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

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The higher ranks of the class *Actinobacteria* were proposed and described in 1997. At each rank, the taxa were delineated from each other solely on the basis of 16S rRNA gene sequence phylogenetic clustering and taxon-specific 16S rRNA signature nucleotides. In the past 10 years, many novel members have been assigned to this class while, at the same time, some members have been reclassified. The new 16S rRNA gene sequence information and the changes in phylogenetic positions of some taxa influence decisions about which 16S rRNA nucleotides to define as taxon-specific. As a consequence, the phylogenetic relationships of *Actinobacteria* at higher levels may need to be reconstructed. Here, we present new 16S rRNA signature nucleotide patterns of taxa above the family level and indicate the affiliation of genera to families. These sets replace the signatures published in 1997. In addition, *Actinopolysporineae* subord. nov. and *Actinopolysporaceae* fam. nov. are proposed to accommodate the genus *Actinopolyspora*, *Kineosporiineae* subord. nov. and *Kineosporiaceae* fam. nov. are proposed to accommodate the genera *Kineococcus*, *Kineosporia* and *Quadrisphaera*, *Beutenbergiaceae* fam. nov. is proposed to accommodate the genera *Beutenbergia*, *Georgenia* and *Salana* and *Cryptosporangiaceae* fam. nov. is proposed to accommodate the genus *Cryptosporangium*. The families *Nocardiaceae* and *Gordoniaceae* are proposed to be combined in an emended family *Nocardiaceae*. Emended descriptions are also proposed for most of the other higher taxa.

INTRODUCTION

The class *Actinobacteria* constitutes one of the main phyla within the *Bacteria* (Ludwig & Klenk, 2001) on the basis of its branching position in 16S rRNA gene trees. Besides the phylogeny of the 16S rRNA gene, some conserved indels in 23S rRNA and protein (e.g. cytochrome-*c* oxidase I, CTP synthetase and glutamyl-tRNA synthetase) sequences

support the distinctness of members of the class from all other bacteria (Gao & Gupta, 2005). The initial hierarchical classification system of the *Actinobacteria* (Stackebrandt *et al.*, 1997) embraced 95 genera, belonging to 30 families and 10 suborders. The phylogenetic relationships of taxa higher than the rank of genus of the *Actinobacteria* were deduced from the clustering of genera in a neighbour-joining dendrogram. The distinction of these ranks from each other was based solely upon taxon-specific 16S rRNA signature nucleotides considered. Phenotypic characteristics, such as chemotaxonomic, morphological and physiological properties, were not taken into account in the delineation of higher ranks. Signature nucleotide patterns, often used in the forthcoming volume 4 of the second edition of *Bergey's Manual of Systematic Bacteriology* at the level of genera and families, are a molecular basis for

Abbreviations: ML, maximum-likelihood; MP, maximum-parsimony; NJ, neighbour-joining.

Trees based on 16S rRNA gene sequences showing relationships between members of the *Corynebacteriineae* using the neighbour-joining method and within the *Actinobacteria* using the maximum-parsimony and maximum-likelihood methods and a tree based on concatenated sequences of seven housekeeping genes are available as supplementary material with the online version of this paper.

positional differences within the 16S rRNA. It is not the 'truth', but an attempt to bring rational order to a group of related organisms, at least for the time being.

It was already obvious in 1997 that the composition of these signatures might change when new sequences were added to the databases. The analysis and determination of signatures were based on published 16S rRNA gene sequences of type strains. 16S rRNA gene sequences of uncultured micro-organisms were not considered, as the quality of such sequences cannot be checked. Nevertheless, the indication of the presence of novel taxa forecast an increase in the phylogenetic richness of the phylum. The availability of novel described taxa is the main reason why patterns of 16S rRNA gene sequence signatures need to be updated regularly.

To date, 219 genera (in 48 families, including some new genera, such as *Catelliglobospora*, *Devriesea*, *Fodinicola*, *Glaciibacter*, *Haloactinospora*, *Hamadaea*, *Humibacillus*, *Klugiella*, *Marihabitans*, *Pseudosporangium* and *Sciscionella*, proposed in papers in press in the *International Journal of Systematic and Evolutionary Microbiology* at the time of writing) have been accommodated in the class *Actinobacteria*, phylum *Actinobacteria*. The subclass *Sphaerobacteridae* was removed from the phylum *Actinobacteria* with the reclassification of *Sphaerobacter thermophilus* as a member of the class *Thermomicrobia*, phylum *Chloroflexi* (Hugenholtz & Stackebrandt, 2004). The description of the families *Catenulisporeaceae* (Busti *et al.*, 2006) and *Actinospicaceae* (Cavaletti *et al.*, 2006) resulted in the description of an eleventh suborder, *Catenulisporinae* (Cavaletti *et al.*, 2006), in the order *Actinomycetales*. As the number of 16S rRNA gene sequences deposited in public databases has increased tremendously, decisions about which 16S rRNA gene sequence nucleotides define taxonomic ranks were likely to be affected. Above all, this was expected to happen in those genera and higher taxa that included only a single type strain in 1997.

Given that scientists actually use the set of signatures for decisions on the description of higher taxa, an update of the phylogenetic structure of the class *Actinobacteria* is called for. In this paper, we update the structure of higher ranks of the class *Actinobacteria* and provide a set of 16S rRNA signature nucleotides between the ranks of family and subclass. Some novel taxa are also proposed as a result of the phylogenetic analysis and signature patterns.

METHODS

16S rRNA gene sequence and alignment. A total of 2642 16S rRNA gene sequences of members of the phylum *Actinobacteria* were obtained from the Ribosomal Database Project (Cole *et al.*, 2007). Sequences shorter than 1300 bp and those containing ambiguous nucleotide sequences were excluded from the database. Sequences of each family were downloaded, together with an *Escherichia coli* 16S rRNA gene sequence (GenBank accession number J01695), in separate files. Alignments were carried out using the CLUSTAL W tool in MEGA version 4.0 (Tamura, *et al.*, 2007). The alignments were then corrected manually using the program BioEdit (Hall, 1999).

Phylogenetic analyses. For reconstruction of the phylogenetic dendrograms, the type species of the type genus of each family were selected as representative. The phylogenetic dendrograms obtained represented a general overview at the higher-taxon level but do not display the branching order at the species level. As lower-taxon branching orders are susceptible to changes depending on the dataset, i.e. the number of sequences available for a given genus, the database was restricted to the type strain of the type species of the type genus of each family. All columns containing gaps in the alignment were deleted manually. The neighbour-joining (NJ), maximum-parsimony (MP) and maximum-likelihood (ML) algorithms were used in phylogenetic tree building. Phylogenetic dendrograms were reconstructed by using the DNAPARS and DNAML programs in the PHYLIP package (Felsenstein, 2005) and MEGA version 4.0 (Tamura, *et al.*, 2007). The distance matrix was produced on the basis of Kimura's two-parameter model (Kimura, 1980). Bootstrap analysis (Felsenstein, 1985) was done with 1000 replicates except in ML, where only 100 replicates were generated.

Deduced amino acid sequences of the proteins AtpD, DnaA, DnaG, DnaK, GyrB, RecA and RpoB were retrieved from the genomes of the following strains for multilocus sequence analysis (MLSA) in order to show the phylogenetic relationships of main groups of *Actinobacteria*: *Acidothermus cellulolyticus* 11B^T, *Actinomyces odontolyticus* ATCC 17982, *Arthrobacter aureus* TC1, *Arthrobacter* sp. FB24, *Bifidobacterium adolescentis* ATCC 15703^T, *Bifidobacterium longum* NCC2705, *Clavibacter michiganensis* subsp. *michiganensis* NCPPB 382, *Corynebacterium efficiens* YS-314^T, *Corynebacterium glutamicum* R, *Frankia alni* ACN14a, *Frankia* sp. CcI3, *Frankia* sp. EAN1pec, *Janibacter* sp. HTCC2649, *Kineococcus radiotolerans* SRS30216^T, *Leifsonia xyli* subsp. *xyli* CTCB07, *Mycobacterium smegmatis* MC2 155, *Mycobacterium ulcerans* Agy99, *Nocardia farcinica* IFM 10152, *Nocardioideis* sp. JS614, *Propionibacterium acnes* KPA171202, *Renibacterium salmoninarum* ATCC 33209^T, *Rhodococcus* sp. RHA1, *Rubrobacter xylanophilus* DSM 9941^T, *Saccharopolyspora erythraea* NRRL 2338^T, *Salinispora arenicola* CNS-205, *Salinispora tropica* CNB-440^T, *Streptomyces avermitilis* MA-4680^T, *Streptomyces coelicolor* A3(2), *Thermobifida fusca* YX and *Tropheryma whippelii* TW08/27. The corresponding proteins in the genomes of *Bacillus clausii* KSM-K16, *Clostridium acetobutylicum* ATCC 824^T and *Escherichia coli* K-12 were used as outgroups. The incongruence length difference (ILD) test (1000 randomizations of datasets; Farris *et al.*, 1995) was performed using PAUP* version 4.0b10 (Swofford, 2002). Hierarchical likelihood-ratio tests were conducted with a batch file supplied with MODELTEST 3.7 (Posada & Hasegawa, 1998) to provide the evolutionary models used in NJ methods.

Signature nucleotide analyses. The complete dataset used for the analyses described in this study contained information on more than 1300 unambiguous nucleotide positions present in all sequences between positions 100 and 1400 (*Escherichia coli* sequence; Brosius *et al.*, 1978). Consensus sequences were calculated by using BioEdit software (Hall, 1999) for each family and used to compare with other families in the same suborder. The threshold consensus value for inclusion of a given nucleotide in a dataset at the family level was 95 %. Variable positions (<95 %) at the level of families and suborders were treated as gaps. Only highly conservative sites were used to detect group-specific signature nucleotides. Positional nucleotide numerical summary (one function of BioEdit) can provide intuitive and tractable statistical data. This approach allows simultaneous identification of those positions that are either above or below the threshold consensus value of 95 %.

RESULTS AND DISCUSSION

The hierarchical classification system based on the phylogeny of 16S rRNA gene sequences does not change the

current descriptions of species and genera, which are in most cases based upon morphological, chemotaxonomic and physiological characteristics (Stackebrandt *et al.*, 1997). These taxa, which provide the working basis for taxonomists, have been revised to constitute phylogenetically coherent taxonomic units in the past several decades. However, the descriptions of taxa above the genus level have not been revisited in the past 10 years. Signature nucleotides are derivatives of the classification process (Stackebrandt *et al.*, 1997). As most signatures are involved in higher order structure, their use in classification expands information from the primary structure (phylogenetic trees) to information on secondary structure idiosyncrasies. However, it is obvious that, at any rank, a significant increase in numbers of species in any of the phylogenetic lineages leads to a decrease in the number of signatures. One example is obvious in the suborder *Corynebacterineae*: the differences between signature patterns of the families *Nocardiaceae* and *Gordoniaceae* disappear with the introduction of the genera *Millisia*, *Skermania* and *Williamsia*. These three genera differed significantly from members of the family *Gordoniaceae* at signature sites 70:98, 293:304, 307, 661:744, 824:876, 825:875, 1002:1038 and 1124:1149. The phylogenetic position of the genera *Millisia*, *Skermania* and *Williamsia* is located between the families *Nocardiaceae* and *Gordoniaceae* (Supplementary Fig. S1, available in IJSEM Online). Hence, the families *Nocardiaceae* and *Gordoniaceae* are proposed here to be combined in an emended family *Nocardiaceae*.

In the past, the genera *Actinocorallia*, *Actinokineospora*, *Excellospora*, *Kineococcus* and *Kineosporia* were excluded from the taxonomic system of *Actinobacteria* because they had either not been investigated by 16S rRNA gene sequence analysis or their phylogenetic affiliation remained undetermined because of uncertainties about their phylogenetic position. The relationship between the members of the family *Thermomonosporaceae* was clarified on the basis of 16S rRNA gene, 16S–23S rRNA internal transcribed spacer and 23S rRNA gene sequences and chemotaxonomic analyses (Zhang *et al.*, 2001). As a consequence, the description of the genus *Actinocorallia* was emended and it was assigned to the family *Thermomonosporaceae*. Simultaneously, the genus *Excellospora* lost its taxonomic status when the type species *Excellospora viridilutea* was transferred to the genus *Actinomadura* as *Actinomadura viridilutea* (Zhang *et al.*, 2001). Phylogenetic analysis of the genera *Actinokineospora*, *Actinosynnema*, *Lentzea* and *Saccharothrix* showed that they are members of the same clade, and distinct from the *Pseudonocardiaceae* (Labeda & Kroppenstedt, 2000). The family *Actinosynnemataceae* was established to accommodate the genera *Actinokineospora*, *Actinosynnema*, *Lentzea* and *Saccharothrix*.

Subsequent studies showed that the genera *Kineococcus* and *Kineosporia* form a cluster with a high bootstrap value (98%) and did not belong to any previously described suborder (Kudo *et al.*, 1998). Furthermore, the evolutionary distance between the two genera seems to be great

enough to separate them at the family level. The genus *Quadrisphaera* was proposed by Maszenan *et al.* (2005) and assigned to the suborder *Frankineae* at that time. In fact, the genera *Kineococcus*, *Kineosporia* and *Quadrisphaera* form a distinct clade (Fig. 1) and share neighbourhood with the suborder *Micrococcineae* when more sequences from each representative were used in reconstruction of the phylogenetic dendrogram. The genera *Kineococcus*, *Kineosporia* and *Quadrisphaera* differed from the suborder *Micrococcineae* at the sites 1165:1171 (G–A vs G–C) and 1163:1173 (G–U vs G–C). Therefore, *Kineosporiineae* subord. nov. and *Kineosporiaceae* fam. nov. are proposed to accommodate the genera *Kineococcus*, *Kineosporia* and *Quadrisphaera*. Similarly, the genus *Actinopolyspora* forms a deep separate branch in the order *Actinomycetales*. *Actinopolysporineae* subord. nov. and *Actinopolysporaceae* fam. nov. are proposed to accommodate the genus *Actinopolyspora*.

The genus *Cryptosporangium* was proposed by Tamura *et al.* (1998), and its phylogenetic position was located in the suborder *Frankineae*. Although the branch was not supported by a high bootstrap value, the relationships with other families remained stable. Noticeably, the signature nucleotides of the genus *Cryptosporangium* differed distinctly from those of other families. Consequently, the genus *Cryptosporangium* should represent a novel family of the suborder *Frankineae*. *Cryptosporangiaceae* fam. nov. is proposed to accommodate the genus *Cryptosporangium*. The genera *Beutenbergia* (Groth *et al.*, 1999b), *Georgenia* (Altenburger *et al.*, 2002a) and *Salana* (von Wintzingerode *et al.*, 2001) were assigned to the suborder *Micrococcineae* as novel lineages at the genus level; *Beutenbergiaceae* fam. nov. is proposed to accommodate the genera *Beutenbergia*, *Georgenia* and *Salana*.

The phylogenetic position of the genus *Thermobispora* was unclear when it was proposed by Wang *et al.* (1996). Even additional analysis, performed to clarify the taxonomic position of *Thermobispora*, did not lead to a reliable higher-order classification. Though the family-level affiliation of *Thermobispora* still can not be determined, the genus should be assigned to the suborder *Streptosporangineae*. In the following updated phylogenetic structure of the class *Actinobacteria*, the genus *Thermobispora* was excluded.

The phylogenetic relatedness of taxa above the genus level is shown in Fig. 1. High bootstrap values are found at deep branching points of lineages such as nodes that separate orders. In contrast, low bootstrap values are found at nodes that separate some suborders and most families of the order *Actinomycetales*. The class *Actinobacteria* contains the subclasses *Acidimicrobidae*, *Rubrobacteridae*, *Coriobacteridae* and *Actinobacteridae*. In comparison with the dendrogram shown in 1997, the phylogenetic relatedness of these lineages (Fig. 1) has been affected by the introduction of novel families described in the past decade.

The order *Rubrobacterales* constitutes one of the deepest branches within the phylum *Actinobacteria*, followed by the

Fig. 1. Intraclass relatedness of the class *Actinobacteria* showing the presence of five orders based on 16S rRNA gene sequence comparison. The phylogenetic relatedness of the families of the class *Actinobacteria* is outlined. Taxa newly described in this paper are highlighted in bold. Bootstrap values of 50 % or more are indicated at branch points. Bar, 2 substitutions per 100 nucleotide positions.

lineages of the orders *Coriobacteriales* and *Acidimicrobiales*. A comparative genomic study has provided convincing evidence that the *Rubrobacterales* is part of the phylum *Actinobacteria* and forms an outgroup of the other actinobacteria (Gao *et al.*, 2006). Within the subclass *Actinobacteridae*, the family *Bifidobacteriaceae* forms a deep-branching lineage. The placement of the bifidobacteria within the *Actinobacteria* and their deep branching within this phylum have also been strongly supported by comparative genomic studies (Gao *et al.*, 2006; Ventura *et al.*, 2007). The phylogenetic relationships among deeply branching lineages within the phylum *Actinobacteria* are stable and supported by high bootstrap values in the NJ tree.

The topological structures of phylogenetic dendrograms calculated on the basis of three different algorithms were compared with each other. The families belonging to the suborder *Frankineae* were separated into distinct clades in the MP and ML trees (Supplementary Figs S2 and S3). The suborders *Actinomycineae*, *Glycomycineae* and *Actinopolysporineae* subord. nov. formed a distinct branch and were positioned within the suborder *Micrococcineae* in the MP

and ML trees. Similarly, the order *Bifidobacteriales* was positioned within the suborder *Micrococcineae* in the MP and ML trees. This confirms the study of Gao *et al.* (2006), indicating that members of *Bifidobacteriales* are related to the *Micrococcineae*. All other families and suborders were positioned at similar branches in NJ, MP and ML trees (Fig. 1 and Supplementary Figs S2 and S3). Phylogenetic analysis based on the 16S rRNA gene sequence as well as comparative genomic studies indicate that the suborders *Streptomycineae*, *Frankineae*, *Pseudonocardineae* and *Corynebacterineae* form late-branching groups within the *Actinobacteria* (Gao *et al.*, 2006).

The *P* value generated from the ILD analysis was 0.001, which indicated that the combination of data would improve the phylogenetic accuracy. Hierarchical likelihood-ratio tests were performed in the selection of the evolutionary model and in the optimization of parameters such as base frequencies, the substitution model and among-site rate variation. The TrN model (Tamura & Nei, 1993) with gamma (Γ) variation and a proportion of invariable sites (I) was used in the NJ analysis. The MLSA

result (Supplementary Fig. S4) indicates that the suborders *Streptomycineae*, *Micromonosporineae*, *Frankineae*, *Pseudonocardineae* and *Corynebacterineae* form late-branching groups within the *Actinobacteria*, as found in comparative genomic studies and 16S rRNA gene sequence phylogeny. The strains *Actinomyces odontolyticus* ATCC 17982, *Bifidobacterium adolescentis* ATCC 15703^T and *Bifidobacterium longum* NCC2705 form a clade within the suborder *Micrococcineae* (see above; viz. *Janibacter* sp. HTCC2649, *Arthrobacter aurescens* TC1, *Arthrobacter* sp. FB24, *Renibacterium salmoninarum* R, *Tropheryma whipplei* TW08/27, *Clavibacter michiganensis* subsp. *michiganensis* NCPPB 382 and *Leifsonia xyli* subsp. *xyli* CTCB07). Similarly, *Kineococcus radiotolerans* SRS30216^T and *Janibacter* sp. HTCC2649 form a clade within the *Micrococcineae*. Nevertheless, as long as the 16S rRNA gene plays the most decisive role in decisions on higher-order structures, topologies of trees from genes coding for housekeeping proteins may be used to support or contradict such arguments; eventually, when genome sequences become available for all type strains, genes other than the 16S rRNA gene may reveal their potential to reflect better the phylogeny of the *Actinobacteria*.

The signatures given below for higher taxa were chosen for their presence in more than 95 % (the same criterion as used by Stackebrandt *et al.*, 1997) of the members of the respective taxon. The genus was treated as the lowest unit for the definition of signature nucleotides. An updated description of the hierarchical classification system of the class *Actinobacteria* is proposed as follows. Some signature nucleotides are in common with the previous patterns. About 207 signature nucleotides proposed by Stackebrandt *et al.* (1997) are not valid today.

Emended description of the subclass *Acidimicrobidae* Stackebrandt *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 242:284 (U–G), 291:309 (U–A), 316:337 (C–G), 819 (U), 952:1229 (C–G) and 1115:1185 (U–G). The subclass contains the order *Acidimicrobiales*. The nomenclatural type is the order *Acidimicrobiales* Stackebrandt *et al.* 1997.

Emended description of the order *Acidimicrobiales* Stackebrandt *et al.* 1997

The 16S rRNA nucleotide signature pattern is as that of the subclass. The order contains the family *Acidimicrobiaceae*. The nomenclatural type is the genus *Acidimicrobium* Clark and Norris 1996.

Emended description of the family *Acidimicrobiaceae* Stackebrandt *et al.* 1997

The 16S rRNA nucleotide signature pattern is as that of the subclass. The family contains the type genus *Acidimicrobium*.

Emended description of the subclass *Coriobacteridae* Stackebrandt *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 242:284 (C–G), 291:309 (C–G), 316:337 (U–G), 819 (A), 952:1229 (U–A) and 1115:1185 (C–G). The subclass contains the order *Coriobacteriales*. The nomenclatural type is the order *Coriobacteriales* Stackebrandt *et al.* 1997.

Emended description of the order *Coriobacteriales* Stackebrandt *et al.* 1997

The 16S rRNA nucleotide signature pattern is as that of the subclass. The order contains the family *Coriobacteriaceae*. The nomenclatural type is the genus *Coriobacterium* Haas and König 1988.

Emended description of the family *Coriobacteriaceae* Stackebrandt *et al.* 1997

The 16S rRNA nucleotide signature pattern is as that of the subclass. The family contains the type genus *Coriobacterium*, as well as the genera *Atopobium* Collins and Wallbanks 1993 (effective publication Collins & Wallbanks, 1992), *Adlercreutzia* Maruo *et al.* 2008, *Collinsella* Kageyama *et al.* 1999, emend. Kageyama and Benno 2000, *Cryptobacterium* Nakazawa *et al.* 1999, *Denitrobacterium* Anderson *et al.* 2000, *Eggerthella* Wade *et al.* 1999, *Olsenella* Dewhirst *et al.* 2001 and *Slackia* Wade *et al.* 1999.

Emended description of the subclass *Rubrobacteridae* Rainey *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 242:284 (C–G), 291:309 (U–A), 316:337 (C–G), 819 (A), 952:1229 (U–A) and 1115:1185 (C–G). The subclass contains the order *Rubrobacterales*. The nomenclatural type is the order *Rubrobacterales* Rainey *et al.* 1997.

Emended description of the order *Rubrobacterales* Rainey *et al.* 1997

The 16S rRNA nucleotide signature pattern is as that of the subclass. The order contains the families *Rubrobacteraceae*, *Conexibacteraceae*, *Patulibacteraceae*, *Solirubrobacteraceae* and *Thermoleophilaceae*. The nomenclatural type is the genus *Rubrobacter* Suzuki *et al.* 1989 (effective publication Suzuki *et al.*, 1988).

Emended description of the family *Rubrobacteraceae* Rainey *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 63:104 (C–G), 144:178 (G–C), 145:177 (G–C), 293:304 (G–U), 377:386 (G–C), 409:433 (C–G), 657:749 (G–C), 681:709 (C–G), 722:733 (G–G), 953:1228 (U–A), 954:1226 (C–G), 1051:1207 (C–G) and 1313:1324 (U–A). The family contains the type genus *Rubrobacter*.

**Emended description of the family
Conexibacteraceae Stackebrandt 2005 (effective
publication Stackebrandt, 2004)**

The pattern of 16S rRNA signatures consists of nucleotides at positions 144:178 (U–A), 145:177 (U–A), 293:304 (G–C), 377:386 (C–G), 408:434 (A–U), 418:425 (U–A), 590:649 (U–A) and 600:638 (U–G). The family contains the type genus *Conexibacter* Monciardini *et al.* 2003.

**Emended description of the family
Patulibacteraceae Takahashi *et al.* 2006**

The pattern of 16S rRNA signatures consists of nucleotides at positions 52:359 (C–G), 144:178 (C–G), 293:304 (G–C), 377:386 (C–G), 502:543 (G–C), 590:649 (U–A), 600:638 (U–G) and 1354:1368 (U–G). The family contains the type genus *Patulibacter* Takahashi *et al.* 2006.

**Emended description of the family
Solirubrobacteraceae Stackebrandt 2005
(effective publication Stackebrandt, 2004)**

The pattern of 16S rRNA signatures consists of nucleotides at positions 52:359 (C–G), 144:178 (C–G), 145:177 (C–G), 293:304 (G–C), 590:649 (C–G) and 600:638 (C–G). The family contains the type genus *Solirubrobacter* Singleton *et al.* 2003.

**Emended description of the family
Thermoleophilaceae Stackebrandt 2005
(effective publication Stackebrandt, 2004)**

The pattern of 16S rRNA signatures consists of nucleotides at positions 52:359 (C–G), 144:178 (C–G), 145:177 (C–G), 293:304 (G–U), 370:391 (G–C), 377:386 (C–G), 590:649 (C–G), 600:638 (C–G), 670:736 (G–C), 681:709 (C–G), 941:1342 (G–C) and 1311:1326 (G–C). The family contains the type genus *Thermoleophilum* Zarilla and Perry 1986 (effective publication Zarilla & Perry, 1984).

**Emended description of the subclass
Actinobacteridae Stackebrandt *et al.* 1997**

The pattern of 16S rRNA signatures consists of nucleotides at positions 242:284 (U–G), 291:309 (C–G), 316:337 (U–G), 819 (G), 952:1229 (C–G) and 1115:1185 (U–G). The subclass contains the orders *Bifidobacteriales* and *Actinomycetales*. The nomenclatural type is the order *Actinomycetales* Buchanan 1917.

**Emended description of the order
Bifidobacteriales Stackebrandt *et al.* 1997**

The pattern of 16S rRNA signatures consists of nucleotides at positions 688:699 (A–U), 701 (U), 823:877 (A–U) and 1060:1197 (C–G). The order contains the family *Bifidobacteriaceae*. The nomenclatural type is the genus *Bifidobacterium* Orla-Jensen 1924.

**Emended description of the family
Bifidobacteriaceae Stackebrandt *et al.* 1997**

The family contains the type genus *Bifidobacterium*, as well as the genera *Aeriscardovia* Simpson *et al.* 2004, *Alloiscardovia* Huys *et al.* 2007, *Gardnerella* Greenwood and Pickett 1980, *Parascardovia* Jian and Dong 2002 and *Scardovia* Jian and Dong 2002. The 16S rRNA nucleotide signature is as that of the order.

**Emended description of the order Actinomycetales
Buchanan 1917, emend. Stackebrandt *et al.* 1997**

The pattern of 16S rRNA signatures consists of nucleotides at positions 688:699 (G–C), 701 (C), 823:877 (G–C) and 1060:1197 (U–A). The order *Actinomycetales* contains the suborders *Actinomycineae*, *Actinopolysporineae*, *Catenulisporineae*, *Corynebacterineae*, *Frankineae*, *Glycomycineae*, *Kineosporiineae*, *Micrococcineae*, *Micromonosporineae*, *Propionibacterineae*, *Pseudonocardineae*, *Streptomycineae* and *Streptosporangineae*. The nomenclatural type is the genus *Actinomyces* Harz 1877.

**Emended description of the suborder
Actinomycineae Stackebrandt *et al.* 1997**

The pattern of 16S rRNA signatures consists of nucleotides at positions 127:234 (R–U), 598:640 (Y–G), 828 (R), 829:857 (G–C), 832:854 (G–Y), 952:1229 (C–G) and 986:1219 (A–U). The suborder contains the family *Actinomycetaceae*. The nomenclatural type is the genus *Actinomyces*.

**Emended description of the family
Actinomycetaceae Buchanan 1918, emend.
Stackebrandt *et al.* 1997**

Genera belonging to the family are the type genus *Actinomyces*, as well as the genera *Actinobaculum* Lawson *et al.* 1997, *Arcanobacterium* Collins *et al.* 1983 (effective publication Collins *et al.*, 1982), *Mobiluncus* Spiegel and Roberts 1984 and *Varibaculum* Hall *et al.* 2003. The 16S rRNA nucleotide signature is as that of the suborder.

**Description of the suborder Actinopolysporineae
subord. nov.**

Actinopolysporineae (Ac.ti'no.po.ly.spo.ri'ne.ae. N.L. fem. n. *Actinopolyspora* type genus of the suborder; -ineae ending to denote a suborder; N.L. fem. pl. n. *Actinopolysporineae* the *Actinopolyspora* suborder).

The pattern of 16S rRNA signatures consists of nucleotides at positions 127:234 (A–U), 242:284 (C–G), 657:749 (G–C), 672:734 (C–G), 828 (A), 829:857 (G–C), 833:853 (U–G), 840:846 (C–G), 986:1219 (U–A), 1100 (U), 1183 (C), 1117:1183 (G–C) and 1309:1328 (G–U). The suborder contains the family *Actinopolysporaceae*. The nomenclatural type is the genus *Actinopolyspora* Gochner *et al.* 1975.

Description of the family *Actinopolysporaceae* fam. nov.

Actinopolysporaceae (Ac.ti'no.po.ly.spo.ra'ce.ae. N.L. fem. n. *Actinopolyspora* type genus of the family; -aceae ending to denote a family; N.L. fem. pl. n. *Actinopolysporaceae* the *Actinopolyspora* family).

The family contains the type genus *Actinopolyspora*. The 16S rRNA nucleotide signature is as that of the suborder.

Emended description of the suborder *Catenulisporineae* Cavaletti et al. 2006

The pattern of 16S rRNA signatures consists of nucleotides at positions 127:234 (G–C), 209 (G), 484 (U), 828 (U), 831:855 (G–G), 840:846 (U–G), 955:1225 (C–G), 986:1219 (U–A) and 987:1218 (G–C). The suborder contains the families *Catenulisporaceae* and *Actinospicaceae*. The nomenclatural type is the genus *Catenulispora* Busti et al. 2006.

Emended description of the family *Catenulisporaceae* Busti et al. 2006

The pattern of 16S rRNA signatures consists of nucleotides at positions 262 (A), 344 (A), 576 (A), 747 (A), 129:232 (U–A), 580:761 (U–A), 658:748 (U–U), 659:746 (C–G), 824:876 (A–U), 825:875 (A–U), 834:852 (G–G), 952:1229 (U–A), 986:1219 (U–A) and 999:1041 (U–U). The family contains the type genus *Catenulispora*.

Emended description of the family *Actinospicaceae* Cavaletti et al. 2006

The pattern of 16S rRNA signatures consists of nucleotides at positions 262 (G), 344 (G), 576 (G), 747 (U), 129:232 (A–G), 580:761 (C–G), 586:755 (C–G), 658:748 (A–U), 659:746 (U–A), 824:876 (C–G), 825:875 (G–C), 834:852 (G–C), 952:1229 (C–G), 986:1219 (A–U) and 999:1041 (C–G). The family contains the type genus *Actinospica* Cavaletti et al. 2006.

Emended description of the suborder *Corynebacterineae* Stackebrandt et al. 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 127:234 (G–Y), 564 (C), 672:734 (U–G), 833:853 (U–G), 952:1229 (U–A) and 986:1219 (U–A). The suborder contains the families *Corynebacteriaceae*, *Dietziaceae*, *Mycobacteriaceae*, *Nocardiaceae*, *Segniliparaceae* and *Tsukamurellaceae*. The nomenclatural type is the genus *Corynebacterium* Lehmann and Neumann 1896.

Emended description of the family *Corynebacteriaceae* Lehmann and Neumann 1907, emend. Stackebrandt et al. 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 250 (U), 316:337 (U–G), 418:425 (C–G),

586:755 (U–G), 599:639 (C–G), 662:743 (U–G), 987:1218 (G–C) and 1059:1198 (U–A). The family contains the type genus *Corynebacterium*, as well as the genus *Turicella* Funke et al. 1994.

Emended description of the family *Dietziaceae* Rainey et al. 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 241:285 (U–G), 250 (U), 316:337 (C–G), 418:425 (U–A), 599:639 (C–G), 662:743 (C–G), 987:1218 (A–U), 1000:1040 (A–U), 1059:1198 (U–A) and 1115:1185 (C–G). The family contains the type genus *Dietzia* Rainey et al. 1995.

Emended description of the family *Mycobacteriaceae* Chester 1897, emend. Stackebrandt et al. 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 128:233 (G–C), 250 (U), 316:337 (C–G), 418:425 (C–G), 586:755 (U–G), 599:639 (U–G), 662:743 (C–G), 987:1218 (G–C), 1000:1040 (A–U) and 1026:1035 (U–G). The family contains the type genus *Mycobacterium* Lehmann and Neumann 1896.

Emended description of the family *Nocardiaceae* Castellani and Chalmers 1919, emend. Rainey et al. 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 250 (U), 316:337 (C–G), 418:425 (C–G), 580:761 (U–A), 599:639 (C–G), 662:743 (C–G), 987:1218 (G–C) and 1000:1040 (A–U). The family contains the type genus *Nocardia* Trevisan 1889, as well as the genera *Gordonia* (ex Tsukamura 1971) Stackebrandt et al. 1989 (effective publication Stackebrandt et al., 1988), *Millisia* Soddell et al. 2006, *Rhodococcus* Zopf 1891, *Skermania* Chun et al. 1997 and *Williamsia* Kämpfer et al. 1999.

Emended description of the family *Segniliparaceae* Butler et al. 2005

The pattern of 16S rRNA signatures consists of nucleotides at positions 128:233 (G–C), 250 (A), 316:337 (C–G), 418:425 (C–G), 586:755 (C–G), 599:639 (C–G), 662:743 (C–G), 987:1218 (G–C), 1000:1040 (A–G) and 1059:1198 (C–G). The family contains the type genus *Segniliparus* Butler et al. 2005.

Emended description of the family *Tsukamurellaceae* Rainey et al. 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 128:233 (G–C), 250 (U), 316:337 (C–G), 418:425 (C–G), 580:761 (C–G), 599:639 (C–G), 987:1218 (G–C), 1000:1040 (A–C) and 1059:1198 (C–G). The family contains the type genus *Tsukamurella* Collins et al. 1988b.

Emended description of the suborder *Frankineae* Stackebrandt *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 127:234 (G–C), 209 (R), 828 (A), 833:853 (U–G), 840:846 (C–G), 844 (A), 845 (C), 1163:1173 (G–C), 1164:1172 (G–U) and 1165:1171 (G–C). The suborder contains the families *Frankiaceae*, *Acidothermaceae*, *Cryptosporangiaceae*, *Geodermatophilaceae*, *Nakamurellaceae* and *Sporichthyaceae*. The nomenclatural type is the genus *Frankia* Brunchorst 1886.

Emended description of the family *Frankiaceae* Becking 1970, emend. Hahn *et al.* 1989, emend. Normand *et al.* 1996, emend. Stackebrandt *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 184:193 (A–C), 195 (A), 196 (U), 582:758 (U–A), 601:637 (G–U), 602:636 (C–G), 841 (C), 952:1229 (U–A), 986:1219 (A–U), 1059:1198 (C–G) and 1308:1329 (C–G). The family contains the type genus *Frankia*.

Emended description of the family *Acidothermaceae* Rainey *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 184:193 (C–U), 195 (G), 196 (C), 203:214 (U–G), 589:650 (U–A), 601:637 (G–U), 602:636 (A–U), 614:626 (A–U), 841 (U), 952:1229 (U–A), 986:1219 (U–A), 1059:1198 (C–G) and 1308:1329 (C–G). The family contains the type genus *Acidothermus* Mohagheghi *et al.* 1986.

Description of the family *Cryptosporangiaceae* fam. nov.

Cryptosporangiaceae (Cryp'to.spo.ran.gi.a'ce.ae. N.L. neut. n. *Cryptosporangium* type genus of the family; -aceae ending to denote a family; N.L. fem. pl. n. *Cryptosporangiaceae* the *Cryptosporangium* family).

The pattern of 16S rRNA signatures consists of nucleotides at positions 195 (U), 196 (C), 601:637 (A–U), 602:636 (C–G), 841 (U), 952:1229 (C–G), 986:1219 (A–U), 1042 (U), 1059:1198 (U–A), 1251 (G) and 1003:1037 (A–C). The family contains the type genus *Cryptosporangium* Tamura *et al.* 1998.

Emended description of the family *Geodermatophilaceae* Normand 2006

The pattern of 16S rRNA signatures consists of nucleotides at positions 157:164 (A–U), 158:163 (A–U), 184:193 (A–C), 195 (C), 196 (A), 293:304 (R–U), 601:637 (G–U), 602:636 (C–G), 841 (A), 952:1229 (U–A), 953:1228 (U–A), 986:1219 (U–A), 1059:1198 (U–A) and 1027:1034 (C–G). The family contains the type genus *Geodermatophilus* Luedemann 1968, as well as the genera *Blastococcus* Ahrens and Moll 1970 and *Modestobacter* Mevs *et al.* 2000.

Emended description of the family *Nakamurellaceae* Tao *et al.* 2004

The pattern of 16S rRNA signatures consists of nucleotides at positions 184:193 (A–C), 195 (C), 196 (A), 589:650 (U–A), 601:637 (A–U), 602:636 (A–U), 670:736 (U–A), 841 (C), 952:1229 (C–G), 955:1225 (A–U), 986:1219 (A–U), 1059:1198 (U–A), 1120:1153 (U–A) and 1027:1034 (C–G). The family contains the type genus *Nakamurella* Tao *et al.* 2004, as well as the genera *Humicoccus* Yoon *et al.* 2007 and *Saxeibacter* Lee *et al.* 2008a.

Emended description of the family *Sporichthyaceae* Rainey *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 184:193 (A–G), 195 (C), 196 (A), 416:427 (G–C), 600:638 (U–G), 601:637 (G–U), 602:636 (C–G), 612:628 (U–A), 841 (U), 952:1229 (U–A), 986:1219 (A–U), 1042 (A) and 1059:1198 (U–A). The family contains the type genus *Sporichthya* Lechevalier *et al.* 1968.

Emended description of the suborder *Glycomycineae* Rainey *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 657:749 (G–U), 672:734 (C–G), 681:709 (A–U), 831:855 (U–G), 832:854 (G–U), 833:853 (G–C), 840:846 (C–U), 952:1229 (C–G), 1064:1192 (G–G) and 1117:1183 (A–U). The suborder contains the family *Glycomycetaceae*. The nomenclatural type is the genus *Glycomyces* Labeda *et al.* 1985.

Emended description of the family *Glycomycetaceae* Rainey *et al.* 1997, emend. Labeda and Kroppenstedt 2005

The family contains the type genus *Glycomyces*, as well as the genus *Stackebrandtia* Labeda and Kroppenstedt 2005. The 16S rRNA nucleotide signature pattern is as that of the suborder.

Description of the suborder *Kineosporiineae* subord. nov.

Kineosporiineae (Ki'ne.o.spo.ri'i.ne.ae. N.L. fem. n. *Kineosporia* type genus of the suborder; -ineae ending to denote a suborder; N.L. fem. pl. n. *Kineosporiineae* the *Kineosporia* suborder).

The pattern of 16S rRNA signatures consists of nucleotides at positions 127:234 (A–U), 142:221 (C–U), 598:640 (U–G), 840:846 (A–C), 845 (A), 986:1218 (A–U), 1163:1173 (G–U), 1164:1172 (G–C) and 1165:1171 (G–A). The suborder contains the family *Kineosporiaceae*. The nomenclatural type is the genus *Kineosporia* Pagani and Parenti 1978.

Description of the family *Kineosporiaceae* fam. nov.

Kineosporiaceae (Ki'ne.o.spo.ri.a'ce.ae. N.L. fem. n. *Kineosporia* type genus of the family; -aceae ending to denote a

family; N.L. fem. pl. n. *Kineosporiaceae* the *Kineosporia* family).

The family contains the type genus *Kineosporia*, as well as the genera *Kineococcus* Yokota *et al.* 1993a and *Quadrisphaera* Maszenan *et al.* 2005. The 16S rRNA nucleotide signature pattern is as that of the suborder.

Emended description of the suborder *Micrococcineae* Stackebrandt *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 127:234 (A–U), 598:640 (U–G), 657:749 (U–A), 953:1228 (G–C), 986:1219 (A–U), 987:1218 (A–U) and 1362 (A). The suborder contains the families *Micrococcaceae*, *Dermatophilaceae*, *Beutenbergiaceae*, *Bogoriellaceae*, *Brevibacteriaceae*, *Cellulomonadaceae*, *Dermabacteraceae*, *Dermacoccaceae*, *Intrasporangiaceae*, *Jonesiaceae*, *Microbacteriaceae*, *Promicromonosporaceae*, *Rarobacteraceae*, *Sanguibacteraceae* and *Yaniellaceae*. The nomenclatural type is the genus *Micrococcus* Cohn 1872. Patterns of 16S rRNA signature nucleotides that define families of the suborder *Micrococcineae* are shown in Table 1.

Emended description of the family *Micrococcaceae* Pribram 1929, emend. Stackebrandt *et al.* 1997

The family contains the type genus *Micrococcus*, as well as the genera *Acaricomes* Pukall *et al.* 2006, *Arthrobacter* Conn and Dimmick 1947, emend. Koch *et al.* 1995, *Citricoccus* Altenburger *et al.* 2002b, *Kocuria* Stackebrandt *et al.* 1995, *Nesterenkonia* Stackebrandt *et al.* 1995, emend. Collins *et al.* 2002, emend. Li *et al.* 2005a, *Renibacterium* Sanders and Fryer 1980, *Rothia* Georg and Brown 1967 and *Zhihengliuella* Zhang *et al.* 2007a. The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the family *Dermatophilaceae* Austwick 1958, emend. Stackebrandt *et al.* 1997, emend. Stackebrandt and Schumann 2000

The family contains the type genus *Dermatophilus* (van Saceghem 1915) Gordon 1964, as well as the genus *Kineosphaera* Liu *et al.* 2002. The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Description of the family *Beutenbergiaceae* fam. nov.

Beutenbergiaceae (Beu'ten.ber.gi.a'ce.ae. N.L. fem. n. *Beutenbergia* type genus of the family; -aceae ending to denote a family; N.L. fem. pl. n. *Beutenbergiaceae* the *Beutenbergia* family).

The family contains the type genus *Beutenbergia* Groth *et al.* 1999b, as well as the genera *Georgenia* Altenburger *et al.* 2002a and *Salana* von Wintzingerode *et al.* 2001. The

pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the family *Bogoriellaceae* Schumann and Stackebrandt 2000 (in Stackebrandt & Schumann, 2000)

The family contains the type genus *Bogoriella* Groth *et al.* 1997a. The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the family *Brevibacteriaceae* Breed 1953, emend. Stackebrandt *et al.* 1997

The family contains the type genus *Brevibacterium* Breed 1953, emend. Collins *et al.* 1980. The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the family *Cellulomonadaceae* Stackebrandt and Prauser 1991, emend. Stackebrandt *et al.* 1997, emend. Stackebrandt and Schumann 2000

The family contains the type genus *Cellulomonas* Bergey *et al.* 1923, emend. Clark 1952, emend. Stackebrandt *et al.* 1982, as well as the genera *Actinotalea* Yi *et al.* 2007, *Demequina* Yi *et al.* 2007, *Oerskovia* Prauser *et al.* 1970, emend. Lechevalier 1972, emend. Stackebrandt *et al.* 2002a and *Tropheryma* La Scola *et al.* 2001. The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the family *Dermabacteraceae* Stackebrandt *et al.* 1997

The family contains the type genus *Dermabacter* Jones and Collins 1989 (effective publication Jones & Collins, 1988), as well as the genus *Brachybacterium* Collins *et al.* 1988a. The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the family *Dermacoccaceae* Schumann and Stackebrandt 2000

The family contains the type genus *Dermacoccus* Stackebrandt *et al.* 1995, as well as the genera *Demetria* Groth *et al.* 1997b and *Kytococcus* Stackebrandt *et al.* 1995. The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the family *Intrasporangiaceae* Rainey *et al.* 1997, emend. Stackebrandt and Schumann 2000

The family contains the type genus *Intrasporangium* Kalakoutskii *et al.* 1967, as well as the genera *Arsenicicoccus* Collins *et al.* 2004, *Humihabitans* Kageyama *et al.* 2007, *Janibacter* Martin *et al.* 1997, *Knoellia* Groth *et al.* 2002, *Kribbia* Jung *et al.* 2006, *Lapillicoccus* Lee and Lee

Table 1. Patterns of 16S rRNA signature nucleotides that define families of the suborder *Micrococccineae*

Families: 1, *Beutenbergiaceae*; 2, *Bogoriellaceae*; 3, *Brevibacteriaceae*; 4, *Cellulomonadaceae*; 5, *Dermabacteraceae*; 6, *Dermacoccaceae*; 7, *Dermatophilaceae*; 8, *Intrasporangiaceae*; 9, *Jonesiaceae*; 10, *Microbacteriaceae*; 11, *Micrococcaceae*; 12, *Promicromonosporaceae*; 13, *Rarobacteraceae*; 14, *Sanguibacteraceae*; 15, *Yaniellaceae*. Residues in lower-case letters are present in some but not all strains.

Position(s)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
120	A	A	A	A	A	A	A	A	A	A	W	A	A	A	U
131:231	C-G	A-G	C-G	C-G	C-G	A-G	Y-K	A-G	A-G	G-R	C-G	A-G	C-G	C-G	A-G
196	G	U	A	U	U	C	A	G	C	U	C	U	A	U	C
342:347	C-G	U-G	C-G	C-G	C-G	C-G	C-G	C-G	C-G	C-G	C-G	C-G	C-G	C-G	C-G
444:490	A-U	A-U	A-U	A-U	A-U	A-U	A-U	a-u	A-U	A-U	A-U	A-U	A-U	A-U	U-U
580:761	C-G	C-A	C-G	C-G	U-A	U-A	U-A	U-A	C-G	C-G	c-g	C-G	C-G	C-G	C-G
602:636	C-G	C-G	C-G	c-g	C-G	C-G	C-G	C-G	C-G	C-G	C-G	G-U	G-U	G-U	C-G
670:736	A-U	A-U	U-A	A-U	A-U	A-U	A-U	A-U	A-U	A-U	A-U	A-U	A-U	A-U	A-U
822:878	G-C	G-C	G-C	G-C	G-C	G-C	G-C	G-C	U-C	G-C	G-C	G-C	G-C	G-C	G-C
823:877	G-C	G-C	G-C	G-C	G-C	G-C	G-C	G-C	A-C	G-C	G-C	G-C	G-C	G-C	G-C
826:874	C-G	C-G	C-G	C-G	C-G	C-G	C-G	C-G	U-G	C-G	C-G	C-G	C-G	C-G	C-G
827	U	U	U	U	U	U	U	U	G	U	U	U	U	U	U
843	U	C	C	U	C	c	U	U	C	C	C	U	U	C	U
950:1231	U-A	U-A	U-A	U-A	U-G	U-A	U-A	U-A	U-A	U-A	U-A	U-A	U-A	U-A	U-A
1047:1210	G-C	G-C	G-U	G-C	G-C	G-C	G-C	G-C	G-C	G-C	G-C	G-C	G-C	G-C	G-C
1109	C	C	C	C	C	C	C	C	C	C	C	C	C	C	G
1145	G	G	A	G	G	G	G	G	G	R	G	G	G	G	G
1309:1328	G-C	A-U	G-C	G-C	G-U	G-C	G-C	G-C	G-C	G-C	G-C	G-C	G-C	G-C	G-C
1361	G	G	G	G	G	G	G	C	G	G	G	G	G	G	G
1383	U	U	C	Y	C	C	C	C	C	C	C	C	C	C	C

2007, *Marihabitans* Kageyama *et al.* 2008, *Ornithinococcus* Groth *et al.* 1999a, *Ornithinimicrobium* Groth *et al.* 2001, *Oryzihumus* Kageyama *et al.* 2005, *Phycococcus* Lee 2006, *Serinicoccus* Yi *et al.* 2004, *Terrabacter* Collins *et al.* 1989, *Terracoccus* Prauser *et al.* 1997 and *Tetrasphaera* Maszenan *et al.* 2000. The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the family *Jonesiaceae* Stackebrandt *et al.* 1997

The family contains the type genus *Jonesia* Rocourt and Stackebrandt 1987 (in Rocourt *et al.*, 1987). The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the family *Microbacteriaceae* Park *et al.* 1995 (effective publication Park *et al.*, 1993), emend. Rainey *et al.* 1997

The family contains the type genus *Microbacterium* Orla-Jensen 1919, emend. Takeuchi and Hatano 1998, as well as the genera *Agreia* Evtushenko *et al.* 2001, *Agrococcus* Groth *et al.* 1996, *Agromyces* Gledhill and Casida 1969, emend. Zgurskaya *et al.* 1992, *Clavibacter* Davis *et al.* 1984, *Cryobacterium* Suzuki *et al.* 1997, *Curtobacterium* Yamada and Komagata 1972, *Frigoribacterium* Kämpfer *et al.* 2000, *Fronidhabitans* Greene *et al.* 2009 (previous illegitimate name *Fronidicola* Zhang *et al.* 2007b), *Glaciibacter* Katayama *et al.* 2009, *Gulosibacter* Manaia *et al.* 2004, *Klugiella* Cook *et al.* 2008, *Labeledella* Lee 2007, *Leifsonia* Evtushenko *et al.*

2000, *Leucobacter* Takeuchi *et al.* 1996, *Microbacterium* Orla-Jensen 1919, emend. Takeuchi and Hatano 1998, *Microcella* Tiago *et al.* 2005, emend. Tiago *et al.* 2006, *Microterricola* Matsumoto *et al.* 2008, *Mycetocola* Tsukamoto *et al.* 2001, *Okibacterium* Evtushenko *et al.* 2002, *Plantibacter* Behrendt *et al.* 2002, *Phycicola* Lee *et al.* 2008b, *Pseudoclavibacter* Manaia *et al.* 2004, *Rathayibacter* Zgurskaya *et al.* 1993, *Rhodoglobus* Sheridan *et al.* 2003, *Salinibacterium* Han *et al.* 2003, *Subtercola* Männistö *et al.* 2000 and *Yonghaparkia* Yoon *et al.* 2006. The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the family *Promicromonosporaceae* Rainey *et al.* 1997

The family contains the type genus *Promicromonospora* Krasil'nikov *et al.* 1961, as well as the genera *Cellulomicrobium* Schumann *et al.* 2001, emend Brown *et al.* 2006, *Isopterica* Stackebrandt *et al.* 2004, *Myceligenans* Cui *et al.* 2004, *Xylanibacterium* Rivas *et al.* 2004, *Xylanimicrobium* Stackebrandt and Schumann 2004 and *Xylanimonas* Rivas *et al.* 2003. The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the family *Rarobacteraceae* Stackebrandt and Schumann 2000

The family contains the type genus *Rarobacter* Yamamoto *et al.* 1988. The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the family *Sanguibacteraceae* Stackebrandt and Schumann 2000

The family contains the type genus *Sanguibacter* Fernández-Garayzábal *et al.* 1995. The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the family *Yaniellaceae* Li *et al.* 2008 (previous illegitimate name *Yaniaceae* Li *et al.* 2005b)

The family contains the type genus *Yaniella* Li *et al.* 2008 (previous illegitimate name *Yania* Li *et al.* 2004, emend. Li *et al.* 2005b). The pattern of 16S rRNA signature nucleotides is shown in Table 1.

Emended description of the suborder *Micromonosporineae* Stackebrandt *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 127:234 (A–U), 209 (G), 534 (G), 831:855 (U–G), 832:854 (G–Y), 833:853 (U–G), 840:846 (Y–G), 845 (G), 955:1225 (A–U), 986:1219 (U–A) and 987:1218 (G–C). The suborder contains the family *Micromonosporaceae*. The nomenclatural type is the genus *Micromonospora* Ørskov 1923.

Emended description of the family *Micromonosporaceae* Krasil'nikov 1938, emend. Koch *et al.* 1996, emend. Stackebrandt *et al.* 1997

The family contains the type genus *Micromonospora*, as well as *Actinocatenispora* Thawai *et al.* 2006, *Actinoplanes* Couch 1950, emend. Stackebrandt and Kroppenstedt 1987, *Asanoa* Lee and Hah 2002, *Catellatospora* Asano and Kawamoto 1986, *Catenuloplanes* Yokota *et al.* 1993b, *Couchioplanes* Tamura *et al.* 1994a, *Dactylosporangium* Thiemann *et al.* 1967b, *Longispora* Matsumoto *et al.* 2003, *Pilimelia* Kane 1966, *Polymorphospora* Tamura *et al.* 2006, *Planosporangium* Wiese *et al.* 2008, *Pseudosporangium* Ara *et al.* 2008, *Salinispora* Maldonado *et al.* 2005, *Spirilliplanes* Tamura *et al.* 1997, *Verrucosispora* Rheims *et al.* 1998 and *Virgisporangium* Tamura *et al.* 2001. The 16S rRNA nucleotide signature is as that of the suborder.

Emended description of the suborder *Propionibacterineae* Rainey *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 127:234 (A–U), 598:640 (U–A), 657:749 (G–C), 828 (U), 829:851 (A–C), 832:854 (U–C), 833:853 (G–U), 952:1229 (C–G) and 986:1219 (U–A). The suborder contains the families *Propionibacteriaceae* and *Nocardioidaceae*. The nomenclatural type is the genus *Propionibacterium* Orla-Jensen 1909.

Emended description of the family *Propionibacteriaceae* Delwiche 1957, emend. Rainey *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 328 (U), 407:435 (C–G), 451 (A), 453 (G), 819 (G), 825:875 (A–U), 827 (C), 828 (U), 832:854 (U–C), 833:853 (G–U) and 844 (U). The family contains the type genus *Propionibacterium*, as well as the genera *Aestuariimicrobium* Jung *et al.* 2007, *Brooklawnia* Rainey *et al.* 2006 (in Bae *et al.* 2006a), *Friedmanniella* Schumann *et al.* 1997, *Granulicoccus* Maszenan *et al.* 2007, *Luteococcus* Tamura *et al.* 1994b, *Microbunatus* Nakamura *et al.* 1995, *Micropruina* Shintani *et al.* 2000, *Propioniceella* Bae *et al.* 2006b, *Propionimonas* Akasaka *et al.* 2003, *Propioniferax* Yokota *et al.* 1994, *Propionimicrobium* Stackebrandt *et al.* 2002b and *Tessaracoccus* Maszenan *et al.* 1999.

Emended description of the family *Nocardioidaceae* Nesterenko *et al.* 1990 (effective publication Nesterenko *et al.*, 1985), emend. Rainey *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 328 (C), 407:435 (A–U), 451 (G), 453 (C), 819 (U), 825:875 (G–C), 827 (U), 828 (A), 832:854 (G–G), 833:853 (U–C) and 844 (C). The family contains the type genus *Nocardioides* Prauser 1976, as well as the genera *Actinopolymorpha* Wang *et al.* 2001, *Aeromicrobium* Miller *et al.* 1991, *Jiangella* Song *et al.* 2005, *Kribbella* Park *et al.* 1999 and *Marmoricola* Urzì *et al.* 2000.

Emended description of the suborder *Pseudonocardineae* Stackebrandt *et al.* 1997

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). The suborder contains the families *Pseudonocardiaceae* and *Actinosynnemataceae*. The nomenclatural type is the genus *Pseudonocardia* Henssen 1957.

Emended description of the family *Pseudonocardiaceae* Embley *et al.* 1989 (effective publication Embley *et al.*, 1988), emend. Stackebrandt *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 211 (G), 480 (U) and 142:221 (C–G). The family contains the type genus *Pseudonocardia*, as well as the genera *Actinomycetospira* Jiang *et al.* 2008, *Allokutzneria* Labeda and Kroppenstedt 2008, *Amycolatopsis* Lechevalier *et al.* 1986, *Saccharopolyspora* Lacey and Goodfellow 1975, *Saccharomonospora* Nonomura and Ohara 1971, *Streptoalloteichus* (ex Tomita *et al.* 1978) Tomita *et al.* 1987, *Kibdelosporangium* Shearer *et al.* 1986, *Thermocrisium* Korn-Wendisch *et al.* 1995, *Kutzneria*

Stackebrandt *et al.* 1994, *Actinoalloteichus* Tamura *et al.* 2000b, *Crossiella* Labeda 2001, *Prauserella* Kim and Goodfellow 1999, emend. Li *et al.* 2003b and *Goodfellowiella* Labeda *et al.* 2008 (previous illegitimate name *Goodfellowia* Labeda and Kroppenstedt 2006).

Emended description of the family *Actinosynnemataceae* Labeda and Kroppenstedt 2000

The pattern of 16S rRNA signatures consists of nucleotides at positions 211 (A), 480 (G) and 142:221 (C–C). The family contains the type genus *Actinosynnema* Hasegawa *et al.* 1978, as well as the genera *Actinokineospira* Hasegawa 1988, *Lechevalieria* Labeda *et al.* 2001, *Lentzea* Yassin *et al.* 1995, emend. Labeda *et al.* 2001, *Saccharothrix* Labeda *et al.* 1984 and *Umezawaea* Labeda and Kroppenstedt 2007.

Emended description of the suborder *Streptomycineae* Rainey *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 127:234 (G–C), 449 (A), 672:734 (C–G), 950:1231 (U–G), 952:1229 (U–A), 955:1225 (C–G), 965 (C), 986:1219 (A–U) and 1362 (C). The suborder contains the family *Streptomycetaceae*. The nomenclatural type is the genus *Streptomyces* Waksman and Henrici 1943.

Emended description of the family *Streptomycetaceae* Waksman and Henrici 1943, emend. Rainey *et al.* 1997, emend. Kim *et al.* 2003

The family contains the type genus *Streptomyces* Waksman and Henrici 1943, emend. Witt and Stackebrandt 1990, emend. Wellington *et al.* 1992, as well as the genera *Kitasatospora* Ōmura *et al.* 1983 (effective publication Ōmura *et al.* 1982), emend. Zhang *et al.* 1997 and *Streptacidiphilus* Kim *et al.* 2003. The 16S rRNA nucleotide signature is as that of the suborder.

Emended description of the suborder *Streptosporangineae* Ward-Rainey *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 127:234 (A–U), 829:857 (G–C), 830:856 (G–C), 953:1228 (U–A), 950:1231 (U–A), 955:1225 (C–G), 986:1219 (A–U) and 987:1218 (A–U). The suborder contains the families *Streptosporangiaceae*, *Nocardiopsaceae* and *Thermomonosporaceae*. The nomenclatural type is the genus *Streptosporangium* Couch 1955.

Emended description of the family *Streptosporangiaceae* Goodfellow *et al.* 1990, emend. Ward-Rainey *et al.* 1997

The pattern of 16S rRNA signatures consists of nucleotides at positions 440:497 (C–G), 485 (U), 501:544 (C–G), 502:543 (G–C), 833:853 (U–G) and 1355:1367 (A–U). The family contains the type genus *Streptosporangium*, as

well as the genera *Acrocarpospora* Tamura *et al.* 2000a, *Herbidospora* Kudo *et al.* 1993, *Microbispora* Nonomura and Ohara 1957, *Microtetrastora* Thiemann *et al.* 1968, *Nonomuraea* Zhang *et al.* 1998, *Planobispora* Thiemann and Beretta 1968, *Planomonospora* Thiemann *et al.* 1967a, *Planotetrastora* Runmao *et al.* 1993, emend. Tamura and Sakane 2004 and *Thermopolyspora* (*ex* Krasil'nikov and Agre 1964) Goodfellow *et al.* 2005.

Emended description of the family *Nocardiopsaceae* Rainey *et al.* 1996, emend. Rainey *et al.* 1997, emend. Zhang *et al.* 1998

The pattern of 16S rRNA signatures consists of nucleotides at positions 440:497 (U–U), 485 (G), 501:544 (G–C), 502:543 (A–U), 833:853 (U–G) and 1355:1367 (G–C). The family contains the type genus *Nocardiopsis* (Brocq-Rousseau 1904) Meyer 1976, as well as the genera *Haloactinospira* Tang *et al.* 2008, *Streptomonospora* Cui *et al.* 2001, emend. Li *et al.* 2003a and *Thermobifida* Zhang *et al.* 1998.

Emended description of the family *Thermomonosporaceae* Rainey *et al.* 1997, emend. Zhang *et al.* 2001

The pattern of 16S rRNA signatures consists of nucleotides at positions 440:497 (C–G), 501:544 (C–G), 502:543 (G–C), 831:855 (G–G), 843 (U), 844 (A) and 1355:1367 (A–U). The family contains the type genus *Thermomonospora* Henssen 1957, as well as the genera *Actinocorallia* Iinuma *et al.* 1994, emend. Zhang *et al.* 2001, *Actinomadura* Lechevalier and Lechevalier 1968 (effective publication Lechevalier & Lechevalier, 1970) and *Spirillospora* Couch 1963.

Note added on revision

Since this article was submitted for publication, an additional order of the subclass *Actinobacteridae* has been described, *Nitriliruptorales* Sorokin *et al.* 2009, to accommodate a new family *Nitriliruptoraceae* and the new genus and species *Nitriliruptor alkaliphilus*.

ACKNOWLEDGEMENTS

The authors are grateful to Dr Jean Euzéby for support with nomenclature. This research was supported by the National Basic Research Program of China (no. 2004CB719601), the National Natural Science Foundation of China (nos 30600001 and 30870005) and the Key Project of Chinese Ministry of Education (no. 206139). W.-J.L. was supported by the Program for New Century Excellent Talents in University.

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