Reassessment of the status of *Streptomyces setonii* and reclassification of *Streptomyces fimicarius* as a later synonym of *Streptomyces setonii* and *Streptomyces albovinaceus* as a later synonym of *Streptomyces globisporus* based on combined 16S rRNA/gyrB gene sequence analysis

Kyoung-Ok Kim,1 Kwang-Soo Shin,1 Mi Na Kim,2 Kee-Sun Shin,2 David P. Labeda,3 Ji-Hye Han4 and Seung Bum Kim4

1Department of Microbiology and Biotechnology, Daejeon University, 96-3 Yongun-dong, Dong-gu, Daejeon 300-716, Republic of Korea
2Korea Research Institute of Bioscience & Biotechnology, 52 Oun-Dong, Yuseong, Daejeon 305-333, Republic of Korea
3National Center for Agricultural Utilization Research, USDA-ARS, Peoria, IL 61604, USA
4Department of Microbiology and Molecular Biology, Chungnam National University, 220 Gung-dong, Yuseong, Daejeon 305-764, Republic of Korea

The 16S rRNA and gyrB genes of 22 *Streptomyces* strains belonging to the *Streptomyces griseus* cluster were sequenced, and their taxonomic positions were re-evaluated. For correct analysis, all of the publicly available sequences of the species were collected and compared with those obtained in this study. Species for which no consensus sequence could be identified were excluded from the phylogenetic analysis. The levels of 16S rRNA gene sequence similarity within the cluster ranged from 98.6 to 100% with a mean value of 99.6 ± 0.3%, and those of the gyrB gene ranged from 93.6 to 99.9% with a mean value of 96.3 ± 1.5%. The observed average nucleotide substitution rate of the gyrB gene was ten times higher than that of the 16S rRNA gene, showing a far higher degree of variation. Strains sharing 99.3% or more gyrB sequence similarity (corresponding to an evolutionary distance of 0.0073) always formed monophyletic groups in both trees. Through the combined analysis of the two genes, clear cases of synonymy could be identified and, according to the priority rule, the assertion of the status of *Streptomyces setonii* as a distinct species and the reclassification of *Streptomyces fimicarius* as a later synonym of *S. setonii* and *Streptomyces albovinaceus* as a later synonym of *Streptomyces globisporus* are proposed. Emended descriptions of *S. setonii* and *S. globisporus* are provided.

INTRODUCTION

The genus *Streptomyces* is a representative member of the phylum *Actinobacteria*, and the industrial significance of the genus as the producer of a wide variety of bioactive compounds has been well documented (Locci, 1989; Han et al., 2008; Bérdy, 2005).

The description of novel *Streptomyces* species has increased continuously since the 1940s. The number of *Streptomyces* species with validly published names is over 500, making it the largest of all prokaryote genera (Euzéby, 2011). However, the description of species has not been based on a fixed taxonomic standard. For example, the descriptions of most species with validly published names were published before the era of gene-based phylogeny, and thus the overall state of the phylogenetic relationships among all members of the genus is not yet clearly understood.

Another problem regarding the taxonomy of *Streptomyces* is that the genus may have been overclassified (Hatano et al., 2003; Lanoot et al., 2002; Rong & Huang, 2010). A number of species apparently share high levels of phenotypic and genotypic similarity with other related species, implying that many of them can be considered synonyms. Cases of
Phylogenetic analysis of the *Streptomyces griseus* cluster

Table 1. *Streptomyces* strains used in the study and sequence accession numbers

<table>
<thead>
<tr>
<th>Species</th>
<th>Strain</th>
<th>Accession number(s)</th>
<th>gyrB</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. acrimycini</em> (= <em>S. fimicarius</em>)</td>
<td>KCTC 9679T</td>
<td>AY999889 (AS 4.1673T), AB184110 (NBRC 12736T)</td>
<td>–</td>
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<tr>
<td><em>S. albovicunaeus</em></td>
<td>NBRC 12739T</td>
<td>AY999799* (JCM 4343T), AB249958 (NBRC 12739T)</td>
<td>HQ995505</td>
</tr>
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<td><em>S. alboviridis</em> (= <em>S. microflavus</em>)</td>
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<td>AB184256* (NBRC 13015T), AY999760 (JCM 4449T)</td>
<td>HQ995506</td>
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<tr>
<td><em>S. bacillaris</em></td>
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<td>AB184439* (NBRC 13487T), AY999817 (KCTC 9018T)</td>
<td>HQ995507</td>
</tr>
<tr>
<td><em>S. californicus</em> (= <em>S. punicus</em>)</td>
<td>DSM 40058T</td>
<td>AB184755 (NBRC 33867T), AB184116 (NBRC 12750T), AY999837 (NBRC 12750T), AY999845 (DSM 40058T)</td>
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<tr>
<td><em>S. cavourensis</em></td>
<td>KCCM 40666T</td>
<td>DQ445791* (NRRL 2740T), AB184264 (NBRC 13026T)</td>
<td>HQ995508</td>
</tr>
<tr>
<td><em>S. chrysomallus</em> (= <em>S. anulatus</em>)</td>
<td>DSM 40128T</td>
<td>AB184120* (NBRC 12755T)</td>
<td>HQ995509</td>
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<tr>
<td><em>S. citreofluorescens</em> (= <em>S. anulatus</em>)</td>
<td>KCTC 9710T</td>
<td>HQ995503*, AY999797 (NRRL B-3362T)</td>
<td>HQ995510</td>
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<tr>
<td><em>S. cyanofuscatus</em></td>
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<td>AY999770* (JCM 4364T), AB184860 (NBRC 13190T)</td>
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<td>AY999784* (ISP 5322T), AB184269 (NBRC 13037T)</td>
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<td><em>S. globisporus</em></td>
<td>KCTC 9026T</td>
<td>HQ995504*, EF178686 (NRRL B-2872T), FJ405901 (AS 4.1968T), AB184203 (NBRC 12867T)</td>
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<td><em>S. griseinus</em> (= <em>S. albovicunaeus</em>)</td>
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<td>AB184205* (NBRC 12869T), AY999891 (AS 4.1875T)</td>
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<tr>
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<td>X61478* (KCTC 9080T), AY207604 (KACC 20084T), AB184699 (NBRC 15744T), AB184211 (NBRC 12875T), AY994371 (ISP 5236T)</td>
<td>–</td>
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<td><em>S. lipmanii</em> (= <em>S. microflavus</em>)</td>
<td>JCM 4058T</td>
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<td>HQ995517</td>
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<tr>
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<td>NBRC 12897T</td>
<td>AB184257* (NBRC 12897T), DQ442535 (NRRL B-3374T)</td>
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<td>DQ442537* (NBRL B-1455T), AB184603 (NBRC 14595T)</td>
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<td><em>S. praceax</em> (= <em>S. anulatus</em>)</td>
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<tr>
<td><em>S. setonii</em> (= <em>S. griseus</em>)</td>
<td>KCTC 9144T</td>
<td>D63872* (ATCC 25497T), AB184300 (NBRC 13085T)</td>
<td>HQ995521</td>
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<tr>
<td><em>S. sindenensis</em></td>
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<td>AB184759* (NBRC 3399T), AY999800 (NBRC 12915T)</td>
<td>HQ995522</td>
</tr>
<tr>
<td><em>S. willmoresi</em> (= <em>S. microflavus</em>)</td>
<td>JCM 4861T</td>
<td>EF178673* (NRRL B-1332T), AB184374 (NBRC 13391T)</td>
<td>HQ995523</td>
</tr>
</tbody>
</table>

*16S rRNA gene sequence used for reconstruction of phylogenetic trees.

The gene encoding the DNA gyrase subunit B is a potential candidate that may replace or supplement the 16S rRNA gene. The gyrB gene is present in all living organisms and encodes the ATPase domain of DNA gyrase, an enzyme essential for DNA replication. A number of studies have shown the potential of the gyrB gene in species delineation for various prokaryote taxa (Han et al., 2012; Hannula & Hänninen, 2007; Hatano et al., 2003; Huang, 1996; Kasai et al., 2000; Parkinson et al., 2009; Suzuki et al., 1999; Wang et al., 2007; Yamamoto et al., 1999), although controversy exists over whether or not the gene is present as a single copy in *Streptomyces* (Labeda, 2011).

Regardless of the sequence examined, problems can occur if a study contains sequences from incorrectly identified strains, since the use of such strains in the analysis may lead to serious confusion and incorrect conclusions. Thus, it is crucial to check the identity of the strains for study when alternative phylogenetic markers are used.

In this study, combined 16S rRNA gene- and gyrB gene-based phylogenetic analyses were carried out to clarify the relationships among *Streptomyces* strains belonging to the 'Streptomyces griseus' cluster (cluster 1-3) as defined previously by numerical taxonomy (Kämpfer et al., 1991). 16S rRNA and gyrB gene sequences were determined for all strains and examined along with publicly available...
sequences to check the authenticity of the strains. Cases of synonymy were identified by using a combination of the two gene sequences, and reclassifications of selected species are proposed accordingly.

**METHODS**

**Bacterial strains and culture conditions.** The Streptomyces type strains used in this study are listed in Table 1. The strains were subcultured and maintained aerobically on Bennett’s medium (0.1% yeast extract, 0.1% beef extract, 0.2% NZ amine type A, 1% glucose and 1.5% agar, pH 7.3) at 28 °C. The same medium was used to obtain the biomass for phylogenetic analysis.

**PCR amplification and sequencing of 16S rRNA and gyrB genes.** Extraction of total DNA from 1-week-old cultures, PCR amplification and sequence determination of the 16S rRNA gene were performed as described previously (Park et al., 2005). PCR amplification and sequencing of the gyrB gene followed the procedures described by Hatano et al. (2003).

**Phylogenetic analysis.** The sequences were proofread, edited and merged into comparable sequences using the PHYDIT program version 3.2 (available at http://plaza.snu.ac.kr/~jchun/phydit). The reconstruction of neighbour-joining trees based on the Jukes–Cantor model and bootstrap analysis followed previously described procedures (Kim et al., 2003). 16S rRNA and gyrB gene sequences derived from the genome sequences of Streptomyces avermitilis MA-4680, *Streptomyces bingchongensis* BCW-1, *Streptomyces griseus* NBRC 13350T and *Streptomyces coelicolor* A3(2) were used as references and outgroups.

**Nucleotide sequence accession numbers.** The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA and gyrB gene sequences determined in this study are listed in Table 1.

**RESULTS**

**Authenticity check of tested strains**

Almost-complete 16S rRNA gene and partial gyrB gene sequences were determined. For the 16S rRNA gene, the sequences with the longest and ‘N’-free stretches were selected as representative sequences for further analysis if all of the available sequences for the species were identical. If there was disagreement between the sequences (more than two nucleotide differences), the species was excluded from further analysis unless any consensus sequence could be identified. The 16S rRNA gene sequences of the *Streptomyces citreofluorescens* and *Streptomyces globisporus* type strains and all of the gyrB gene sequences used in the analysis were deposited in the GenBank database.

No consensus 16S rRNA gene sequences could be identified for *Streptomyces acrimycini*, *Streptomyces californicus* or *Streptomyces griseobrunneus*, and the three species were excluded from subsequent analyses. In the case of *S. acrimycini*, large differences were observed between the two available sequences and the sequence obtained in this study (ranging from 95.2 to 97.6%). In the case of *S. californicus*, disagreement was observed among the five sequences (four earlier sequences and the sequence obtained in this study), although all five could be recovered as a monophyletic group in the tree (not shown). In the case of *S. griseobrunneus*, the sequences deposited as AB249912 and AY999888 differed by two bases, and differed from the sequence determined in this study by 12 and 14 bases, respectively.

**Properties of 16S rRNA and gyrB gene sequences and substitution patterns**

G+C contents and base substitution patterns were calculated from the 16S rRNA (1412 bases) and gyrB (1236 bases) gene sequences of 19 strains. The G+C contents of the 16S rRNA genes ranged from 58.2 to 58.6 mol%, and the mean was 58.4 ± 0.1 mol%. In contrast, the G+C content of the gyrB gene was in the range 65.5–66.9 mol% with a mean of 66.4 ± 0.4 mol%, which was in better agreement with the high G+C contents of *Streptomyces* strains (Locci, 1989). The level of 16S rRNA gene sequence similarity among the strains of cluster 1-3 was 98.6–100%, with a mean of 99.6 ± 0.3%, and that of the gyrB gene was 93.6–99.9% with a mean of 96.3 ± 1.5%.

Analysis of base substitution patterns indicated that the transition/transversion ratio was 0.72 among the 16S rRNA gene sequences and 0.61 among the gyrB gene sequences. Therefore, the substitution patterns for the two genes were found to be closer to the Jukes–Cantor model (Jukes & Cantor, 1969) than to Kimura’s two-parameter model (Kimura, 1980). Accordingly, the Jukes–Cantor model was used to reconstruct phylogenetic trees for both genes. The stability of the tree topology was similar in trees constructed from the two models (not shown).

A total of 789 nucleotide differences were observed from pairwise comparison among the 16S rRNA gene sequences of the 19 strains (171 pairs in total). The mean number of substitutions in 16S rRNA genes was therefore 4.61 per molecule between strains. In contrast, 7890 nucleotide differences were observed among the gyrB gene sequences of the 19 strains, among which 1594 cases of non-synonymous substitutions were identified, accounting for 20.2% of the total substitutions. The mean number of nucleotide substitutions in the gyrB genes was therefore 46.1 per molecule between strains, and that of amino acid substitutions was 9.32.

**Phylogenetic relationships based on 16S rRNA and gyrB gene sequences**

In the phylogenetic tree based on the 16S rRNA gene, 13 branches could be recognized, excluding the root position (Fig. 1). Of them, only five branches were also recovered in the gyrB gene-based tree (Fig. 2). However, all five consensus branches were terminal branches directly connecting operational taxonomic units, and only two other such terminal branches (*Streptomyces cyanoseoppins–S. griseus* and *Streptomyces parvus–Streptomyces sindenensis*) were not recovered in the gyrB gene-based tree. Four
groups in which the strains exhibited identical 16S rRNA gene sequences could be identified, and all four groups could also be recovered in the gyrB gene tree, albeit with higher degrees of variation (Table 2). The members of each group are listed in Table 2, where representative genetic properties are also explained.

The S. globisporus group (designated following the species having nomenclatural priority) contained three species, Streptomyces albovinaceus, S. globisporus and Streptomyces griseinus. The mean gyrB gene sequence similarity within the group was 99.75%. The substitutions were synonymous except for those between S. globisporus and each of the other two species.

The Streptomyces microflavus group contained four species, Streptomyces alboviridis, Streptomyces lipmanii, S. microflavus and Streptomyces willmorei. The mean gyrB gene sequence similarity within this group was 99.6%, and there were two non-synonymous substitutions between S. alboviridis and S. willmorei and none between S. lipmanii and S. microflavus. Each of the other pairs in the group had one non-synonymous substitution.

The Streptomyces anulatus group contained four species, S. anulatus, S. citreofluorescens, Streptomyces chrysomallus and Streptomyces praecox, the latter three all reclassified as later synonyms of S. anulatus. The mean gyrB gene sequence similarity within the group was 99.7%. All substitutions within the group were synonymous.

The Streptomyces setonii group contained two species, Streptomyces fimicarius and S. setonii. The gyrB gene sequence similarity between the two was 99.8%, and one of the two substitutions was non-synonymous.

Streptomyces bacillaris and Streptomyces cavourensis were recovered as a clade in both trees, but the gyrB gene sequence similarity between the two was 98.1%. Each of the pairs S. cyaneofuscatus–S. griseus (sharing 95.5% gyrB

![Fig. 1. 16S rRNA gene sequence-based (1412 bases) neighbour-joining tree of the S. griseus cluster using Jukes–Cantor distances. Numbers at nodes indicate percentages of bootstrap support. Only values over 50% are given. Filled circles indicate nodes that were also recovered in Fig. 2. All such clades were also recovered in maximum-likelihood and maximum-parsimony trees. Bar, 0.001 substitutions per nucleotide position.](http://ijs.sgmjournals.org)

![Fig. 2. gyrB gene sequence-based (1236 bases) neighbour-joining tree of the S. griseus cluster using Jukes–Cantor distances. See the legend to Fig. 1 for an explanation of the numbers at nodes. Filled circles indicate nodes that were also recovered in Fig. 1. All such clades were also recovered in maximum-likelihood and maximum-parsimony trees. Bar, 0.01 substitutions per nucleotide position.](http://ijs.sgmjournals.org)
gene sequence similarity) and S. parvus–S. sindenensis (sharing 96.6 % gyrB gene sequence similarity) were clustered together in the 16S rRNA gene tree with low bootstrap support, but not in the gyrB gene tree.

Correlation between 16S rRNA and gyrB gene sequence similarity

Pearson’s correlation coefficient between the gyrB and 16S rRNA gene sequence similarities was 0.664, showing that a weak correlation was found between the similarity of the two genes. In cases of 100 % 16S rRNA gene sequence similarity, however, the range of gyrB gene similarity was 99.3–99.9 % (Fig. 3a).

The correlation coefficient between the 16S rRNA gene sequence similarity and the amino acid sequence identity of GyrB sequences was 0.466. In contrast, that between the nucleotide sequence similarity of the gyrB gene and amino acid identity of the GyrB sequence was 0.834 (Fig. 3b). Notably, when the nucleotide similarity of the gyrB gene exceeded 99.5 %, the amino acid identity was always over 99.5 % (corresponding to two amino acid substitutions or fewer), as indicated by a circle in Fig. 3(b), and vice versa, with one exception (S. cavourensis and S. sindenensis shared 96.2 % gyrB gene sequence similarity and differed by two amino acids in their GyrB sequences).

**DISCUSSION**

The accumulation of sequence data for the same organisms has enabled simple authenticity checks of the strains to be carried out. In this study, 16S rRNA gene sequences were determined for all tested strains and compared with all available sequences of the corresponding type strains. Heterogeneity was found in almost all cases (one or two base differences), although most of the heterogeneity appears to have come from sequencing errors, i.e. heterogeneity found in conserved regions. For a few species, however, the discrepancy was substantial, as described in Results. As even a few base differences in

<table>
<thead>
<tr>
<th>Species group</th>
<th>16S rRNA gene</th>
<th>gyrB</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Similarity (%) [distance]</td>
<td>Similarity (%) [distance]</td>
</tr>
<tr>
<td>S. anulatus group (S. chrysonallus, S. citreofluorescens, S. praecox)</td>
<td>100 [0]</td>
<td>99.7–99.8 [0.0016–0.0032]</td>
</tr>
<tr>
<td>S. setonii group (S. finicarius, S. setonii)</td>
<td>100 [0]</td>
<td>99.8 [0.0016]</td>
</tr>
<tr>
<td>S. globisporus group (S. albovinaceus, S. globisporus, S. griseinus)</td>
<td>100 [0]</td>
<td>99.7–99.8 [0.0016–0.0032]</td>
</tr>
<tr>
<td>S. microflavus group (S. alboviridis, S. lipmanii, S. microflavus, S. willmorei)</td>
<td>100 [0]</td>
<td>99.3–99.9 [0.00081–0.0073]</td>
</tr>
</tbody>
</table>

16S rRNA gene sequences may imply ten times as much variation in gyrB gene sequences, an authenticity check of the tested strains in taxonomic studies, for multigene studies in particular, should always be considered essential.

The gyrB gene apparently has a higher degree of correlation to DNA–DNA relatedness than does the 16S rRNA gene (Hatano et al., 2003; Kasai et al., 2000; Wang et al., 2007). In addition, the gyrB gene has the following advantages over the 16S rRNA gene as a phylogenetic marker: the gyrB gene gives greater resolution than the 16S rRNA gene at the species level and below and, in addition to nucleotide

**Table 2.** Monophyletic groups recovered in both 16S rRNA gene- and gyrB-based trees and their properties

The Jukes–Cantor model was used for both the 16S rRNA and gyrB genes.
sequence data, information on amino acid sequences can also be utilized. Regarding the question of whether the gyrB gene exists as a single copy in a genome, there are gyrB gene-like segments in the publicly available genome sequences of *Streptomyces* strains, but the sequence similarities with known gyrB genes were found to be fairly low and the currently used PCR primers would not amplify them (not shown). On the other hand, the lack of universal gyrB gene primers and extensive databases, long sequences and ineffectiveness for comparison at higher taxonomic levels due to high substitution rates are problems to overcome.

Different levels of gyrB gene similarity have been proposed for species delineation of various prokaryotic taxa, ranging from 95.0 to 98.5 %, or genetic distances from 0.014 to 0.04, depending on the taxonomic groups and the lengths of the analysed fragments (Everest & Meyers, 2009; Hatano et al., 2003; Kirby et al., 2010; Wang et al., 2007; Yamamoto et al., 1999).

In this study, a gap could be recognized in the sequence similarity range of the gyrB gene lying between 98.5 and 99.3 % (corresponding to evolutionary distances of 0.016 and 0.0073, respectively), in contrast to the continual distribution of 16S rRNA gene sequence similarity (Fig. 3). This observation is consistent with the suggested cut-off value of 98.5 % nucleotide sequence similarity or a genetic distance of 0.014 for species delineation, as strains sharing similarity above this value formed monophyletic groups in both trees (Figs 1 and 2). This also supports previous work proposing reclassification of selected species, as indicated in Table 1.

**Taxonomic conclusions**

Based on the present study, *S. albominaceus*, *S. globisporus* and *S. griseinus* share identical 16S rRNA gene sequences and 99.7–99.8 % gyrB gene sequence similarity (an evolutionary distance of 0.0016–0.0032), and should therefore be considered a single species. According to the rules of priority (Lapage et al., 1992), *Streptomyces albominaceus* (Kudrina 1957) Pridham et al. 1958 and *Streptomyces griseinus* Waksman 1959 are proposed as later heterotypic synonyms of *Streptomyces globisporus* (Krasil’nikov 1941) Waksman 1953. This is supported by similarities in morphology and carbon source utilization patterns among the three taxa (Shirling & Gottlieb, 1968, 1969) and also by the DNA–DNA relatedness value of 87.5 ± 6.3 % between *S. albominaceus* NBRC 12739T and *S. globisporus* KCTC 9026T determined in this study.

*Streptomyces setonii* was previously proposed as a synonym of *Streptomyces griseus* (Liu et al., 2005; Rong & Huang, 2010), but it is obvious from this study that *S. setonii* is phylogenetically distant from *S. griseus*, with a 16S rRNA gene sequence similarity of 99.8 % and gyrB gene similarity of 97.6 % (corresponding to an evolutionary distance of 0.025), which is in contrast to the multilocus analysis by Rong & Huang (2010). However, our observation is in line with a low level of DNA–DNA relatedness between the two type strains (43 %) observed in an earlier study (Healy & Lambert, 1991). Furthermore, a comparison of earlier phenotypic descriptions of the two species, such as melanin production by *S. griseus* in tyrosine agar in contrast to *S. setonii* and differences in carbon source utilization patterns between the two (Shirling & Gottlieb, 1968, 1969), clearly supports our observation. Thus, the previous proposal for the reclassification of *S. setonii* as a synonym of *S. griseus* seems to be based on incorrect information. This was confirmed by the DNA–DNA relatedness value of 35.5 ± 2.1 % between *S. setonii* KCTC 9144T and *S. griseus* KCTC 9135T obtained in this study. In addition, it is proposed that *S. setonii* and *S. fimicarius*, sharing identical 16S rRNA gene sequences and 99.8 % gyrB sequence similarity (corresponding to an evolutionary distance of 0.0016), should be considered a single species. This was also supported by the phenotypic similarity between *S. setonii* and *S. fimicarius* (Shirling & Gottlieb, 1969) and a DNA–DNA relatedness value of 88.5 ± 0.7 % between the two type strains obtained in this study. The name *Streptomyces setonii* (Millard and Burr 1926) Waksman 1953 has priority over *Streptomyces fimicarius* (Duché 1934) Waksman and Henrici 1948 and, accordingly, the status of *S. setonii* as a distinct species is reasserted and reclassification of *Streptomyces fimicarius* as a later heterotypic synonym of *Streptomyces setonii* is proposed.

**Emended description of Streptomyces setonii** (Millard and Burr 1926) Waksman 1953

The species description is as given previously (Shirling & Gottlieb, 1969). Previous proposals (Liu et al., 2005; Rong & Huang, 2010) for the reclassification of *S. setonii* as a later synonym of *Streptomyces griseus* seem to be based on incorrect information. The species now includes the following heterotypic synonym: *Streptomyces fimicarius* (Duché 1934) Waksman and Henrici 1948.

**Emended description of Streptomyces globisporus** (Krasil’nikov 1941) Waksman 1953

The species description is as given previously (Shirling & Gottlieb, 1968). The species now includes the following heterotypic synonyms: *Streptomyces albominaceus* (Kudrina 1957) Pridham et al. 1958; *Streptomyces griseinus* Waksman 1959.

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