

Phylogenetic study of the species within the family *Streptomycetaceae*

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Abstract Species of the genus *Streptomyces*, which constitute the vast majority of taxa within the family *Streptomycetaceae*, are a predominant component of the microbial population in soils throughout the world and have been the subject of extensive isolation and screening efforts over the years because they are a major source of commercially and medically important secondary metabolites. Taxonomic characterization of *Streptomyces* strains has been a challenge due to the large number of described species, greater than

any other microbial genus, resulting from academic and industrial activities. The methods used for characterization have evolved through several phases over the years from those based largely on morphological observations, to subsequent classifications based on numerical taxonomic analyses of standardized sets of phenotypic characters and, most recently, to the use of molecular phylogenetic analyses of gene sequences. The present phylogenetic study examines almost all described species (615 taxa) within the family *Streptomycetaceae* based on 16S rRNA gene sequences and illustrates the species diversity within this family, which is observed to contain 130 statistically

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supported clades, as well as many unsupported and single member clusters. Many of the observed clades are consistent with earlier morphological and numerical taxonomic studies, but it is apparent that insufficient variation is present in the 16S rRNA gene sequence within the species of this family to permit bootstrap-supported resolution of relationships between many of the individual clusters.

Keywords *Actinobacteria* · Systematics · *Streptomycetales* · Actinomycetes

Introduction

The systematics of the genus *Streptomyces* have had a long and convoluted history with numerous different approaches taken to the delineation of species within the genus. Early descriptions of species relied heavily on morphologically procedures, such as colour of aerial and substrate mycelia and spore chain morphology along with rudimentary physiological features (Krainsky 1914; Waksman and Curtis 1916; Waksman 1919). However, substantial interest in the genus only arose because of their commercial potential following the discoveries of actinomycin and streptomycin by *Streptomyces antibioticus* (Waksman and Woodruff 1941) and *Streptomyces griseus* (Schatz et al. 1944), respectively. The advent of large-scale industrial isolation and screening of *Streptomyces* species resulted in the naming of approximately 3,000 species by 1970, mainly on the basis of small differences in morphological and cultural properties, with many of these new names found only in the patent literature (Trejo 1970).

The problems facing streptomycete systematists were addressed in a series of cooperative studies, the most notable of which was the International *Streptomyces* Project (ISP). The project was planned and enacted by the Subcommittee on Taxonomy of Actinomycetes of the International Committee on Bacteriological Nomenclature and the Subcommittee of Actinomycetales of the Committee on Taxonomy of the American Society of Microbiology. The primary aim of the study was to provide reliable descriptions of extant and authentic type strains of *Streptomyces* and *Streptoverticillium* species. Existing type and neotype

strains of species assigned to these genera were sent, under code, to at least three experts in different countries. The strains were examined in each laboratory using strictly standardized media and experimental conditions to determine morphological and pigmentation properties, and carbon utilization profiles (Shirling and Gottlieb 1966). The characters evaluated had been selected based on data from previous international cooperative studies (Küster 1959; Gottlieb 1961, 1963). The methods and descriptions resulting from these studies were published (Shirling and Gottlieb 1968a, b, 1969, 1972) and the type strains deposited in several internationally recognized service collections. The classification of the genera *Streptomyces* and *Streptoverticillium* in the eighth edition of Bergey's Manual of Determinative Bacteriology was based on the results of the International *Streptomyces* Project (Pridham and Tresner 1974).

The ISP study, like earlier attempts to classify streptomycetes, was largely based on a limited number of features, with a heavy emphasis on morphology and pigmentation. Sneath (1970) considered that a rigorous application of the numerical taxonomic procedure provided the only way of reclassifying the plethora of *Streptomyces* species since reliance on a few selected characters could not be expected to reveal natural phenetic groups. The first comprehensive numerical taxonomic study of the genus *Streptomyces* was undertaken by Williams et al. (1983) who assigned type strains of *Streptomyces* species to 23 major (6–71 strains), 20 minor (2–5 strains) and 25 single membered clusters which were named, where possible, after the earliest validly described species they contained. The minor and single membered clusters were considered to be species and the major clusters species-groups. The largest cluster, the *Streptomyces albidoflavus* species-group, encompassed three subgroups which were recovered as separate, albeit related, clusters in an extension of the earlier study (Goodfellow et al. 1992). Most of the major clusters defined by Williams and his colleagues were recognized in an even more extensive numerical taxonomic study carried out by Kämpfer et al. (1991). The circumscription of most *Streptomyces* species described in Bergey's Manual of Systematic Bacteriology, volume 4 (Williams et al. 1989) is based on the numerical taxonomic survey of Williams et al. (1983).

Relatively few attempts have been made to evaluate phenotypes delineated in the extensive numerical taxonomic surveys of streptomycetes and streptovorticillia (Williams et al. 1983; Kämpfer et al. 1991; Goodfellow et al. 1992), using independent taxonomic approaches, other than somewhat *ad hoc* studies focused on representatives of specific clusters. The taxonomic status of some phenotypes circumscribed by Williams and his colleagues have been underpinned by chemotaxonomic and DNA:DNA relatedness data as exemplified by subcluster 1A (*S. albidoflavus*) (Mordarski et al. 1986; Manchester et al. 1990; Ferguson et al. 1997). In addition, Ridell et al. (1986) found that streptomycetes which shared a high number of precipitinogens belonged to the same numerically defined clusters whereas those less serologically related tended to fall into different clusters. In contrast, other taxa, such as clusters 10 (*Streptomyces fulvissimus*), 17 (*Streptomyces griseoviridis*), 18 (*Streptomyces cyaneus*) and 61 (*Streptomyces lavendulae*) have been shown to be heterogeneous (Saddler et al. 1987; Labeda 1992, 1993, 1998; Labeda and Lyons 1991a), notably with respect to DNA:DNA pairing data. However, in some instances better correlation was found when DNA:DNA pairing data were compared with the groupings of Kämpfer et al. (1991), as outlined by Kämpfer (2011).

Numerical taxonomic data also helped resolve intergeneric relationships within the family *Streptomycetaceae* as shown by the transfer of the genera *Actinopycnidium*, *Actinosporangium*, *Chainia*, *Ehytrosporangium*, *Kitasatoa*, *Microellobosporia* and *Streptovorticillium* to the genus *Streptomyces* (Goodfellow et al. 1986a, b, c, d; Witt and Stackebrandt 1990). However, the relationships between the genera *Kitasatospora* (Ōmura et al. 1982) and *Streptacidiphilus* (Kim et al. 2003) remains contentious (Anderson and Wellington 2001; Kämpfer 2011).

The present collaborative study was designed to generate a comprehensive 16S rRNA *Streptomyces* gene tree in order to (a) clarify relationships between the type strains of closely related *Streptomyces* species, (b) to evaluate the taxonomic informativeness of standard morphological markers, (c) to cast light onto the status of the genera *Kitasatospora* and *Streptacidiphilus* and (d) to allow the selection of representative strains for further studies, not least for comparative whole genome sequence analyses.

Methods

The type strains for almost all valid species in the family *Streptomycetaceae* as well as those in press on October 1, 2010 were included in the study (as can be seen online in Supplemental Table 1). Some sequences were obtained from the public sequence databanks, but the vast majority were determined and deposited during the current study. DNA was isolated and approximately 1320 almost-complete 16S rRNA gene sequences were determined in the various collaborating laboratories using previously described methods (Chun and Goodfellow 1995; Goodfellow et al. 2007; Kim et al. 1996; Kumar and Goodfellow 2008; Labeda and Kroppenstedt 2000; Labeda et al. 2009; Lu et al. 2001; Park et al. 2005).

Sequence data were organized, aligned and subjected to preliminary analysis within the ARB software package (Ludwig et al. 2004). Duplicate sequences for individual type strains from different collaborators were evaluated for both length and quality and the best sequence was retained for analysis. The sequence data were subsequently filtered to trim all sequences so that only the 1303 bp of sequence data devoid of missing data at either end of the gene sequence were exported for subsequent analysis. Final editing of the sequence alignment was done using BioEdit (Hall 1999) and phylogenetic analysis was performed with version 5 of the MEGA software package (Tamura et al. 2011) using the Tamura-Nei (Tamura and Nei 1993) distance coefficient with neighbor-joining (Saitou and Nei 1987) together with 1,000 bootstrap replications (Felsenstein 1985). The dataset was also analyzed using the the maximum parsimony (close-neighbor interchange on random trees) (Felsenstein 1993) and maximum likelihood (Tamura-Nei substitution model, uniform rates, and nearest neighbor-interchange heuristic method) (Felsenstein 1993) algorithms with 100 bootstrap replications. The node labels for each strain also contain the morphological characteristics used for the classical characterization of species within the genus *Streptomyces*, as in the International *Streptomyces* Project (Shirling and Gottlieb, 1966) and the cluster assignment from the numerical taxonomic study of Williams et al. (1983), where relevant. *Streptoalloteichus tenebarius* NBRC 16175^T (16S rRNA gene sequence AB184721) was used as the outgroup for calculations because this strain was originally described

as a species within the genus *Streptomyces* until it was recently correctly identified by Tamura et al. (2008a).

Results and discussion

The phylogenetic tree shown in Fig. 1a through j consists of 130 clades defined at greater than 60% bootstrap support, as summarized in Table 1, although other clusters and single member clusters can also be observed. It is reassuring that 106 of these clades (82%) were also observed in phylogenetic trees constructed by the maximum-parsimony and maximum-likelihood algorithms, as indicated by branches marked with an asterisk in Fig. 1a–j. Although the phylogenetic relationships within these are consistent between the computational methods, the weak statistical support for the backbone of the tree is reflected by the rearrangement of relationships between the clades in the different methods. A subset of the data deposited for this study had also been included in the all-species living tree project of Yarza et al. (2008) and demonstrated similar topography, but their tree did not designate individual species clusters based on bootstrap support. This highlights the strength of the sequence of the 16S rRNA gene in identifying relationships between closely related species in this family, but demonstrates that this gene is not particularly useful for accurately determining phylogenetic relationships between the clades.

For the most part, there is excellent correlation between the phylogeny of the well supported clades and morphological properties observed within them. The results were also observed to correlate well in many instances with the data from earlier phenotypic numerical taxonomy studies (Williams et al. 1983; Kämpfer et al. 1991). For instance, all of the strains in Clade 6 (Fig. 1a) produce green-colored, spiny surfaced spores borne in spiral chains (RA or RA-S). In this particular clade, there is also good correlation with the results of the numerical taxonomic study of Williams et al. (1983) in that most of the strains belong to their Cluster 37 in the simple matching coefficient tree. Similarly, the majority of the strains in Clades 38 and 39 (Fig. 1d) produce smooth-surfaced, red-colored spores borne in chains forming open loops (RA). Many of these species were found in Cluster 61 in the Williams et al. (1983) study. Lastly, Clades 112 and 113 (Fig. 1i) contain the strains of subcluster 1A

(*S. albidoflavus*) in the Williams et al. study and all produce smooth-surfaced, olive-buff colored spores carried in flexuous chains.

Four of the five neutrotolerant acidophilic species (Kim et al. 2004; Xu et al. 2006) formed Clades 121 and 122, to which the remaining one, *Streptomyces guanduensis*, was associated (Fig. 1j); all of these organisms formed flexuous chains (RF) of smooth surfaced spores and, with a single exception, a gray aerial spore mass. Four of the ten thermophilic streptomycetes formed Clade 105 to which the *Streptomyces thermocrophilus* strain was loosely associated (Fig. 1i); all of these strains form a gray aerial spore mass and produce smooth- or warty-ornamented spores in either spiral or flexuous spore chains. Three other thermophilic strains, *Streptomyces thermocarboxydovorans*, *Streptomyces thermodiastaticus* and *Streptomyces thermoviolaceus*, formed a loose grouping (Fig. 1i); these strains also had a gray aerial spore mass. The *Streptomyces thermolineatus* strain was associated with Clade 127, a well defined group formed by the strains of *Streptomyces glaucosporus*, *Streptomyces macrosporus*, *Streptomyces megasporus* and *Streptomyces radiopugnans*, whereas the *Streptomyces thermospinosisorus* was associated with Clade 104 (Fig. 1h). The final thermophilic strain, *Streptomyces thermocarboxyidus*, formed Clade 109 together with *Streptomyces lusitanus*.

The situation outlined above is not uniformly true for all of the clusters defined in the numerical taxonomy study since the taxa reported to comprise Cluster 18 (the *S. cyaneus* species-group) are found scattered between 9 major clades and numerous single member clades. This is not particularly surprising, however, since the DNA relatedness study of Labeda and Lyons (1991a) and the fatty acid analyses of Saddler et al. (1987) demonstrated that this group was taxonomically heterogeneous.

It is interesting that the species of the genus *Streptacidiphilus* are monophyletic and are found in Clade 53 (Fig. 1e), except for the type strain of *Streptacidiphilus oryzae* which is found in neighboring Clade 54. The *Streptacidiphilus* species clade is well supported in all three computational methods, and appears phylogenetically closely related to the genus *Kitasatospora*, whose species segregate into a large, statistically unsupported clade which also contains a number of *Streptomyces* species. The species of both of these genera are found within the

radiation of the species of the genus *Streptomyces* in the present study, and hence might only be considered as taxonomically valid if the genus *Streptomyces* is truly polyphyletic.

It was disappointing to observe that those species forming verticillate chains of spores, formerly classified in the genus *Streptovorticillium*, did not segregate into a single cluster group, but rather were found in three unsupported larger clusters, including Clades 49, 50, 51 and 52 (Fig. 1e) in the first, Clades 61, 62, 63, 64, 65, 66 (Fig. 1e) in the second, and Clades 82, 83 and 84 (Fig. 1g) in the third. Given the separation of these groups within the radiation of the genus *Streptomyces* and the apparent lack of phylogenetic resolution within the backbone structure of this phylogenetic tree provided by the limited variability of the 16S rRNA, and hence the relationships between the individual clades, it would be premature to speculate if there is enough support for revival of the verticillate species as multiple distinct genera.

Other taxa exhibiting morphological traits used to differentiate them into separate genera in the past were also noted. Species formerly classified in the genus *Microellobosporia* were found to segregate into a single clade (Clade 16), as can be seen in Fig. 1b, but again this cluster resides within the radiation of *Streptomyces* species, making any argument for the revival of this genus dubious. The three species originally assigned to the genus *Elyrosporangium*; *Streptomyces brasiliensis*, *Streptomyces carpinensis* and *Streptomyces spiralis*, were loosely associated albeit with other *Streptomyces* species (Fig. 1g, h) which have spiral spore chains. Those taxa formerly classified within the genus *Chainia* were found in several distinct clusters, including Clades 73, 74, 87, 91 and 92 (Fig. 1f–h).

Taxa producing spores with a rugose or rough surface were found among the closely related group of Clades 75, 76, 77, 78, 79, and 80 (Fig. 1f, g), perhaps indicative of the taxonomic significance of this spore surface property as highlighted in recent polyphasic studies where such strains were assigned to the *Streptomyces violaceusniger* 16S rRNA clade (Goodfellow et al. 2007; Kumar and Goodfellow 2008). The type strain of *Streptomyces hygrosopicus* produces rugose spores whereas six other strains bearing the name do not, these organisms form distinct branches in the 16S rRNA *Streptomyces* tree (Kumar and Goodfellow 2010).

The clade containing *Streptomyces albus* (Clade 126 in Fig. 1j), the type species of the genus *Streptomyces*, is very basal with respect to the phylogeny of the rest of the species in this genus. All of the species in Clade 126, including *Streptomyces albus*, *Streptomyces almquistii*, *Streptomyces gibsonii*, *Streptomyces rangoonensis*, *Streptomyces flocculus*, are morphologically similar and those studied had been assigned to Cluster 16 in the Williams et al. study. In spite of the fact that the summary of physiological properties reported by Pridham and Tresner (1974) exhibited differences in terms of sugar utilization patterns among these species, it is likely that they represent the same species.

The high similarity of 16S rRNA gene sequences among all taxa within the *Streptomycetaceae* weakens the statistical support for the backbone structure of the phylogenetic tree for this family, generally providing little statistical support for the phylogenetic relationships among the 130 individual clades. The taxonomic value for the sequence of this gene locus is primarily in the identification or confirmation of novelty of unknown isolates of streptomycetes, particularly since there seems to be at least some correlation with morphological and physiological traits. It is not really possible to propose a defined 16S rRNA gene sequence similarity at which an unknown isolate is or is not a member of described species, although it appears that the 98.5% level proposed in the literature (Stackebrandt and Ebers 2006) is likely not valid for the genus *Streptomyces*.

Because of the aforementioned issue of high 16S rRNA gene sequence similarity among species, the use of partial sequences of multiple house-keeping genes, or multi-locus sequence typing (MLST) has been applied to the systematics of the species of the *Streptomycetaceae*. Phylogeny based on the 16S rRNA gene exhibits good agreement with the data reported by Rong et al. (2009) for their MLST study of the *S. albidoflavus* group using partial sequences of five house-keeping genes (*atpD*, *gyrB*, *recA*, *rpoB*, and *trpB*) and all of the species that they proposed to be later heterotypic synonyms of *S. albidoflavus*, including *Streptomyces canescens*, *Streptomyces champavatii*, *Streptomyces coelicolor*, *Streptomyces felleus*, *Streptomyces globisporus* subsp. *caucasicus*, *S. griseus* subsp. *solvifaciens*, *Streptomyces limosus*, *Streptomyces odorifer*, and *Streptomyces sampsonii*, are also found in Clade 112 (Fig. 1i) which has excellent

bootstrap support (99%) and was also observed in trees constructed using maximum likelihood and maximum parsimony algorithms.

The congruence between the MLST data presented by Guo et al. (2009) and Rong and Huang (2010) for the *S. griseus* group, as well as the accompanying taxonomic proposals for these strains, with the 16S rRNA gene phylogeny presented here is fairly good. There is a definite lack of resolution in the region of the 16S rRNA gene phylogenetic tree containing many of the species studied by Guo et al. (2009) and Rong and Huang (2010), providing virtually no bootstrap support for many of the branches present in this region (Fig. 1c between Clade 34 and Clade 35), which makes it very difficult to compare results. The phylogenies presented in their analyses resulting from the concatenation of five partial house-keeping genes exhibit much higher bootstrap support, not surprising considering the higher degree of sequence variability observed in these loci. The inclusion of virtually all validly described *Streptomyces* species in the phylogenetic tree presented in the 16S rRNA gene phylogeny resulting from the present study should make it possible to extend the proposed species revisions by suggesting the addition of species not included in the pilot MLST studies as possible synonyms. For example, the proposal for reduction of *Streptomyces flavogriseus* to a later heterotypic synonym of *Streptomyces flavovirens* is well supported in the 16S rRNA gene phylogeny (Clade 37, Fig. 1c) although perhaps *Streptomyces nigrifaciens* might also be included as a later synonym. Likewise it is clear that, as proposed by Rong and Huang (2010), *Streptomyces californicus* and *Streptomyces floridae* should be considered as later heterotypic synonyms of *Streptomyces puniceus* (Clade 33, Fig. 1c), but it also seems likely from the 16S rRNA gene phylogeny that *Streptomyces phaeofaciens* should likely be also considered as a synonym. Determination of the house-keeping gene sequences for the type strains of *Streptomyces nigrifaciens* and *Streptomyces phaeofaciens* will quickly determine if these suggestions are valid.

In general, strong congruence was observed between the 16S rRNA gene sequence phylogeny and that constructed using concatenated partial sequences of house-keeping genes *atpD*, *recA*, *rpoB*, and *trpB* in a recent study of phytopathogenic *Streptomyces* species and near neighbors by Labeda (2011). Strains observed within Clades 23, 24, and 25 (Fig. 1b) were found to

Fig. 1 a through **1 j**. Phylogenetic tree for an analysis calculated from sequences of the 16S rRNA gene (1303 bp) using the Tamura-Nei evolutionary distance method (1993) and the neighbor-joining algorithm of Saitou and Nei (1987). Branches conserved in phylogenetic trees constructed using the maximum parsimony and maximum likelihood algorithms (Felsenstein 1993) are indicated with an asterisk. Node labels also contain morphological information regarding spore color, spore surface properties, and sporophore morphology (*RF Rectiflexibiles* or flexuous spore chains; *RA Retinaculiperti* or spore chains in open loops; *S Spirales* or spores in spiral chains) as well as the cluster assignment (*WC* Williams et al. cluster number) for the simple matching coefficient in the numerical taxonomic study of Williams et al. (1983), with SMC referring to single member cluster. Percentages at the nodes represent levels of bootstrap support from 1,000 re-sampled datasets (Felsenstein 1985) with values less than 60% not shown. Bar equals 0.005 nucleotide substitutions per site

cluster similarly based on the sequences of house-keeping genes. The potato scab-producing species *Streptomyces scabiei*, *Streptomyces europaescabiei* and *Streptomyces stelliscabiei* were observed to represent distinct taxa and a similar topography was observed in trees constructed using 16S rRNA gene sequences or sequences of the concatenated four house-keeping genes. In the MLST study, however, *Streptomyces ipomoea* was observed to be phylogenetically closer to *Streptomyces puniscabiei*, while *Streptomyces acidiscabiei* was observed to be phylogenetically nearer to *Streptomyces niveiscabiei*. The close phylogenetic relationship between *S. reticuliscabiei* and *S. turgidiscabiei* observed in the 16S rRNA gene phylogeny (Clade 22) was also observed in phylogenetic trees constructed from the partial house-keeping gene sequences. It was possible, however, to differentiate between these taxa based on *atpD* and *trpB* gene sequences, supporting the proposal of Boucek-Mechiche et al. (2006) that these be retained as separate taxa.

The species within Clades 18 and 19 in the 16S rRNA phylogenetic tree (Fig. 1b) were found to cluster similarly in the 4-gene tree (Labeda 2011) with the exception that *Streptomyces cinereoruber* subsp. *fructofermentans* was observed to be closely related to *Streptomyces aurantiacus* and *Streptomyces tauricus* in the MLST study, while it is observed to be more closely related to *Streptomyces reticuliscabiei* and *Streptomyces turgidiscabies* (Clade 22, Fig. 1b) in the 16S rRNA gene tree. Moreover, the species observed in Clade 48 (Fig. 1d) in the 16S rRNA phylogenetic tree, including *Streptomyces gobitricini*,

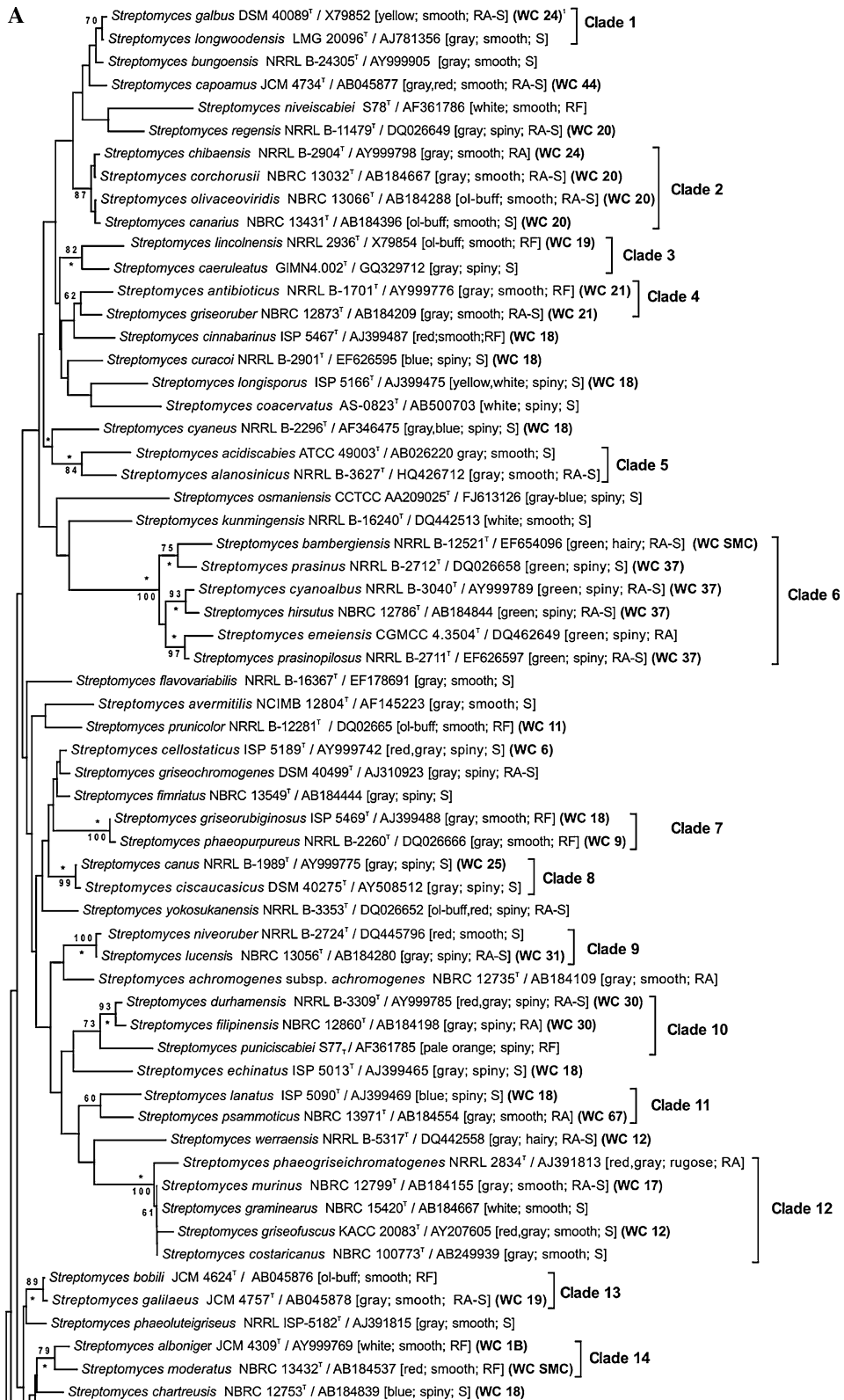


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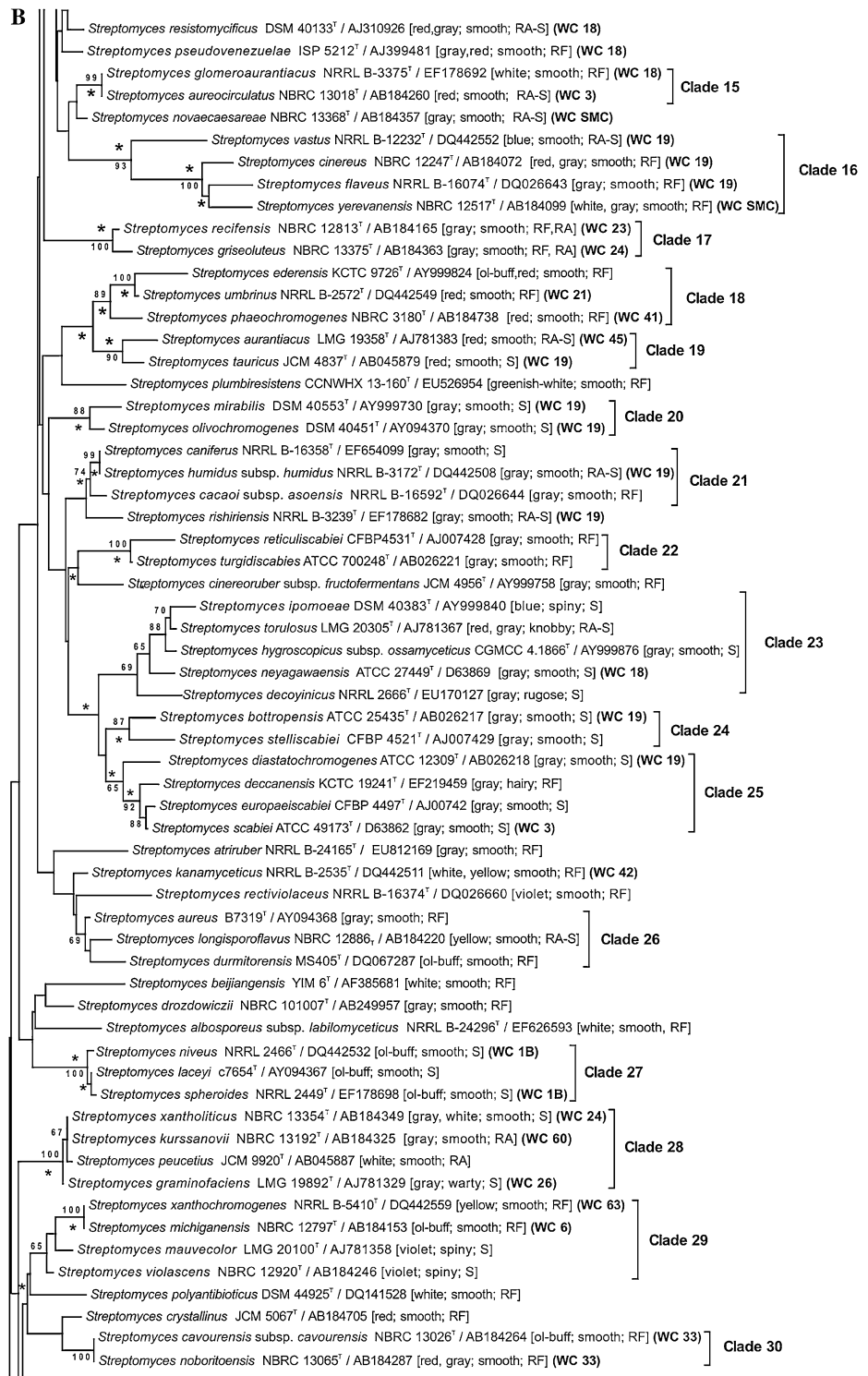


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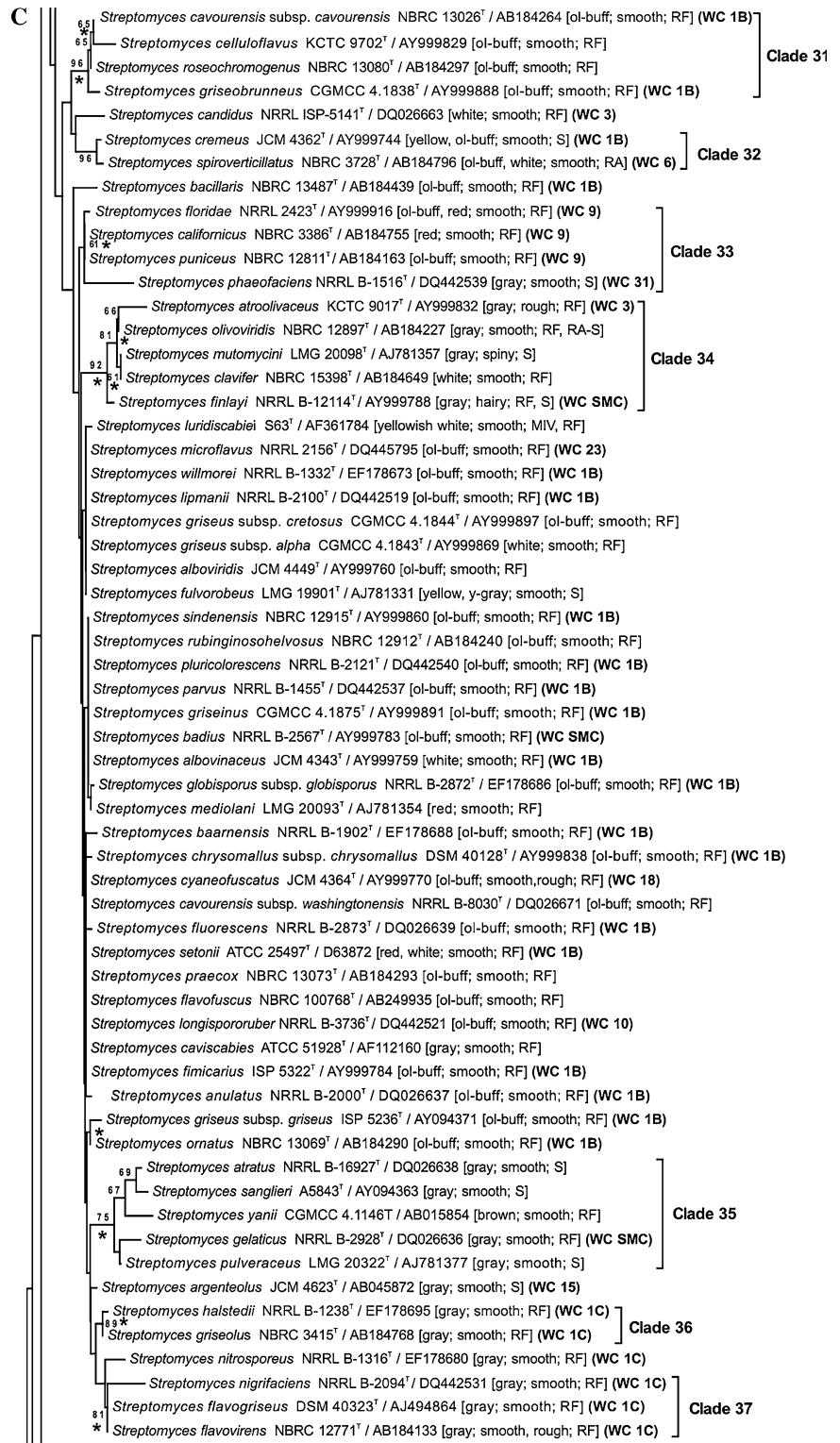


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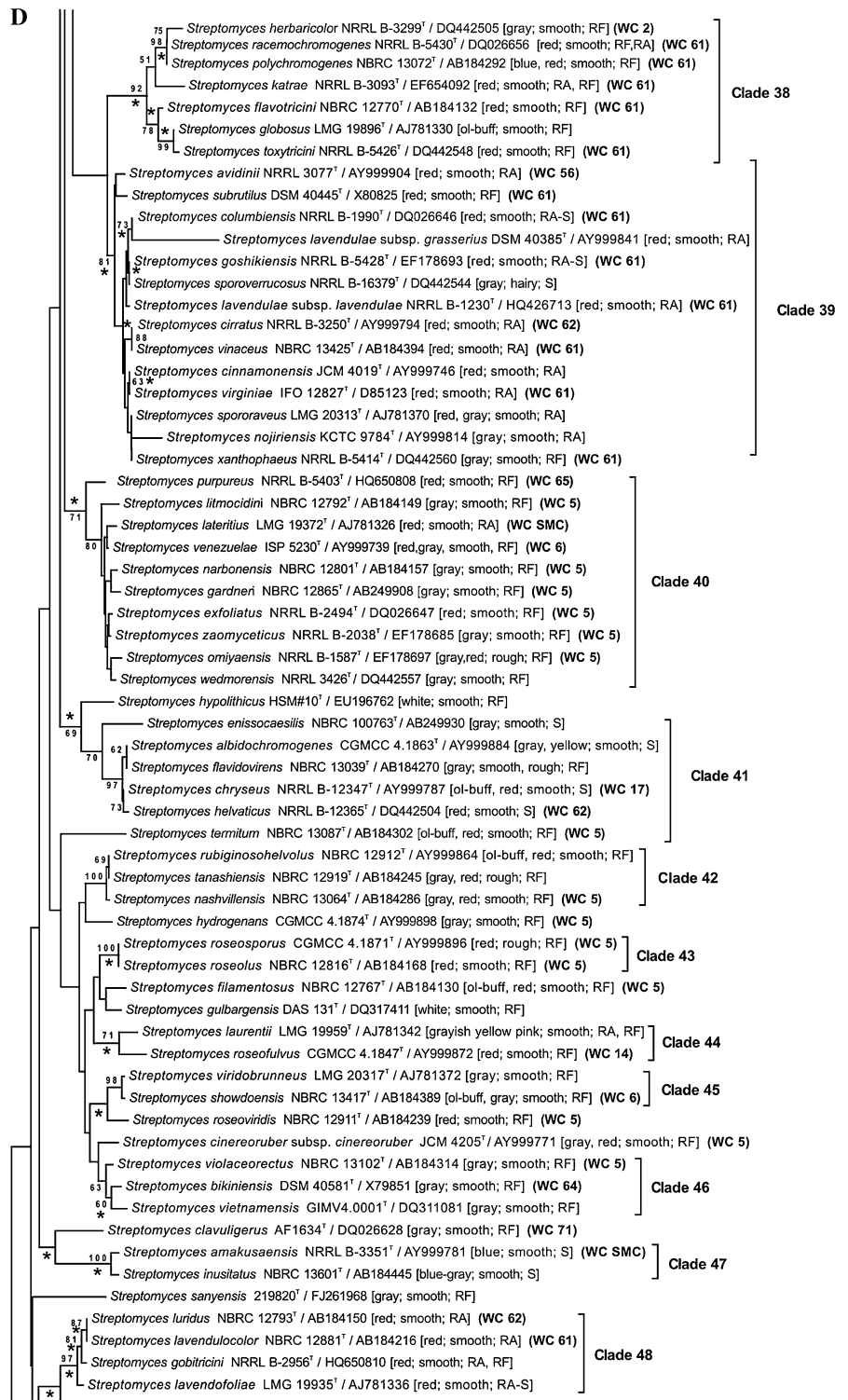


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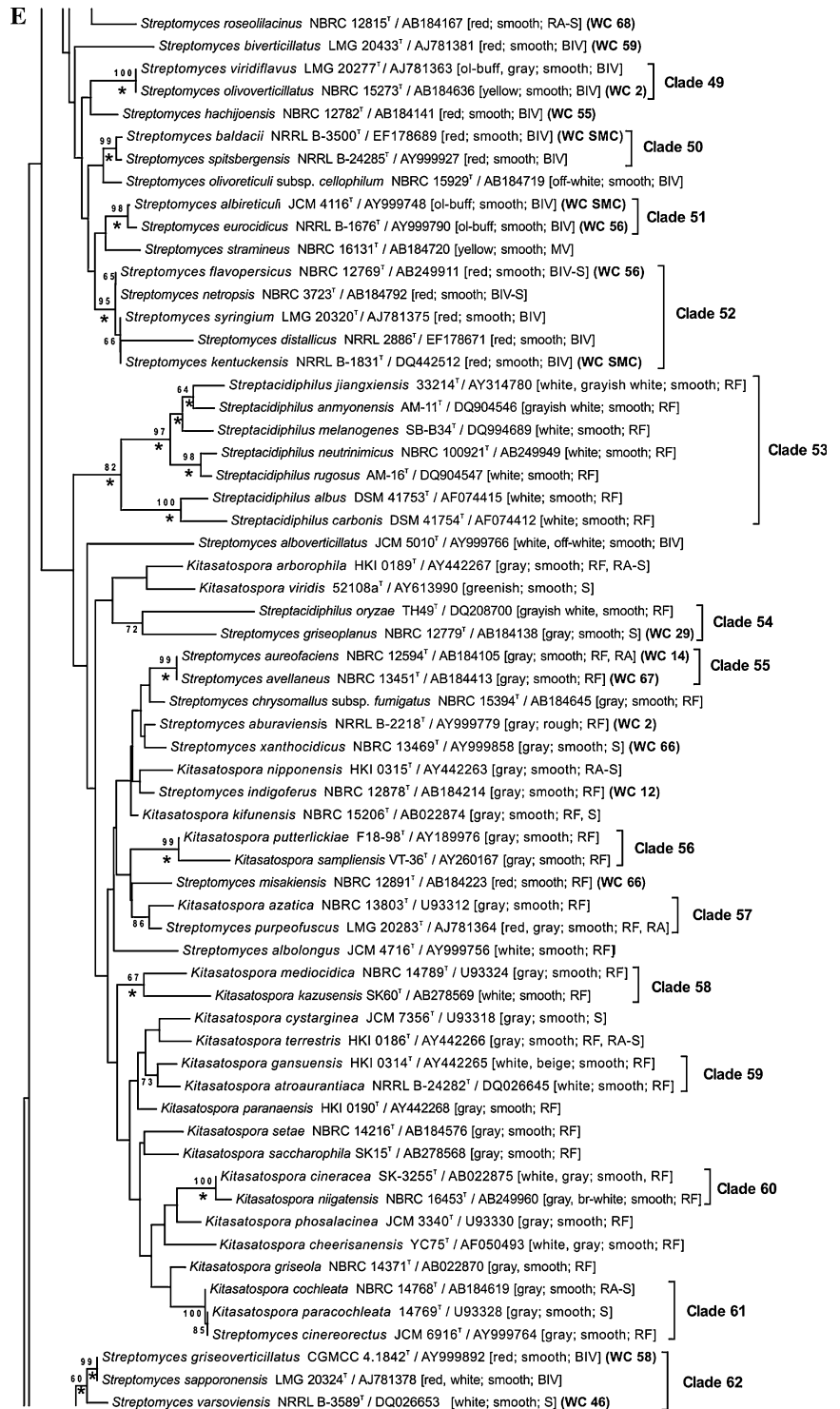


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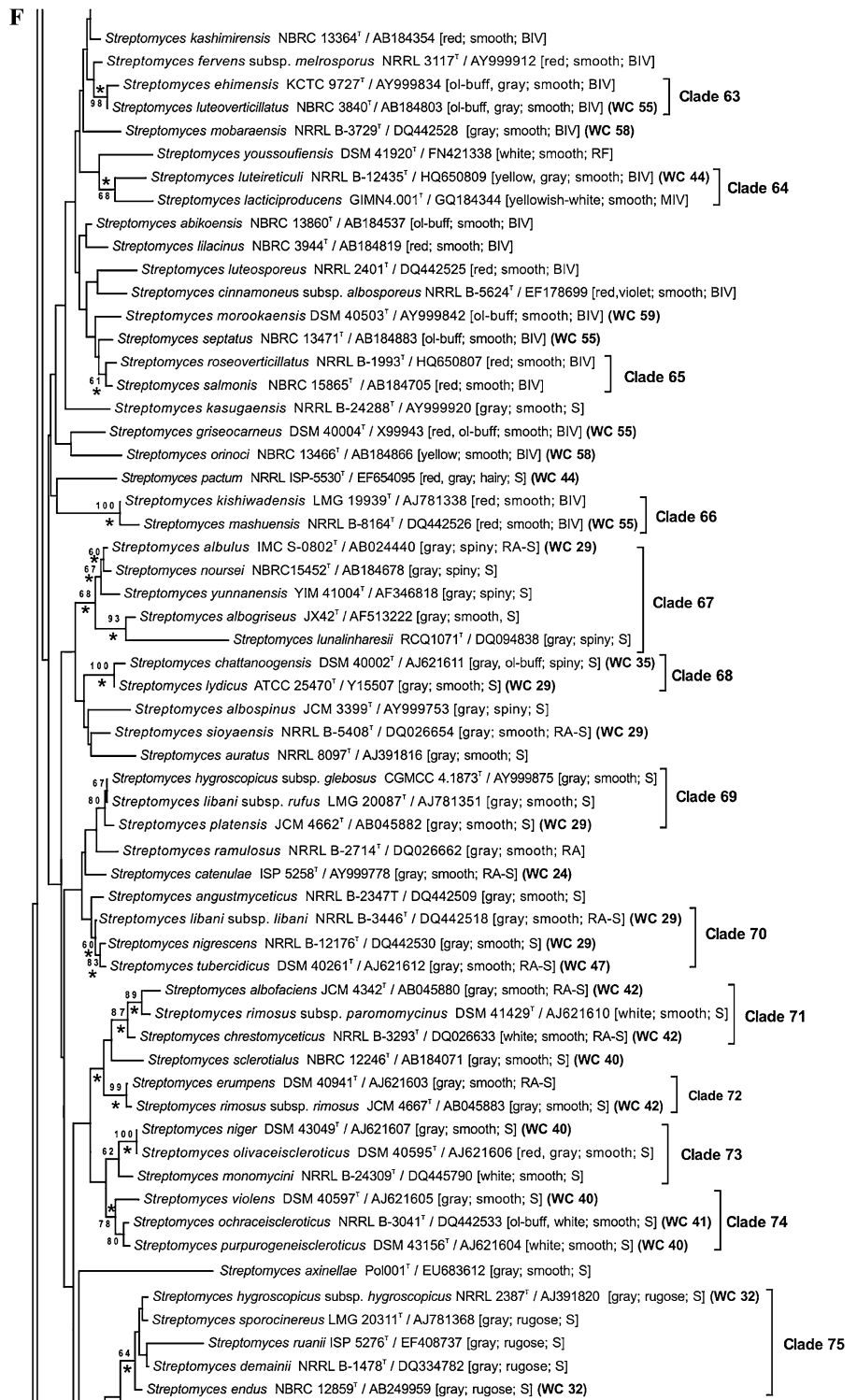


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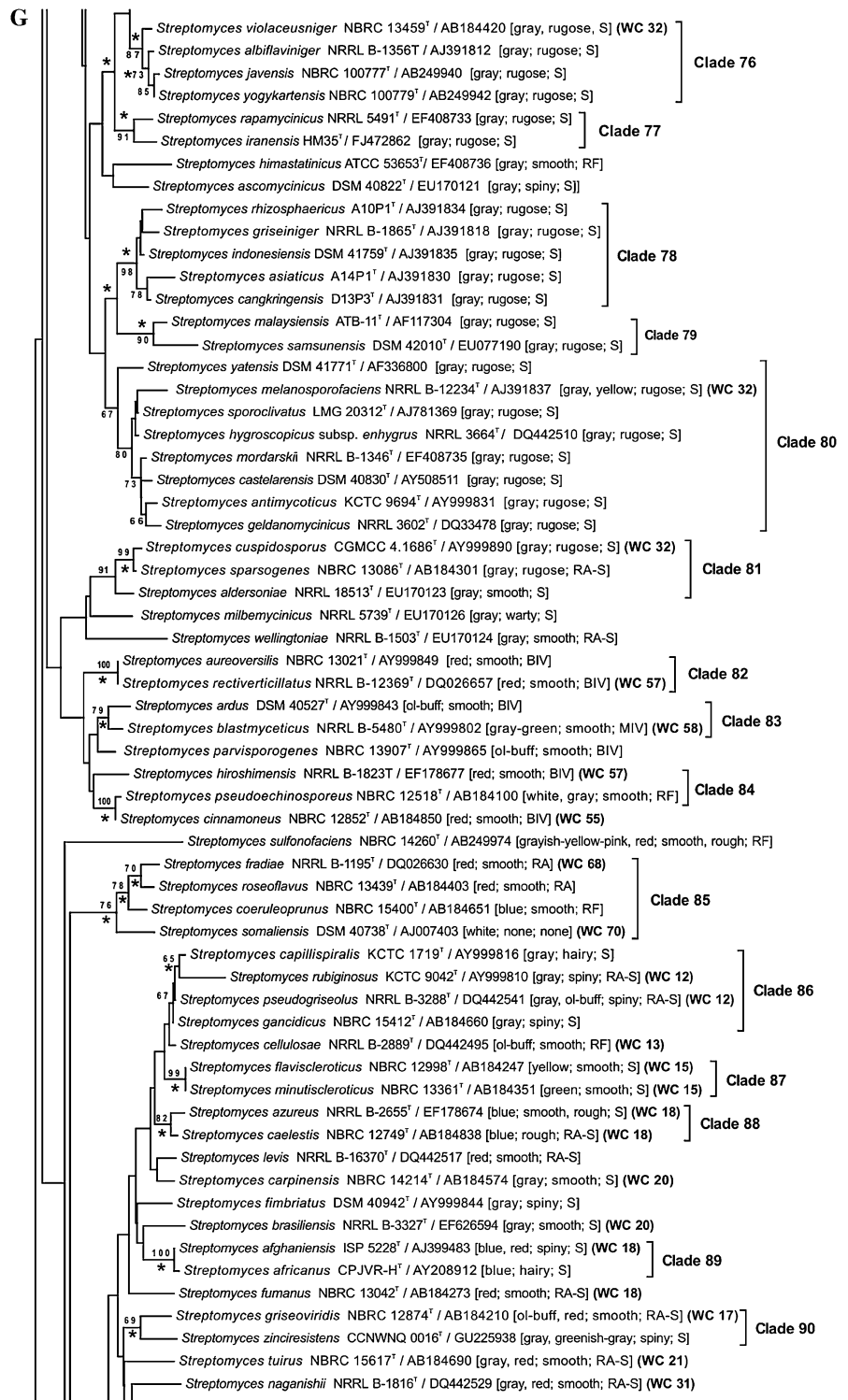


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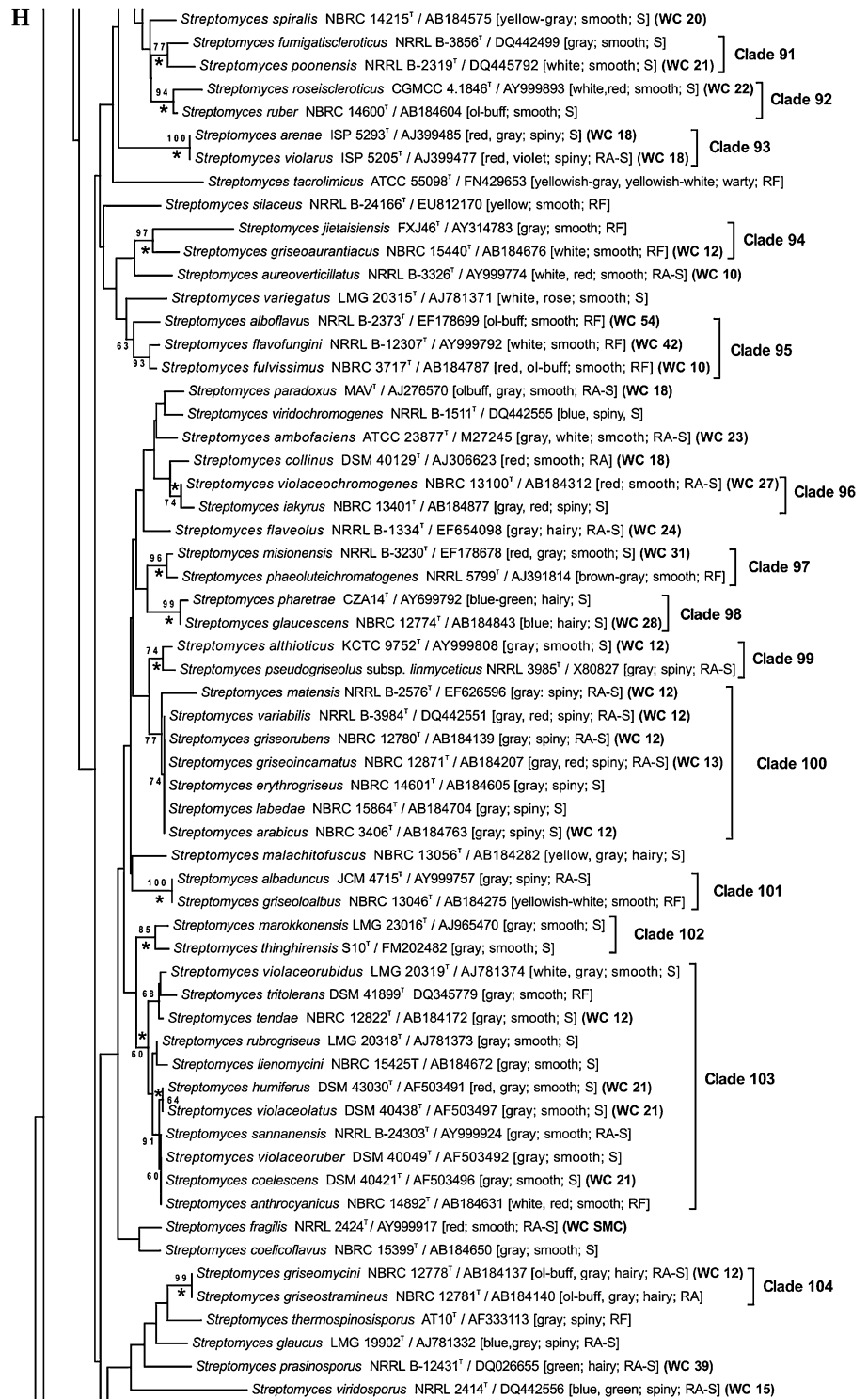


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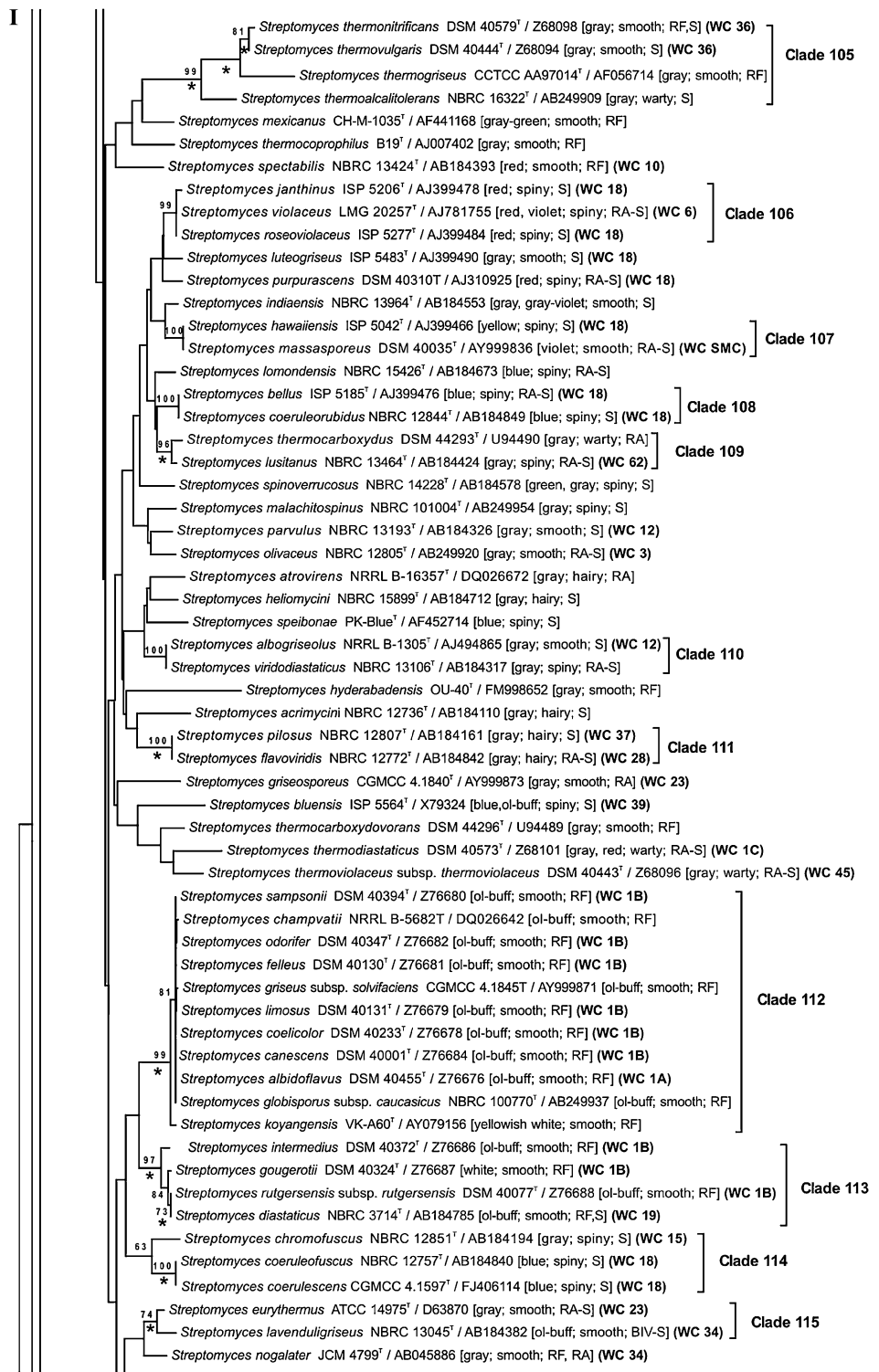
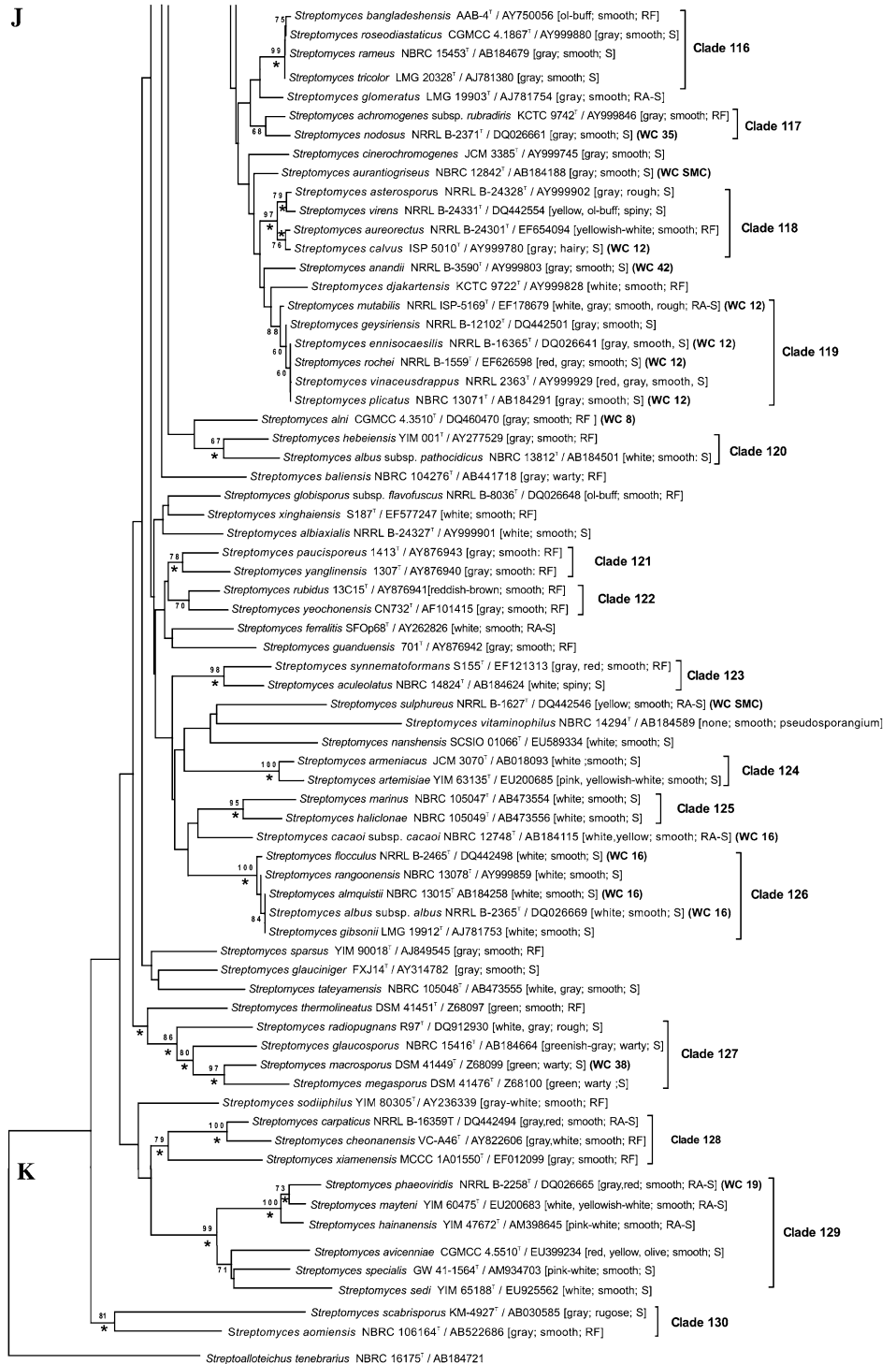


Fig. 1 continued



Streptomyces lavendofoliae, *Streptomyces lavendulicolor*, and *Streptomyces luridus*, as well as the nearest outlying species *Streptomyces roseolilacinus* were observed to exhibit identical tree topography in the phylogenetic tree constructed from the four concatenated house-keeping genes.

It was reassuring to observe that phylogenetic relations of taxa in the trees constructed from the largely conserved 16S rRNA gene sequences confirmed that the “classic” phenotypic, and largely morphological, characteristics used for classification schemes for species of the genus *Streptomyces* are generally quite useful for species identification and grouping of similar taxa. These traits, including spore color, spore surface ornamentation, if present, and the morphology of the sporophores on which they are borne, are highly similar within the vast majority of phylogenetically well defined clades that exhibit acceptable bootstrap support. It is obvious in considering the distribution of different spore colors, such as red or blue, over the entire phylogenetic tree that there is no support for the separation of the species of the genus into defined spore color groups as had been done by Pridham and Tresner (1974) for the 8th edition of Bergey’s Manual of Determinative Bacteriology. Examination of the morphological properties within clades provided evidence that no differentiation should be made between spore chains formed in large open loops (RA or *Retinaculum*-Apertum) or in tight spirals (*Spira*), since both categories were routinely observed together in many of the well supported clades (for example Clades 1, 2, 5, 6 and others). Generally, well supported clades that contained species with flexuous (RF or *Rectus Flexibilis*) chains of spores did not contain member species with spore chains in loops or spirals (for example Clades 18, 22, 30, 31 and others).

Concordance between the arrangement of taxa observed in 16S rRNA gene phylogenetic tree with the clusters formed by species in the numerical taxonomic studies of Williams et al. (1983) and Kämpfer et al. (1991) was not as clear since species highly similar both in 16S rRNA gene sequence and in phenotypic characteristics not surprisingly were clustered in both the phylogenetic and numerical taxonomic studies (Clade 126). The distribution of less similar taxa, determined in the numerical taxonomic studies on the 16S rRNA tree is not predictable, as can be seen with the extended distribution of strains from Williams

et al. Cluster 1B across a range of the clusters seen in Fig. 1b, C.

The percentage of 16S rRNA gene sequence similarity corresponding to species-level similarity is a frequent issue when dealing with newly discovered representatives within existing genera. The sequence similarity among *Streptomyces niveus*, *Streptomyces laceyi*, and *Streptomyces spheroides*, the members of Clade 27, was observed to be 99.8 to 99.9% and Tamura et al. (2008b) described these taxa as members of the same, with *S. laceyi* and *S. spheroides* designated as later synonyms of *S. niveus* on the basis of identical MALDI-TOF MS patterns and the discovery that all three strains produce the antibiotic novobiocin.

An assessment of the 16S rRNA gene similarity between several species for which DNA homology was determined in the past (Labeda and Lyons 1991a, b; Labeda 1993) found that DNA relatedness values of greater than 84% (including *S. lavendulae* subsp. *lavendulae*, *S. lavendulae* subsp. *grasserius*, and *S. columbiensis* from Clade 39, *S. hygrosopicus* subsp. *hygrosopicus* and *S. endus* from Clade 75, and *S. bellus* and *S. coeruleorubidus* from Clade 108) was reflected in sequence similarity values ranging from 98.5 to 99.8%. It is interesting to note that in the bootstrap-supported Clade 106, *S. albus* subsp. *albus*, *S. almquistii*, *S. flocculus*, *S. gibsonii* and *S. rangoonensis*, cluster very closely and share 100% sequence similarity with only one exception (*S. albus* subsp. *albus* and *S. flocculus* are only 99.8% similar), possibly indicating that these taxa represent a single species, *S. albus* subsp. *albus* given that they also appear very morphologically similar (white, smooth-surfaced spores borne in flexuous chains) in culture. Clade 6 had 100% bootstrap support and was reproduced in maximum parsimony and maximum likelihood trees. This clade, consisting of *S. bambergensis*, *S. cyaneoalbus*, *S. emeiensis*, *S. hirsutus*, *S. prasino-pilosus*, and *S. prasinus*, also contained taxa with very similar morphology in culture (green, spiny- to hairy-surfaced spores borne in spiral chains) and the 16S rRNA gene sequence similarity among the members ranged from 98 to 99.7%. It is possible that these taxa represent a single species, particularly since most were also found in the same phenotypic cluster group (Cluster 37) in the study of Williams et al. (1983) but additional studies would be necessary.

It is disappointing that this phylogenetic analysis did not clarify the status of the genera *Kitasatospora* or

Table 1 Clades supported by bootstrap values greater than 60% and their member taxa

Clade 1 (70% bootstrap support)

Streptomyces galbus DSM 40089^T/×79852 [yellow; smooth; RA-S^a] (Williams et al. Cluster 24)

Streptomyces longwoodensis LMG 20096^T/AJ781356 [gray; smooth; S]

Clade 2 (87% bootstrap support)

Streptomyces canarius NBRC 13431^T/AB184396 [ol-buff^b; smooth; S] (Williams et al. Cluster 20)

Streptomyces chibaensis NRRL B-2904^T/AY999798 [gray; smooth; RA] (Williams et al. Cluster 24)

Streptomyces corchorusii NBRC 13032^T/AB184667 [gray; smooth; RA-S] (Williams et al. Cluster 20)

Streptomyces olivaceoviridis NBRC 13066^T/AB184288 [ol-buff; smooth; RA-S] (Williams et al. Cluster 20)

Clade 3 (82% bootstrap support)

Streptomyces caeruleatus GIMN4.002^T/GQ329712 [gray; spiny; S]

Streptomyces lincolnensis NRRL 2936^T/×79854 [ol-buff; smooth; RF] (Williams et al. Cluster 19)

Clade 4 (62% bootstrap support)

Streptomyces antibioticus NRRL B-1701^T/AY999776 [gray; smooth; RF] (Williams et al. Cluster 21)

Streptomyces griseoruber NBRC 12873^T/AB184209 [gray; smooth; RA-S] (Williams et al. Cluster 21)

Clade 5 (84% bootstrap support)

Streptomyces acidiscabies ATCC 49003^T/AB026220 gray; smooth; S]

Streptomyces alanosinicus NRRL B-3627^T/HQ426712 [gray; smooth; RA-S]

Clade 6 (100% bootstrap support)

Streptomyces bambergiensis NRRL B-12521^T/EF654096 [green; hairy; RA-S] (Williams et al. Single Member Cluster)

Streptomyces cyanoalbus NRRL B-3040^T/AY999789 [green; spiny; RA-S] (Williams et al. Cluster 37)

Streptomyces emeiensis CGMCC 4.3504^T/DQ462649 [green; spiny; RA]

Streptomyces hirsutus NBRC 12786^T/AB184844 [green; spiny; RA-S] (Williams et al. Cluster 37)

Streptomyces prasinopilosus NRRL B-2711^T/EF626597 [green; spiny; RA-S] (Williams et al. Cluster 37)

Streptomyces prasinus NRRL B-2712^T/DQ026658 [green; spiny; S] (Williams et al. Cluster 37)

Clade 7 (100% bootstrap support)

Streptomyces griseorubiginosus ISP 5469^T/AJ399488 [gray; smooth; RF] (Williams et al. Cluster 18)

Streptomyces phaeoauripureus NRRL B-2260^T/DQ026666 [gray; smooth; RF] (Williams et al. Cluster 9)

Clade 8 (99% bootstrap support)

Streptomyces canus NRRL B-1989^T/AY999775 [gray; spiny; S] (Williams et al. Cluster 25)

Streptomyces ciscaucasicus DSM 40275^T/AY508512 [gray; spiny; S]

Clade 9 (100% bootstrap support)

Streptomyces lucensis NBRC 13056^T/AB184280 [gray; spiny; RA-S] (Williams et al. Cluster 31)

Streptomyces niveoruber NRRL B-2724^T/DQ445796 [red; smooth; S]

Clade 10 (73% bootstrap support)

Streptomyces durhamensis NRRL B-3309^T/AY999785 [red,gray; spiny; RA-S] (Williams et al. Cluster 30)

Streptomyces filipinensis NBRC 12860^T/AB184198 [gray; spiny; RA] (Williams et al. Cluster 30)

Streptomyces puniscabiei S77^T/AF361785 [pale orange; spiny; RF]

Clade 11 (60% bootstrap support)

Streptomyces lanatus ISP 5090^T/AJ399469 [blue; spiny; S] (Williams et al. Cluster 18)

Streptomyces psammiticus NBRC 13971^T/AB184554 [gray; smooth; RA] (Williams et al. Cluster 67)

Clade 12 (100% bootstrap support)

Streptomyces costaricanus NBRC 100773^T/AB249939 [gray; smooth; S]

Streptomyces graminearus NBRC 15420^T/AB184667 [white; smooth; S]

Streptomyces griseofuscus KACC 220083^T/AY207605 [red, gray; smooth; S] (WC 12)

Streptomyces murinus NBRC 12799^T/AB184155 [gray; smooth; RA-S] (Williams et al. Cluster 17)

Streptomyces phaeoigriseichromatogenes NRRL 2834^T/AJ391813 [red,gray; rugose; RA]

Table 1 continued

Clade 13 (89% bootstrap support)

Streptomyces bobili JCM 4624^T/AB045876 [ol-buff; smooth; RF]

Streptomyces galilaeus JCM 4757^T/AB045878 [gray; smooth; RA-S] (Williams et al. Cluster 19)

Clade 14 (79% bootstrap support)

Streptomyces alboniger JCM 4309^T/AY999769 [white; smooth; RF] (Williams et al. Cluster 1B)

Streptomyces moderatus NBRC 13432^T/AB184537 [red; smooth; RF] (Williams et al. Single member cluster)

Clade 15 (99% bootstrap support)

Streptomyces aureocirculatus NBRC 13018^T/AB184260 [red; smooth; RA-S] (Williams et al. Cluster 3)

Streptomyces glomeroaurantiacus NRRL B-3375^T/EF178692 [white; smooth; RF] (Williams et al. Cluster 19)

Clade 16 (93% bootstrap support)

Streptomyces cinereus NBRC 12247^T/AB184072 [red, gray; smooth; RF] (Williams et al. Cluster 19)

Streptomyces flaveus NRRL B-16074^T/DQ026643 [gray; smooth; RF] (Williams et al. Cluster 19)

Streptomyces vastus NRRL B-12232^T/DQ442552 [blue; smooth; RA-S] (Williams et al. Cluster 19)

Streptomyces yerevanensis NBRC 12517^T/AB184099 [white, gray; smooth; RF] (Williams et al. Single member cluster)

Clade 17 (100% bootstrap support)

Streptomyces griseoluteus NBRC 13375^T/AB184363 [gray; smooth; RF, RA] (Williams et al. Cluster 24)

Streptomyces recifensis NBRC 12813^T/AB184165 [gray; smooth; RF, RA] (Williams et al. Cluster 23)

Clade 18 (89% bootstrap support)

Streptomyces ederensis KCTC 9726^T/AY999824 [ol-buff, red; smooth; RF]

Streptomyces phaeochromogenes NBRC 3180^T/AB184738 [red; smooth; RF] (Williams et al. Cluster 41)

Streptomyces umbrinus NRRL B-2572^T/DQ442549 [red; smooth; RF] (Williams et al. Cluster 21)

Clade 19 (90% bootstrap support)

Streptomyces aurantiacus LMG 19358^T/AJ781383 [red; smooth; RA-S] (Williams et al. Cluster 45)

Streptomyces tauricus JCM 4837^T/AB045879 [red; smooth; S] (Williams et al. Cluster 19)

Clade 20 (88% bootstrap support)

Streptomyces mirabilis DSM 40553^T/AY999730 [gray; smooth; S] (Williams et al. Cluster 19)

Streptomyces olivochromogenes DSM 40451^T/AY094370 [gray; smooth; S] (Williams et al. Cluster 19)

Clade 21 (74% bootstrap support)

Streptomyces cacaoi subsp. *asoensis* NRRL B-16592^T/DQ026644 [gray; smooth; RF]

Streptomyces caniferus NRRL B-16358^T/EF654099 [gray; smooth; S]

Streptomyces humidus subsp. *humidus* NRRL B-3172^T/DQ442508 [gray; smooth; RA-S] (Williams et al. Cluster 19)

Clade 22 (100% bootstrap support)

Streptomyces reticuliscabiei CFBP4531^T/AJ007428 [gray; smooth; RF]

Streptomyces turgidiscabies ATCC 700248^T/AB026221 [gray; smooth; RF]

Clade 23 (69% bootstrap support)

Streptomyces decoyinus NRRL 2666^T/EU170127 [gray; rugose; S]

Streptomyces hygroscopicus subsp. *ossamyceticus* CGMCC 4.1866^T/AY999876 [gray; smooth; S]

Streptomyces ipomoeae DSM 40383^T/AY999840 [blue; spiny; S]

Streptomyces neyagawaensis ATCC 27449^T/D63869 [gray; smooth; S] (Williams et al. Cluster 18)

Streptomyces torulosus LMG 20305^T/AJ781367 [red, gray; knobby; RA-S]

Clade 24 (87% bootstrap support)

Streptomyces bottropensis ATCC 25435^T/AB026217 [gray; smooth; S] (Williams et al. Cluster 19)

Streptomyces stelliscabiei CFBP 4521^T/AJ007429 [gray; smooth; S]

Clade 25 (65% bootstrap support)

Streptomyces deccanensis KCTC 19241^T/EF219459 [gray; hairy; RF]

Streptomyces diastatochromogenes ATCC 12309^T/AB026218 [gray; smooth; S] (Williams et al. Cluster 19)

Table 1 continued

Streptomyces europaeiscabiei CFBP 4497^T/AJ00742 [gray; smooth; S]
Streptomyces scabiei ATCC 49173^T/D63862 [gray; smooth; S] (Williams et al. Cluster 3)

Clade 26 (69% bootstrap support)
Streptomyces aureus B7319^T/AY094368 [gray; smooth; RF] (Williams et al. Cluster 1B)
Streptomyces durmitorensis MS405^T/DQ067287 [ol-buff; smooth; RF]
Streptomyces longisporoflavus NBRC 12886^T/AB184220 [yellow; smooth; RA-S] (Williams et al. Cluster 39)

Clade 27 (100% bootstrap support)
Streptomyces laceyi c7654^T/AY094367 [ol-buff; smooth; S]
Streptomyces niveus NRRL 2466^T/DQ442532 [ol-buff; smooth; S] (Williams et al. Cluster 1B)
Streptomyces spheroides NRRL 2449^T/EF178698 [ol-buff; smooth; S] (Williams et al. Cluster 1B)

Clade 28 (100% bootstrap support)
Streptomyces graminofaciens LMG 19892^T/AJ781329 [gray; warty; S] (Williams et al. Cluster 26)
Streptomyces kurssanovii NBRC 13192^T/AB184325 [gray; smooth; RA] (Williams et al. Cluster 60)
Streptomyces peucetius JCM 9920^T/AB045887 [white; smooth; RA]
Streptomyces xantholiticus NBRC 13354^T/AB184349 [gray,white; smooth; S] (Williams et al. Cluster 24)

Clade 29 (65% bootstrap support)
Streptomyces mauvecolor LMG 20100^T/AJ781358 [violet; spiny; S]
Streptomyces michiganensis NBRC 12797^T/AB184153 [ol-buff; smooth; RF] (Williams et al. Cluster 6)
Streptomyces violascens NBRC 12920^T/AB184246 [violet; spiny; S]
Streptomyces xanthochromogenes NRRL B-5410^T/DQ442559 [yellow; smooth; RF] (Williams et al. Cluster 63)

Clade 30 (100% bootstrap support)
Streptomyces melanogenes NRRL B-2072^T/DQ4425527 [gray; smooth; RF] (Williams et al. Cluster 33)
Streptomyces noboritoensis NBRC 13065^T/AB18428⁷ [red, gray; smooth; RF] (Williams et al. Cluster 33)

Clade 31 (96% bootstrap support)
Streptomyces cavourensis subsp. *cavourensis* NBRC 13026^T/AB184264 [ol-buff; smooth; RF] (Williams et al. Cluster 1B)
Streptomyces celluloflavus KCTC 9702^T/AY999829 [ol-buff; smooth; RF]
Streptomyces griseobrunneus CGMCC 4.1838^T/AY999888 [ol-buff; smooth; RF]
Streptomyces roseochromogenus NBRC 13080^T/AB184297 [ol-buff; smooth; RF]

Clade 32 (96% bootstrap support)
Streptomyces cremeus JCM 4362^T/AY999744 [yellow, ol-buff; smooth; S] (Williams et al. Cluster 1B)
Streptomyces spiroverticillatus NBRC 3728^T/AB184796 [ol-buff, white; smooth; RA] (Williams et al. Cluster 6)

Clade 33 (61% bootstrap support)
Streptomyces californicus NBRC 3386^T/AB184755 [red; smooth; RF] (Williams et al. Cluster 9)
Streptomyces floridae NRRL 2423^T/AY999916 [ol-buff, red; smooth; RF] (Williams et al. Cluster 9)
Streptomyces puniceus NBRC 12811^T/AB184163 [ol-buff; smooth; RF]
Streptomyces phaeofaciens NRRL B-1516^T/DQ442539 [gray; smooth; S] (Williams et al. Cluster 31)

Clade 34 (92% bootstrap support)
Streptomyces atroolivaceus KCTC 9017^T/AY999832 [gray; rough; RF] (Williams et al. Cluster 3)
Streptomyces clavifer NBRC 15398^T/AB184649 [white; smooth; RF]
Streptomyces finlayi NRRL B-12114^T/AY999788 [gray; hairy; RF, S] (Williams et al. Single member cluster)
Streptomyces mutomycini LMG 20098^T/AJ781357 [gray; spiny; S]
Streptomyces olivoviridis NBRC 12897^T/AB184227 [gray; smooth; RF, RA-S]

Clade 35 (75% bootstrap support)
Streptomyces atratus NRRL B-16927^T/DQ026638 [gray; smooth; S]
Streptomyces gelaticus NRRL B-2928^T/DQ026636 [gray; smooth; RF] (Williams et al. Single member cluster)
Streptomyces pulveraceus LMG 20322^T/AJ781377 [gray; smooth; S]

Table 1 continued

Streptomyces sanglieri A5843^T/AY094363 [gray; smooth; S]
Streptomyces yanii CGMCC 4.1146^T/AB015854 [brown; smooth; RF]

Clade 36 (89% bootstrap support)
Streptomyces griseolus NBRC 3415^T/AB184768 [gray; smooth; RF] (Williams et al. Cluster 1C)
Streptomyces halstedii NRRL B-1238^T/EF178695 [gray; smooth; RF] (Williams et al. Cluster 1C)

Clade 37 (81% bootstrap support)
Streptomyces flavogriseus DSM 40323^T/AJ494864 [gray; smooth; RF] (Williams et al. Cluster 1C)
Streptomyces flavovirens NBRC 12771^T/AB184133 [gray; smooth, rough; RF] (Williams et al. Cluster 1C)
Streptomyces nigrifaciens NRRL B-2094^T/DQ442531 [gray; smooth; RF] (Williams et al. Cluster 1C)

Clade 38 (92% bootstrap support)
Streptomyces flavotricini NBRC 12770^T/AB184132 [red; smooth; RF] (Williams et al. Cluster 61)
Streptomyces globosus LMG 19896^T/AJ781330 [ol-buff; smooth; RF]
Streptomyces herbaricolor NRRL B-3299^T/DQ442505 [gray; smooth; RF] (Williams et al. Cluster 2)
Streptomyces katrae NRRL B-3093^T/EF654092 [red; smooth; RA, RF] (Williams et al. Cluster 61)
Streptomyces polychromogenes NBRC 13072^T/AB184292 [blue, red; smooth; RF] (Williams et al. Cluster 61)
Streptomyces racemochromogenes NRRL B-5430^T/DQ026656 [red; smooth; RF,RA] (Williams et al. Cluster 61)
Streptomyces toxytricini NRRL B-5426^T/DQ442548 [red; smooth; RF] (Williams et al. Cluster 61)

Clade 39 (81% bootstrap support)
Streptomyces avidinii NRRL 3077^T/AY999904 [red; smooth; RA] (Williams et al. Cluster 56)
Streptomyces cinnamomensis JCM 4019^T/AY999746 [red; smooth; RA]
Streptomyces cirratus NRRL B-3250^T/AY999794 [red; smooth; RA] (Williams et al. Cluster 62)
Streptomyces columbiensis NRRL B-1990^T/DQ026646 [red; smooth; RA-S] (Williams et al. Cluster 61)
Streptomyces goshikiensis NRRL B-5428^T/EF178693 [red; smooth; RA-S] (Williams et al. Cluster 61)
Streptomyces lavendulae subsp. *grasseri* DSM 4038^{5T}/AY999841 [red; smooth; RA]
Streptomyces lavendulae subsp. *lavendulae* NRRL B-1230^T/HQ426713 [red; smooth; RA] (Williams et al. Cluster 61)
Streptomyces nojiriensis KCTC 9784^T/AY999814 [gray; smooth; RA]
Streptomyces spororaveus LMG 20313^T/AJ781370 [red, gray; smooth; RA]
Streptomyces sporoverrucosus NRRL B-16379^T/DQ442544 [gray; hairy; S]
Streptomyces subrutillus DSM 40445^T/×80825 [red; smooth; RF] (Williams et al. Cluster 61)
Streptomyces vinaceus NBRC 13425^T/AB184394 [red; smooth; RA] (Williams et al. Cluster 6)
Streptomyces virginiae IFO 12827^T/D85123 [red; smooth; RA] (Williams et al. Cluster 61)
Streptomyces xanthophaeus NRRL B-5414^T/DQ442560 [gray; smooth; RF] (Williams et al. Cluster 61)

Clade 40 (71% bootstrap support)
Streptomyces exfoliatus NRRL B-2494^T/DQ026647 [red; smooth; RF] (Williams et al. Cluster 5)
Streptomyces gardneri NBRC 12865^T/AB249908 [gray; smooth; RF] (Williams et al. Cluster 5)
Streptomyces lateritius LMG 19372^T/AJ781326 [red; smooth; RA] (Williams et al. Single member cluster)
Streptomyces litmocidini NBRC 12792^T/AB184149 [gray; smooth; RF] (Williams et al. Cluster 5)
Streptomyces narbonensis NBRC 12801^T/AB184157 [gray; smooth; RF] (Williams et al. Cluster 5)
Streptomyces omiyaensis NRRL B-1587^T/EF178697 [gray, red; rough; RF] (Williams et al. Cluster 5)
Streptomyces purpureus NRRL B-5403^T/HQ650808 [red; smooth; RF] (Williams et al. Cluster 65)
Streptomyces venezuelae ISP 5230^T/AY999739 [red, gray, smooth, RF] (Williams et al. Cluster 6)
Streptomyces wedmorensis NRRL 3426^T/DQ442557 [gray; smooth; RF]
Streptomyces zaomyceticus NRRL B-2038^T/EF178685 [gray; smooth; RF] (Williams et al. Cluster 5)

Clade 41 (69% bootstrap support)
Streptomyces albidochromogenes CGMCC 4.1863^T/AY999884 [gray, yellow; smooth; S]
Streptomyces chryseus NRRL B-12347^T/AY999787 [ol-buff, red; smooth; S] (Williams et al. Cluster 17)

Table 1 continued

Streptomyces enissocaecilus NBRC 100763^T/AB249930 [gray; smooth; S]
Streptomyces flavidovirens NBRC 13039^T/AB184270 [gray; smooth, rough; RF]
Streptomyces helveticus NRRL B-12365^T/DQ442504 [red; smooth; S] (Williams et al. Cluster 62)
Streptomyces hypolithicus HSM#10^T/EU196762 [white; smooth; RF]

Clade 42 (100% bootstrap support)
Streptomyces nashvillensis NBRC 13064^T/AB184286 [gray, red; smooth; RF] (Williams et al. Cluster 5)
Streptomyces rubiginosohelvolus NBRC 12912^T/AY999864 [ol-buff, red; smooth; RF]
Streptomyces tanashiensis NBRC 12919^T/AB184245 [gray, red; rough; RF]

Clade 43 (100% bootstrap support)
Streptomyces roseolus NBRC 12816^T/AB184168 [red; smooth; RF] (Williams et al. Cluster 5)
Streptomyces roseosporus CGMCC 4.1871^T/AY999896 [red; rough; RF] (Williams et al. Cluster 5)

Clade 44 (71% bootstrap support)
Streptomyces laurentii LMG 19959^T/AJ781342 [grayish yellow pink; smooth; RA, RF]
Streptomyces roseofulvus CGMCC 4.1847^T/AY999872 [red; smooth; RF] (Williams et al. Cluster 14)

Clade 45 (98% bootstrap support)
Streptomyces showdoensis NBRC 13417^T/AB184389 [ol-buff, gray; smooth; RF] (Williams et al. Cluster 6)
Streptomyces viridobrunneus LMG 20317^T/AJ781372 [gray; smooth; RF]

Clade 46 (63% bootstrap support)
Streptomyces bikiniensis DSM 40581^T/×79851 [gray; smooth; RF] (Williams et al. Cluster 64)
Streptomyces vietnamensis GIMV4.0001^T/DQ311081 [gray; smooth; RF]
Streptomyces violaceorectus NBRC 13102^T/AB184314 [gray; smooth; RF] (Williams et al. Cluster 5)

Clade 47 (100% bootstrap support)
Streptomyces amakusaensis NRRL B-3351^T/AY999781 [blue; smooth; S] (Williams et al. Single member cluster)
Streptomyces inusitatus NBRC 13601^T/AB184445 [blue-gray; smooth; S]

Clade 48 (97% bootstrap support)
Streptomyces gobitricini NRRL B-2956^T/HQ650810 [red; smooth; RA]
Streptomyces lavendofoliae LMG 19935^T/AJ781336 [red; smooth; RA-S]
Streptomyces lavendulocolor NBRC 12881^T/AB184216 [red; smooth; RA] (Williams et al. Cluster 61)
Streptomyces luridus NBRC 12793^T/AB184150 [red; smooth; RA] (Williams et al. Cluster 62)

Clade 49 (100% bootstrap support)
Streptomyces olivovorticillatus NBRC 15273^T/AB184636 [yellow; smooth; BIV] (Williams et al. Cluster 2)
Streptomyces viridiflavus LMG 20277^T/AJ781363 [ol-buff, gray; smooth; BIV]

Clade 50 (99% bootstrap support)
Streptomyces baldacii NRRL B-3500^T/EF178689 [red; smooth; BIV] (Williams et al. Single member cluster)
Streptomyces spitsbergensis NRRL B-24285^T/AY999927 [red; smooth; BIV]

Clade 51 (98% bootstrap support)
Streptomyces albireticuli JCM 4116^T/AY999748 [ol-buff; smooth; BIV] (Williams et al. Single member cluster)
Streptomyces eurocidicus NRRL B-1676^T/AY999790 [ol-buff; smooth; BIV] (Williams et al. Cluster 56)

Clade 52 (95% bootstrap support)
Streptomyces distallicus NRRL 2886^T/EF178671 [red; smooth; BIV] (Williams et al. Cluster 56)
Streptomyces flavopersicus NBRC 12769^T/AB249911 [red; smooth; BIV-S] (Williams et al. Single member cluster)
Streptomyces kentuckensis NRRL B-1831^T/DQ442512 [red; smooth; BIV]
Streptomyces netropsis NBRC 3723^T/AB184792 [red; smooth; BIV-S]
Streptomyces syringium LMG 20320^T/AJ781375 [red; smooth; BIV]

Table 1 continued

Clade 53 (82% bootstrap support)

- Streptacidiphilus albus* DSM 41753^T/AF074415 [white; smooth; RF]
- Streptacidiphilus anmyonensis* AM-11^T/DQ904546 [grayish white; smooth; RF]
- Streptacidiphilus carbonis* DSM 41754^T/AF074412 [white; smooth; RF]
- Streptacidiphilus jiangxiensis* 33214^T/AY314780 [white, grayish white; smooth; RF]
- Streptacidiphilus melanogenes* SB-B34^T/DQ994689 [white; smooth; RF]
- Streptacidiphilus neutrinimicus* NBRC 100921^T/AB249949 [white; smooth; RF]
- Streptacidiphilus rugosus* AM-16^T/DQ904547 [white; smooth; RF]

Clade 54 (72% bootstrap support)

- Streptomyces griseoplanus* NBRC 12779^T/AB184138 [gray; smooth; S] (Williams et al. Cluster 29)
- Streptacidiphilus oryzae* TH49^T/DQ208700 [grayish white, smooth; RF]

Clade 55 (99% bootstrap support)

- Streptomyces avellaneus* NBRC 13451^T/AB184413 [gray; smooth; RF] (Williams et al. Cluster 67)
- Streptomyces aureofaciens* NBRC 12594^T/AB184105 [gray; smooth; RF, RA] (Williams et al. Cluster 14)

Clade 56 (99% bootstrap support)

- Kitasatospora putterlickiae* F18-98^T/AY189976 [gray; smooth; RF]
- Kitasatospora sampliensis* VT-36^T/AY260167 [gray; smooth; RF]

Clade 57 (86% bootstrap support)

- Kitasatospora azatica* NBRC 13803^T/U93312 [gray; smooth; RF]
- Streptomyces purpeofuscus* LMG 20283^T/AJ781364 [red, gray; smooth; RF, RA]

Clade 58 (67% bootstrap support)

- Kitasatospora kazusensis* SK60^T/AB278569 [white; smooth; RF]
- Kitasatospora mediocidica* NBRC 14789^T/U93324 [gray; smooth; RF]

Clade 59 (73% bootstrap support)

- Kitasatospora atroaurantiaca* NRRL B-24282^T/DQ026645 [white; smooth; RF]
- Kitasatospora gansuensis* HKI 0314^T/AY442265 [white, beige; smooth; RF]

Clade 60 (100% bootstrap support)

- Kitasatospora cineracea* SK-3255^T/AB022875 [white, gray; smooth, RF]
- Kitasatospora niigatensis* NBRC 16453^T/AB249960 [gray, br-white; smooth; RF]

Clade 61 (100% bootstrap support)

- Kitasatospora cochleata* NBRC 14768^T/AB184619 [gray; smooth; RA-S]
- Kitasatospora paracochleata* 4769^T/U93328 [gray; smooth; S]
- Streptomyces cinereorectus* JCM 6916^T/AY999764 [gray; smooth; RF]

Clade 62 (60% bootstrap support)

- Streptomyces griseovorticillatus* CGMCC 4.1842^T/AY999892 [red; smooth; BIV] (Williams et al. Cluster 58)
- Streptomyces sapporonensis* LMG 20324^T/AJ781378 [red, white; smooth; BIV]
- Streptomyces varsoviensis* NRRL B-3589^T/DQ026653 [white; smooth; S]

Clade 63 (98% bootstrap support)

- Streptomyces ehimensis* KCTC 9727^T/AY999834 [ol-buff, gray; smooth; BIV] (Williams et al. Cluster 55)
- Streptomyces luteovorticillatus* NBRC 3840^T/AB184803 [ol-buff, gray; smooth; BIV]

Clade 64 (68% bootstrap support)

- Streptomyces lacticiproducens* GIMN4.001^T/GQ184344 [yellowish-white; smooth; MIV]
- Streptomyces luteireticuli* NRRL B-12435^T/HQ650809 [yellow, gray; smooth; BIV] (Williams et al. Cluster 44)

Clade 65 (61% bootstrap support)

- Streptomyces roseovorticillatus* NRRL B-1993^T/HQ650807 [red; smooth; BIV]
- Streptomyces salmonis* NBRC 15865^T/AB184705 [red; smooth; BIV]

Table 1 continued

Clade 66 (100% bootstrap support)

Streptomyces kishiwadensis LMG 19939^T/AJ781338 [red; smooth; BIV]*Streptomyces mashiensis* NRRL B-8164^T/DQ442526 [red; smooth; BIV] (Williams et al. Cluster 55)

Clade 67 (68% bootstrap support)

Streptomyces albogriseus JX42^T/AF513222 [gray; smooth; S]*Streptomyces albulus* IMC S-0802^T/AB024440 [gray; spiny; RA-S] (Williams et al. Cluster 29)*Streptomyces lunalinharesii* RCQ1071^T/DQ094838 [gray; spiny; S]*Streptomyces noursei* NBRC15452^T/AB184678 [gray; spiny; S]*Streptomyces yunnanensis* YIM 41004^T/AF346818 [gray; spiny; S]

Clade 68 (100% bootstrap support)

Streptomyces chattanoogensis DSM 40002^T/AJ621611 [gray, ol-buff; spiny; S] (Williams et al. Cluster 35)*Streptomyces lydicus* ATCC 25470^T/Y15507 [gray; smooth; S] (Williams et al. Cluster 29)

Clade 69 (80% bootstrap support)

Streptomyces hygroscopicus subsp. *glebosus* CGMCC 4.1873^T/AY999875 [gray; smooth; S]*Streptomyces libani* subsp. *rufus* LMG 20087^T/AJ781351 [gray; smooth; S]*Streptomyces platensis* JCM 4662^T/AB045882 [gray; smooth; S] (Williams et al. Cluster 29)

Clade 70 (60% bootstrap support)

Streptomyces libani subsp. *libani* NRRL B-3446^T/DQ442518 [gray; smooth; RA-S] (Williams et al. Cluster 29)*Streptomyces nigrescens* NRRL B-12176^T/DQ442530 [gray; smooth; S] (Williams et al. Cluster 29)*Streptomyces tubercidicus* DSM 40261^T/AJ621612 [gray; smooth; RA-S] (Williams et al. Cluster 47)

Clade 71 (87% bootstrap support)

Streptomyces albofaciens JCM 4342^T/AB045880 [gray; smooth; RA-S] (Williams et al. Cluster 42)*Streptomyces chrestomyceticus* NRRL B-3293^T/DQ026633 [white; smooth; RA-S] (Williams et al. Cluster 42)*Streptomyces rimosus* subsp. *paromomycinus* DSM 41429^T/AJ621610 [white; smooth; S]

Clade 72 (99% bootstrap support)

Streptomyces erumpens DSM 40941^T/AJ621603 [gray; smooth; RA-S]*Streptomyces rimosus* subsp. *rimosus* JCM 4667^T/AB045883 [gray; smooth; S] (Williams et al. Cluster 42)

Clade 73 (62% bootstrap support)

Streptomyces olivaceiscleroticus DSM 40595^T/AJ621606 [red, gray; smooth; S]*Streptomyces monomycini* NRRL B-24309^T/DQ445790 [white; smooth; S]*Streptomyces niger* DSM 43049^T/AJ621607 [gray; smooth; S] (Williams et al. Cluster 40)

Clade 74 (78% bootstrap support)

Streptomyces ochraceiscleroticus NRRL B-3041^T/DQ442533 [ol-buff, white; smooth; S] (Williams et al. Cluster 41)*Streptomyces purpurogeneiscleroticus* DSM 43156^T/AJ621604 [white; smooth; S] (Williams et al. Cluster 40)*Streptomyces violens* DSM 40597^T/AJ621605 [gray; smooth; S] (Williams et al. Cluster 40)

Clade 75 (64% bootstrap support)

Streptomyces demainii NRRL B-1478^T/DQ334782 [gray; rugose; S]*Streptomyces endus* NBRC 12859^T/AB249959 [gray; rugose; S] (Williams et al. Cluster 32)*Streptomyces hygroscopicus* subsp. *hygroscopicus* NRRL 2387^T/AJ391820 [gray; rugose; S] (Williams et al. Cluster 32)*Streptomyces ruanii* ISP 5276^T/EF408737 [gray; rugose; S]*Streptomyces sporocinereus* LMG 20311^T/AJ781368 [gray; rugose; S]

Clade 76 (87% bootstrap support)

Streptomyces albiflaviniiger NRRL B-1356^T/AJ391812 [gray; rugose; S]*Streptomyces javensis* NBRC 100777^T/AB249940 [gray; rugose; S]*Streptomyces violaceusniger* NBRC 13459^T/AB184420 [gray, rugose, S] (Williams et al. Cluster 32)*Streptomyces yogykartensis* NBRC 100779^T/AB249942 [gray; rugose; S]

Table 1 continued

Clade 77 (91% bootstrap support)

- Streptomyces iranensis* HM35^T/FJ472862 [gray; rugose; S]
Streptomyces rapamycinicus NRRL 5491^T/EF408733 [gray; rugose; S]

Clade 78 (98% bootstrap support)

- Streptomyces asiaticus* A14P1^T/AJ391830 [gray; rugose; S]
Streptomyces cangkringensis D13P3^T/AJ391831 [gray; rugose; S]
Streptomyces griseiniger NRRL B-1865^T/AJ391818 [gray; rugose; S]
Streptomyces indonesiensis DSM 41759^T/AJ391835 [gray; rugose; S]
Streptomyces rhizosphaericus A10P1^T/AJ391834 [gray; rugose; S]

Clade 79 (90% bootstrap support)

- Streptomyces malaysiensis* ATB-11^T/AF117304 [gray; rugose; S]
Streptomyces samsunensis DSM 42010^T/EU077190 [gray; rugose; S]

Clade 80 (67% bootstrap support)

- Streptomyces antimycoticus* KCTC 9694^T/AY999831 [gray; rugose; S]
Streptomyces castelarensis DSM 40830^T/AY508511 [gray; rugose; S]
Streptomyces geldanomycinicus NRRL 3602^T/DQ33478 [gray; rugose; S]
Streptomyces hygrosopicus subsp. *enhygrus* NRRL 3664^T/DQ442510 [gray; rugose; S]
Streptomyces melanosporofaciens NRRL B-12234^T/AJ391837 [gray, yellow; rugose; S] (Williams et al. Cluster 32)
Streptomyces mordarskii NRRL B-1346^T/EF408735 [gray; rugose; S]
Streptomyces sporoclivatus LMG 20312^T/AJ781369 [gray; rugose; S]

Clade 81 (91% bootstrap support)

- Streptomyces aldersoniae* NRRL 18513^T/EU170123 [gray; smooth; S]
Streptomyces cuspidosporus CGMCC 4.1686^T/AY999890 [gray; rugose; S]
Streptomyces sparsogenes NBRC 13086^T/AB184301 [gray; ridged; RA-S] (Williams et al. Cluster 32)

Clade 82 (100% bootstrap support)

- Streptomyces aureoversilis* NBRC 13021^T/AY999849 [red; smooth; BIV]
Streptomyces reactivicillatus NRRL B-12369^T/DQ026657 [red; smooth; BIV] (Williams et al. Cluster 57)

Clade 83 (79% bootstrap support)

- Streptomyces arduus* DSM 40527^T/AY999843 [ol-buff; smooth; BIV]
Streptomyces blastmyceticus NRRL B-5480^T/AY999802 [gray-green; smooth; MIV] (Williams et al. Cluster 58)

Clade 84 (100% bootstrap support)

- Streptomyces cinnamoneus* NBRC 12852^T/AB184850 [red; smooth; BIV] (Williams et al. Cluster 55)
Streptomyces pseudoehinosporus NBRC 12518^T/AB184100 [white, gray; smooth; RF]

Clade 85 (76% bootstrap support)

- Streptomyces coeruleoprunus* NBRC 15400^T/AB184651 [blue; smooth; RF]
Streptomyces fradiae NRRL B-1195^T/DQ026630 [red; smooth; RA] (Williams et al. Cluster 68)
Streptomyces roseoflavus NBRC 13439^T/AB184403 [red; smooth; RA]
Streptomyces somaliensis DSM 40738^T/AJ007403 [white; none; none] (Williams et al. Cluster 70)

Clade 86 (67% bootstrap support)

- Streptomyces capillispiralis* KCTC 1719^T/AY999816 [gray; hairy; S]
Streptomyces gancidicus NBRC 15412^T/AB184660 [gray; spiny; S]
Streptomyces pseudogriseolus NRRL B-3288^T/DQ442541 [gray, ol-buff; spiny; RA-S] (Williams et al. Cluster 12)
Streptomyces rubiginosus KCTC 9042^T/AY999810 [gray; spiny; RA-S] (Williams et al. Cluster 12)

Clade 87 (99% bootstrap support)

- Streptomyces flaviscleroticus* NBRC 12998^T/AB184247 [yellow; smooth; S] (Williams et al. Cluster 15)
Streptomyces minutiscleroticus NBRC 13361^T/AB184351 [green; smooth; S] (Williams et al. Cluster 15)

Table 1 continued

Clade 88 (82% bootstrap support)
<i>Streptomyces azureus</i> NRRL B-2655 ^T /EF178674 [blue; smooth, rough; S] (Williams et al. Cluster 18)
<i>Streptomyces caelestis</i> NBRC 12749 ^T /AB184838 [blue; rough; RA-S] (Williams et al. Cluster 18)
Clade 89 (100% bootstrap support)
<i>Streptomyces afghaniensis</i> ISP 5228 ^T /AJ399483 [blue, red; spiny; S] (Williams et al. Cluster 18)
<i>Streptomyces africanus</i> CPJVR-H ^T /AY208912 [blue; hairy; S]
Clade 90 (69% bootstrap support)
<i>Streptomyces griseoviridis</i> NBRC 12874 ^T /AB184210 [ol-buff, red; smooth; RA-S] (Williams et al. Cluster 17)
<i>Streptomyces zinciresistens</i> CCNWNQ 0016 ^T /GU225938 [gray, greenish-gray; spiny; S]
Clade 91 (77% bootstrap support)
<i>Streptomyces fumigatiscleroticus</i> NRRL B-3856 ^T /DQ442499 [gray; smooth; S]
<i>Streptomyces poonensis</i> NRRL B-2319 ^T /DQ445792 [white; smooth; S] (Williams et al. Cluster 22)
Clade 92 (94% bootstrap support)
<i>Streptomyces roseiscleroticus</i> CGMCC 4.1846 ^T /AY999893 [white, red; smooth; S] (Williams et al. Cluster 22)
<i>Streptomyces ruber</i> NBRC 14600 ^T /AB184604 [ol-buff; smooth; S]
Clade 93 (100% bootstrap support)
<i>Streptomyces arenae</i> ISP 5293 ^T /AJ399485 [red, gray; spiny; S] (Williams et al. Cluster 18)
<i>Streptomyces violarus</i> ISP 5205 ^T /AJ399477 [red, violet; spiny; RA-S] (Williams et al. Cluster 18)
Clade 94 (97% bootstrap support)
<i>Streptomyces griseoaurantiacus</i> NBRC 15440 ^T /AB184676 [white; smooth; RF] (Williams et al. Cluster 12)
<i>Streptomyces jietaisiensis</i> FXJ46 ^T /AY314783 [gray; smooth; RF]
Clade 95 (63% bootstrap support)
<i>Streptomyces alboflavus</i> NRRL B-2373 ^T /EF178699 [ol-buff; smooth; RF] (Williams et al. Cluster 54)
<i>Streptomyces flavofungini</i> NRRL B-12307 ^T /AY999792 [white; smooth; RF] (Williams et al. Cluster 42)
<i>Streptomyces fulvissimus</i> NBRC 3717 ^T /AB184787 [red, ol-buff; smooth; RF] (Williams et al. Single member cluster)
Clade 96 (74% bootstrap support)
<i>Streptomyces iakyrus</i> NBRC 13401 ^T /AB184877 [gray, red; spiny; S]
<i>Streptomyces violaceochromogenes</i> NBRC 13100 ^T /AB184312 [red; smooth; RA-S]
Clade 97 (96% bootstrap support)
<i>Streptomyces misionensis</i> NRRL B-3230 ^T /EF178678 [red, gray; smooth; S] (Williams et al. Cluster 31)
<i>Streptomyces phaeoluteichromatogenes</i> NRRL 5799 ^T /AJ391814 [brown-gray; smooth; RF]
Clade 98 (99% bootstrap support)
<i>Streptomyces glaucescens</i> NBRC 12774 ^T /AB184843 [blue; hairy; S] (Williams et al. Cluster 28)
<i>Streptomyces pharetrae</i> CZA14 ^T /AY699792 [blue-green; hairy; S]
Clade 99 (74% bootstrap support)
<i>Streptomyces althioticus</i> KCTC 9752 ^T /AY999808 [gray; smooth; S] (Williams et al. Cluster 12)
<i>Streptomyces pseudogriseolus</i> subsp. <i>linmyceticus</i> NRRL 3985 ^T /×80827 [gray; spiny; RA-S]
Clade 100 (77% bootstrap support)
<i>Streptomyces arabicus</i> NBRC 3406 ^T /AB184763 [gray; spiny; S] (Williams et al. Cluster 12)
<i>Streptomyces erythrogriseus</i> NBRC 14601 ^T /AB184605 [gray; spiny; S]
<i>Streptomyces griseoincarnatus</i> NBRC 12871 ^T /AB184207 [gray, red; spiny; RA-S] (Williams et al. Cluster 13)
<i>Streptomyces griseorubens</i> NBRC 12780 ^T /AB184139 [gray; spiny; RA-S]
<i>Streptomyces labedae</i> NBRC 15864 ^T /AB184704 [gray; spiny; S]
<i>Streptomyces matensis</i> NRRL B-2576 ^T /EF626596 [gray; spiny; RA-S] (Williams et al. Cluster 12)
<i>Streptomyces variabilis</i> NRRL B-3984 ^T /DQ442551 [gray, red; spiny; RA-S] (Williams et al. Cluster 12)

Table 1 continued

Clade 101 (100% bootstrap support)

Streptomyces albaduncus JCM 4715^T/AY999757 [gray; spiny; RA-S]*Streptomyces griseoloalbus* NBRC 13046^T/AB184275 [yellowish-white; smooth; RF]

Clade 102 (85% bootstrap support)

Streptomyces marokkonensis LMG 23016^T/AJ965470 [gray; smooth; S]*Streptomyces thinghirensis* S10^T/FM202482 [gray; smooth; S]

Clade 103 (60% bootstrap support)

Streptomyces anthrocyanicus NBRC 14892^T/AB184631 [white, red; smooth; RF]*Streptomyces coelestis* DSM 40421^T/AF503496 [gray; smooth; S] (Williams et al. Cluster 21)*Streptomyces humiferus* DSM 43030^T/AF503491 [red, gray; smooth; S] (Williams et al. Cluster 21)*Streptomyces lienomycini* NBRC 15425^T/AB184672 [gray; smooth; S]*Streptomyces rubrogriseus* LMG 20318^T/AJ781373 [gray; smooth; S]*Streptomyces sannanensis* NRRL B-24303^T/AY999924 [gray; smooth; RA-S]*Streptomyces tendae* NBRC 12822^T/AB184172 [gray; smooth; S] (Williams et al. Cluster 12)*Streptomyces tritolerans* DSM 41899^T/DQ345779 [gray; smooth; RF]*Streptomyces violaceolatus* DSM 40438^T/AF503497 [gray; smooth; S] (Williams et al. Cluster 21)*Streptomyces violaceoruber* DSM 40049^T/AF503492 [gray; smooth; S]*Streptomyces violaceorubidus* LMG 20319^T/AJ781374 [white, gray; smooth; S]

Clade 104 (99% bootstrap support)

Streptomyces griseomycini NBRC 12778^T/AB184137 [ol-buff, gray; hairy; RA-S] (Williams et al. Cluster 12)*Streptomyces griseostramineus* NBRC 12781^T/AB184140 [ol-buff, gray; hairy; RA] (Williams et al. Cluster 60)

Clade 105 (99% bootstrap support)

Streptomyces thermoalcalitolerans NBRC 16322^T/AB249909 [gray; warty; S]*Streptomyces thermogriseus* CCTCC AA97014^T/AF056714 [gray; smooth; RF]*Streptomyces thermotrificans* DSM 40579^T/Z68098 [gray; smooth; RF,S] (Williams et al. Cluster 36)*Streptomyces thermovulgaris* DSM 40444^T/Z68094 [gray; smooth; S] (Williams et al. Cluster 36)

Clade 106 (99% bootstrap support)

Streptomyces janthinus ISP 5206^T/AJ399478 [red; spiny; S] (Williams et al. Cluster 18)*Streptomyces roseoviolaceus* ISP 5277^T/AJ399484 [red; spiny; S] (Williams et al. Cluster 18)*Streptomyces violaceus* LMG 20257^T/AJ781755 [red, violet; spiny; RA-S] (Williams et al. Cluster 6)

Clade 107 (100% bootstrap support)

Streptomyces hawaiiensis ISP 5042^T/AJ399466 [yellow; spiny; S] (Williams et al. Cluster 18)*Streptomyces massaporeus* DSM 40035^T/AY999836 [violet; smooth; RA-S] (Williams et al. Single member cluster)

Clade 108 (100% bootstrap support)

Streptomyces bellus ISP 5185^T/AJ399476 [blue; spiny; RA-S] (Williams et al. Cluster 18)*Streptomyces coeruleorubidus* NBRC 12844^T/AB184849 [blue; spiny; S] (Williams et al. Cluster 18)

Clade 109 (96% bootstrap support)

Streptomyces lusitanus NBRC 13464^T/AB184424 [gray; spiny; RA-S] (Williams et al. Cluster 44)*Streptomyces thermocarboxydus* DSM 44293^T/U94490 [gray; warty; RA]

Clade 110 (100% bootstrap support)

Streptomyces albogriseolus NRRL B-1305^T/AJ494865 [gray; smooth; S] (Williams et al. Cluster 12)*Streptomyces viridodiastaticus* NBRC 13106^T/AB184317 [gray; spiny; RA-S]

Clade 111 (100% bootstrap support)

Streptomyces flavoviridis NBRC 12772^T/AB184842 [gray; hairy; RA-S] (Williams et al. Cluster 28)*Streptomyces pilosus* NBRC 12807^T/AB184161 [gray; hairy; S] (Williams et al. Cluster 37)

Table 1 continued

Clade 112 (99% bootstrap support)

- Streptomyces albidoflavus* DSM 40455^T/Z76676 [ol-buff; smooth; RF] (Williams et al. Cluster 1A)
Streptomyces canescens DSM 40001^T/Z76684 [ol-buff; smooth; RF] (Williams et al. Cluster 1B)
Streptomyces champvatii NRRL B-5682^T/DQ026642 [ol-buff; smooth; RF]
Streptomyces coelicolor DSM 40233^T/Z76678 [ol-buff; smooth; RF] (Williams et al. Cluster 1B)
Streptomyces felleus DSM 40130^T/Z76681 [ol-buff; smooth; RF] (Williams et al. Cluster 1B)
Streptomyces globisporus subsp. *caucasicus* NBRC 100770^T/AB249937 [ol-buff; smooth; RF]
Streptomyces griseus subsp. *solvifaciens* CGMCC 4.1845^T/AY999871 [ol-buff; smooth; RF]
Streptomyces koyangensis VK-A60^T/AY079156 [yellowish white; smooth; RF]
Streptomyces limosus DSM 40131^T/Z76679 [ol-buff; smooth; RF] (Williams et al. Cluster 1B)
Streptomyces odorifer DSM 40347^T/Z76682 [ol-buff; smooth; RF] (Williams et al. Cluster 1B)
Streptomyces sampsonii DSM 40394^T/Z76680 [ol-buff; smooth; RF] (Williams et al. Cluster 1B)

Clade 113 (97% bootstrap support)

- Streptomyces diastaticus* NBRC 3714^T/AB184785 [ol-buff; smooth; RF, S] (Williams et al. Cluster 19)
Streptomyces gougerotii DSM 40324^T/Z76687 [white; smooth; RF] (Williams et al. Cluster 1B)
Streptomyces intermedius DSM 40372^T/Z76686 [ol-buff; smooth; RF] (Williams et al. Cluster 18)
Streptomyces rutgersensis subsp. *rutgersensis* DSM 40077^T/Z76688 [ol-buff; smooth; RF] (Williams et al. Cluster 1B)

Clade 114 (63% bootstrap support)

- Streptomyces chromofuscus* NBRC 12851^T/AB184194 [gray; spiny; S] (Williams et al. Cluster 15)
Streptomyces coeruleofuscus NBRC 12757^T/AB184840 [blue; spiny; S] (Williams et al. Cluster 18)
Streptomyces coerulescens CGMCC 4.1597^T/FJ406114 [blue; spiny; S] (Williams et al. Cluster 18)

Clade 115 (74% bootstrap support)

- Streptomyces eurhythmus* ATCC 14975^T/D63870 [gray; smooth; RA-S] (Williams et al. Cluster 23)
Streptomyces lavenduligriseus NBRC 13045^T/AB184382 [ol-buff; smooth; BIV-S] (Williams et al. Cluster 34)

Clade 116 (99% bootstrap support)

- Streptomyces bangladeshensis* AAB-4^T/AY750056 [ol-buff; smooth; RF]
Streptomyces rameus NBRC 15453^T/AB184679 [gray; smooth; S]
Streptomyces roseodiataticus CGMCC 4.1867^T/AY999880 [gray; smooth; S]
Streptomyces tricolor LMG 20328^T/AJ781380 [gray; smooth; S]

Clade 117 (68% bootstrap support)

- Streptomyces achromogenes* subsp. *rubradiris* KCTC 9742^T/AY999846 [gray; smooth; RF]
Streptomyces nodosus NRRL B-2371^T/DQ026661 [gray; smooth; S] (Williams et al. Cluster 35)

Clade 118 (97% bootstrap support)

- Streptomyces asterosporus* NRRL B-24328^T/AY999902 [gray; rough; S]
Streptomyces aureorectus NRRL B-24301^T/EF654094 [yellowish-white; smooth; RF]
Streptomyces calvus ISP 5010^T/AY999780 [gray; hairy; S] (Williams et al. Cluster 12)
Streptomyces virens NRRL B-24331^T/DQ442554 [yellow, ol-buff; spiny; S]

Clade 119 (88% bootstrap support)

- Streptomyces ennisocaeilis* NRRL B-16365^T/DQ026641 [gray, smooth, S]
Streptomyces geysiriensis NRRL B-12102^T/DQ442501 [gray; smooth; S]
Streptomyces mutabilis NRRL ISP-5169^T/EF178679 [white, gray; smooth, rough; RA-S] (Williams et al. Cluster 12)
Streptomyces plicatus NBRC 13071^T/AB184291 [gray; smooth; S] (Williams et al. Cluster 12)
Streptomyces rochei NRRL B-1559^T/EF626598 [red, gray; smooth, S] (Williams et al. Cluster 12)
Streptomyces vinaceusdrappus NRRL 2363^T/AY999929 [red, gray, smooth, S] (Williams et al. Cluster 12)

Table 1 continued

Clade 120 (67% bootstrap support)

Streptomyces albus subsp. *pathocidicus* NBRC 13812^T/AB184501 [white; smooth; S]

Streptomyces hebeiensis YIM 001^T/AY277529 [gray; smooth; RF]

Clade 121 (78% bootstrap support)

Streptomyces paucisporeus 1413^T/AY876943 [gray; smooth; RF]

Streptomyces yanglinensis 1307^T/AY876940 [gray; smooth; RF]

Clade 122 (70% bootstrap support)

Streptomyces rubidus 13C15^T/AY876941 [reddish-brown; smooth; RF]

Streptomyces yeochonensis CN732^T/AF101415 [gray; smooth; RF]

Clade 123(98% bootstrap support)

Streptomyces aculeolatus NBRC 14824^T/AB184624 [white; spiny; S]

Streptomyces synnematoformans S155^T/EF121313 [gray, red; smooth; RF]

Clade 124 (100% bootstrap support)

Streptomyces armeniacus JCM 3070^T/AB018093 [white; smooth; S]

Streptomyces artemisiae YIM 63135^T/EU200685 [pink, yellowish-white; smooth; S]

Clade 125 (95% bootstrap support)

Streptomyces haliclona NBRC 105049^T/AB473556 [white; smooth; S]

Streptomyces marinus NBRC 105047^T/AB473554 [white; smooth; S]

Clade 126 (100% bootstrap support)

Streptomyces albus subsp. *albus* NRRL B-2365^T/DQ026669 [white; smooth; S] (Williams et al. Cluster 16)

Streptomyces almquistii NBRC 13015^T AB184258 [white; smooth; S] (Williams et al. Cluster 16)

Streptomyces flocculus NRRL B-2465^T/DQ442498 [white; smooth; S] (Williams et al. Cluster 16)

Streptomyces gibsonii LMG 19912^T/AJ781753 [white; smooth; S]

Streptomyces ragoonensis NBRC 13078^T/AY999859 [white; smooth; S]

Clade 127 (86% bootstrap support)

Streptomyces glaucosporus NBRC 15416^T/AB184664 [greenish-gray; warty; S]

Streptomyces macrosporus DSM 41449^T/Z68099 [green; warty; S] (Williams et al. Cluster 38)

Streptomyces megasporus DSM 41476^T/Z68100 [green; warty; S]

Streptomyces radiopugnans R97^T/DQ912930 [white, gray; rough; S]

Clade 128 (79% bootstrap support)

Streptomyces carpaticus NRRL B-16359^T/DQ442494 [gray, red; smooth; RA-S]

Streptomyces cheonanensis VC-A46^T/AY822606 [gray, white; smooth; RF]

Streptomyces xiamenensis MCCC 1A01550^T/EF012099 [gray; smooth; RF]

Clade 129 (99% bootstrap support)

Streptomyces avicenniae CGMCC 4.5510^T/EU399234 [red, yellow, olive; smooth; S]

Streptomyces hainanensis YIM 47672^T/AM398645 [pink-white; smooth; RA-S]

Streptomyces mayteni YIM 60475^T/EU200683 [white, yellowish-white; smooth; RA-S]

Streptomyces phaeoviridis NRRL B-2258^T/DQ026665 [gray, red; smooth; RA-S] (Williams et al. Cluster 19)

Streptomyces sedi YIM 65188^T/EU925562 [white; smooth; S]

Streptomyces specialis GW 41-1564^T/AM934703 [pink-white; smooth; S]

Clade 130 (81% bootstrap support)

Streptomyces aomiensis NBRC 106164^T/AB522686 [gray; smooth; RF]

Streptomyces scabrisporus KM-4927^T/AB030585 [gray; rugose; S]

RF, *Rectiflexibles* or flexuous spore chains; RA, *Retinaculiaperti* or spore chains in open loops; S *Spirales* or spores in spiral chains; ol-buff, olive-buff color

Streptacidiphilus as well as the species of the former genus *Streptoverticillium*. The location of the species of these genera in the current tree would suggest that they could only be valid if the genus *Streptomyces* were polyphyletic but, because of the highly conserved nature of the 16S ribosomal RNA gene, there is insufficient variability and hence phylogenetic signal present to provide statistical support for the backbone of the tree. As a result of this limitation, it is not possible at this time to predict the relationships of most of the individual clades with each other. A major value of the phylogenetic tree and associated data presented in this study is as the guide map for further studies, either utilizing sequencing of multiple house-keeping genes as has been already demonstrated by the studies of Guo et al. (2008); Rong et al. (2009); Rong and Huang (2010), and Labeda (2011), or in selecting appropriate species for genome sequencing projects as the cost of these studies continue to decline.

As additional genome sequences for type strains of *Streptomyces* species become available and expanded studies of the sequences of numerous house-keeping genes are completed, it may be possible to construct a more robust, statistically supported phylogeny of the family *Streptomycetaceae* but it is just as likely that the propensity of streptomycetes to happily exchange genetic information will continue to confound efforts to propose a species concept for the genus *Streptomyces*.

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References

A co-operative study, Gottlieb D (1961) An evaluation of criteria and procedures used in the description and characterization of the streptomycetes. *Appl Microbiol* 9:55–65

Anderson AS, Wellington EMH (2001) The taxonomy of *Streptomyces* and related genera. *Int J Syst Evol Microbiol* 51:797–814

Bouček-Mechiche K, Gardan L, Andrivon D, Normand P (2006) *Streptomyces turgidiscabies* and *Streptomyces reticuliscabies*: one genomic species, two pathogenic groups. *Int J Syst Evol Microbiol* 56:2771–2776

Chun J, Goodfellow M (1995) A phylogenetic analysis of the genus *Nocardia* with 16S rRNA gene sequences. *Int J Syst Bacteriol* 45:240–245

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39:783–791

Felsenstein J (1993) Phylogeny inference package (PHYLIP) version 3.5. University of Washington, Seattle

Ferguson EV, Ward AC, Sanglier J-J, Goodfellow M (1997) Evaluation of *Streptomyces* species-groups by pyrolysis mass spectrometry. *Zbl Bakt* 285:169–181

Goodfellow M, Williams ST, Alderson G (1986a) Transfer of *Elytrosporangium brasiliense* Falcão de Moraes et al., *Elytrosporangium spirale* Falcão de Moraes et al., *Microellobosporia flava* Cross et al., *Microellobosporia grisea* (Konev et al.) Pridham and *Microellobosporia violacea* (Tsyganov et al.) Pridham to the genus *Streptomyces*, with emended descriptions of the species. *Syst Appl Microbiol* 8:48–54

Goodfellow M, Williams ST, Alderson G (1986b) Transfer of *Chainia* species to the genus *Streptomyces* with emended description of species. *Syst Appl Microbiol* 8:55–60

Goodfellow M, Williams ST, Alderson G (1986c) Transfer of *Actinosporangium violaceum* Krasil'nikov and Yuan, *Actinosporangium vitaminophilum* Shomura et al. and *Actinopyridium caeruleum* Krasil'nikov to the genus *Streptomyces*, with emended descriptions of the species. *Syst Appl Microbiol* 8:61–64

Goodfellow M, Williams ST, Alderson G (1986d) Transfer of *Kitasatoa purpurea* Matsumae and Hata to the genus *Streptomyces* as *Streptomyces purpureus* comb. nov. *Syst Appl Microbiol* 8:65–66

Goodfellow M, Ferguson EV, Sanglier J-J (1992) Numerical classification and identification of *Streptomyces* species—a review. *Gene* 115:225–233

Goodfellow M, Kumar Y, Labeda DP, Sembiring L (2007) The *Streptomyces violaceusniger* clade: a home for streptomycetes with rugose ornamented spores. *Antonie van Leeuwenhoek* 92:173–197

Gottlieb D (1963) Recommendations for description of some *Actinomycetales* appearing in patent applications. *Int Bull Bacteriol Nomencl Taxon* 13:159–160

Guo Y, Zheng W, Rong X, Huang Y (2008) A multilocus phylogeny of the *Streptomyces griseus* 16S rRNA gene clade: use of multilocus sequence analysis for streptomycete systematics. *Int J Syst Evol Microbiol* 58:149–159

Hall TA (1999) BioEdit, a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symp Ser* 41:95–98

Kämpfer P (2011) Genus *Streptomyces* Waksman and Henrici 1943, 339^{AL} emend. Witt and Stackebrandt 1990, 370, emend. Wellington, Stackebrandt, Sanders, Wolstrup and Jørgensen, 1992, 159. In: Goodfellow M, Kämpfer P, Busse H-J, Trujillo M, Suzuki KE, Ludwig W, Whitman WB (eds) *Bergey's Manual of Systematic Bacteriology*, 2nd edn, volume 5 Springer, USA (in press)

Kämpfer P, Kroppenstedt RM, Dott W (1991) A numerical classification of the genera *Streptomyces* and *Streptoverticillium* using miniaturized physiological tests. *J Gen Microbiol* 137:1831–1891

Kim D, Chun J, Sahin N, Hah YC, Goodfellow M (1996) Analysis of thermophilic clades within the genus

- Streptomyces* by 16S ribosomal DNA sequence comparisons. *Int J Syst Bacteriol* 46:581–587
- Kim SB, Lonsdale JT, Seong C-N, Goodfellow M (2003) *Streptacidiphilus* gen. nov., a home for acidiphilic actinomycetes with a wall chemotype 1 and emendation of the family *Streptomycetaceae* (Waksman & Henrici 1943 emend Rainey et al. 1997) *Antonie van Leeuwenhoek* 83:107–116
- Krainsky A (1914) Die Aktinomyceten und ihren Bedeutung in der Natur. *Zentrbl Bacteriol Parasiterikd Infektionkr Hyg II Abt* 41:649–688
- Kumar Y, Goodfellow M (2008) Five new members of the *Streptomyces violaceusniger* 16S rRNA gene clade: *Streptomyces castelarensis* comb. nov., *S. himastatinicus* sp. nov., *S. mordarskii* sp. nov., *S. rapamycinicus* sp. nov. and *S. ruanii* sp. nov. *Int J Syst Evol Microbiol* 58: 1369–1378
- Kumar Y, Goodfellow M (2010) Reclassification of *Streptomyces hygroscopicus* strains as *Streptomyces aldersoniae* sp. nov., *Streptomyces augustinyceticus* sp. nov., comb. nov., *Streptomyces ascomycinicus* sp. nov. *Streptomyces decoyicus* sp. nov., comb. nov., *Streptomyces milbemycinicus* sp. nov. and *Streptomyces wellingtoniae* sp. nov. *Int J Syst Evol Microbiol* 60:769–775
- Küster E (1959) Outline of a comparative study of criteria used in characterization of the actinomycetes. *Int Bull Bacteriol Nomencl Taxon* 9:97–104
- Labeda DP (1992) DNA:DNA hybridization in the systematics of *Streptomyces*. *Gene* 115:249–253
- Labeda DP (1993) DNA:DNA relatedness among strains of the *Streptomyces lavendulae* phenotypic cluster group. *Int J Syst Evol Microbiol* 53:822–825
- Labeda DP (1998) DNA:DNA relatedness among the *Streptomyces fulvissimus* and *Streptomyces griseoviridis* phenotypic cluster groups. *Int J Syst Evol Microbiol* 48:829–832
- Labeda DP (2011) Multilocus sequence analysis of phytopathogenic *Streptomyces* species. *Int J Syst Evol Microbiol* 61:2379–2383
- Labeda D, Kroppenstedt RM (2000) Phylogenetic analysis of *Saccharothrix* and related taxa: proposal for *Actinosynnemataceae* fam. nov. *Int J Syst Evol Microbiol* 50:331–336
- Labeda DP, Lyons AJ (1991a) Deoxyribonucleic acid relatedness among species of the “*Streptomyces cyaneus*” cluster. *Syst Appl Microbiol* 14:158–164
- Labeda DP, Lyons AJ (1991b) The *Streptomyces violaceusniger* cluster is heterogeneous in DNA relatedness among strains: emendation of the descriptions of *S. violaceusniger* and *Streptomyces hygroscopicus*. *Int J Syst Bacteriol* 41:398–401
- Labeda DP, Price NP, Kroppenstedt RM, Donahue JM, Williams NM, Sells SF (2009) *Streptomyces atriruber* sp. nov. and *Streptomyces silaceus* sp. nov., two novel species of equine origin. *Int J Syst Evol Microbiol* 59:2899–2903
- Lu Z, Liu Z, Wang L, Zhang Y, Qi W, Goodfellow M (2001) *Saccharopolyspora flava* sp. nov. and *Saccharopolyspora thermophila* sp. nov., novel actinomycetes from soil. *Int J Syst Evol Microbiol* 51:319–325
- Ludwig W, Strunk O, Westram R, Richter L, Meier H, Buchner A, Yadhukumar Lai, Steppi S et al (2004) ARB: a software environment for sequence data. *Nucleic Acids Res* 32: 1363–1371
- Manchester L, Pot B, Kersters K, Goodfellow M (1990) Classification of *Streptomyces* and *Streptovercillium* species by numerical analysis of electrophoretic protein patterns. *Syst Appl Microbiol* 13:333–337
- Mordarski M, Goodfellow M, Williams ST, Sneath PHA (1986) Evaluation of species groups in the genus *Streptomyces*. In: Szabó G, Biró S, Goodfellow M (eds) *Biological, biochemical and biomedical aspects of actinomycetes*. Akademiai Kiadó, Budapest, pp 517–525
- Ōmura S, Takahashi Y, Iwai Y, Tamaka H (1982) *Kitasatosporia*, a new genus of the order *Actinomycetales*. *J Antibiot* 35:1013–1019
- Park MS, Jung SR, Lee MS, Kim KO, Do JO, Lee KH, Kim SB, Bae KS (2005) Isolation and characterization of bacteria associated with two sand dune plant species, *Calystegia soldanella* and *Elymus mollis*. *J Microbiol* 43:219–227
- Pridham TG, Tresner HD (1974) Genus I. *Streptomyces* Waksman and Henrici 1943, 339. In: Buchanan RE, Gibbons NE (eds) *Bergey’s Manual of Determinative Bacteriology*, 8th edn. Williams and Wilkins Company, Baltimore, pp 748–829
- Ridell M, Wallerstrom G, Williams ST (1986) Immunodiffusion analysis of phenetically defined strains of *Streptomyces*, *Streptovercillium* and *Nocardopsis*. *Syst Appl Microbiol* 8:24–27
- Rong X, Huang Y (2010) Taxonomic evaluation of the *Streptomyces griseus* clade using multilocus sequence analysis and DNA–DNA hybridization, with proposal to combine 29 species and three subspecies as 11 genomic species. *Int J Syst Evol Microbiol* 60:696–703
- Rong X, Gou Y, Huang Y (2009) Proposal to reclassify the *Streptomyces albidoflavus* clade based on the basis of multilocus sequence analysis and DNA–DNA hybridization, and taxonomic elucidation of *Streptomyces griseus* subsp. *solvifaciens*. *Syst Appl Microbiol* 32:314–322
- Saddler GS, O’Donnell AG, Goodfellow M, Minnikin DE (1987) SIMCA pattern recognition in the analysis of streptomycete fatty acids. *J Gen Microbiol* 133:1137–1147
- Saitou N, Nei M (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol Biol Evol* 4:406–425
- Schatz A, Bugie E, Waksman SA (1944) Streptomycin, a substance inhibiting antibiotic activity against gram-positive and gram-negative bacteria. *Proc Soc Exp Biol Med* 55: 66–69
- Shirling EB, Gottlieb D (1966) Methods for characterization of *Streptomyces* species. *Int J Syst Bacteriol* 16:313–340
- Shirling EB, Gottlieb D (1968a) Cooperative description of type cultures of *Streptomyces*. II. Species descriptions from first study. *Int J Syst Bacteriol* 38:69–189
- Shirling EB, Gottlieb D (1968b) Cooperative description of type cultures of *Streptomyces*. III. Additional species descriptions from first and second studies. *Int J Syst Bacteriol* 18:279–292
- Shirling EB, Gottlieb (1969) Cooperative description of type cultures of *Streptomyces*. IV. Species descriptions from the second, third and fourth studies. *Int J Syst Bacteriol* 19:391–512
- Shirling EB, Gottlieb D (1972) Cooperative description of type strains of *Streptomyces* V. Additional descriptions. *Int J Syst Bacteriol* 22:265–394

- Sneath PHA (1970) Application of numerical taxonomy to Actinomycetales: problems and perspectives. In: Prauser H (ed) The Actinomycetales. Gustav Fischer, Jena, pp 371–378
- Stackebrandt E, Ebers J (2006) Taxonomic parameters revisited: tarnished gold standards. *Microbiol Today* Nov 06: 152–155
- Tamura K, Nei M (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Mol Biol Evol* 10:512–526
- Tamura T, Ishida Y, Otoguro M, Hatano K, Suzuki K (2008a) Classification of ‘*Streptomyces tenebrarius*’ Higgins and Kastner as *Streptoalloteichus tenebrarius* nom. rev., comb. nov., and emended description of the genus *Streptoalloteichus*. *Int J Syst Evol Microbiol* 58:688–691
- Tamura T, Ishida Y, Otoguro M, Hatano K, Labeda D, Price NP, Suzuki K (2008b) Reclassification of *Streptomyces caeruleus* as a synonym of *Actinoalloteichus cyanogriseus* and reclassification of *Streptomyces spheroides* and *Streptomyces laceyi* as later synonyms of *Streptomyces niveus*. *Int J Syst Evol Microbiol* 58:2812–2813
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: molecular evolutionary genetics analysis using likelihood, distance, and parsimony methods. *Mol Biol Evol* 28 (in press)
- Trejo WH (1970) An evaluation of some concepts and criteria used in the speciation of streptomycetes. *Trans NY Acad Sci Ser II* 32:989–997
- Waksman SA (1919) Cultural studies of species of *Actinomycetes*. *Soil Sci* 8:71–215
- Waksman SA, Curtis RE (1916) The actinomycetes of the soil. *Soil Sci* 1:99–134
- Waksman SA, Woodruff HB (1941) *Actinomycetes antibioticus*, a new soil organism antagonistic to pathogenic and non-pathogenic bacteria. *J Bacteriol* 42:231–249
- Williams ST, Goodfellow M, Alderson G, Wellington EMH, Sneath PHA, Sackin MJ (1983) Numerical classification of *Streptomyces* and related genera. *J Gen Microbiol* 129: 1743–1813
- Williams ST, Goodfellow M, Alderson G (1989) Genus *Streptomyces* Waksman and Henrici 1943, 339AL. In: Williams ST, Sharpe ME, Holt JG (eds) *Bergey’s manual of determinative bacteriology*, volume 4. Williams and Wilkins, Baltimore, pp 2453–2492
- Witt D, Stackebrandt E (1990) Unification of the genera *Streptoverticillium*, *Streptomyces*, emendation of *Streptomyces* Waksman, Henrici 1943 339AL. *Syst Appl Microbiol* 13:361–371
- Xu C, Wang W, Cui Q, Huang Y, Liu Z, Zheng G, Goodfellow M (2006) Neutrotolerant acidiphilic *Streptomyces* species isolated from acidic-soils in China: *Streptomyces guanduensis* sp. nov., *Streptomyces paucisporeus* sp. nov., *Streptomyces rubidus* sp. nov. and *Streptomyces yanglinensis* sp. nov. *Int J Syst Evol Microbiol* 56:1109–1115
- Yarza P, Richter M, Peplies J, Euzéby J, Amann R, Schleifer K-H, Ludwig W, Glöckner FO, Roselló-Móra R (2008) The all-species living tree project: a 16S rRNA-based phylogenetic tree for all sequenced type strains. *Syst Appl Microbiol* 31:241–250