. coelicolor</i>	Strain assigned to cluster 86: <i>Streptomyces coelicolor</i> (1) *DSM 40674	Category I	Species no. 01
87	68	<i>A. autotrophica</i>	Strain assigned to cluster 87: <i>Amicolata autotrophica</i> (1) DSM 40011 ATCC 19727 ISP 5011 I 69		

† Number of cluster (and subcluster) in the UPGMA/ S_{SM} analysis.

‡ Number of cluster (and subcluster) in the UPGMA/ S_j analysis (numbers of strains for each cluster and subcluster are given in the text).

§ Designation of strain as received from the German Collection of Micro-organisms (DSM). The 20 strains included in the test reproducibility study are marked #.

|| Strains are marked with an asterisk when the species name is listed in the Approved Lists of Bacterial Names (Skerman *et al.*, 1980). A superscript T denotes the type strain of the species according to Williams *et al.* (1989); a superscript (T) denotes the type strain of the nomenspecies in the Approved Lists. Abbreviations of culture collections, etc.: ATCC, American Type Culture Collection, Rockville, MD, USA; DSM, Deutsche Sammlung von Mikroorganismen und Zellkulturen, Braunschweig, FRG; IFO, Institute for Fermentation, Osaka, Japan; ISP, International Streptomyces Project; IMRU, Institute of Microbiology, Rutgers-State University, NJ, USA; NCIB, National Collection of Industrial Bacteria, Aberdeen, UK; NRRL, Northern Utilization Research and Development Division, Peoria, IL, USA.

¶ Cluster-group and number of the numerical analysis of Williams *et al.* (1983a).

†† Assignment of strains to species according to *Bergey's Manual of Systematic Bacteriology*, vol. 4. For the genus *Streptomyces*, species categories I to IV are shown, with the species number within the category according to Williams *et al.* (1989); for species category IV the 'series' assignment is also given, according to spore colour. For the genus *Streptoverticillium*, species numbers are according to Locci & Schofield (1989).

Williams *et al.* (1983a), the name proposed by these authors was chosen for the phenon.

The following description of the phenon is presented in comparison with the study of Williams *et al.* (1983a) and the resulting species descriptions in *Bergey's Manual of Systematic Bacteriology*, vol. 4 (Williams *et al.*, 1989). The clusters of Williams *et al.* (1983a) are in places referred to as 'Williams groups', to avoid confusion with the clusters obtained in the present study. The three categories of the spore chains, viz. (a) straight to flexuous (Rectiflexibilis; RF), (b) hooks, loops or spirals with one to two turns (Retinaculiaperti; RA), and (c) spirals (Spirales; SP), are also given, although it is generally accepted that more than one category can be observed in the same species and the distinction between Retinaculiaperti and Spirales is not clear (Williams & Wellington, 1980; Williams *et al.*, 1989). The colour of the spore mass is also given, although its determination is not always easy (Kutzner, 1981), but 'species' assignment to different series within category IV (Williams *et al.*, 1989) is still based on these morphological properties. Physiological characters most representative of each cluster are marked in Table 2.

Composition and characteristics of the major clusters

Cluster 1 (*S. albidoflavus*/*S. griseus*/*S. antibioticus*) was the largest cluster of the analysis and contained 206 strains. The majority of these strains formed RF or RA spore chains with smooth, white, grey or yellow spores. It could be divided into eight subclusters (1-1 to 1-8) at the 84.0% similarity level (S_{SM}).

Subcluster 1-1 (*S. albidoflavus*) contained 52 strains, the majority of them from Williams cluster group A1A (*S. albidoflavus*). Additionally, eight strains were found in this cluster which were not tested by Williams *et al.* (1983a), but which belong to this species (Williams *et al.*, 1989). This subcluster also contained strain ISP 5139 (*S. badius*) from Williams cluster group C (single-member cluster), strain ISP 5557 (*S. alni*) from group A8, strain ISP 5335 (*S. prunicolor*) from group A11 and strain ISP 5496 (*S. diastaticus*) from group A19. In this cluster, three strains of *S. albus* were found, which proved to be wrongly designated. The cluster contained in addition *S. somaliensis* strain ISP 5267 which belongs to the yellow series according to Shirling & Gottlieb, 1968b. All strains formed smooth, yellow or white spores in RF chains.

Table 2. Distribution of positive characters to major subclusters and clusters defined at the 81.5% and 84.0% similarity levels (S_{SM})

Values are the percentage of strains with positive character states. Character states which are most representative within each cluster are marked with an asterisk.

Character	Cluster no. . . .	Subcluster . . .	No. of strains . . .	<i>S. albidoflavus</i>	<i>S. halstedii</i>	<i>S. griseus</i>	<i>S. olivaceus</i>	<i>S. antibioticus</i>	<i>S. flaveolus</i>	<i>S. diastachromogenes</i>	<i>S. exfoliatus</i>	<i>S. graminofaciens</i>	<i>S. rochei</i>	<i>S. prasinophilus</i>	<i>S. violaceus</i>	<i>S. niveoruber</i>	<i>S. chrysomallus</i>	<i>Se. griseocarinum</i>	<i>S. lavendulae</i>	<i>S. mitsukensis</i>	<i>S. fradiae</i>	<i>S. lydicus</i>	<i>S. albus</i>	<i>S. alboflavus</i>	<i>S. rimosus</i>	<i>S. ochraceiscleroticus</i>	<i>Streptomyces</i> sp./ <i>Nocardia</i> sp.	
Carbon source used for growth:																												
Carbohydrates and sugar derivatives																												
N-Acetyl-D-glucosamine																												
Amygdalin	100	44	33	43	0	47	6	44	40	17	38	57	22	44	17	0	100	43	53	98	100	100	95	96	100	100	89	
D-Arabinose	2	0	1	0	0	0	0	8	100	87	100	99	100	98	100	67	0	0*	0*	0*	0*	0*	0*	0	0	0	0	
L-Arabinose	100	100	40	100	100	100	75	100	0	0	0	0	1	14	3	0	50	0	0	0	0	0	0	0	0	0	0	
Arabinic acid	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
p-Arbutin	88	50	83	17	47	31	64	97	100	85	100	91	89	83	4	79	35	29	18	76	95	17	90	11	11	11	11	
D-Cellobiose	98	100*	99	100	95	100	100	100	100	97	100	100	100	100	100	100	8*	72	88	94	29	100	100	71	100	0	0	
Dextran	42	17	22	0	32	0	32	0	20	0	50	53	14	14	78	17	0	5	0	0	0	82	37	0	80	11	11	
D-Fructose	100	100	100	100	100	100	94	100	94	100	57	100	99	100	97	100	100	53	47	71	0*	100	88	100*	96	100	67	
D-Fucose	2	0	0	0	0	0	0	0	0	4	0	4	14	3	33	0	2	0	2	0	0	0	16	4	70	0	0	
L-Fucose	8	17	21	100*	26	0	20	33	50	29	43	92*	78	33	0*	7	18	0	65	35	79	8	60	0	60	0	0	
D-Galactose	92	100	99	100	95	100	100	95	100	99	100	99	100	99	100	83	39	65	100	24	100	100	100	100	100	0	0	
α-D-Galacturonate	0	17	5	17	21	0	6	12	7	17	35	0	42	67	17	0	0	9	6	0	0	12	6	11	0	80	0	
D-Glucarate	2	0	5	100*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	11	11	
Gluconate	96	83	99	100	95	100	94	100	100	83	97	100	98	100	100	100	98	88	100	100	88	100	88	100	96	100	56	
D-Glucosamine	92	100	96	100	74	100	94	100	96	100	100	100	100	100	95	100	100	95	82	65	88	100	100	100	100	100	22	
D-Glucosaminic acid	94	67	91	100	89	69	80	67	83	87	100	81	100	100	100	100	55	47	41	6	100	100	100	100	100	100	22	
D-Glucose	98	100	99	100	100	100	100	100	100	100	100	99	100	98	100	100	100	100	100	100	100	100	100	100	100	100	100	
D-Glucuronate	2	50	41	33	21	50	68	23	83	78	43	74	78	50	2	16	12	6	18	6	18	6	79	29	100	0	0	
Glycogen	98	83	100	100	95	100	100	100	100	100	100	99	100	99	100	89	100	98	100	100	100	24	95	100	100	0*	0*	
Glycyrhizinic acid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Inulin	48	67	52	33	53	62	80	73	83	54	71	68	56	100	67	4*	80	49	47	71	35	65	53	54	100	78	78	
Lactose	96	100	69	67	89	75	96	80	100	97	100	97	100	100	100	67	4*	12*	41	35	47	94	47	67	100	0	0	
Lactulose	85	33	22	17	21	62	92	27	67	94*	71	90	100	17	0	0	0	9	12	12	59	94	26	58	90	0	0	
D-Lyxose	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
L-Lyxose	0	17	23	83	0	19	44	0	19	44	0	33	70	86	67	89	17	0	0	0	0	0	11	0	60	0	0	
D-Maltose	98	100	99	100	100	94	100	100	100	100	100	99	100	100	100	100	94	98	94	100	100	100	100	100	100	100	11	
D-Mannose	96	100	99	100	100	89	100	100	100	100	100	83	99	100	99	100	83	94	98	53	94	100	100	100	100	100	11	
L-Mannose	0	50	28	50	0	25	48	0	33	47	0	66	100*	17	2	0	0	0	0	0	0	0	0	11	0	80	0	0
D-Mannoheptulose	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	18	0	0	0	0	
α-D-Melezitose	6	0	1	0	5	0	0	0	17	3	0	0	0	0	0	0	0	0	0	0	0	53	24	5	4	100*	0	0
α-D-Melibiose	2	0	0*	0	79	50	64	20	100*	54	14	96*	89	50	0	0	0	0	12	0	0	82	0	84	71	70	0	0
Methyl α-D-glucopyranoside	42	0	12	0	0	0	4	0	83	62	86	24	100*	33	0	0	0	0	0	0	0	47	94	68	0	90	0	0
Methyl α-D-mannoside	0	0	0	0	0	0	26	19	4	3	67	47	14	25	100*	0	22	0	0	0	0	0	100*	32	58	20	0	0
Methyl β-D-xyloside	8	0	5	0	0	0	0	0	0	0	0	4	0	0	0	0	0	2	0	0	0	82	5	0	0	0	0	0

Urea	6	17	7	0	0	0	0	8	7	0	3	43	4	11	0	6	7	0	0	0	0	6	0	0	17	10	0	
Hexylamine	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	2	6	0	0	6	0	0	0	0	0	0	
Putrescine	100	50	99	67	100	94	100	96	100	100	99	86	100	100	83	86	100	100	100	100	100	100	100	100	100	100	0*	
Spermidine	98	50	100	100	100	100	100	96	100	100	100	100	99	89	83	78	100	94	6*	94	88	100	96	100	100	100	11	
Spermine	0	0	9	0	11	6	4	87	17	0	0	5	0	17	49	74	76	12	29	0	21	96*	0	0	0	0	0	
Taurine	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	
Trigonelline	0	0	0	0	0	0	0	0	0	0	1	0	4	0	0	0	0	0	0	0	0	0	0	0	50	0	0	
Tryptamine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Tyramine	0	0	16	0	63	25	48	27	0	14	0	66	11	0	27	16	0	0	0	0	0	0	0	4	60	0	0	
Miscellaneous nitrogenous compounds																												
Acetamide	4	0	0	17	0	0	0	0	0	0	5	14	3	0	0	2	0	0	6	6	12	16	8	10	11	0	0	
Allantoin	2	0	5	83	11	0	8	3	0	16	14	51	44	0	2	0	0	0	0	0	6	59	37	8	30	0	0	
Cytosine	6	0	0	0	0	0	8	0	0	6	0	9	0	0	0	0	0	0	0	0	0	0	12	0	11	0	0	
Glycinamide	8	0	5	0	11	69	32	13	0	24	43	47	33	50	59	9	12	6	18	29	79	38	20	0	0	0	0	
Hippurate	0	0	1	0	0	6	4	0	0	9	29	3	22	0	2	0	0	0	0	12	18	0	54	100*	11	0	0	
Indole-3-acetate	6	0	5	0	11	6	0	3	17	6	14	5	0	0	14	2	0	0	0	6	0	0	10	0	0	0	0	
L-Leucinamide	77	33	36	83	5*	25	56	77	100	56	86	50	78	67	80	56	53	35	12	76	84	75	100	56	0	0	0	
Oxamic acid	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Salicylamide	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Thiamin	2	0	0	0	0	0	0	0	0	1	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Uracil	4	0	0	0	0	12	0	3	0	1	0	0	22	0	18	5	0	0	0	6	11	8	0	0	0	0	0	
Ureidosuccinate	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
L-Valinamide	69	50	69	33	42	38	88	57	100	70	71	89	83	86	56	59	35	71	94	95	83	100	22	0	0	0	0	
Aromatic compounds																												
Anthraniolate	2	0	6	0	5	19	0	7	17	6	0	17	67	17	2	5	12	0	6	0	16	0	10	0	0	0	0	
3-Aminobenzoate	0	0	0	0	0	6	4	0	0	6	29	1	11	0	0	0	0	0	0	12	0	8	0	0	0	0	0	
4-Aminobenzoate	0	0	0	0	0	0	4	0	0	1	0	2	0	0	0	2	0	0	0	0	5	0	0	0	0	0	0	
Benzoate	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	70	11	0	0	
Furan-2-carbonic acid	0	0	1	0	0	0	0	0	0	1	0	0	0	0	2	0	0	6	0	6	0	0	20	0	0	0	0	
3-Hydroxybenzoate	4	33	1	0	0	6	4	0	0	14	57	8	22	17	0	2	0	12	12	0	8	20	22	0	0	0	0	
4-Hydroxybenzoate	0	0	0	0	0	32	25	36	57	0	44	29	48	78	17	0	16	18	0	29	0	37	62	80	0	0	0	
2-Hydroxyphenylacetate	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	6	6	0	0	0	0	0	0	0	
3-Hydroxyphenylacetate	0	0	6	17	5	12	0	13	17	8	29	20	33	17	4	16	6	0	18	0	5	4	30	0	0	0	0	
4-Hydroxyphenylacetate	0	0	0	0	0	21	12	0	0	4	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Isophthalate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
D-Mandelate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
L-Mandelate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Phenoxyacetate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	
Phenylacetate	96	83	77	100	53	75	72	90	50	89	57	78	89	83	43	49	53	53	88	29	47	88	80	11	0	0	0	
Phenyllactate	90	17	9	50	26	62	32	43	17	68	100	51	89	50	57	21	53	12	53	100	100	92	70	0	0	0	0	
Phenylpropionate	12	0	0	0	0	0	12	0	0	5	0	11	11	0	6	5	6	6	0	0	0	0	20	11	0	0	0	
Phenylpyruvate	40	0	40	100	32	44	36	67	17	44	14	64	89	50	65	74	29	41	29	88	95	92	50	0	0	0	0	
Phthalate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	
Protocatechuate	4	0	2	0	11	6	20	17	33	48	57	40	56	0	2	5	0	12	12	0	32	38	50	0	0	0	0	
Quinate	0	0	0	0	0	5	0	4	0	33	28	46	33	0	0	0	0	0	0	6	0	0	70	0	0	0	0	
Salicylate	0	0	0	0	0	0	0	0	0	0	0	14	11	11	0	6	6	0	0	0	0	0	50	0	0	0	0	
Tropate	2	0	2	0	0	0	4	3	0	0	0	2	0	0	0	2	0	0	0	0	0	8	0	0	0	0	0	
Vanillate	0	0	0	0	5	0	4	3	0	9	0	56	11	0	0	0	0	0	0	6	11	0	10	0	0	0	0	
Growth with:																												
Glucose + 1% NaCl	100	100	99	100	100	100	100	100	100	99	100	100	100	100	83	100	100	100	100	100	100	100	100	89	0	0	0	0
Glucose + 2% NaCl	100	100	99	100	95	100	92	100	100	97	100	100	100	100	83	100	100	100	100	100	100	100	100	89	0	0	0	0
Glucose + 5% NaCl	96	83	94	83	58	75	88	97	67	94	100	92	100	100	100	86	79	47	88	100	100	100	100	56	0	0	0	0
Glucose + 7% NaCl	94	83	90	50	47	62	76	93	67	94	100	83	100	83	100	83	67	49	29	82	94	100	100	44	0	0	0	0
Glucose + 10% NaCl	88	33	78	50	37	44	52	60	67	86	86	65	56	67	25	16	0	76	65	100	100	100	100	44	0	0	0	0
Glucose + 0.005% NaN ₃	21	0	32	67	26	25	32	40	17	32	43	67	56	100	82	44	35	53	59	71	68	79	80	56	0	0	0	0
Glucose + 0.01% NaN ₃	19	0	28	67	26	25	28	30	0*	33	57	65	78	100	90	42	29	59	59	76	68	75	80	56	0	0	0	0
Glucose + 0.02% NaN ₃	10	0	12	67	16	0	4	13	0	6	14	36	44	83	55	23	12	53	35	53	58	60	44	0	0	0	0	0

Subcluster 1-2 (*S. halstedii*) consisted of six strains. Five of these belonged to Williams group A1C (*S. halstedii*); the other strain, DSM 40859 (*S. scabies*), is probably wrongly designated. All strains of this cluster formed smooth, grey spores in RF chains.

Subcluster 1-3 (*S. griseus*) contained 81 strains, the majority of them belonging to Williams group A1B (*S. anulatus*). This cluster also contained one strain each from the Williams clusters A6, A9 and A23, and *S. floridae* and *S. praecox* (category IV, yellow series), in addition to three strains grouped into cluster A3. These strains shared the morphological properties of the majority of the strains in subcluster 1-3 (yellow spore mass, smooth spores in RF chains). *S. acrimycini* (category IV, green series) was also recovered in this subcluster, despite its morphological characteristics (green spores with a hairy surface, SP or RA spore chains). In addition to these strains in subcluster 1-3, two strains of *S. fradiae* and two strains of *S. lavendulae* were found which were obviously wrongly designated. Subcluster 1-3 also contained strain ISP 5078, designated as *S. scabies* and grouped into cluster A3 of Williams *et al.* (1983a) but not included in the revival of *S. scabies* by Lambert & Loria (1989a). *S. setonii* ATCC 25497, which was considered to be a strain of *S. griseus* by Hütter (1967), also fell within this subcluster. Strain *S. anulatus* ISP 5361, responsible for the name of the corresponding cluster A1B (*S. anulatus*) of Williams *et al.* (1983a) formed single-member cluster 47 in the present analysis.

Subcluster 1-4 (*S. olivaceus*) consisted of six strains, four of them named *S. olivaceus* and all sharing the morphological properties of strains grouped into subcluster 1-2. In addition, one strain named *S. scabies* (DSM 40611) was found in this subcluster.

The four subclusters 1-1 to 1-4 were joined at the 82.3% similarity level S_{SM} .

Subcluster 1-5 (*S. antibioticus*) contained 19 strains, most of them received as *S. antibioticus*. All strains formed grey spores; the majority had a smooth surface. Spore chains were RF, RA or SP. Williams *et al.* (1983a) grouped five strains into a heterogeneous cluster (A31) named *S. antibioticus*. Only one strain (*S. lucensis*, ISP 5317) of this Williams cluster was recovered in subcluster 1-5. However, two further strains from Williams cluster A31 were found in subcluster 1-6 (*S. flaveolus*), thus confirming the heterogeneity of the species. Furthermore, all three strains of Williams group A34 (*S. nogalater*) which were later classified into different species (Williams *et al.*, 1989) were found in subcluster 1-5. The strain named '*S. lavenduligriseus*' ISP 5487 is classified in the genus *Streptovercillium* (*Sv. lavenduligriseum*) according to Locci & Schofield (1989). The subcluster contained further strains from different Williams groups which are listed in detail in Table 1.

Subcluster 1-6 (*S. flaveolus*) was composed of 16 strains, 10 of them tested by Williams *et al.* (1983a) and grouped into clusters A1B, A12, A17, A18, A24, A31 and A33. All strains, with the exception of *S. alboniger* (ISP 5043) produced grey or red, smooth or hairy spores in SP or RF spore chains.

Subcluster 1-7 (*S. diastatochromogenes*) contained 25 strains. Three of these were strains from Williams group A19 (*S. diastaticus*) which were not grouped into our cluster 9 containing the majority of strains from A19. Besides these strains, members of the Williams groups A12, A18, A23 and A31, *S. bobili* (ISP 5056) of category IV, white series, and *S. ghanaensis* (DSM 40746), green series (Williams *et al.*, 1989) were also found. Three strains of *S. glaucescens* not tested by these workers were additionally recovered in this subcluster. Most strains had the morphological properties found in other subclusters of cluster 1, but this subcluster had no corresponding cluster in the study of Williams *et al.* (1983a).

Subcluster 1-8 ('*Sv. luteoreticuli*') contained only strain ISP 5509, which was classified as *Sv. mobaraense* by Locci & Schofield (1989).

The subclusters 1-5 to 1-8 were joined at the 83% S_{SM} similarity level.

Cluster 2 (*S. exfoliatus*) was composed of 30 strains. Of these, 12 strains belonged to Williams group A5 (*S. exfoliatus*) and three to the strongly related Williams group A6 (*S. violaceus*), in addition to one strain of Williams group A7. All strains, including strain *S. tanashiensis* ISP 5195 (category IV, grey series of Williams *et al.*, 1989) produced RF chains of smooth, red, grey or white spores.

Cluster 4 (*S. graminofaciens*) was composed of six strains and contained both the strains from Williams group A26 (*S. graminofaciens*) in addition to strains from different Williams groups. It has no corresponding cluster in the study of Williams *et al.* (1983a).

Cluster 6 (*S. rochei*) was composed of 79 strains, the majority of them belonging to Williams groups A12 (*S. rochei*) and A21 (*S. griseoruber*). Single strains from the Williams groups A1C, A13, A15, A37, A38 and C44 were also recovered. This cluster also contained ten strains from category IV (Williams *et al.*, 1989): eight strains of the grey series, one strain of the red series (*S. rubiginosohelvolus* ISP 5176) and one strain of the green series (*S. griseostramineus* ISP 5161). Most strains produced SP or RF chains of smooth grey spores, and produced no melanin or other pigments.

Cluster 7 (*S. prasinopilosus*) consisted of seven strains, three of them classified in cluster A37 (*S. griseoflavus*) of Williams *et al.*, 1983a). They produced ornamented, green spores in RA or SP chains and were melanin negative.

Cluster 9 (*S. violaceus*) was the third-biggest cluster of the S_{SM} analysis, containing 118 strains. Most of these strains were classified into clusters A18 (*S. cyaneus*) and A19 (*S. diastaticus*) of Williams *et al.* (1983a). Furthermore, the cluster contained all four strains of cluster A30 (*S. filipinensis*), three of the five strains of cluster A33 (*S. chromogenus*), many strains designated as *S. viridochromogenes* and *S. chartreusis*, and six strains of category IV, three belonging to the grey series, two belonging to the blue series and one strain belonging to the red series (Williams *et al.*, 1989). The cluster contained many strains producing blue, spiny spores (*S. chartreusis*). Other strains produced grey or red spores in RF or SP chains.

Cluster 13 (*S. niveoruber*) was composed of nine strains, which produced grey, smooth spores in SP or RF chains, and of which only one (*S. toyocaensis* ISP 5030) was tested by Williams *et al.* (1983a) and grouped into cluster A29. Three of the strains in cluster 13 are currently classified within category IV of Williams *et al.* (1989).

Cluster 20 (*S. chrysomallus*) was composed of six strains, none of them included in the study of Williams *et al.* (1983a). These strains shared many morphological properties with strains grouped into subclusters 1-1 (*S. albidoflavus*) and 1-3 (*S. griseus*). The cluster contained *S. celluloflavus* DSM 40839 belonging to the category IV, yellow series of Williams *et al.* (1989).

Cluster 22 (*Streptoverticillium* sp./*S. lavendulae*/*S. fradiae*) contained 133 strains. It could be divided into five subclusters (22-1 to 22-5) at the 84.0% similarity level (S_{SM}).

Subcluster 22-1 (*Streptoverticillium griseocarneum*) contained 50 strains of the genus *Streptoverticillium* in addition to '*Streptomyces mediocidicus*' ISP 5021. This strain was recovered as a single-member cluster in cluster group F of Williams *et al.* (1983a) and shared the morphological properties of the genus *Streptoverticillium*. Subcluster 22-1 was very homogeneous and all strains conformed to the genus description of *Streptoverticillium* of Locci & Schofield (1989). The groupings of Locci *et al.* (1981) and, hence, the classification of Locci & Schofield (1989) could not be confirmed in our investigation.

Subcluster 22-2 (*S. roseoviridis*) was composed of five strains, two of them from Williams group A5 (*S. exfoliatus*) and one each from Williams groups A6 (*S. violaceus*) and A38 (*S. prasinosporus*). The other strain in this cluster was designated as *S. olivaceus*.

Subcluster 22-3 (*S. lavendulae*) was a heterogeneous subcluster containing 43 strains, most of them classified within the groups F61 (*S. lavendulae*) and F62 (*S. luridus*) of Williams *et al.* (1983a) and most of them producing smooth, red spores in RF chains. The majority of the strains were melanin-positive. In addition to single

strains of Williams groups A2, A6, A10, A17 and A29, the subcluster contained four strains currently classified within category IV of Williams *et al.* (1989), two of them belonging to the red series (*S. lavendofoliae* ISP 5217 and *S. cinnamomensis* DSM 40803) and two belonging to the grey series (*S. globosus* DSM 40815 and *S. purpeofuscus* DSM 40283). These strains shared many morphological and physiological properties with the other members of the subcluster.

Subcluster 22-4 (*S. misakiensis*) was composed of 17 strains sharing many physiological properties with the strains found in subcluster 22-3. Three strains of Williams group F66 (*S. misakiensis*) were found in this cluster, as well as strains from groups A2, A12, A14 and C44. Many strains produced a grey spore mass in RF or SP chains. Only a few strains were melanin-positive. The subcluster contained *S. cuspidosporus* DSM 41424 from category IV, grey series (Williams *et al.*, 1989).

Subcluster 22-5 (*S. fradiae*) was homogeneous and contained 17 melanin-negative strains, most of them producing smooth, red spores in RF or SP chains. It included *S. clavuligerus* DSM 40751, category IV, grey series, and *S. roseoflavus* ISP 5536, category IV, red series of Williams *et al.* (1989).

The four subclusters 22-2 to 22-5 fused at the 83.4% S_{SM} similarity level.

Cluster 25 (*S. lydicus*) consisted of 17 strains, the majority of which belonging to Williams group A29 (*S. lydicus*), in addition to four strains designated as *S. hygrosopicus*, which are currently classified within *S. violaceusniger* (Williams *et al.*, 1989). In most cases, the strains had SP spore chains and their spores were grey and smooth. The cluster contained *S. kurssanovii* ISP 5162 and *S. noursei* DSM 40635 from category IV, grey series of Williams *et al.* (1989).

Cluster 30 (*S. albus*) was a homogeneous cluster, containing 17 strains, composed mainly of strains from Williams group A16 (*S. albus*). The strains produced smooth, white or yellow spores in SP chains and produced no melanin, thus sharing the features of two strains from the white series of category IV (*S. gibsonii* DSM 40959 and *S. rangoon* ISP 5452) according to Williams *et al.* (1989). One strain designated as *S. antibioticus*, sharing the morphological features of strains found in that cluster but different from those strains of subcluster 1-5, was also grouped within cluster 30.

Cluster 33 (*S. alboflavus*) contained many strains from Williams group A10 (*S. fulvissimus*) and all three members of Williams group E54 (*S. alboflavus*). In addition to these, some strains of *S. kanamyceticus* were found which were grouped into cluster B42 (*S. rimosus*) by Williams *et al.* (1983a). All the strains produced smooth, white or red spores in RT chains.

Cluster 35 (*S. rimosus*) consisted of the majority of the *S. rimosus* strains (Williams group B42) and additionally contained two strains (*S. djakartensis* DSM 40743 and *S. erumpens* DSM 40941) from the grey series, *S. peucetius* DSM 40754 from the red series and *S. mauvecolor* (DSM 40827) from the violet series of category IV (Williams *et al.*, 1989). It was a homogeneous cluster and the majority of strains produced smooth spores in SP chains, or rarely in RF or RA chains.

Cluster 69 (*S. ochraceiscleroticus*) comprised 10 strains, four of them belonging to cluster A40 (*S. phaeochromogenes*) of Williams *et al.* (1983a). Several strains of the former genus *Chainia* were also grouped within that cluster. Strains produced smooth spores in SP chains. Two strains from the grey series of Williams *et al.* (1989) were found within cluster 69 and also shared the morphological features of the cluster, among them the type strain of *S. violaceoruber* ISP 5049^T, which was not recovered with the majority of related strains in cluster 6 (*S. rochei*).

Cluster 76 (*Streptomyces* sp./*Nocardia* sp.) contained strains assigned to different genera (Table 1).

Composition and characteristics of the minor clusters and single-member clusters

Cluster 3 (*S. gelaticus*) contained three strains, two of them from cluster A1C and a single-member cluster of Williams *et al.* (1983a). They produced smooth, grey spores in RA or RF chains.

Cluster 5 (*S. parvus*) contained five strains, all from different clusters of Williams *et al.* (1983a). They produced smooth, yellow spores in RF or SP chains. No strain was able to produce melanin.

Cluster 8 (*Streptomyces* sp.) contained four strains, of which two were designated as *S. scabies*. None of these strains were used in the studies of Williams *et al.* (1983a) or Lambert & Loria (1989a, b).

Cluster 10 (*S. sparsogenes*) was composed of two strains, which produced grey spores in SP chains but were physiologically different from other *S. violaceus-niger* and *S. hygroscopicus* strains found in clusters 51 and 53 to 57 of the present UPGMA/ S_{SM} analysis.

Cluster 11 (*S. psammoticus*) contained five strains which had grey, blue or green spores in SP or RF chains. The strains shared many properties with those found in major cluster 9. These two clusters were joined at the 80.5% S_{SM} level.

Cluster 12 (*S. aurantiacus*) comprised two strains producing smooth, red coloured spores in RT chains, which were similar to the strains in cluster 13 (*S. niveoruber*). These two clusters fused at the 80.6% similarity level (S_{SM}).

Cluster 14 (*Streptomyces* sp.) contained two strains, designated as *S. albus* and *S. scabies*, respectively.

Clusters 15 (*S. massasporeus*), producing violet, smooth spores, 16 (*S. lanatus*), producing blue, spiny spores, 18 (*S. griseoruber*) and 19 (*S. cyaneogriseus*), both producing grey, smooth spores, were single-member clusters. Two of them (clusters 15 and 19) were also recovered as single-member clusters by Williams *et al.* (1983a). All these strains had SP spore chains.

Cluster 17 (*S. griseoalbus*) consisted of two strains with yellow, smooth spores in RF chains; of these, strain *S. griseoalbus* ISP 5468 is grouped into species category IV, yellow series of Williams *et al.* (1989).

In cluster 21 (*S. thermovulgaris*), three thermophilic strains were recovered (Williams group A36), in addition to two mesophilic strains producing grey, smooth spores in SP chains.

Cluster 23 (*S. griseolus*) contained two strains, producing RA chains of smooth red or red-greyish spores and physiologically very similar to subcluster 22-5. This cluster contained *Sv. avidinii* ISP 5526, which is currently classified as *species incertae sedis* in the genus *Streptoverticillium* (Locci & Schofield, 1989), although it has been described as a typical streptomycete (Shirling & Gottlieb, 1972).

Cluster 24 (*S. fungicidicus*) was composed of four strains, producing grey, rugose or smooth spores in SP chains and showing much similarity to the strains found in major cluster 25 (*S. lydicus*). These two clusters were joined at the 81.3% S_{SM} level.

Cluster 26 (*S. flavidovirens*) contained two strains producing smooth, yellow or greyish spores in RF or RA chains.

Cluster 27 (*S. fradiae*) contained a further two strains of *S. fradiae* showing the morphological properties of strains grouped into major subcluster 22-5, but physiologically different from strains grouped into subcluster 22-5 (see Tables 2 and 3).

Cluster 28 (*S. prasinus*) contained two strains not considered in the study of Williams *et al.* (1983a). The strains were morphologically different. *S. prasinus* DSM 40774 formed green spores in RA chains, while *S. achromogenes* subsp. *rubradiris* formed white spores in RF chains.

Cluster 29 (*S. loidensis*) was a single-member cluster and was not considered in the study of Williams *et al.* (1983a).

Strains of cluster 31 (*S. cacaoi*) and single-member cluster 32 (*S. albus*), which contained the type strain of *S. albus*, ISP 5313^T, joined the major cluster 30 (*S. albus*) at similarity levels of 81.4% and 80.0% (S_{SM}), respectively. They shared all of the morphological and many of the physiological properties of strains found in major cluster 30.

Single-member cluster 34 (*S. fulvissimus*) contained the type strain and joined major cluster 33 (*S. alboflavus*) at a similarity level of 80.4% (S_{SM}).

Two strains of *S. rimosus* were grouped into cluster 36 (*S. rimosus*). They shared the morphological properties of strains grouped within major cluster 35 (*S. rimosus*) and joined this cluster at a similarity level of 81.0% S_{SM} .

Clusters 37 (*S. varsoviensis*), producing yellow, smooth spores in RF chains, 38 (*Actinomadura luteofluorescens*), producing yellow spores in RA chains, 39 (*S. caelicus*) and 40 (*S. spheroides*), both producing yellow, smooth spores, were recovered as single-member clusters. Two of them (clusters 38 and 39) were not included in the study of Williams *et al.* (1983a).

Cluster 41 (*S. endus*) was composed of two strains, both producing rugose, grey spores in SP chains. These strains were physiologically different from those found in clusters 10, 51, 53 and 54, which all contained strains currently grouped into *S. violaceusniger* (Williams *et al.*, 1989).

Single-member clusters 42 (*S. olivaceus* ISP 5072) and 43 (*S. niveus* ISP 5088) contained strains grouped within Williams groups A1C and A1B, respectively. These strains shared the morphological properties of cluster 1, but were physiologically different from strains grouped into subclusters 1-4 and 1-2.

Clusters 44 and 65 (*Streptomyces* sp.) were each composed of two strains, not assigned to named species, and single-member cluster 45 contained a strain designated as *S. scabies* which differed from those found in clusters 6, 8, and 9. Single-member cluster 46 (*S. pallidus*) contained a strain grouped into cluster A18 (*S. cyaneus*) of Williams *et al.* (1983a), but not listed among the synonyms of that cluster (Williams *et al.*, 1989). Single-member cluster 47 (*S. anulatus*) produced yellow, smooth spores in RF chains and 48 (*S. parvulus*) produced grey spores in SP chains.

Cluster 49 (*S. roseiscleroticus*) contained two strains producing greyish, smooth spores in SP chains, one of them (*S. ruber*) currently classified within the red series of category IV (Williams *et al.*, 1989). Both strains belonged to the former genus *Chainia* which has been reclassified into the genus *Streptomyces* (Goodfellow *et al.*, 1986).

Cluster 50 (*S. violatus*) was also composed of two strains with grey or white spores in SP spore chains.

Clusters 51 to 57 (*S. violaceusniger*, *S. hygroscopicus*) were formed from the majority of strains designated as *S. hygroscopicus* and *S. violaceusniger* (Table 1). The strains produced grey, rugose spores in SP chains and produced no melanin. One strain of the grey series of category IV (*S. antimycoticus* ISP 5284) was also found in cluster 51, sharing the morphological properties of the majority of

strains. Single-member cluster 58 (*S. caeruleus* ISP 5103) classified within the grey series of category IV, was morphologically and physiologically very similar to strains found in clusters 51 to 57.

Single-member cluster 52 (*S. bluensis*) produced smooth, blue spores, clusters 60 (*S. malachiticus*) and 62 (*S. xantholiticus*) formed smooth, grey spores, and cluster 61 (*S. bellus*) produced blue spores, all in SP chains

Single-member cluster 63 (*S. albosporus*) of the red series of category IV of Williams *et al.* (1989) also produced smooth spores in SP chains.

Cluster 64 ('*S. longissimus*') contained three strains not included in the study of Williams *et al.* (1983a). The cluster contained strains possibly not belonging to the genus *Streptomyces*, with '*S. mediterranei*' now classified into the genus *Nocardia* as *N. mediterranei*, and '*S. longissimus*' listed as *species incertae sedis* in Bergey's *Manual of Determinative Bacteriology*, 8th edn (Pridham & Tresner, 1974b).

Cluster 66 (*S. flocculus*) was composed of strains morphologically similar to those grouped into clusters 30, 31 and 32, but physiologically different (see Table 3).

Single-member cluster 67 (*Nocardia* sp.) contained a strain morphologically and chemotaxonomically different from *Streptomyces*. It could be assigned to the genus *Nocardia* on the basis of chemotaxonomic analyses (unpublished results).

Cluster 68 (*S. sulphureus*) was composed of two strains producing smooth, yellow spores in SP chains.

Single-member cluster 70 contained a strain of *S. fradiae* physiologically different from those found in subcluster 22-5 and cluster 27 (Tables 2 and 3). Strain *S. poonensis* ISP 5596 formed single-member cluster 71. This strain shared many properties with those found in cluster 49 (*S. roseiscleroticus*). Single-member cluster 72 contained a strain not assigned to a species and single-member cluster 73 comprised a strain of *S. olivaceus* which was physiologically different from those found in subclusters 1-2 and 1-4 (Table 2). Single-member cluster 74 was comprised of *S. erythrorhizus*, which is currently classified in the red series of category IV (Williams *et al.*, 1989). Single-member cluster 75 (*S. bambergiensis*) contained a strain producing green spores with a hairy surface in RA chains, also recovered as a single-member cluster in the study of Williams *et al.* (1983a).

Single-member cluster 77 (*S. ipomoeae*) comprised a strain currently classified within the blue series of category IV (Williams *et al.*, 1989). Clusters 78 to 87 contained small numbers of strains or were single-member clusters, in several cases named after recognized species or clusters, but different in their physiological properties (Tables 2, 3 and 4) and thus forming separate phenotypes (see Table 1).

Table 3. Distribution of positive characters for minor subclusters and clusters defined at the 81.5% and 84.0% similarity levels (S_{SM})

Values are the number of strains with positive character states.

Character	Cluster no. . . .	No. of strains . . .	<i>S. gelatus</i>	<i>S. parvus</i>	<i>Streptomyces</i> sp.	<i>S. sparsogenes</i>	<i>S. psammoticus</i>	<i>S. aurantiacus</i>	<i>Streptomyces</i> sp.	<i>S. griseoalbus</i>	<i>S. thermovulgaris</i>	<i>S. roseoviridis</i>	<i>S. griseolus</i>	<i>S. fungicidicus</i>	<i>S. flavidotrens</i>	<i>S. fradiae</i>	<i>S. prasinus</i>	<i>S. cacaoi</i>	<i>S. rimosus</i>	<i>S. endus</i>	<i>Streptomyces</i> sp.	<i>S. roseiscleroticus</i>	<i>S. violatus</i>	<i>S. violaceusniger</i>	<i>S. violaceusniger</i>	<i>S. violaceusniger</i>	<i>S. hygroscopicus</i>	<i>S. hygroscopicus</i>	<i>S. longissimus</i>	<i>Streptomyces</i> sp.	<i>S. flocculus</i>	<i>S. sulphureus</i>	<i>S. fragilis</i>	<i>S. lipmanii</i>	<i>Streptomyces</i> sp.	<i>Streptomyces</i> sp.
<i>Carbon source used for growth:</i>																																				
Carbohydrates and sugar derivatives																																				
<i>N</i> -Acetyl-D-galactosamine																																				
<i>N</i> -Acetyl-D-glucosamine																																				
Amygdalin																																				
D-Arabinose																																				
L-Arabinose																																				
Arabonic acid																																				
<i>p</i> -Arbutin																																				
D-Cellobiose																																				
Dextran																																				
D-Fructose																																				
D-Fucose																																				
L-Fucose																																				
D-Galactose																																				
α -D-Galacturonate																																				
D-Glucarate																																				
Gluconate																																				
D-Glucosamine																																				
D-Glucosaminic acid																																				
D-Glucose																																				
D-Glucuronate																																				
Glycogen																																				
Glycyrrhizinic acid																																				
Inulin																																				
Lactose																																				
Lactulose																																				
D-Lyxose																																				
L-Lyxose																																				
D-Maltose																																				
D-Mannose																																				
L-Mannose																																				
D-Mannoheptulose																																				
α -D-Melezitose																																				
α -D-Melibiose																																				
Methyl α -D-glucopyranoside																																				
Methyl α -D-mannoside																																				
Methyl β -D-xyloside																																				
Mucate																																				
5-Oxogluconate																																				
α -D-Raffinose																																				
L-Rhamnose																																				

Overlap of clusters

Only statistically insignificant or no overlaps with other major clusters and subclusters were found for the S_{SM} subclusters 1-1 (*S. albidoflavus*, Williams group A1A), 1-2 (*S. halstedii*, Williams group A1C) and 1-3 (*S. griseus*, Williams group A1B), cluster 2 (*S. exfoliatus*, Williams groups A5 and A6), cluster 9 (*S. violaceus*, Williams groups A18 and A19), subcluster 22-5 (*S. fradiae*), and cluster 30 (*S. albus*). Cluster 33 (*S. albobiflavus*) overlapped significantly with cluster 35 (*S. rimosus*). Subcluster 22-1 (*Sv. griseocarneum*) overlapped with subcluster 22-3 (*S. lavendulae*) with an index of overlap $V_G > 10\%$. Subcluster 22-4 (*S. misakiensis*) also showed overlap with subcluster 22-3 (*S. lavendulae*) with V_G just over 9%.

Most of the overlaps were found between major clusters and adjacent minor clusters, with V_G values ranging between 9% and 22%. The major cluster 9 (*S. violaceus*) showed overlap with clusters 11 (*S. psammoticus*), 12 (*S. aurantiacus*) and 13 (*S. niveroruber*), with V_G values of 9%, 16% and 18%, respectively. All minor clusters 51, 53, 54, 55 and 57, containing strains of *S. violaceusniger* and *S. hygroscopicus*, showed overlaps with one another. Cluster 30 (*S. albus*) overlapped with cluster 31 (*S. cacaoi*), with a V_G exceeding 25%. Similarly, there was an extensive overlap between cluster 35 (*S. rimosus*) and cluster 36, which also contained two strains of *S. rimosus*.

Clustering of strains using the UPGMA algorithm with the S_J coefficient

The study using S_J coefficient considered only positive matches and therefore revealed a changed phenogram with reduced similarity levels at which the phenons were recognized. The cophenetic correlation coefficient r_{cs} as a measure of correlation between corresponding pairs from the similarity matrix and the cophenetic matrix was 0.6929.

Taking a similarity level of 59.6% (S_J), a total of 78 clusters was defined.

S_{SM} cluster 1 was further subdivided into 35 subclusters at a similarity level of 64.6% (S_J). The assignment to different clusters and differences from the UPGMA/ S_{SM} analysis are given in Table 1 and the rearrangements are described in comparison with the S_{SM} clusters in detail below. All of the major and most of the minor clusters were recognized, with some changes in the cluster composition.

S_{SM} subclusters 1-1 (*S. albidoflavus*) and 1-2 (*S. halstedii*) were each recovered in their entirety in the UPGMA/ S_J analysis, as S_J subclusters 1-1 and S_J cluster 15, respectively. The 81 strains grouped within S_{SM}

subcluster 1-3 (*S. griseus*) fell into S_J subclusters 1-2 (70 strains) and 1-20 (three strains), and S_J clusters 4 (one strain), 8 (two strains), 10 (three strains), 30 (one strain) and 47 (one strain). The corresponding S_J cluster 1-2 contained the two further strains *S. rubiginosohelvolus* ISP 5176 and *S. baarnensis* ISP 5232, both found in S_{SM} cluster 6 (*S. rochei*). All six strains of S_{SM} subcluster 1-4 (*S. olivaceus*) were found in the corresponding S_J subcluster (1-4), in addition to strain *S. viridogenes* ISP 5454, which was grouped into S_{SM} cluster 6 (*S. rochei*). Strains found in subcluster 1-5 (*S. antibioticus*) of the UPGMA/ S_{SM} analysis formed S_J cluster 11 (four strains) and were further found in S_J subclusters 1-16 (three strains) and S_J clusters 9 (11 strains) and 59 (*S. recifensis* ISP 5115), which became a single-member cluster. S_{SM} subcluster 1-6 (*S. flaveolus*) was split into S_J subclusters 1-10, 1-12 (single-member cluster '*S. umbrosus*' ISP 5242), 1-13 (single-member cluster *S. flaveolus* ISP 5061^T), 1-14, 1-15, 1-16 and 1-31 (single-member cluster *S. alboniger* ISP 5043). Strains of S_{SM} subcluster 1-7 (*S. diastatochromogenes*) were found in S_J subclusters 1-14, 1-15, 1-19 and 1-21. Thus all strains of S_J subcluster 1-14 and the majority of strains from S_J subcluster 1-15 were grouped into S_{SM} subclusters 1-6 and 1-7. S_{SM} single-member cluster 1-8 (*Sv. luteoreticuli* ISP 5509) remained as single-member cluster 1-17 in the UPGMA/ S_J analysis.

All strains of S_{SM} cluster 2 (*S. exfoliatus*) were grouped into S_J subcluster 1-7 with the exception of *S. cinereoruber* ISP 5012, which formed S_J single-member cluster 38. The S_J subcluster 1-7 contained a further two strains grouped into S_{SM} subcluster 22-4 (*S. misakiensis*). S_{SM} cluster 3 (*S. gelaticus*) remained intact as S_J subcluster 1-3. Four strains of S_{SM} cluster 4 (*S. graminofaciens*) were found in S_J subcluster 1-23. This subcluster contained five strains; the fifth strain belonged to S_{SM} cluster 25. The two remaining strains of S_{SM} cluster 4 formed S_J cluster 6. S_J cluster 10 was composed of 11 strains, one from S_{SM} cluster 5 (*S. parvus*) and two from S_{SM} subcluster 1-3 (*S. griseus*); the remaining strains were found in S_{SM} cluster 6. S_{SM} cluster 6 (*S. rochei*) was split into S_J subclusters 1-18 (61 strains), 1-10 (seven strains), S_J single-member clusters 1-11 (*S. nodosus* ISP 5109), 1-4 and 1-2, and S_J cluster 10 (six strains). The remaining strain from S_J subcluster 1-18 was grouped into S_{SM} cluster 13 (*S. niveoruber*); the remaining strain from S_J subcluster 1-10 fell into S_{SM} subcluster 1-6 (*S. flaveolus*).

S_{SM} cluster 7 (*S. prasinopilosus*) was recovered as cluster 3 in the UPGMA/ S_J analysis. Cluster 8 (*Streptomyces* sp.) contained one strain which fell into S_J cluster 20 and three strains which fell into S_J cluster 19. The remaining strains forming S_J cluster 20 (five strains) were found in S_{SM} cluster 9 (*S. violaceus*). S_{SM} cluster 9

Table 4 (continued)

Character	Single-member cluster number . . .	1-8	15	16	18	19	29	32	34	37	38	39	40	42	43	45	46	47
Polyalcohols and glycols																		
Adonitol		0	1	1	0	0	0	1	1	0	1	0	1	0	1	1	1	0
D-Arabitol		1	1	1	0	0	1	1	1	1	0	1	1	1	1	1	1	1
L-Arabitol		0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Dulcitol		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
m-Erythritol		0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0
Glycerol		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
i-Inositol		1	1	1	1	0	1	1	1	0	0	1	0	1	1	1	1	0
Maltitol		0	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0
D-Mannitol		1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Tributyrin		0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
D-Xylitol		0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1
Fatty acids																		
Acetate		0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Butyrate		0	1	1	1	1	1	1	0	1	1	0	1	0	1	0	1	1
Caprate		0	1	1	1	1	0	1	1	1	1	0	0	0	0	0	1	1
Heptanoate		0	1	1	0	0	0	1	0	1	0	1	0	1	0	0	0	0
Isobutyrate		1	0	1	1	0	0	1	1	1	1	1	0	1	0	1	1	1
Isovalerate		1	1	1	1	0	0	1	1	1	1	1	0	1	0	1	1	1
Propionate		1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
Sorbinic acid		1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Miscellaneous organic acids																		
cis-Aconitate		1	1	1	1	0	1	0	1	1	1	1	0	1	1	1	1	1
trans-Aconitate		0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1
Adipate		0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Azelate		1	0	1	1	1	1	0	1	0	1	1	0	0	0	1	1	1
Citraconate		0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Citrate		0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Fumarate		0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Glutarate		0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0
Glycerate		0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
Glycerophosphate		0	1	1	0	0	1	1	1	1	0	0	0	1	1	1	1	0
Glycolate		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glyoxylate		0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0
DL-3-Hydroxybutyrate		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4-Hydroxybutyrate		0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
DL-2-Hydroxyisobutyrate		0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
L-2-Hydroxyisocaproate		0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1
DL-2-Hydroxyisovalerate		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
2-Hydroxyvalerate		0	0	0	1	1	1	1	1	0	1	0	1	0	0	0	1	1
DL-Isocitrate		0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1
Itaconate		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D-Lactate		0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	1
DL-Lactate		1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	0	1
L-Lactate		0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
Laevulinat		1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
DL-Malate		0	1	0	1	1	1	0	1	1	1	1	1	0	0	1	1	1
L-Malate		0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0
Maleate		0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	1	1
Malonate		0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1
Mesaconate		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesoxalate		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxalacetate		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2-Oxoglutarate		1	1	1	0	1	0	1	0	0	1	1	1	1	0	1	1	1
2-Oxoisocaproate		0	0	0	1	1	0	0	1	1	1	1	1	1	0	1	1	1
Pimelate		0	0	0	1	1	0	0	1	0	0	0	1	1	0	1	0	1
Pyruvate		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Suberate		0	1	1	1	1	1	0	1	0	1	1	0	1	0	1	1	1
Succinate		0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1
D-Tartrate		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
m-Tartrate		0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0
L-Tartrate		0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1
Tartronate		0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Alcohols																		
1-Butanol		0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0
2-Butanol		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0

Table 4 (continued)

[illegible]

Table 4 (continued)

Character	Single-member cluster number . . .	1-8	15	16	18	19	29	32	34	37	38	39	40	42	43	45	46	47
L-Tryptophan		1	1	1	1	1	1	0	1	0	0	0	0	1	1	1	1	0
L-Valine		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Amines																		
Butylamine		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cadaverine		1	0	1	1	0	1	0	1	0	0	1	0	0	0	0	1	0
Carnitine		0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Creatine		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Creatinine		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ethanolamine		1	1	1	1	1	1	0	1	1	0	0	1	0	1	1	1	1
Ethylamine		0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Urea		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Hexylamine		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Putrescine		1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Spermidine		1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1
Spermine		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Taurine		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonelline		0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Tryptamine		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tyramine		1	1	1	1	1	0	0	0	0	0	1	0	0	0	1	1	0
Miscellaneous nitrogenous compounds																		
Acetamide		0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Allantoin		0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0
Cytosine		0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Glycinamide		0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0
Hippurate		0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Indole-3-acetate		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L-Leucinamide		0	1	0	0	1	0	1	1	0	1	1	1	0	0	1	1	1
Oxamic acid		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salicylamide		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thiamin		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Uracil		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Ureidosuccinate		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L-Valinamide		1	1	1	1	1	1	0	1	1	0	0	1	0	0	0	1	1
Aromatic compounds																		
Anthranilate		0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0
3-Aminobenzoate		0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
4-Aminobenzoate		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Benzoate		0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
Furan-2-carboxylic acid		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3-Hydroxybenzoate		0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
4-Hydroxybenzoate		0	0	1	0	0	1	0	0	1	1	0	0	1	1	1	0	1
2-Hydroxyphenylacetate		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
3-Hydroxyphenylacetate		0	0	0	0	1	0	0	1	1	0	0	0	0	1	1	0	0
4-Hydroxyphenylacetate		1	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0
Isophthalate		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D-Mandelate		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L-Mandelate		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phenoxyacetate		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phenylacetate		1	1	0	1	0	0	1	1	1	0	1	1	1	1	1	1	1
Phenyllactate		1	0	1	1	1	1	0	1	0	1	0	0	1	1	0	1	1
Phenylpropionate		0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0
Phenylpyruvate		0	0	0	0	1	1	0	1	1	0	1	1	1	1	1	0	0
Phthalate		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocatechuate		0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0
Quinate		0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0	1
Salicylate		0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0
Tropate		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Vanillate		0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Growth with:																		
Glucose + 1% NaCl		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Glucose + 2% NaCl		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Glucose + 5% NaCl		0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Glucose + 7% NaCl		0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Glucose + 10% NaCl		0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1
Glucose + 0.005% NaN ₃		1	1	1	0	1	1	0	1	1	1	1	0	0	0	1	0	1
Glucose + 0.01% NaN ₃		1	1	1	0	1	1	0	1	1	1	1	0	0	0	1	0	1
Glucose + 0.02% NaN ₃		1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0

Table 4 (continued)

[illegible]

Table 4 (continued)

Character	Single-member cluster number . . .	1-8	15	16	18	19	29	32	34	37	38	39	40	42	43	45	46	47
L-Lyxose		0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
D-Maltose		0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
D-Mannose		0	0	0	0	0	1	0	1	1	0	0	0	0	1	1	0	1
α -D-Melezitose		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
α -D-Melibiose		0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	1
Methyl α -D-glucopyranoside		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Methyl α -D-mannoside		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Methyl β -D-xyloside		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mucate		0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
α -D-Raffinose		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L-Rhamnose		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D-Ribose		0	1	1	0	0	1	1	1	0	0	0	0	1	0	1	0	0
D-Sucrose		0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Salicin		0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
L-Sorbose		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Starch		0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0
D-Tagatose		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D-Trehalose		0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0
D-Turanose		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D-Xylose		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
L-Xylose		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyalcohols and glycols																		
Dulcitol		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>m</i> -Erythritol		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Glycerol		0	1	1	0	0	1	1	0	1	0	0	0	1	0	1	1	1
<i>i</i> -Inositol		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maltitol		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D-Mannitol		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D-Xylitol		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tributyrin		0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0

contained a further 105 of the 125 strains grouped into S_j subcluster 1-19, and four of the eight strains from S_j subcluster 1-9. One additional strain from S_j subcluster 1-19 was found in S_{SM} cluster 10 (*S. sparsogenes*), which also contained a strain of S_j subcluster 1-29; the remaining strains of S_j subcluster 1-19 were found in S_{SM} clusters 12 (*S. aurantiacus*) and 13 (*S. niveoruber*) and the single-member clusters 15, 16 and 46. Cluster 11 of the UPGMA/ S_{SM} analysis (*S. psammoticus*) contained four of the eight strains from S_j subcluster 1-20 and one strain from S_j subcluster 1-21; further strains of S_j subcluster 1-20 were found in S_{SM} cluster 20 (one strain) and, as mentioned above, in S_j subcluster 1-2 (three strains). The remaining strain of S_j subcluster 1-21 (*S. ghanaensis* DSM 40746) was grouped into S_{SM} subcluster 1-7 (*S. diastatochromogenes*). S_{SM} clusters 14 (*Streptomyces* sp.) and 17 (*S. griseoalbus*) were recovered as S_j clusters 21 and 7, respectively. The two S_{SM} single-member clusters 18 (*S. griseoruber*) and 19 (*S. cyaneogriseus*) were joined to form S_j cluster 23. Four strains of S_{SM} cluster 20 (*S. chrysomallus*) formed S_j cluster 32; one of the remaining two strains was grouped into S_j subcluster 1-8, which contained the remaining 10 strains of the S_{SM} subcluster

22-3 (*S. lavendulae*), the other was assigned to S_j subcluster 1-20. The three thermophilic *Streptomyces* strains assigned to S_{SM} cluster 21 (*S. thermovulgaris*) were grouped into S_j cluster 2, which also contained the two strains of cluster 68 (*S. sulphureus*). The remaining two strains of S_{SM} cluster 21 were found in S_j subcluster 1-5, which contained two additional strains, from S_{SM} subclusters 22-3 (*S. lavendulae*) and 22-5 (*S. fradiae*), respectively.

The subclusters of S_{SM} cluster 22 (*Streptoverticillium* sp./*S. lavendulae*/*S. fradiae*) were largely recovered as clusters in the UPGMA/ S_j analysis. Subcluster 22-1 (*St. griseocarneum*) was found in its entirety as S_j cluster 40. Four strains of subcluster 22-2 (*S. roseoviridis*) formed S_j cluster 37; one further strain was grouped into S_j subcluster 1-15, which contained 18 strains, 15 of which were found in S_{SM} subcluster 1-7 (*S. diastatochromogenes*). The remaining two strains of S_j subcluster 1-15 were found in S_{SM} subcluster 1-6 (*S. flaveolus*) and in cluster 25 (*S. lydicus*). Strains of S_{SM} subcluster 22-3 (*S. lavendulae*) were grouped into S_j subclusters 1-5, 1-7, 1-9 (one strain) and 1-8 (nine strains) and into S_j clusters 42 (27 strains) and 43 (three strains). The S_j cluster 42

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Table 5. Comparison of clusters and subcultures of the UPGMA/ S_{SM} analysis with corresponding phenotypes of the study of Williams et al. (1983a)

Cluster/ subcluster no(s).	Phenon	Corresponding cluster(s) of Williams <i>et al.</i> (1983 <i>a</i>)	No. of strains used in both studies	No. of strains found in corresponding phena	Agreement (%)
1-1	<i>S. albidoflavus</i>	A1A	15	15	100.0
1-2	<i>S. halstedii</i>	A1C	9	5	55.5
1-3	<i>S. griseus</i>	A1B	29	23	79.3
2	<i>S. exfoliatus</i>	A5 + A6	15 + 9	12 + 3	62.5
6	<i>S. rochei</i>	A12 + A21	22 + 9	18 + 7	80.6
9	<i>S. violaceus</i>	A18 + A19 + A20	36 + 14 + 4	28 + 8 + 4	74.1
22-3	<i>S. lavendulae</i>	F61 + F62	12 + 3	11 + 3	93.3
22-5	<i>S. fradiae</i>	G68	2	2	100.0
25	<i>S. lydicus</i>	A29	11	7	63.6
30, 31, 32	<i>S. albus</i>	A16	6	5	83.3
33	<i>S. alboflavus</i>	E54	3	3	100.0
35, 36	<i>S. rimosus</i>	B42	6	4	66.7
51, 53-57	<i>S. violaceusniger</i>	A32	5	2	40.0
69	<i>S. ochraceiscleroticus</i>	A40	5	4	80.0
Total			215	164	76.3

contained 27 strains, almost exclusively found in clusters F61 and F62 of Williams *et al.* (1983a). A further 11 strains of S_J cluster 43 were grouped into S_{SM} subcluster 22-4 (*S. misakiensis*), which contained one strain of S_J subcluster 1-6, and S_J clusters 35 and 62 (single-member

cluster '*S. pyridomyceticus*' ISP 5024), and two strains of *S_J* subcluster 1-7. With the exception of two strains, one of them forming *S_J* single-member cluster 38 (*S. clavuligerus* DSM 40751), subcluster 22-5 (*S. fradiae*) was recovered as *S_J* cluster 39.

The two strains of S_{SM} cluster 23 (*S. griseolus*) and strain *S. roseochromogenes* ISP 5463 (S_{SM} subcluster 1-3) formed S_J cluster 4. S_{SM} cluster 24 (*S. fungicidicus*) was split into the S_J clusters 56 and 57 (single-member cluster). The remaining strain was grouped into S_J cluster 5, containing 13 strains, 12 of which were found in S_{SM} cluster 25 (*S. lydicus*). This cluster contained a further three strains from S_J subcluster 1-9 and one strain each from S_J subclusters 1-15 and 1-23. S_{SM} cluster 26 (*S. flavidovirens*) was split into S_J single-member cluster 33 and S_J cluster 27, which contained one further strain (S_{SM} single-member cluster 32, *S. albus* ISP 5313^T). S_{SM} cluster 27 (*S. fradiae*) was recovered as S_J cluster 31; S_{SM} cluster 28 (*S. prasinus*) contained the two remaining strains of S_J cluster 9 not grouped into S_{SM} subcluster 1-5 (*S. antibioticus*). S_{SM} clusters 30 (*S. albus*) and 31 (*S. cacaoi*) were joined as S_J subcluster 1-34 with the exception of *S. antibioticus* DSM 41568, which formed S_J single-member cluster 46. The S_{SM} clusters 33 (*S. alboflavus*), 34 (*S. fulvissimus*) and 35 (*S. rimosus*) were joined to form S_J subcluster 1-33, with the exception of two strains which formed S_J cluster 41. S_{SM} clusters 36 (*S. rimosus*) and 49 (*S. roseiscleroticus*) were recovered as S_J clusters 45 and 22, respectively. The two strains of S_{SM} cluster 41 (*S. endus*) were recovered as S_J cluster 12, which contained in addition the strain forming S_{SM} single-member cluster 85. S_{SM} clusters 44 (*Streptomyces* sp.) and single-member cluster 45 were joined in S_J subcluster 1-24. The two strains of S_{SM} cluster 50 (*S. violatus*) were grouped into S_J cluster 19, which contained further strains found in S_{SM} clusters 8, 9 and 12. S_{SM} clusters 51, 53, 54 and 55, all containing strains of *S. violaceusniger*, *S. hygroscopicus* and related organisms, were joined in S_J cluster 18, with the exception of one strain classified within the genus *Nocardia* ('*N. capreola*'), which was grouped into S_J subcluster 1-30 together with the three strains of S_{SM} cluster 64 (*S. longissimus*). S_{SM} cluster 57 (*S. hygroscopicus*) was split into S_J single-member clusters 52 and 53. The two strains of S_{SM} cluster 65 (*Streptomyces* sp.) were clustered into S_J subcluster 1-29 together with one strain from S_{SM} cluster 10. S_{SM} clusters 66 (*S. flocculus*) and 67 (*Nocardia* sp.) were joined into S_J cluster 34. S_{SM} cluster 68 (*S. sulphureus*) was grouped with three thermophilic strains from S_{SM} cluster 21 into S_J cluster 2.

S_{SM} cluster 69 (*S. ochraceiscleroticus*) and the single-member clusters 70, 72 and 73 were joined into S_J subcluster 1-26. S_{SM} single-member cluster 71 (*S. poonensis*) fell within the large S_J subcluster 1-19. S_{SM} cluster 76 (*Streptomyces* sp./*Nocardia* sp.) was divided into the S_J clusters 69 (four strains), 71 (two strains), and the two single-member clusters 72 and 73. The S_{SM} clusters 78 (*S. fragilis*), 79 (*S. lipmanii*), 80 (*Streptomyces* sp.) and 82 (*Streptomyces* sp.) were split into S_J single-member clusters (Table 1).

The following single-member clusters of the UPGMA/ S_{SM} analysis were recovered also as S_J single-member clusters: 29, 37-40, 42, 43, 47, 48, 52, 56, 58-63, 74, 75, 77, 81, 83, 84, 86 and 87 (Table 1).

Discussion

The numerical taxonomic study of Williams *et al.* (1983a) was the guiding survey for a taxonomic framework of the genus *Streptomyces*. As pointed out by these authors, the phena defined by numerical taxonomic studies are polythetic: no single character is indispensable or sufficient for group membership (Williams *et al.*, 1983a). Numerical taxonomic studies are thus in sharp contrast to traditional concepts in streptomycete taxonomy, which used a few subjectively chosen characters for the recognition of taxa (Gause *et al.*, 1957; Pridham *et al.*, 1958; Hütter, 1967; Pridham & Tresner, 1974a, b; Pridham, 1976).

Possible problems in numerical taxonomic studies can be minimized by the choice of suitable tests and statistics (Sneath & Johnson, 1972; Austin & Colwell, 1977; O'Brien & Colwell, 1987). It is necessary that all the tests can be employed for all strains, that test reproducibility is high and that the majority of phena show a low overlap with other phena (Sneath, 1974, 1979). Additionally, the results of numerical taxonomic studies should be compared to other numerical surveys and to classifications based on chemical, genetical and serological data (Goodfellow, 1986).

In the present study, test reproducibility was assessed using the methods of Sneath & Johnson (1972). Overall test error was low ($p = 3.11\%$) and comparable to other studies ($p = 3.12\%$, Holmberg & Nord, 1975; $p = 1.6\%$, Schofield & Schaal, 1981; $p = 3.7\%$, Goodfellow & Alderson, 1977; $p = 2.1\%$, Goodfellow & Pirouz, 1982; $p = 3.36\%$, Williams *et al.*, 1983a). Acid production from a range of sugars gave scores for the probability of erroneous results ($p = 7.09\%$). These tests were also difficult to read photometrically. A comparison of test results obtained visually and photometrically gave discrepancies of 7.45% for all results; however, test results of sugar fermentations showed high inconsistencies of 20.5%. Often the growth of the streptomycetes resulted in the production of cell agglomerates, thus preventing a homogeneous turbidity in the test wells of the microplates and requiring that all test results be checked visually. The 20 strains chosen for the reproducibility studies (Table 1) showed marked differences in their growth characteristics, so we did not exclude tests beforehand on the basis of the triplicate results of these strains, because the extent of variation due to the high variability within the genus could not be estimated.

Sneath & Johnson (1972) recommended that tests with more than 10–15% error should be rejected. In our study, these values were only observed for a few sugar acidification tests. As already mentioned, inconsistencies and instabilities in tests for all strains were noted, and only those tests showing a high degree of stability for all strains were chosen for identification purposes (Kämpfer & Kroppenstedt, 1991). The assessment of cluster overlap revealed some overlap between the phena, confirming earlier numerical taxonomic studies (Gyllenberg, 1970; Gyllenberg *et al.*, 1967; Paszkiewicz, 1972). The overlap of clusters can be explained by the high number of test organisms, the high number of tests, and the physiological heterogeneity of strains within the genus *Streptomyces*. In the study of Williams *et al.* (1983a), only slight overlap was found between the phena. As pointed out by these authors, the overlap may reflect inadequacies in some of the tests in the analysis. The overlap of clusters 30 and 31 containing *S. albus* and related strains, 35 and 36 containing *S. rimosus* strains, and 51, 53 to 57 with *S. violaceusniger* and related organisms may indicate that these clusters represent one cluster. This is supported by the UPGMA/ S_j analysis.

Well-defined clusters showed only low or no overlap with other phena, thus confirming in part the results of Williams *et al.* (1983a). The majority of overlaps were found in pairs of clusters containing only a few strains and in those which could not be recovered in the UPGMA/ S_j analysis. As pointed out by Williams *et al.* (1983a), it would be unrealistic to demand very low values given the present state of streptomycete taxonomy.

The result of numerical phenetic studies have to be interpreted carefully and the results of different statistics have to be considered, including the use of different similarity coefficients and calculations of overlaps between the phena to determine the content and quality of the classifications.

The choice of the similarity coefficient has a marked influence on cluster composition. The Jaccard coefficient (S_j) considers exclusively positive matches. Therefore, the composition of clusters created with this coefficient depends on the number of positive test results for the strains. Isolates which show a majority of negative test results can be grouped into a single cluster using the simple-matching coefficient, S_{SM} whereas this grouping can be considerably changed using the Jaccard coefficient. The delineation of clusters and subclusters at the 81.5% (S_{SM}) and the 84.0% (S_{SM}) S-levels is arbitrary, but was chosen because several clusters of the study of Williams *et al.* (1983a) could be recovered, in addition to the agreement of groups defined by other studies (Korn *et al.*, 1978; Mordarski *et al.*, 1986; Ridell *et al.*, 1986).

Although it is the standard practice in numerical

phenetics to use a single cut-off point in each analysis, it is obvious that in the UPGMA/ S_M analysis some closely related strains were assigned to different clusters (clusters 30, 31 and 32, *S. albus* and related strains; clusters 35 and 36, *S. rimosus*; clusters 51 and 53 to 57, *S. violaceusniger* and *S. hygroscopicus*). A delineation in a staggered line, as used by Priest *et al.* (1988) in their UPGMA/ S_j analysis of *Bacillus* species, is probably a better way to define phena in numerical surveys with large numbers of strains and tests.

The number of tests employed in our study is unusually high. Although an upper limit of 200 characters has been recommended (O'Brien & Colwell, 1987) this is not stringent, and an argument in favour of using large numbers of tests is that the effects of plasmid-borne traits will be relatively small (Harwood, 1980). There is no universal criterion of the goodness of a classification (Sneath & Sokal, 1973), but in numerical phenetics a classification is considered to be optimal if it represents as closely as possible the original similarity matrix among the OTUs. This can be estimated by the calculation of cophenetic correlations (Sneath & Sokal, 1973). In our study, values for cophenetic correlation coefficients of 0.6929 and 0.8239 were found for the UPGMA/ S_j and UPGMA/ S_{SM} classifications, respectively. It has generally been found that r_{cs} values vary from 0.6 to 0.95 (Sneath & Sokal, 1973).

As pointed out by Williams *et al.* (1989), streptomycete taxonomy should be improved by the application of statistical methods for the significance and integrity of groups and their application to all validly published species. Furthermore, the correlation between numerical phenetic, chemotaxonomic and molecular genetic data has to be assessed. Chemotaxonomic methods have to be improved for the analysis of quantitative data (O'Donnell, 1988; Williams *et al.*, 1989).

Cluster-groups as defined by Williams *et al.* (1983a) in their UPGMA/ S_{SM} analysis could not be detected in our analysis, although some parallels to some of these groups were observed. Taking a similarity level of 79.5% (S_{SM}), it can be seen from Fig. 1 that the clusters 1 to 17 fell within a cluster-group containing the majority of strains (223 to 280 inclusive) assigned to cluster group A of Williams *et al.* (1983a). The clusters 33 to 36, joined at the 79.5% (S_{SM}) similarity level of our analysis, representing *S. alboflavus*, *S. rimosus* and related organisms, shared many features with cluster group B of Williams *et al.* (1983a), which consisted of the major cluster *S. rimosus* and the single-member cluster *S. amakusaensis*. Similar groupings to cluster groups C, D, and E of Williams *et al.* (1983a) could not be detected in our numerical survey. Clusters 22 to 26 contained most of the strains grouped within cluster groups F and G of Williams *et al.* (1983a). Only a few strains of cluster

groups H, I, and J of Williams *et al.* (1983a) were included in our study. These strains formed single-member clusters 19 and 87, or fell within subclusters 22-1, 22-3 and 22-4, and clusters 4 and 51. The cluster-groups of Williams *et al.* (1983a) could not be recovered in their UPGMA/ S_j analysis, and were not found in our UPGMA/ S_j analysis.

There seems to be no reason to doubt the species status of the S_{SM} subcluster 1-1 (*S. albidoflavus*, Williams group A1A), subcluster 1-2 (*S. halstedii*, Williams group A1C) and subcluster 1-3 (*S. griseus*, Williams group A1B). These groups were also found in earlier studies (Kutzner *et al.*, 1978; Kurylowicz *et al.*, 1970, 1975). Studies of DNA-DNA homology have confirmed the species status of these subclusters: the Williams clusters A1A, A1B and A1C were recovered, with some changes, in the studies of Mordarski *et al.* (1986). The strains *S. albidus* ISP 5320 and *S. alboniger* ISP 5043 were not assigned to the Williams group 1A (subcluster 1-1 of the present investigation), but were found in subcluster 1-3 and subcluster 1-7, respectively. *S. olivaceus* ISP 5072 was recovered as single-member cluster 42 and was not included in subcluster 1-4, which contained four strains of *S. olivaceus*. This subcluster overlapped with subcluster 1-2 (*S. halstedii*) at a V_G level of 16%, thus showing the strong relationship suggested by Williams *et al.* (1983a). Mordarski *et al.* (1986) could not assign *S. olivaceus* ISP 5072 to the expected DNA-homology group. The DNA homology results of Mordarski *et al.* (1986), who assigned *S. coelicolor*, *S. albidoflavus*, *S. albidus*, *S. alboniger*, *S. canescens*, '*S. citreus*', *S. fellus*, *S. limosus*, *S. rutgersensis* and *S. sampsonii* to one taxon, and *S. alboviridis*, '*S. cratifer*' and '*S. oligocarbophilus*' to another genospecies, are strongly supported by our phenetic data. The *S. coelicolor* group of Korn *et al.* (1978), containing 28 strains, was found in subcluster 1-1 (*S. albidoflavus*) with the exception of the one strain *S. coelicolor* DSM 40674, which formed the single-member cluster 86.

Of the 30 strains of the *S. griseus* group investigated by Korn *et al.* (1978), 24 were recovered in subcluster 1-3 (*S. griseus*) of the present study, two strains in subcluster 22-3 (*S. chryseus* DSM 40420 and *S. vinaceus* DSM 40515) and one in each of subcluster 1-1 (*S. badius* DSM 40138), cluster 6 (*S. baarnensis* DSM 40232) and single-member cluster 47 (*S. anulatus* DSM 40361). Many strains of subcluster 1-2 (*S. griseus*) have been shown to comprise a distinct DNA homology group (Okanishi *et al.*, 1972) and the results are in line with the earlier studies of Hütter (1967) and Gyllenberg (1970).

Subclusters 1-5 (*S. antibioticus*), 1-6 (*S. flaveolus*) and 1-7 (*S. diastatochromogenes*) have no corresponding phenon in the study of Williams *et al.* (1983a). Strains grouped into the heterogeneous cluster A31 (*S. antibioticus*) of

Williams *et al.* (1983a) were found in all three subclusters, which overlapped with each other at V_G levels of 10 to 13%.

The recognition of cluster 2 (*S. exfoliatus*, Williams groups A5 and A6) supports the view of Williams *et al.* (1983a), who found considerable overlap between their phenon A5 (*S. exfoliatus*) and A6 (*S. violaceus*), that these strains should be grouped within one species. Cluster 6 (*S. rochei*) was a large cluster containing the majority of strains of Williams groups A12 (*S. rochei*) and A21 (*S. griseoruber*) in addition to many strains of the grey series of category IV (Williams *et al.*, 1989). The *S. violaceoruber* group defined by phage typing (Korn *et al.*, 1978) was recovered in this cluster, with the exception of the type strain *S. violaceoruber* DSM 40049^T, which was shown to be physiologically different (Tables 2 to 4) and therefore grouped into cluster 69. Cluster 6 also contained '*S. lividans*', thus showing the relationship between this strain and strains of *S. violaceoruber*, and confirming group IV of the numerical survey of Kurylowicz *et al.* (1975). Cluster 7 (*S. prasinopilosus*) contained the majority of strains found in Williams group A37. This cluster was recovered in the UPGMA/ S_j analysis and all strains produced ornamented, green spores in RA or SP chains and were melanin negative. Cluster 9 (*S. violaceus*) was composed of the majority of strains from Williams groups A18 (*S. cyaneus*) and A19 (*S. diastaticus*). These clusters showed no overlap in the study of Williams *et al.* (1983a), but they overlapped with Williams cluster A40, from which one strain was also found in our cluster 9. Most of the strains found in cluster 9 produced blue, spiny spores. Strains of the *S. viridochromogenes* group studied by phage typing (Korn *et al.*, 1978) were found within cluster 9 (*S. violaceus*). Many strains of *S. chartreusis* were also found in this cluster, thus confirming the relationship between these species (Hütter, 1967). With the exception of five strains, this cluster contained all the *S. cyaneus* strains studied by Saddler *et al.* (1987) in their investigations using quantitative fatty acid data. Their grouping was not supported by our investigation. The significance of fatty acid data in defining taxa at the species level remains unresolved. Cluster 9 also contained three strains of *S. scabies* and may be the home for the majority of strains studied by Lambert & Loria (1989a, b).

The majority of strains of the genus *Streptovorticillium* were found in subcluster 22-1 of the UPGMA/ S_{SM} study. This cluster was also recovered in the UPGMA/ S_j analysis. Only three strains belonging to the genus *Streptovorticillium* are found in other clusters: *Sv. lavenduligriseum* ISP 5487 in subcluster 1-5; '*Sv. luteoreticuli*' ISP 5509 in subcluster 1-8; and *Sv. albireticuli* ISP 5051 in cluster 76. The other strains were physiologically homogeneous. The groups obtained in the study of Locci

et al. (1981) could not be recovered in the present investigation. It is widely accepted that the genera *Streptomyces* and *Streptovorticillium* are closely related. Both have cell-wall type I (Lechevalier & Lechevalier, 1970*a, b*), a high content of GC in their DNA (Pridham & Tresner, 1974*a, b*) and high similarities in DNA homology (Okanishi & Gregory, 1970; Okanishi *et al.*, 1972; Kroppenstedt *et al.*, 1981), and are lysed by the same phages (Prauser, 1976; Wellington & Williams, 1981). Additionally, they contain similar menaquinones, fatty acids and polar lipids (Collins *et al.*, 1977; Kroppenstedt & Kutzner, 1976; Lechevalier *et al.*, 1977). Immunodiffusion studies (Ridell *et al.*, 1986) further support the affinity between the two genera, especially the relationship between streptovorticillia and *Streptomyces lavendulae*. This relationship was confirmed in our study, as the subclusters 22-1 (*Sv. griseocarneum*) and 22-3 (*S. lavendulae*) were shown to be phenetically closely related as indicated by their degree of overlap. As pointed out by Kutzner (1981) and confirmed here (Table 2), the streptovorticillia utilize only a limited number of carbon sources. The only support for distinguishing between *Streptomyces* and *Streptovorticillium* has come from DNA-RNA pairing studies (Gladek *et al.*, 1985). The current recognition of *Streptovorticillium* as a separate genus is nonetheless still a practical proposition. The basis of the classification within the genus *Streptovorticillium* (Locci *et al.*, 1981) could not be confirmed in the present study.

Subcluster 22-3 (*S. lavendulae*) was heterogeneous and was split into several clusters in the UPGMA/ S_J analysis. However, strains of *S. lavendulae* and synonyms were physiologically homogeneous and were found largely in S_J cluster 42. The strong relationship of *S. lavendulae* to streptovorticillia shown by serological studies (Ridell *et al.*, 1986) was confirmed. Subcluster 22-5 (*S. fradiae*) was also found to be related to *S. lavendulae* and *Streptovorticillium* strains, thus supporting the findings of Williams *et al.* (1983*a*).

Cluster 25 (*S. lydicus*) contained seven strains of the *S. lydicus* phenon (A29) of Williams *et al.* (1983*a*). This cluster additionally contained four strains of *S. hygroscopicus*, currently regarded as a synonym of *S. violaceus-niger*. These strains were different from those strains grouped into clusters 53 to 57. It is obvious that strains designated as *S. hygroscopicus* are heterogeneous, and this is confirmed by fatty acid data (R. M. Kroppenstedt, unpublished).

Cluster 30 (*S. albus*) was a homogeneous phenon, showing high similarities to the overlapping clusters 31 and 32, which also contained strains of *S. albus* or synonyms. These results are in accordance with Korn *et al.* (1976) and Williams *et al.* (1989). Taking a similarity level of 79.5% (S_{SM}), clusters 30 to 32 formed a relatively

distinct group, separate from other *Streptomyces* species, thus confirming the isolated position of the type species of the genus, which can be further demonstrated by its temperature range, pathogenicity and fatty acid data (R. M. Kroppenstedt, unpublished).

Strains grouped within cluster 33 (*S. alboflavus*) which showed a strong relationship to those found in cluster 35 (*S. rimosus*) were grouped into subcluster 1-33 of the UPGMA/ S_J analysis. They were morphologically very similar, most of them producing a white or yellow spore mass and no melanin. Cluster 35 (*S. rimosus*) was also found by Williams *et al.* (1983*a*), in their cluster group B, distant from other streptomycetes, which was confirmed in our study.

Strains of *S. violaceus-niger* and *S. hygroscopicus* were found in the related and overlapping clusters 51 and 53 to 57, confirming the results of Williams *et al.* (1983*a*). As mentioned above, a delineation of the dendrogram in a staggered line would have clustered these strains together.

A comparison of major phenons of the UPGMA/ S_{SM} analysis with the corresponding clusters of the study of Williams *et al.* (1983*a*) is given in Table 5. Although in some cases it was difficult to define corresponding clusters, of 215 strains, 164 (76.3%) were found in comparable phenons. Predominant character states of morphological features are also in line with the study of Williams *et al.* (1983*a*) (see Table 9 of that study). The species status of the minor clusters in our analysis is difficult to evaluate, because most of them contained strains grouped into different clusters of Williams *et al.* (1983*a*). Their taxonomic position will require confirmation by genetical, improved chemotaxonomic and serological data.

With respect to morphological criteria, our study supports the view of Williams *et al.* (1983*a*) that these traditional criteria, which are often difficult to determine (Gottlieb & Shirling, 1967; Williams & Wellington, 1980; Kutzner, 1981), are inadequate for classification. Although streptomycetes producing a blue spore mass were largely grouped together (cluster 9, *S. violaceus*), *Streptomyces* species producing a green, red or violet spore mass were found in different clusters, thus confirming the studies of Kurylowicz *et al.* (1975) and Williams *et al.* (1983*a*). The classification of 'species' currently classified within category IV of Williams *et al.* (1989) is improved by allocation of most of these strains to major clusters of the UPGMA/ S_{SM} analysis. Physiological characters are therefore indispensable for classification and identification of *Streptomyces*. Carbon source utilization tests were often used in earlier taxonomic studies. The utilization of carbohydrates such as sucrose, L-arabinose, *D*-inositol, mannitol, rhamnose and raffinose was recommended as an aid in species differentiation in

the International Streptomyces Project (Shirling & Gottlieb, 1966; 1968*a, b*, 1969, 1972) and these tests are included in species descriptions in *Bergey's Manual of Determinative Bacteriology*, 8th edn (Pridham & Tresner, 1974*b*). The differentiation potential of these tests, especially the utilization of different polyalcohols, can be readily seen from Tables 2 to 4. The use of qualitative enzyme tests for differentiation of streptomycetes has been recently applied to 88 strains belonging to different species-groups of *Streptomyces* (Goodfellow *et al.*, 1987). These tests were performed as growth-independent hydrolysis tests of fluorogenic, methylumbelliferyl-linked substrates. In comparison to our growth-dependent enzyme tests with nitrophenyl- or nitroanilide-linked substrates, several corresponding results, but also some differences, were observed. All or the majority of strains were able to produce acid and alkaline phosphatases, α -D-glucosidase, β -D-glucosidase and *N*-acetyl- β -D-glucosaminidase, which was also found by Goodfellow *et al.* (1987). Even the ability of β -L-fucosidase to differentiate between *S. albidoflavus* and *S. griseus* (*S. anulatus*) could be observed. In contrast to the results of Goodfellow *et al.* (1987), not all strains produced β -D-galactosidase, and other profiles were obtained for β -D-glucuronidase and sulphatase production. It seems that these tests may be important for characterization of streptomycetes, but cannot be used for their unambiguous identification. Quantitative chemotaxonomic methods have also been applied to some species of the genus *Streptomyces* (O'Donnell, 1988), but the differentiation potential of quantitative fatty acid data at the species level remains questionable (Saddler *et al.*, 1987).

Our study showed that many strains of the genus *Streptomyces* deposited in culture collections are poorly characterized and assigned to the wrong species. As an example, the three strains of *S. albus* found in subcluster 1-1 (*S. albidoflavus*) were shown by fatty acid profiles to belong to *S. albidoflavus* (R. M. Kroppenstedt, unpublished). In contrast, several strains of the same species were found in different phena, because of their atypical physiological reactions. Examples are *S. anulatus* ISP 5361^T, which was not grouped into subcluster 1-3 (*S. griseus*) as expected, but formed single-member cluster 47, and *S. violaceoruber* ISP 5049^T, which was not found in cluster 6 (*S. rochei*), but in cluster 69 (*S. ochraceiscleroticus*). The reasons for the atypical physiological patterns of such strains are difficult to determine. Test conditions, for example the time of reading of tests, incubation temperatures, test media, and the source and size of inoculum may not be optimal for all test strains, or the deviations may be due to mutations. As pointed out by Hill (1974), numerical taxonomy should be regarded as any other theory, and as such should be modified and

refined by further testing, including the use of genetical methods.

Conclusions

This study confirms the extensive species reduction within the genus *Streptomyces* proposed by Williams *et al.* (1983*a*) and supports the view of Sneath (1970) that numerical analysis is a practical way of dealing with the overspeciation in the genus. The taxonomic position of many strains currently classified within species category IV (Williams *et al.*, 1989) could be evaluated (Table 1). The results of our study indicate that the genus *Streptomyces* is still overspeciated.

There is evidence that the major subclusters and major clusters *S. albidoflavus*, *S. halstedii*, *S. griseus*, *S. exfoliatus*, *S. rochei*, *S. lydicus*, *S. fradiae*, *S. lavendulae*, *S. rimosus* and *S. albus* can be regarded as species, in addition to *S. violaceusniger*, strains of which were found in closely related and overlapping clusters. The taxonomic status of these species is supported by other taxonomic methods. Our results support the view that strains placed in the genus *Streptoverticillium* should be reclassified into the genus *Streptomyces*. However, the species status of many phena, including the minor clusters and single-member clusters, remains questionable. Species grouped into category III and category IV of Williams *et al.* (1989) should be regarded as in a state of transition until further genetical information is available. The nomenclature for phena used in our study was according to the procedure proposed by Williams *et al.* (1983*a*). Any necessary nomenclatural changes will be published elsewhere.

Note added in proof

Since the completion of this study the formal proposal has been made to unify the genera *Streptoverticillium* and *Streptomyces* in an amended genus *Streptomyces* based on phylogenetic similarities (Witt & Stackebrandt, 1990). In this study and in a further study by Labeda & Lyons (1991), extensive DNA-DNA hybridizations were carried out on members of the Williams clusters A21 (*S. griseoruber*), F61 (*S. lavendulae*) and A18 (*S. cyaneus*). In both studies, the hybridization values spanned a wide range, and in most cases intracluster pairing values were as low as those found between members of different Williams clusters. In some cases several strains grouped within the same cluster by Williams *et al.* (1983*a*), and showing very low intracluster hybridization values, were not grouped into the corresponding cluster in our study (e.g. Williams cluster A21: *S. griseoruber* ISP 5281^T, *S. griseoruber* ISP 5275^T; Williams group F61: *S. xanthophaeus* ISP 5134^T;

Williams group A18: *S. amakusaensis* ISP 5219^T, *S. fumanus* ISP 5154^T and *S. griseochromogenes* ISP 5499^T). However, as pointed out by Witt & Stackebrandt (1990) it is not possible to determine the phylogenetic depth of the phenetic clusters solely by DNA-DNA hybridization, and the question about their phylogenetic coherency cannot be answered at present.

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