Revival of the genus *Lentzea* and proposal for *Lechevalieria* gen. nov.

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The genus *Saccharothrix* is phylogenetically heterogeneous on the basis of analysis of almost complete 16S rDNA sequences. An evaluation of chemotaxonomic, morphological and physiological properties in the light of the molecular phylogeny data revealed that several species are misclassified. *Saccharothrix aerocolonigenes* NRRL B-3298^T and *Saccharothrix flava* NRRL B-16131^T constitute a lineage distinct from *Saccharothrix* and separate from *Lentzea*. The genus *Lechevalieria* gen. nov. is proposed for these species. *Lechevalieria aerocolonigenes* comb. nov. is the type species and *S. flava* is transferred as *Lechevalieria flava* comb. nov. Although *Lentzea albidocapillata*, the type species of the genus *Lentzea*, was transferred recently to the genus *Saccharothrix*, the revival of *Lentzea* is clearly supported by molecular phylogenetic and chemotaxonomic data. The description of the revived genus is emended to include galactose, mannose and traces of ribose as diagnostic whole-cell sugars and MK-9(H₄) as the principal menaquinone and elimination of tuberculostearic acid as a diagnostic component in the fatty acid profile. *Saccharothrix waywayandensis* NRRL B-16159^T, *S. aerocolonigenes* NRRL B-16137 and '*Asiosporangium albidum*' IFO 16102 are members of the amended genus *Lentzea* on the basis of phylogenetic and chemotaxonomic properties. *S. waywayandensis* is transferred to *Lentzea* as *Lentzea waywayandensis* comb. nov., while the new species *Lentzea californiensis* sp. nov. and *Lentzea albida* sp. nov. are described for *S. aerocolonigenes* NRRL B-16137 and '*A. albidum*' IFO 16102, respectively. Nucleotide signatures in the 16S rDNA sequences are defined that are diagnostic for the genera *Lechevalieria*, *Lentzea* and *Saccharothrix*.

Keywords: *Pseudonocardineae*, *Actinosynnemataceae*, *Saccharothrix*

INTRODUCTION

A phylogenetic analysis of species of the genus *Saccharothrix* and allied taxa within the family *Actinosynnemataceae*, based on partial 16S rDNA sequences (Labeda & Kroppenstedt, 2000), demonstrated that *Saccharothrix* is phylogenetically heterogeneous and that several of the described species are misclassified. It was noted that *Saccharothrix waywayandensis* NRRL B-16159^T is more closely related phylogenetically to *Lentzea albidocapillata* than to *Saccharothrix sensu stricto* and that *Saccharothrix aerocolonigenes* NRRL

B-3298^T and *Saccharothrix flava* NRRL B-16131^T form a lineage distinct from *Saccharothrix* and separate from *Lentzea*. The previous study of Tamura & Hatano (1998) also demonstrated that '*Asiosporangium albidum*' IFO 16102 is phylogenetically related to *Saccharothrix* and *Lentzea*. A recent proposal (Lee *et al.*, 2000) suggested that *Lentzea albidocapillata*, the type species of the genus *Lentzea*, be transferred into the genus *Saccharothrix*, thus effectively abolishing this genus under the rules of the Bacteriological Code of Nomenclature (Lapage *et al.*, 1992), but the phylogenetic and chemotaxonomic data in the present study do not support this proposal. An evaluation of the chemotaxonomic, morphological and physiological properties of these actinomycetes was undertaken to clarify their taxonomic position.

The GenBank accession number for the almost complete sequence of the 16S rDNA gene of *Saccharothrix aerocolonigenes* NRRL B-16137 is AF174435.

METHODS

Strains, cultivation and maintenance. The strains evaluated in the present study are listed in Fig. 1. Primary storage of strains was as lyophilized ampoules of mycelial and spore suspensions in sterile beef serum held at 4 °C. Working stock cultures were maintained on slants of ATCC medium no. 172 (Cote *et al.*, 1984) and stored at 4 °C until needed. Biomass for extraction of DNA was grown as 7 d streak cultures on ATCC medium no. 172 agar plates.

Chemotaxonomy. Chemotaxonomic analysis of strains for menaquinones, fatty acids and whole-cell sugars was performed using methods described previously (Grund & Kroppenstedt, 1989).

Physiological tests. Physiological tests, including those for the production of acid from carbohydrates, the utilization of organic acids and the hydrolysis and decomposition of adenine, guanine, hypoxanthine, tyrosine, xanthine, casein, aesculin, urea and hippurate, were evaluated by using the media of Gordon *et al.* (1974). Allantoin hydrolysis was evaluated in the basal medium suggested by Gordon *et al.* (1974) for aesculin hydrolysis. Phosphatase activity was evaluated by using the method of Kurup & Schmitt (1973). The temperature range for growth was determined on slants of ATCC medium no. 172 agar (Cote *et al.*, 1984).

DNA isolation, 16S rDNA gene amplification and sequencing. Genomic DNA was isolated, purified and sequenced using

procedures described previously (Labeda & Kroppenstedt, 2000).

Phylogenetic analysis. The 16S rDNA sequences obtained in this study were aligned manually with actinomycete reference sequences obtained from the Ribosomal Database Project (Maidak *et al.*, 1994) and GenBank in the ARB software environment for sequence data that was developed by Wolfgang Ludwig and Oliver Strunk (Lehrstuhl für Mikrobiologie, University of Munich, Germany). The program PHYLO_WIN (Galtier *et al.*, 1996) was used to calculate evolutionary distances (using the method of Kimura, 1980) and linkages (using the neighbour-joining method of Saitou & Nei, 1987) and to perform maximum-parsimony and maximum-likelihood analyses. The topographies of the trees resulting from neighbour-joining and maximum-parsimony analyses were evaluated by bootstrap analysis of the data (with 500 resamplings).

RESULTS AND DISCUSSION

The neighbour-joining dendrogram for the family *Actinosynnemataceae*, resulting from phylogenetic analysis of 16S rDNA sequences, is shown in Fig. 1; it can be clearly observed that the genus *Saccharothrix sensu lato* exhibits phylogenetic heterogeneity upon analysis based on almost complete sequences of 16S rDNA. Similar tree topographies resulted from analy-

Fig. 1. Phylogenetic dendrogram reconstructed from evolutionary distances (Kimura, 1980) by the neighbour-joining method (Saitou & Nei, 1987), indicating the positions of species of the genera within the family *Actinosynnemataceae*. Bar, 0.1 nucleotide substitutions per site.

	601	611	621	841	1001
<i>Lechevalieria aerocolonigenes</i> NRRL B-3298 ^T	AAACTTGGGG	CTTAACCCCG	AGCCTGCGGT	ACGTTCTCCG	GAAACCGGTA
<i>Lechevalieria flava</i> NRRL B-16131 ^T					
<i>Lentzea albida</i> IFO 16102 ^T		T..A	...T.....	...CC...T.	A...
<i>Lentzea albidocapillata</i> DSM 44073 ^T		T..A	...T.....	...CC...T.	G.TC..
<i>Lentzea californiensis</i> NRRL B-16137 ^T		T..A	...T...C..	...CC...T.	A...
<i>Lentzea violacea</i> IMSNU 50388 ^T		T..A	...T.....	...CC...T.	G.TC..
<i>Lentzea waywayandensis</i> NRRL B-16159 ^T		T..A	...T.....	...CC...T.	TC..
<i>Actinosynnema mirum</i> DSM 43827 ^T				...C.....	A...
<i>Actinosynnema pretiosum</i> subsp. <i>pretiosum</i> NRRL B-16060 ^T			...T.....	...C.....	A...
<i>Saccharothrix australiensis</i> NRRL 11239 ^T	CAC.	GTG.		...C.....	TCC.
<i>Saccharothrix coeruleofusca</i> NRRL B-16115 ^T	CAC.	GTG.		...C.....	T.C.
<i>Saccharothrix espanaensis</i> NRRL 15764 ^T	CAC.	GTG.		...C.....	T.C.
<i>Saccharothrix longispora</i> NRRL B-16116 ^T	CAC.	GTG.	A..	...C.....	A...
<i>Saccharothrix mutabilis</i> subsp. <i>capreolus</i> DSM 40225 ^T	CAC.	..N..GTG.		...C.....	TCC.
<i>Saccharothrix mutabilis</i> subsp. <i>mutabilis</i> DSM 43853 ^T	CAC.	..N..GTG.		...C.....	TCC.
<i>Saccharothrix syringae</i> NRRL B-16468 ^T	CAC.	GTG.		...C.....	T.C.
<i>Saccharothrix texasensis</i> NRRL B-16134 ^T	CAC.	GTG.	A..	...C.....	T.C.

Fig. 2. Signatures in the 16S rDNA sequence for the genera *Lechevalieria*, *Lentzea* and *Saccharothrix*.

ses using the maximum-parsimony and maximum-likelihood algorithms (trees not shown). The phylogenetic position of *Saccharothrix cryophilis* NRRL B-16238^T indicates that this species does not belong in the genus *Saccharothrix* and that it probably does not belong within the family *Actinosynnemataceae*, but this will be the subject of another detailed paper. *S. aerocolonigenes* NRRL B-16137, *Saccharothrix violacea* IMNSU 50388^T, *S. waywayandensis* NRRL B-16159^T and 'A. albidum' IFO 16102 form a lineage that contains *Lentzea albidocapillata* DSM 44073^T (97.8% mean intrageneric nucleotide similarity), the type species of the genus, which is also clearly separated phylogenetically from *Saccharothrix sensu stricto*, with a mean nucleotide similarity of 95.8% between all species of both genera. These strains also share similar chemotaxonomic characteristics, and it is proposed that they be transferred to the revived and emended genus *Lentzea*.

The type strains of *S. aerocolonigenes* and *S. flava*, respectively NRRL B-3298^T and NRRL B-16131^T, consistently formed a monophyletic lineage distinct from *Saccharothrix* (mean nucleotide similarity of 96.8% to species of this genus) and intermediate between *Lentzea* (mean nucleotide similarity of 96.7% to species of this genus) and *Actinosynnema* (mean nucleotide similarity of 97.3% to species of this genus) for all of the algorithms tested. The phylogenetic validity of the genera *Actinosynnema*, *Lentzea* and *Saccharothrix* was consistently well supported statistically by all algorithms used; the *S. aerocolonigenes* and *S. flava* lineage was consistently found between *Actinosynnema* and *Lentzea*, regardless of which algorithm was used. An examination of the aligned sequences for the 16S rDNA gene (Fig. 2) revealed that diagnostic nucleotide signatures can be used to differentiate the *S. aerocolonigenes*–*S. flava* lineage from *Lentzea* and *Actinosynnema* and that they can also be used to differentiate them from the other

genera of the *Actinosynnemataceae*. Although *S. aerocolonigenes* and *S. flava* appear to be phylogenetically close to the genus *Actinosynnema*, neither has been observed to produce coremia with chains of motile spores (this feature being characteristic of this genus). It is therefore proposed that the *S. aerocolonigenes*–*S. flava* lineage represents a new genus, to be called *Lechevalieria* gen. nov.

Analysis of the chemotaxonomic characteristics of *Lentzea albidocapillata* DSM 44073^T in the present study revealed the presence of galactose, mannose and ribose as diagnostic sugars and menaquinone MK-9(H₄) as the predominant menaquinone and the absence of any significant amount of 10-methyl C18:0 fatty acids (tuberculostearic acid). This is largely in agreement with the observations of Lee *et al.* (2000) regarding this strain. Galactose and mannose were found as diagnostic sugars in whole-cell hydrolysates of all strains examined, but 'A. albidum' IFO 16102 and *S. aerocolonigenes* NRRL B-16137 contained ribose, while *S. waywayandensis* NRRL B-16159^T, *S. aerocolonigenes* NRRL B-3298^T and *S. flava* NRRL B-16131^T did not. Whilst the genera *Lechevalieria* and *Lentzea* (including 'A. albidum', *S. aerocolonigenes* NRRL B-16137 and *S. waywayandensis* NRRL B-16159^T) share many diagnostic chemotaxonomic characteristics with *Saccharothrix*, they can be distinguished from this genus by the lack of hydroxy-substituted fatty acids in the phosphatidyl ethanolamine component of their phospholipids (Table 1). *Saccharothrix* and *Lechevalieria* strains tend to contain varying amounts of rhamnose in whole-cell hydrolysates, whereas *Lentzea* strains were observed to lack (or contain only trace amounts of) rhamnose, and might also contain ribose.

All species of *Lentzea* produce branching substrate mycelium, and the aerial mycelium fragments into rod-shaped elements, although *Lentzea waywayandensis*

Table 1. Chemotaxonomic characteristics of *Lechevalieria* compared with other genera of the family *Actinosynnemataceae*

All of the genera have *meso*-diaminopimelic acid as the cell wall diamino acid, are of cell wall chemotype III and contain straight-chain, mono-unsaturated, iso and anteiso fatty acids. Abbreviations: DPG, diphosphatidyl glycerol; PE, phosphatidyl ethanolamine; PG, phosphatidyl glycerol; PI, phosphatidyl inositol; PIMs, phosphatidyl inositol mannosides; PME, phosphatidyl methylethanolamine.

Characteristic	<i>Actinokineospora</i>	<i>Actinosynnema</i>	<i>Asiosporangium</i>	<i>Lechevalieria</i>	<i>Lentzea</i>	<i>Saccharothrix</i>
Whole-cell sugar pattern	Galactose, mannose, rhamnose	Galactose, mannose	Galactose, mannose, ribose	Galactose, mannose, rhamnose	Galactose, mannose, ribose	Galactose, rhamnose, mannose (trace)
Phospholipid type	PII	PII	PII	PII	PII	PII, PIV
Phospholipids	PE, OH-PE	PE, OH-PE, PI, PIMs, DPG	PE	PE	PE, DPG, PG, PI	PE, OH-PE, PI, PIMs, DPG, PG
Predominant menaquinones	MK-9(H ₄)	MK-9(H ₄), MK-9(H ₆)	MK-9(H ₄)	MK-9(H ₄)	MK-9(H ₄)	MK-10(H ₄), MK-9(H ₄)

Table 2. Differential physiological properties of *Lentzea* species

w, Weak positive reaction. Data for *Lentzea violacea* were taken from Lee *et al.* (2000).

Property	<i>Lentzea albidocapillata</i> NRRL B-24057 ^T	<i>Lentzea albida</i> NRRL B-24073 ^T	<i>Lentzea californiensis</i> NRRL B-16137 ^T	<i>Lentzea violacea</i> IMSNU 50388 ^T	<i>Lentzea waywayandensis</i> NRRL B-16159 ^T
Hydrolysis of urea	w	w	+	+	+
Nitrate reductase production	—	—	+	—	+
Assimilation of:					
Acetate	—	+	+	+	+
Citrate	—	+	+	—	+
Lactate	—	—	—	+	+
Malate	+	+	+	—	+
Production of acid from:					
Adonitol	+	+	—	—	+
Cellobiose	+	+	+	—	+
Inositol	+	+	+	—	+
Maltose	+	+	+	—	+
Mannitol	+	+	+	—	+
Raffinose	w	—	+	+	+
Rhamnose	+	+	+	—	+
Sucrose	+	+	+	—	+
Trehalose	+	+	+	—	+
Xylose	+	+	+	—	+
Growth at:					
10 °C	+	—	+	+	+
37 °C	+	+	+	+	w
42 °C	—	+	—	—	—
45 °C	—	+	—	—	—

NRRL B-16159^T produces only relatively sparse aerial mycelium in comparison with the other *Lentzea* species. Both species of *Lechevalieria* produce very sparse aerial mycelium on agar media and have not been observed to produce sporangia, coremia or motile spores, which differentiates them from *Actinokineospora* and *Actinosynnema*.

It is proposed that the formal description of the revived genus *Lentzea* be emended to include updated chemotaxonomic data from both the present study and that of Lee *et al.* (2000). On the basis of the data presented,

S. violacea is transferred as *Lentzea violacea* comb. nov., *S. waywayandensis* is transferred as *Lentzea waywayandensis* comb. nov. and '*A. albidum*' IFO 16102 is validly described as *Lentzea albida* sp. nov. Because it is proposed that the type strain of *S. aerocolonigenes* be transferred to the new genus *Lechevalieria* and as strain NRRL B-16137 is a member of the genus *Lentzea*, it is described as the new species *Lentzea californiensis* sp. nov. The physiological properties that differentiate these species are shown in Table 2 and the formal descriptions are given below.

Table 3. Differential physiological properties of *Lechevalieria* species

w, Weak positive reaction.

Property	<i>Lechevalieria aerocolonigenes</i> NRRL B-3298 ^T	<i>Lechevalieria flava</i> NRRL B-16131 ^T
Growth in the presence of:		
4 % NaCl	+	—
5 % NaCl	+	—
Utilization of lactate	+	—
Production of acid from:		
Adonitol	+	w
Salicin	+	—
Growth at 45 °C	—	+

The physiological properties that differentiate the *Lechevalieria* species can be seen in Table 3 and the formal descriptions of the genus *Lechevalieria* and the species *Lechevalieria aerocolonigenes* and *Lechevalieria flava* are also given below.

Emended description of *Lentzea* nom. rev., emend.

The formal description of Yassin *et al.* (1995) is emended to reflect the following changes in the chemotaxonomic characteristics. The diagnostic whole-cell sugars include galactose and mannose and might also include ribose. The major menaquinone is MK-9(H₄). Tuberculostearic acid is found only in trace quantities, if at all, in fatty acid profiles. The sequence of the 16S rRNA gene contains a genus-specific diagnostic nucleotide signature pattern, namely TCCA (617–620) and GCC (843–845).

Description of *Lentzea albida* sp. nov.

Lentzea albida (al'bi.da. L. fem. adj. *albida* whitish, referring to the colour of the aerial mycelium).

Substrate mycelium is a yellowish-orange in colour on most media. Copious white aerial mycelium is produced. Soluble pigments are not produced. Casein, aesculin, hypoxanthine, starch and tyrosine are hydrolysed. No hydrolysis of adenine, allantoin or xanthine. Growth occurs in the presence of 4 and 5 % NaCl. Assimilates acetate, citrate, malate, propionate and succinate. Does not assimilate benzoate, lactate, mucate, oxalate or tartrate. Acid is produced from adonitol, arabinose, cellobiose, dextrin, fructose, galactose, glucose, glycerol, inositol, maltose, mannitol, mannose, melibiose, rhamnose, sucrose, trehalose and xylose. Acid is weakly produced from lactose. No acid is produced from dulcitol, erythritol, methyl β -xyloside, raffinose or sorbitol. Grows at 37 and 42 °C but not at 45 °C. Isolated from a soil sample collected in Jianbxi Province, People's Republic of China. The

type strain of *Lentzea albida* is IFO 16102^T (= NRRL B-24073^T).

Description of *Lentzea californiensis* sp. nov.

Lentzea californiensis (cal.i.for.ni.en'sis. N.L. gen. n. *californiensis* of California, referring to the source of this isolate, soil from California).

Substrate mycelium is yellow to orange-brown. White aerial mycelium is produced. Orange, soluble pigments may be produced on Czapek's agar. Casein, aesculin, hypoxanthine, starch and tyrosine are hydrolysed. Does not hydrolyse adenine, allantoin or xanthine. Grows in the presence of 5 % NaCl. Assimilates citrate, malate, propionate and succinate. Does not assimilate acetate, benzoate, lactate, mucate, oxalate or tartrate. Acid is produced from arabinose, cellobiose, dextrin, fructose, galactose, glucose, glycerol, inositol, lactose, maltose, mannitol, mannose, melibiose, raffinose, rhamnose, sucrose, trehalose and xylose; acid is not produced from adonitol, dulcitol, erythritol, methyl β -xyloside or sorbitol. Grows at 37 °C but not at 42 °C. Isolated from a soil sample from California. Strain NRRL B-16137 was originally classified as *Saccharothrix aerocolonigenes*. The type strain of *Lentzea californiensis* is NRRL B-16137^T (= DSM 43393^T = IMRU 550^T).

Description of *Lentzea violacea* comb. nov.

Basonym *Saccharothrix violacea* Lee *et al.* 2000.

The morphological and physiological properties of this species have been described previously (Lee *et al.*, 2000). The type strain of *Lentzea violacea* is IMSNU 50388^T.

Description of *Lentzea waywayandensis* comb. nov.

Basonym *Saccharothrix waywayandensis* Labeda and Lyons 1989.

The morphological and physiological properties of this species have been described previously (Labeda & Lyons, 1989). The type strain of *Lentzea waywayandensis* is NRRL B-16159^T (= DSM 44232^T = IFO 14970^T).

Description of *Lechevalieria* gen. nov.

Lechevalieria (Le.che.val.i.er'i.a. N.L. fem. n. *Lechevalieria* of Lechevalier, named after the American microbiologists Hubert and Mary Lechevalier, who contributed substantially to the field of actinomycete biology during their careers at the Waksman Institute of Microbiology).

Branching vegetative mycelium (approx. 0.5 μ m in diameter) is produced. Very scant aerial mycelium is produced on some media. Gram-positive. Lysozyme-resistant. Catalase-positive and aerobic. The cell wall

is of type III (*meso*-diaminopimelic acid). The whole-cell sugar pattern consists of galactose, mannose and traces of rhamnose. Possesses the type PII phospholipid pattern, with significant quantities of phosphatidyl ethanolamine lacking hydroxylated fatty acids. The predominant menaquinone is MK-9(H₄). The fatty acid profile consists of saturated and mono-unsaturated iso and anteiso fatty acids. Phylogenetically, the genus represents a line of descent in the *Actinosynnemataceae* adjacent to the genus *Saccharothrix* and close to the genera *Actinosynnema* and *Lentzea*. The sequence of the 16S rRNA gene contains a genus-specific diagnostic nucleotide signature pattern, namely TT (844–845) and GGT (1107–1109). The type species is *Lechevalieria aerocolonigenes*.

Description of *Lechevalieria aerocolonigenes* comb. nov.

Basonym *Saccharothrix aerocolonigenes* (ex Shinobu and Kawato 1960) Labeda 1986.

The morphological and physiological properties of this species have been described previously (Labeda, 1986). The type strain of *Lechevalieria aerocolonigenes* is NRRL B-3298^T (= ATCC 23870^T = CCRC 13661^T = DSM 40034^T = IFO 13195^T = JCM 4150^T).

Description of *Lechevalieria flava* comb. nov.

Basonym *Saccharothrix flava* (Gauze *et al.* 1974) Grund and Kroppenstedt 1990.

The morphological and physiological properties of this species have been described previously (Grund & Kroppenstedt, 1989). The type strain of *Lechevalieria flava* is NRRL B-16131^T (= ATCC 29533^T = CCRC 13328^T = DSM 43885^T = IFO 14521^T = INA 2171^T = JCM 3296^T).

ACKNOWLEDGEMENTS

The able technical assistance of E. N. Hoekstra during the analysis of physiological properties, the isolation and purification of DNA, the PCR amplification of 16S rDNA and the sequence determinations for this study is gratefully acknowledged.

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