

# Reassessment of the systematics of the suborder *Pseudonocardineae*: transfer of the genera within the family *Actinosynnemataceae* Labeda and Kroppenstedt 2000 emend. Zhi *et al.* 2009 into an emended family *Pseudonocardiaceae* Embley *et al.* 1989 emend. Zhi *et al.* 2009

D. P. Labeda,<sup>1</sup> M. Goodfellow,<sup>2</sup> J. Chun,<sup>3</sup> X.-Y. Zhi<sup>4</sup> and W.-J. Li<sup>4</sup>

## Correspondence

D. P. Labeda

David.Labeda@ars.usda.gov

<sup>1</sup>National Center for Agricultural Utilization Research, USDA-ARS, Peoria, IL 61604, USA

<sup>2</sup>School of Biology, University of Newcastle, Newcastle upon Tyne NE1 7RU, UK

<sup>3</sup>School of Biological Sciences, Seoul National University, Shillim-dong, Kwanak-gu, Seoul 151-742, Republic of Korea

<sup>4</sup>The Key Laboratory for Microbial Resources of the Ministry of Education and Laboratory for Conservation and Utilization of Bio-Resources, Yunnan Institute of Microbiology, Yunnan University, Kunming 650091, PR China

The taxonomic status of the families *Actinosynnemataceae* and *Pseudonocardiaceae* was assessed based on 16S rRNA gene sequence data available for the 151 taxa with validly published names, as well as chemotaxonomic and morphological properties available from the literature. 16S rRNA gene sequences for the type strains of all taxa within the suborder *Pseudonocardineae* were subjected to phylogenetic analyses using different algorithms in ARB and PHYLIP. The description of many new genera and species within the suborder *Pseudonocardineae* since the family *Actinosynnemataceae* was proposed in 2000 has resulted in a markedly different distribution of chemotaxonomic markers within the suborder from that observed at that time. For instance, it is noted that species of the genera *Actinokineospora* and *Allokutzneria* contain arabinose in whole-cell hydrolysates, which is not observed in the other genera within the *Actinosynnemataceae*, and that there are many genera within the family *Pseudonocardiaceae* as currently described that do not contain arabinose. Phylogenetic analyses of 16S rRNA gene sequences for all taxa within the suborder do not provide any statistical support for the family *Actinosynnemataceae*, nor are signature nucleotides found that support its continued differentiation from the family *Pseudonocardiaceae*. The description of the family *Pseudonocardiaceae* is therefore emended to include the genera previously classified within the family *Actinosynnemataceae* and the description of the suborder *Pseudonocardineae* is also emended to reflect this reclassification.

The suborder *Pseudonocardineae* as proposed by Stackebrandt *et al.* (1997) contained only a single family, the *Pseudonocardiaceae* Embley *et al.* 1989. Subsequently, Labeda & Kroppenstedt (2000) proposed that, on the basis of phylogenetic analysis of 16S rRNA gene sequences for a subset of all taxa within the family, the genera *Actinosynnema*, *Actinokineospora*, *Lentzea* and *Saccharothrix* should be placed in the new family *Actinosynnemataceae*. The description of the family *Actinosynnemataceae* was recently emended by Zhi *et al.* (2009) to include member

genera described since 2000, namely *Lechevalieria* Labeda *et al.* 2001 and *Umezawaea* Labeda and Kroppenstedt 2007.

The taxonomic status of the families *Actinosynnemataceae* and *Pseudonocardiaceae* was assessed in the present study on the basis of phylogenetic analysis of 151 currently available 16S rRNA gene sequences and previously described chemotaxonomic and morphological properties of the member genera and species. It was observed that there is inadequate phylogenetic or chemotaxonomic support to maintain the family *Actinosynnemataceae*, as currently delineated, and it is proposed that the taxa within this family be transferred to the family *Pseudonocardiaceae*,

A supplementary table is available with the online version of this paper.

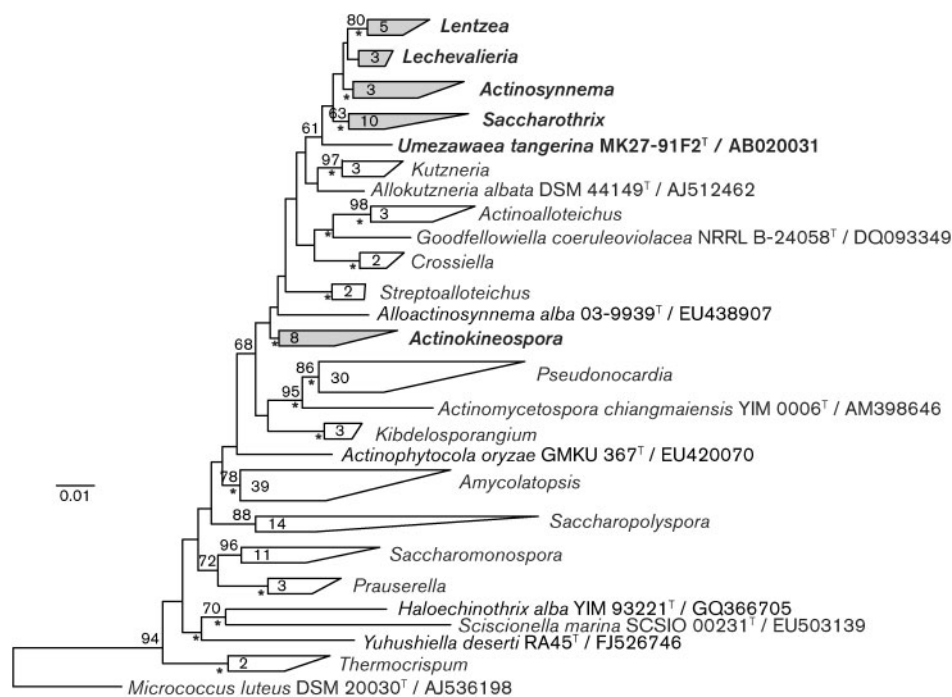
whose description is emended to accommodate these genera.

The 16S rRNA gene sequences for the type strains of all taxa within the suborder *Pseudonocardineae* were obtained from the SILVA database maintained at the Technical University of Munich (<http://www.arb-silva.de/>) or from locally maintained alignments, and subjected to phylogenetic analyses using ARB (Ludwig *et al.*, 2004). The list of taxa, their strain numbers and the accession numbers of their 16S rRNA gene sequences in the public databases can be found in Supplementary Table S1, available in IJSEM Online. The alignment was trimmed at both ends to include only positions that contained data for all strains, totalling 1276 bases. The 16S rRNA gene sequence of *Micrococcus luteus* DSM 20030<sup>T</sup> was used as the outgroup for analyses. This dataset was also subsequently evaluated using jPhydit (Jeon *et al.*, 2005) to filter out the hypervariable loop regions from the analyses in order to determine the phylogenetic impact of these regions (not shown).

Phylogenetic analyses of 16S rRNA gene sequence data for all taxa currently described within the suborder *Pseudonocardineae* do not support the current description of the family *Actinosynnemataceae*, as can be seen in Fig. 1.

The species of the genus *Actinokineospora* are the most distant members of the clade that contains the other genera currently described within the family, namely *Actinosynnema*, *Lechevalieria*, *Lentzea*, *Saccharothrix* and *Umezawaea*, but this clade also contains the genera *Actinoalloteichus*, *Alloactinosynnema*, *Allokutzneria*, *Crossiella*, *Goodfellowiella*, *Kutzneria* and *Streptoalloteichus*. From a cursory examination of this phylogenetic tree, one can easily conclude that the suborder could be divided into three or more families rather than the current two, but these observations do not have statistical support in the present dataset, nor can signature nucleotide patterns be found that support any subdivision. Evaluation of the phylogeny of the 16S rRNA gene sequence alignment with all hypervariable loop regions removed (not shown) also did not demonstrate phylogenetic support for subdivision of the suborder into more than one family.

An evaluation of the previously reported chemotaxonomic properties of the genera within the suborder *Pseudonocardineae* (Table 1) demonstrates that certain properties, such as the presence of *meso*-diaminopimelic acid and galactose in whole-cell hydrolysates and, generally, the presence of tetrahydrogenated menaquinones with nine



**Fig. 1.** Phylogenetic tree for the genera of the suborder *Pseudonocardineae* calculated from almost-complete 16S rRNA gene sequences (1276 nt) using Kimura's evolutionary-distance method (Kimura, 1980) and the neighbour-joining algorithm of Saitou & Nei (1987). Percentages at nodes represent levels of bootstrap support from 1000 resampled datasets; values less than 60% are not shown. Numbers within each clustered group indicate the total number of taxa with validly published names included in the phylogenetic analyses that made up each cluster. The taxa, strain numbers and accession numbers of 16S rRNA gene sequences can be found in Supplementary Table S1. Branches also conserved in maximum-parsimony (Felsenstein, 1989) and maximum-likelihood (Stamatakis *et al.*, 2002) trees are marked with asterisks. Genera currently defined as members of the family *Actinosynnemataceae* are identified in bold. Bar, 0.01 substitutions per nucleotide site.

repeating units [i.e. MK-9(H<sub>4</sub>)], are common to all, but there is no observed segregation of properties that supports subdivision of the suborder into more than one family. For instance, the presence of arabinose in whole-cell hydrolysates is observed within genera scattered over the phylogenetic tree, such as *Actinokineospora*, *Actinophytocola*, *Actinomycetospora*, *Allokutzneria*, *Amycolatopsis*, *Kibdelosporangium*, *Prauserella*, *Pseudonocardia*, *Saccharomonospora*, *Saccharopolyspora*, *Scissionella*, *Thermocrispum* and *Yuhushiella*, and therefore cannot be used to differentiate between members of the major clades within the suborder. Morphological properties, such as production of sporangia and motile spores, are also distributed throughout the taxa shown in Fig. 1, so they are of little differential use in grouping the genera into separate families.

In light of the lack of phylogenetic, chemotaxonomic and morphological support for differentiation of the genera within the family *Actinosynnemataceae* from those in the family *Pseudonocardiaceae*, as well as a lack of any strong support for any other subdivision of the suborder *Pseudonocardineae* at this time, it would appear that these genera should be transferred from the family *Actinosynnemataceae* into an emended family *Pseudonocardiaceae*. With the discovery, description and sequencing of many new taxa within the suborder *Pseudonocardineae* in the future, it might be possible to propose subdivision into additional families at a later date.

Formal emended descriptions of the family *Pseudonocardiaceae* and suborder *Pseudonocardineae* follow.

### **Emended description of the family *Pseudonocardiaceae* Embley *et al.* 1989 emend. Zhi *et al.* 2009**

*Pseudonocardiaceae* (Pseu.do.no.car'di.ac.e.ae. N.L. fem. n. *Pseudonocardia* the type genus of the family; L. suff. *-aceae* ending to denote a family; N.L. fem. pl. n. *Pseudonocardiaceae* the *Pseudonocardia* family).

The family contains the type genus *Pseudonocardia* Henssen 1957 (Approved Lists 1980) emend. Park *et al.* 2008, as well as the genera *Actinoalloteichus* Tamura *et al.* 2000, *Actinokineospora* Hasegawa 1988b emend. Labeda *et al.* 2010 (effective publication Hasegawa, 1988a), *Actinomycetospora* Jiang *et al.* 2008, *Actinophytocola* Indananda *et al.* 2010, *Actinosynnema* Hasegawa *et al.* 1978, *Alloactinosynnema* Yuan *et al.* 2010, *Allokutzneria* Labeda and Kroppenstedt 2008, *Amycolatopsis* Lechevalier *et al.* 1986 emend. Lee 2009, *Crossiella* Labeda 2001, *Goodfellowiella* Labeda *et al.* 2008 (previous illegitimate name *Goodfellowia* Labeda and Kroppenstedt 2006), *Haloechinotrix* Tang *et al.* 2010, *Kibdelosporangium* Shearer *et al.* 1986, *Kutzneria* Stackebrandt *et al.* 1994, *Lechevalieria* Labeda *et al.* 2001, *Lentzea* Yassin *et al.* 1995 emend. Labeda *et al.* 2001, *Prauserella* Kim and Goodfellow 1999 emend. Li *et al.* 2003, *Saccharomonospora* Nonomura and Ohara 1971 (Approved Lists 1980), *Saccharopolyspora*

Lacey and Goodfellow 1975 (Approved Lists 1980) emend. Korn-Wendisch *et al.* 1989, *Saccharothrix* Labeda *et al.* 1984 emend. Labeda and Lechevalier 1989, *Scissionella* Tian *et al.* 2009, *Streptoalloteichus* Tomita *et al.* 1987 emend. Tamura *et al.* 2008, *Thermocrispum* Korn-Wendisch *et al.* 1995, *Umezawaea* Labeda and Kroppenstedt 2007 and *Yuhushiella* Mao *et al.* 2011.

Aerobic, mesophilic or thermophilic, catalase-positive actinomycetes. Gram-positive. Not acid-fast. Morphologically heterogeneous; single or short chains of spores may be present on both aerial mycelium and substrate mycelium. Vegetative mycelium branches, diameter approximately 0.5–0.7 µm; aerial mycelium is produced and fragments in some genera into single smooth-surfaced, rod-shaped elements or chains of such elements. Some taxa may fail to produce aerial mycelium. Marked fragmentation of hyphae occurs in some taxa, but is absent in others. Other structures such as synnemata or dome-like bodies, sporangia or pseudosporangia may be produced in some genera. Motile spores may be produced in some genera. Most taxa are chemo-organotrophic, although some are autotrophic. A few taxa are halophilic. All genera contain *meso*-diaminopimelic acid as the diamino acid in their peptidoglycan and all except *Haloechinotrix* contain galactose as one of many diagnostic whole-cell sugars. Mycolic acids are not present in any of the genera. Tetrahydrogenated menaquinones of nine isoprene units are characteristic components, although menaquinones containing eight isoprene units predominate in the genus *Pseudonocardia*. The phospholipid profile generally includes phosphatidylethanolamine, sometimes containing hydroxylated fatty acids, as a major constituent, although representatives of one or more genera may also contain phosphatidylcholine. Resistant to lysozyme. The G+C content of the DNA ranges from 66 to 74 mol%. The pattern of 16S rRNA signatures consists of nucleotides at positions 127:234 (G–C), 564 (U), 672:734 (U–G), 831:855 (U–G), 832:854 (G–Y), 833:853 (U–G), 952:1229 (U–A) and 986:1219 (U–A). Members of the family are found in a variety of environments, including soils, plant material, manure and clinical or veterinary samples. The type genus is *Pseudonocardia* Henssen 1957 (Approved Lists 1980) emend. Park *et al.* 2008.

### **Emended description of the suborder *Pseudonocardineae* Stackebrandt *et al.* 1997 emend. Zhi *et al.* 2009**

*Pseudonocardineae* (Pseu.do.no.car'di.ne.ae. N.L. fem. n. *Pseudonocardia* the type genus of the suborder; N.L. suff. *-ineae* ending to denote a suborder; N.L. fem. pl. n. *Pseudonocardineae* the *Pseudonocardia* suborder).

Aerobic, mesophilic or thermophilic, catalase-positive actinomycetes comprising the family *Pseudonocardiaceae*, including the former members of the family *Actinosynnemataceae*. Morphology, chemotaxonomy, phylogeny and 16S rRNA signature nucleotides are those of the

**Table 1.** Comparison of chemotaxonomic profiles of genera within the order *Pseudonocardineae*Data were obtained from the original and emended descriptions listed in the emended description of the family *Pseudonocardiaceae*.

Genus	Sporangia produced	Motile spores	Whole-cell sugars*	Phospholipids†	Predominant menaquinone(s)	DNA G + C content (mol%)
<i>Actinoalloteichus</i>	None	No	Glc, Gal, Man, Rib	PE, PIM, PI, PG, DPG, PME	9(H <sub>4</sub> )	72–72.5
<i>Actinokineospora</i>	None	Variable	Gal, Ara, Rha, Man	PE, DPG, PI	9(H <sub>4</sub> )	72.0
<i>Actinomycespora</i>	None	No	Ara, Gal	PC, PI, PG	9(H <sub>4</sub> )	69.0
<i>Actinophytocola</i>	None	No	Ara, Gal, Man, Rha, Rib	PE, OH-PE	9(H <sub>4</sub> )	71.1
<i>Actinosynnema</i>	Synnemata	Yes	Gal, Man	PE, OH-PE, DPG	9(H <sub>4</sub> ), some 9(H <sub>6</sub> )	73.0
<i>Alloactinosynnema</i>	Pseudosporangia	No	Gal, Rib	DPG, PG, PC	9(H <sub>4</sub> )	68.2
<i>Allokutzneria</i>	Yes; no spores	No	Ara, Gal, Man	PE, PME, OH-PE, PI, lyso-PME, DPG, PG, lyso-PE	9(H <sub>4</sub> )	71.6
<i>Amycolatopsis</i>	None	No	Ara, Gal	PE, DPG, PG, PI	9(H <sub>4</sub> )	66.0–69.0
<i>Crossiella</i>	None	No	Gal, Man, Rha, Rib	PE, PME, PI, PIM	9(H <sub>4</sub> )	74.1
<i>Goodfellowiella</i>	None	No	Gal, Rib	PE, DPG, OH-PE, PME	9(H <sub>4</sub> ), 10(H <sub>4</sub> )	69.2
<i>Haloethinotrix</i>	None	No	Glc, Man, GlcN, NK	DPG, PG, PE, PI, PIM, PL	8(H <sub>4</sub> )	68.1
<i>Kibdelosporangium</i>	Yes	No	Ara, Gal, Mad (v), Glc (v), Rha (v)	PE, PI, PME, PG, DPG, PIM	9(H <sub>4</sub> ), 9(H <sub>6</sub> ), 9(H <sub>10</sub> )	66
<i>Kutzneria</i>	Yes	No	Gal, Rha	PE, DPG, PI, PG, PME	9(H <sub>4</sub> )	70.3–70.7
<i>Lechevalieria</i>	None	No	Gal, Man, Rha (tr)	PE, DPG, PG, PI	9(H <sub>4</sub> )	68.0–71.4
<i>Lentzea</i>	None	No	Gal, Man, Rib	PE, DPG, PI	9(H <sub>4</sub> )	71.4
<i>Prauserella</i>	None	No	Ara, Gal	DPG, PE	9(H <sub>2</sub> ), 9(H <sub>4</sub> )	67–68.9
<i>Pseudonocardia</i>	None	No	Ara, Gal	PC, PE, PME, PI, PIM, OH-PE	8(H <sub>4</sub> )	68–69
<i>Saccharomonospora</i>	None	No	Ara, Gal	PE, DPG, PG, PI	9(H <sub>4</sub> )	66.0–70.0
<i>Saccharopolyspora</i>	None	No	Ara, Gal	PC, PE, DPG, PG, PI	9(H <sub>4</sub> )	66.0–74.0
<i>Saccharothrix</i>	None	No	Gal, Rha, Man (tr)	PE, OH-PE, DPG, PG, PI, PIM	9(H <sub>4</sub> ), 10(H <sub>4</sub> )	71.4
<i>Scissionella</i>	None	No	Ara, Gal, Glc	DPG, PC, PE, PI, PL, PME	9(H <sub>4</sub> )	69.0
<i>Streptoalloteichus</i>	Pseudosporangia	Variable	Gal, Man, Rha	PE, DPG, PI, PIM, PME	9(H <sub>6</sub> ), 10(H <sub>6</sub> )	71.6
<i>Thermocrispum</i>	Pseudosporangia	No	Ara, Man, Glc, Gal (tr)	PE, PI, OH-PE	9(H <sub>4</sub> )	69.0–73.0
<i>Umezawaea</i>	None	No	Gal, Man, Rib, Rha (tr)	PE, PI, OH-PE, lyso-PE	9(H <sub>4</sub> ), 10(H <sub>4</sub> )	74.0
<i>Yuhushiella</i>	Pseudosporangia	No	Ara, Gal, Glc, Rib	PE, PIM, PME, DPG, PL, GlcNu	9(H <sub>4</sub> )	69.9

\*Ara, Arabinose; Gal, galactose; Glc, glucose; GlcN, glucosamine; Mad, madurose; Man, mannose; Rha, rhamnose; Rib, ribose; NK, unknown sugar; tr, trace; v, sugar is variably present in whole-cell hydrolysates.

†DPG, Diphosphatidylglycerol; GlcNu, phospholipids of unknown structure containing glucosamine; OH-PE, phosphatidylethanolamine with hydroxy fatty acids; lyso-PE, phosphatidylethanolamine where one fatty acid chain is missing from the glycerol backbone; lyso-PME, phosphatidylmethylethanolamine where one fatty acid chain is missing from the glycerol backbone; PC, phosphatidylcholine; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; PI, phosphatidylinositol; PIM, phosphatidylinositol mannosides; PL, unknown phospholipids; PME, phosphatidylmethylethanolamine.

family *Pseudonocardiaceae*. The type genus is *Pseudonocardia* Henssen 1957 (Approved Lists 1980) emend. Park *et al.* 2008.

## Acknowledgements

Names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of others that may also be suitable.

## References

- Embley, M. T., Smida, J. & Stackebrandt, E. (1989). *Pseudonocardiaceae* fam. nov. In *Validation of the Publication of New Names and New Combinations Previously Effectively Published Outside the IJSB*, List no. 29. *Int J Syst Bacteriol* **39**, 205–206.
- Felsenstein, J. (1989). PHYLIP (phylogeny inference package) version 3.5.1. Department of Genome Sciences, University of Washington, Seattle, USA.
- Hasegawa, T. (1988a). *Actinokineospora*: a new genus of the Actinomycetales. *Actinomycetologica* **2**, 31–45.
- Hasegawa, T. (1988b). *Actinokineospora* gen. nov. In *Validation of the Publication of New Names and New Combinations Previously Effectively Published Outside the IJSB*, List no. 27. *Int J Syst Bacteriol* **38**, 449.
- Hasegawa, T., Lechevalier, M. P. & Lechevalier, H. A. (1978). A new genus of Actinomycetales: *Actinosynnema* gen. nov. *Int J Syst Bacteriol* **28**, 304–310.
- Henssen, A. (1957). Beiträge zur Morphologie und Systematik der thermophilen Actinomyceten. *Arch Mikrobiol* **26**, 373–414 (in German).
- Indananda, C., Matsumoto, A., Inahashi, Y., Takahashi, Y., Duangmal, K. & Thamchaipenet, A. (2010). *Actinophytocola oryzae* gen. nov., sp. nov., isolated from the roots of Thai glutinous rice plants, a new member of the family *Pseudonocardiaceae*. *Int J Syst Evol Microbiol* **60**, 1141–1146.
- Jeon, Y.-S., Chung, H., Park, S., Hur, I., Lee, J.-H. & Chun, J. (2005). jPHYDIT: a JAVA-based integrated environment for molecular phylogeny of ribosomal RNA sequences. *Bioinformatics* **21**, 3171–3173.
- Jiang, Y., Wiese, J., Tang, S. K., Xu, L. H., Imhoff, J. F. & Jiang, C. L. (2008). *Actinomycetospora chiangmaiensis* gen. nov., sp. nov., a new member of the family *Pseudonocardiaceae*. *Int J Syst Evol Microbiol* **58**, 408–413.
- Kim, S. B. & Goodfellow, M. (1999). Reclassification of *Amycolatopsis rugosa* Lechevalier *et al.* 1986 as *Prauserella rugosa* gen. nov., comb. nov. *Int J Syst Bacteriol* **49**, 507–512.
- Kimura, M. (1980). A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *J Mol Evol* **16**, 111–120.
- Korn-Wendisch, F., Kempf, A., Grund, E., Kroppenstedt, R. M. & Kutzner, H. J. (1989). Transfer of *Faenia rectivirgula* Kurup and Agre 1983 to the genus *Saccharopolyspora* Lacey and Goodfellow 1975, elevation of *Saccharopolyspora hirsuta* subsp. *taberi* Labeda 1987 to species level, and emended description of the genus *Saccharopolyspora*. *Int J Syst Bacteriol* **39**, 430–441.
- Korn-Wendisch, F., Rainey, F., Kroppenstedt, R. M., Kempf, A., Majazza, A., Kutzner, H. J. & Stackebrandt, E. (1995). *Thermocrispum* gen. nov., a new genus of the order Actinomycetales, and description of *Thermocrispum municipale* sp. nov. and *Thermocrispum agreste* sp. nov. *Int J Syst Bacteriol* **45**, 67–77.
- Labeda, D. P. (2001). *Crossiella* gen. nov., a new genus related to *Streptoalloteichus*. *Int J Syst Evol Microbiol* **51**, 1575–1579.
- Labeda, D. P. & Kroppenstedt, R. M. (2000). Phylogenetic analysis of *Saccharothrix* and related taxa: proposal for *Actinosynnemataceae* fam. nov. *Int J Syst Evol Microbiol* **50**, 331–336.
- Labeda, D. P. & Kroppenstedt, R. M. (2006). *Goodfellowia* gen. nov., a new genus of the *Pseudonocardineae* related to *Actinoalloteichus*, containing *Goodfellowia coeruleoviolacea* gen. nov., comb. nov. *Int J Syst Evol Microbiol* **56**, 1203–1207.
- Labeda, D. P. & Kroppenstedt, R. M. (2007). Proposal of *Umezawaea* gen. nov., a new genus of the *Actinosynnemataceae* related to *Saccharothrix*, and transfer of *Saccharothrix tangerinus* Kinoshita *et al.* 2000 as *Umezawaea tangerina* gen. nov., comb. nov. *Int J Syst Evol Microbiol* **57**, 2758–2761.
- Labeda, D. P. & Kroppenstedt, R. M. (2008). Proposal for the new genus *Allokutzneria* gen. nov. within the suborder *Pseudonocardineae* and transfer of *Kibdelosporangium albatum* Tomita *et al.* 1993 as *Allokutzneria albata* comb. nov. *Int J Syst Evol Microbiol* **58**, 1472–1475.
- Labeda, D. P. & Lechevalier, M. P. (1989). Amendment of the genus *Saccharothrix* Labeda *et al.* 1984 and descriptions of *Saccharothrix espanaensis* sp. nov., *Saccharothrix cryophilis* sp. nov., and *Saccharothrix mutabilis* comb. nov. *Int J Syst Bacteriol* **39**, 420–423.
- Labeda, D. P., Testa, R. T., Lechevalier, M. P. & Lechevalier, H. A. (1984). *Saccharothrix*: a new genus of the Actinomycetales related to *Nocardopsis*. *Int J Syst Bacteriol* **34**, 426–431.
- Labeda, D. P., Hatano, K., Kroppenstedt, R. M. & Tamura, T. (2001). Revival of the genus *Lentzea* and proposal for *Lechevalieria* gen. nov. *Int J Syst Evol Microbiol* **51**, 1045–1050.
- Labeda, D. P., Kroppenstedt, R. M., Euzéby, J. P. & Tindall, B. J. (2008). Proposal of *Goodfellowiella* gen. nov. to replace the illegitimate genus name *Goodfellowia* Labeda and Kroppenstedt 2006. *Int J Syst Evol Microbiol* **58**, 1047–1048.
- Labeda, D. P., Price, N. P., Tan, G. Y. A., Goodfellow, M. & Klenk, H.-P. (2010). Emended description of the genus *Actinokineospora* Hasegawa 1988 and transfer of *Amycolatopsis fastidiosa* Henssen *et al.* 1987 as *Actinokineospora fastidiosa* comb. nov. *Int J Syst Evol Microbiol* **60**, 1444–1449.
- Lacey, J. & Goodfellow, M. (1975). A novel actinomycete from sugar-cane bagasse: *Saccharopolyspora hirsuta* gen. et sp. nov. *J Gen Microbiol* **88**, 75–85.
- Lechevalier, M. P., Prauser, H., Labeda, D. P. & Ruan, J. S. (1986). Two new genera of nocardioform actinomycetes: *Amycolata* gen. nov. and *Amycolatopsis* gen. nov. *Int J Syst Bacteriol* **36**, 29–37.
- Lee, S. D. (2009). *Amycolatopsis ultiminotia* sp. nov., isolated from rhizosphere soil, and emended description of the genus *Amycolatopsis*. *Int J Syst Evol Microbiol* **59**, 1401–1404.
- Li, W. J., Xu, P., Tang, S. K., Xu, L. H., Kroppenstedt, R. M., Stackebrandt, E. & Jiang, C. L. (2003). *Prauserella halophila* sp. nov. and *Prauserella alba* sp. nov., moderately halophilic actinomycetes from saline soil. *Int J Syst Evol Microbiol* **53**, 1545–1549.
- Ludwig, W., Strunk, O., Westram, R., Richter, L., Meier, H., Yadhukumar, Buchner, A., Lai, T., Steppi, S. & other authors (2004). ARB: a software environment for sequence data. *Nucleic Acids Res* **32**, 1363–1371.
- Mao, J., Wang, J., Dai, H. Q., Zhang, Z. D., Tang, Q. Y., Ren, B., Yang, N., Goodfellow, M., Zhang, L. X. & Liu, Z. H. (2011). *Yuhushiella deserti* gen. nov., sp. nov., a new member of the suborder *Pseudonocardineae*. *Int J Syst Evol Microbiol* **61**, 621–630.
- Nonomura, H. & Ohara, Y. (1971). Distribution of actinomycetes in soil. X. New genus and species of monosporic actinomycetes in soil. *J Ferment Technol* **49**, 895–903.

- Park, S. W., Park, S. T., Lee, J. E. & Kim, Y. M. (2008). *Pseudonocardia carboxydivorans* sp. nov., a carbon monoxide-oxidizing actinomycete, and an emended description of the genus *Pseudonocardia*. *Int J Syst Evol Microbiol* **58**, 2475–2478.
- Saitou, N. & Nei, M. (1987). The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol Biol Evol* **4**, 406–425.
- Shearer, M. C., Colman, P. M., Ferrin, R. M., Nisbet, L. J. & Nash, C. H., III (1986). New genus of the Actinomycetales: *Kibdelosporangium aridum* gen. nov., sp. nov. *Int J Syst Bacteriol* **36**, 47–54.
- Stackebrandt, E., Kroppenstedt, R. M., Jahnke, K. D., Kemmerling, C. & Gürtler, H. (1994). Transfer of *Streptosporangium viridogriseum* (Okuda et al. 1966), *Streptosporangium viridogriseum* subsp. *kofuense* (Nonomura and Ohara 1969), and *Streptosporangium albidum* (Furumai et al. 1968) to *Kutzneria* gen. nov. as *Kutzneria viridogrisea* comb. nov., *Kutzneria kofuensis* comb. nov., and *Kutzneria albida* comb. nov., respectively, and emendation of the genus *Streptosporangium*. *Int J Syst Bacteriol* **44**, 265–269.
- Stackebrandt, E., Rainey, F. A. & Ward-Rainey, N. L. (1997). Proposal for a new hierarchic classification system, Actinobacteria classis nov. *Int J Syst Bacteriol* **47**, 479–491.
- Stamatakis, A. P., Ludwig, T., Meier, H. & Wolf, M. J. (2002). AxML: a fast program for sequential and parallel phylogenetic tree calculations based on the maximum likelihood method. *Proc IEEE Comput Soc Bioinform Conf* **1**, 21–28.
- Tamura, T., Zhiheng, L., Yamei, Z. & Hatano, K. (2000). *Actinoalloteichus cyanogriseus* gen. nov., sp. nov. *Int J Syst Evol Microbiol* **50**, 1435–1440.
- Tamura, T., Ishida, Y., Otoguro, M., Hatano, K. & Suzuki, K. (2008). 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.
- Tang, S.-K., Wang, Y., Zhang, H., Lee, J.-C., Lou, K., Kim, C.-J. & Li, W.-J. (2010). *Haloechothrix alba* gen. nov., sp. nov., a halophilic filamentous actinomycete of the suborder *Pseudonocardineae*. *Int J Syst Evol Microbiol* **60**, 2154–2158.
- Tian, X. P., Zhi, X. Y., Qiu, Y. Q., Zhang, Y. Q., Tang, S. K., Xu, L. H., Zhang, S. & Li, W.-J. (2009). *Sciscionella marina* gen. nov., sp. nov., a marine actinomycete isolated from a sediment in the northern South China Sea. *Int J Syst Evol Microbiol* **59**, 222–228.
- Tomita, K., Nakakita, Y., Hoshino, Y., Numata, K. & Kawaguchi, H. (1987). New genus of the Actinomycetales: *Streptoalloteichus hindustanus* gen. nov., nom. rev.; sp. nov., nom. rev. *Int J Syst Bacteriol* **37**, 211–213.
- Yassin, A. F., Rainey, F. A., Brzezinka, H., Jahnke, K.-D., Weissbrodt, H., Budzikiewicz, H., Stackebrandt, E. & Schaal, K. P. (1995). *Lentzea* gen. nov., a new genus of the order Actinomycetales. *Int J Syst Bacteriol* **45**, 357–363.
- Yuan, L.-J., Zhang, Y.-Q., Yu, L.-Y., Liu, H.-Y., Guan, Y., Lee, J.-C., Kim, C.-J. & Zhang, Y.-Q. (2010). *Alloactinosynnema album* gen. nov., sp. nov., a member of the family Actinosynnemataceae isolated from soil. *Int J Syst Evol Microbiol* **60**, 39–43.
- Zhi, X. Y., Li, W.-J. & Stackebrandt, E. (2009). An update of the structure and 16S rRNA gene sequence-based definition of higher ranks of the class Actinobacteria, with the proposal of two new suborders and four new families and emended descriptions of the existing higher taxa. *Int J Syst Evol Microbiol* **59**, 589–608.