

Proposal for a New Hierarchic Classification System, *Actinobacteria* classis nov.

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A new hierarchic classification structure for the taxa between the taxonomic levels of genus and class is proposed for the actinomycete line of descent as defined by analysis of small subunit (16S) rRNA and genes coding for this molecule (rDNA). While the traditional circumscription of a genus of the actinomycete subphylum is by and large in accord with the 16S rRNA/rDNA-based phylogenetic clustering of these organisms, most of the higher taxa proposed in the past do not take into account the phylogenetic clustering of genera. The rich chemical, morphological and physiological diversity of phylogenetically closely related genera makes the description of families and higher taxa so broad that they become meaningless for the description of the enclosed taxa. Here we present a classification system in which phylogenetically neighboring taxa at the genus level are clustered into families, suborders, orders, subclasses, and a class irrespective of those phenotypic characteristics on which the delineation of taxa has been based in the past. Rather than being based on a listing of a wide array of chemotaxonomic, morphological, and physiological properties, the delineation is based solely on 16S rDNA/rRNA sequence-based phylogenetic clustering and the presence of taxon-specific 16S rDNA/RNA signature nucleotides.

In their publication "On the nature of global classification," Wheelis et al. (177) based the definition of higher taxa on the molecular level of universally homologous functions. This statement is derived from the high correlation of genealogical trees inferred from several such molecules, e.g., genes coding for 16S rRNA (16S rDNA) (179), 23S rDNA (96), elongation factors involved in the translation process, and the β -subunit of ATPase (97). The authors (177) stress that a basic requirement of a global classification is uniformity in methods and characteristics used in defining and ranking taxa. Nonhomologous characteristics, on the other hand, may be useful in confirming the molecular groupings. Application of this classification strategy led to the description of domains for the three highest taxa recognized today, the *Archaea*, *Bacteria*, and *Eucarya* (180). As a consequence of the description of kingdoms for the major lineages within the domain *Eucarya* (plants, animals, fungi, and protozoa), Woese et al. (180) described the two main lineages within the domain *Archaea* as the kingdom *Crenarchaeota* and the kingdom *Euryarchaeota*.

Within the domain *Bacteria*, more than 15 lineages, which in phylogenetic uniqueness and ancestry are comparable to the archaeal kingdoms, have been identified. The taxonomic rank of kingdom has not yet been proposed for any of these lineages. The taxon class *Proteobacteria* has been proposed for a phylogenetically broad cluster of gram-negative genera, and several orders have been described for some of the phylogenetic lineages that emerged from the comparison of evolutionarily conserved macromolecules; e.g., *Aquificales* (15), *Thermotogales* (67), *Verrucomicrobiales* (173), and *Planctomycetales* (138). These phylogenetically coherent taxa are now used side by side with higher taxa that were described at the beginning of the pre-molecular era, i.e., before or around 1984. While the phylogenetic coherence of the division *Firmacutes* (53), the class *Mollicutes*, and the orders *Chlamydiales*, *Spirochaetales*, and *Myxobacterales* were by and large confirmed following 16S

rDNA analyses of their members, the majority of higher taxa represent a collection of phylogenetically diverse families and genera. Examples are the classes *Actinomycetes* (81) and *Photobacteria* (53) and the orders *Clostridiales* and *Bacillales* (119), which need to be redefined in order to make classification consistent with phylogenetic structure.

One of the main lines of descent within the domain *Bacteria* includes a wide range of morphologically diverse organisms, most of which, on the basis of a gram-positive staining reaction, can be considered members of the division *Firmacutes* (53). This lineage comprises organisms with a DNA base composition which generally is above 50 mol% G+C (with a few exceptions) and includes representatives of the class *Actinomycetes* (81), the orders *Actinomycetales* (13) and *Micrococcales* (118), the tribes *Brevibacteriae* and *Micrococceae* (120), and several families of the order *Actinomycetales* as well as additional organisms which were identified as members of this lineage by phylogenetic analyses. This lineage encompasses a wide range of bacteria that irrespective of Gram stain reaction, base composition of DNA, morphology, chemotaxonomic properties, and other characteristics used to delineate bacterial taxa in the past, have a common ancestry (Fig. 1).

The modern era in the classification of organisms that are proposed as members of the class *Actinobacteria* has its origin in three sources: firstly, the establishment of chemotaxonomy that detects differences in the chemical composition of cell constituents such as peptidoglycan, polar lipids and fatty acids, isoprenoid quinones, cytochromes, and the base composition of DNA; secondly, the introduction of DNA-DNA reassociation experiments that measure the gross similarities between single-stranded DNA of strains of closely related species (144); and thirdly, the determination of 16S rRNA and rDNA sequence similarities, which reveals the extent of sequence variation among strains at all levels of relatedness (148). Each of these approaches has contributed to the success of a classification strategy which has been termed polyphasic by Colwell (34).

Although the appropriate methods have been available for decades, it took about 30 years to achieve a comprehensive overview of the relatedness among actinomycete bacteria that would allow a proposal for a unified classification system. The

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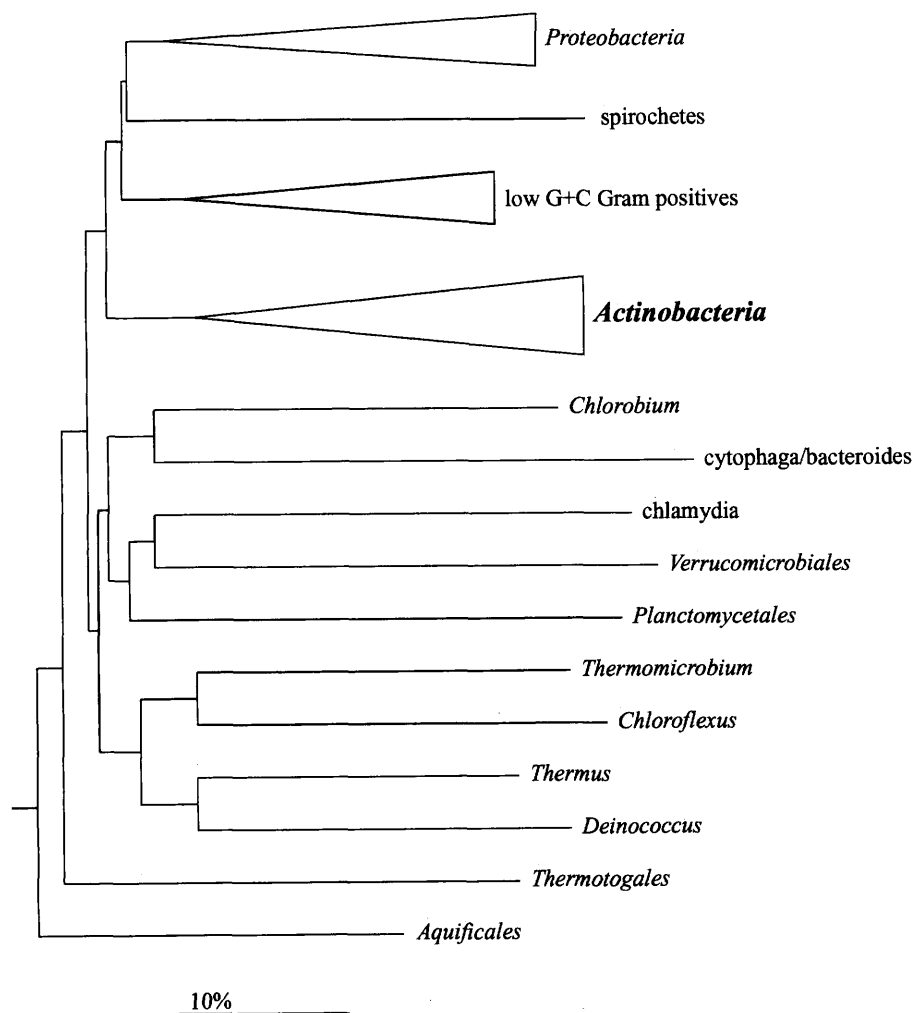


FIG. 1. Dendrogram of 16S rDNA/rRNA relationships showing the phylogenetic position of the proposed class *Actinobacteria* within the domain *Bacteria*. Sequences of *Archaea* were used to root the dendrogram. The recovery of the main lines of descent is as published by Woese (179). The scale bar represents 10 nucleotide substitutions per 100 nucleotides.

reasons were manifold. The most obvious one is the late introduction of 16S rRNA/DNA sequence analysis that, better than any other taxonomic method, places an organism in the framework of phylogenetic relationships. The restricted information on the degree of relatedness obtained by DNA-DNA reassociation studies (143) only allowed analysis of highly related species, while elucidation of more remote relationships had to wait for analysis of conservative genes. Another reason was the tremendous amount of work needed to analyze the phylogenetic relatedness of the type strains of several hundred species which in the end led to the recognition of those properties at the epigenetic level that could be used to unambiguously circumscribe species at the genus level.

MATERIALS AND METHODS

Phylogenetic analyses. As this publication reviews published data, no emphasis is placed on methods. Rather we refer to relevant publications, most of which contain original or cited data on phylogeny, chemotaxonomy, and other phenotypic data used in the classification of actinomycetes above the species level.

An alignment of all 16S rRNA/DNA sequences currently available for members of the actinomycete lineage was created by using the ae2 editor (99). The sequences included in this alignment were obtained from the Ribosomal Database Project (99) and the ARB package (a software environment for sequence data) (156) as well as our own entries. The 16S rRNA/DNA sequences were

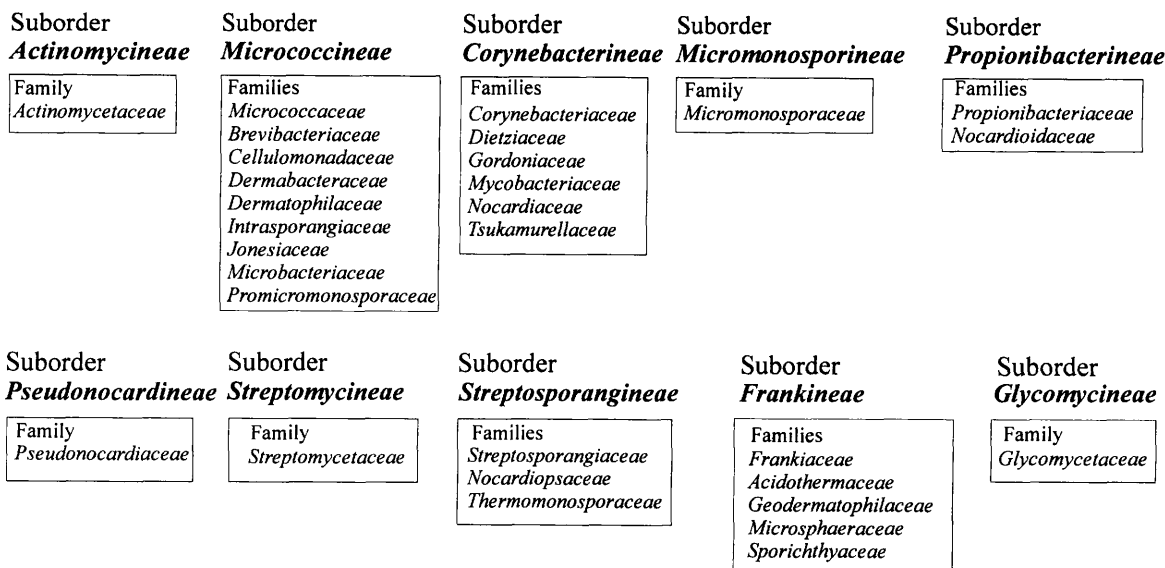
manually aligned to provide a secondary structure-based optimal alignment. The best sequences available were chosen in all cases, but due to the fact that many of the actinomycete reference sequences obtained from the databases are partial sequences consisting of fewer than 1,300 nucleotides, an ideal data set could not be constructed.

The complete data set used for the analyses described in this study contained information on more than 1,000 unambiguous nucleotide positions present in all sequences between positions 150 and 1400 (*Escherichia coli* sequence [11]). Individual data sets, which in many cases comprised more than 1,300 nucleotides, were used for the determination of the relationships within the groups of the proposed taxonomic structure of the actinomycetes. The data set consisting of the type strains of the type species of the genera included in this study can be requested from the authors. The following genera have either not yet been investigated by 16S rDNA sequence analysis and their phylogenetic affiliation remains undetermined or their exact phylogenetic position is unclear: *Actinocorallia* (68), *Actinokineospora* (64), *Excellospora* (1), *Kineococcus* (186), *Kineosporia* (112), and *Micropolyspora* (93).

For the reconstruction of the phylogenetic dendrograms, evolutionary distances were calculated by the method of Jukes and Cantor (70). Phylogenetic dendrograms were reconstructed by using treeing algorithms contained in the PHYLIP package (46) and the ARB package (156). The robustness of tree topologies was evaluated by bootstrap analyses (45) of the neighbor-joining (136) data by performing 1,000 resamplings. The phylogenetic dendrograms presented in many cases represent a general overview at the higher-taxon level and do not show the individual branching order at the genus and species level. These lower-taxon branching orders are susceptible to changes depending on the data set used in the analysis, but the compositions of taxa above the genus level will not be affected.

Class *Actinobacteria*

Subclass *Acidimicrobidae* Order *Acidimicrobiales* Family *Acidimicrobiaceae*
 Subclass *Rubrobacteridae* Order *Rubrobacterales* Family *Rubrobacteraceae*
 Subclass *Coriobacteridae* Order *Coriobacterales* Family *Coriobacteriaceae*
 Subclass *Sphaerobacteridae* Order *Sphaerobacterales* Family *Sphaerobacteraceae*
 Subclass *Actinobacteridae* Order *Actinomycetales*



Order *Bifidobacteriales* Family *Bifidobacteriaceae*

FIG. 2. Proposed hierarchic classification system of the class *Actinobacteria* based on the phylogenetic analyses of the 16S rDNA/rRNA sequence data.

RESULTS AND DISCUSSION

The basis for the proposal of a novel hierarchic structure (Fig. 2) for the phylogenetically coherent group of actinomycete bacteria and relatives is membership of the same phylogenetic group which was formerly described as a 16S rRNA subdivision or subphylum of the gram-positive bacteria. The common ancestry of the actinomycetes proper and the second subdivision of gram-positive bacteria, defined by clostridia, bacilli, and their relatives, has not yet been convincingly demonstrated by 16S rDNA analyses. However, sequence analyses of glutamine synthetase, glutamate dehydrogenase, and the heat shock protein HSP70 reveal a common ancestry of the gram-positive bacteria (59, 60). The phylogenetic coherence of these organisms supports the description of a kingdom for the *Firmacutes* which would contain two or more classes, one of which embraces the actinomycetes proper. If the results of future studies were to unambiguously demonstrate the common ancestry of members of the two subphyla they could be united under the umbrella of a common higher taxon, the kingdom.

Membership of a new strain to the class *Actinobacteria* is indicated by 16S rDNA sequence similarity values above 80% as determined by comparison of almost-complete 16S rDNA sequences of the new strain and the most deeply branching members of the class, such as *Rubrobacter radiotolerans*, *Acidimicrobium ferrooxidans*, or *Coriobacterium glomerans*, and the presence of signature nucleotides. We are aware that the phylogenetic tree, upon which the conclusions outlined below

are based, is a mathematical model of how bacterial evolution occurs. Signature nucleotides are derivatives of the classification process; i.e., signatures are determined for those organisms that are contained within a particular data set. It is also known that a significant increase in species numbers in any of the phylogenetic lineages may lead to a decrease in the number of signatures as the 16S rDNA of more slowly or more rapidly evolving strains may not contain the signature. It is hoped that this proposal will stimulate analyses of other conservative genes from organisms that cluster together by 16S rDNA analyses, so that taxonomic information is provided from additional, independently selected genes and properties and the hierarchic structure proposed here can be tested.

The signatures given below for the higher taxa were chosen for their presence in more than 95% of the members of the respective taxon. The signature pattern for monospecific families must be considered tentative. It should be mentioned that the pattern of signature nucleotides, but not necessarily each individual nucleotide, is indicative of the membership of a taxon to a higher taxon. Bootstrap values (not shown) were determined for the branching points shown in Fig. 3 and were higher than 90% in only a few cases, indicating a lack of statistical significance of the respective branching points. Despite the finding that the majority of branching points are not supported by high bootstrap values, the orders, suborders, and families described previously and below are consistently recoverable from phylogenetic analyses. The lack of high bootstrap

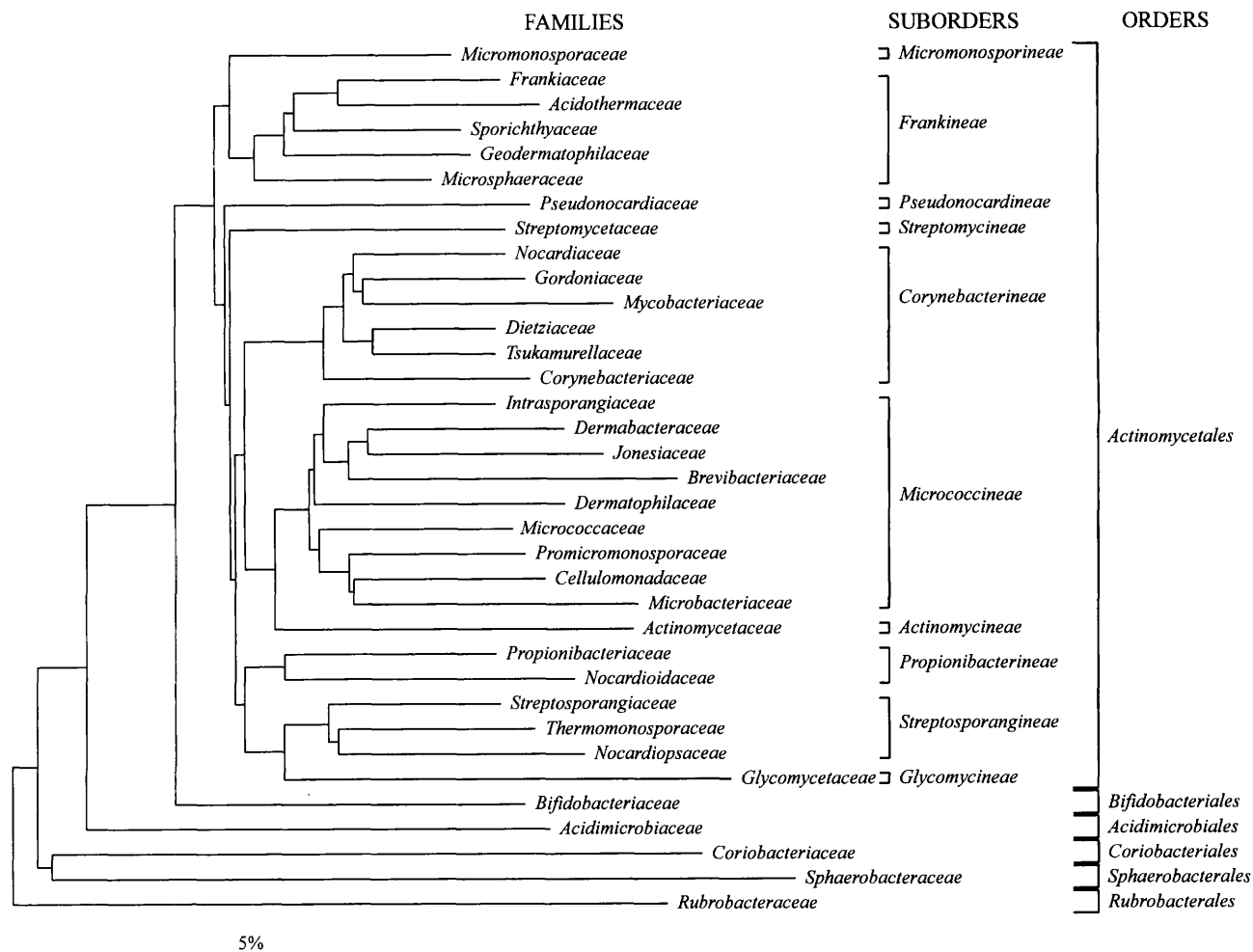


FIG. 3. Intra-class relatedness of *Actinobacteria* showing the presence of six orders as well as the 10 suborders of the order *Actinomycetales* based upon 16S rDNA/rRNA sequence comparison. The phylogenetic relatedness of the families of the class *Actinobacteria* is outlined. The scale bar represents 5 nucleotide substitutions per 100 nucleotides.

values is probably due to the small differences in the primary structure of 16S rDNA of members of most of the neighboring families. Many of the signature nucleotides and idiosyncrasies are located in highly variable and hypervariable regions of the 16S rDNA molecule, which means that dendrograms of relatedness are mostly derived from nucleotide positions that are subject to changes. Also, low bootstrap values are found when the radiation of lineages occurs within a short evolutionary time span, like those found for the radiation of most suborders of the order *Actinomycetales*. Nevertheless, the separate branching of these suborders is found in any of the trees generated, irrespective of the algorithm used. This means that even if the branching points of taxa above the genus level change within the narrow margin at which the higher taxa separate from each other, their phylogenetic uniqueness remains unchanged and their affiliation to the next higher taxon will not be greatly affected. As indicated above, the patterns of signature nucleotides may need to be emended when analysis of novel members of the families indicates the necessity for doing so. In this respect, the taxa defined by molecular data reflect the most recent state-of-the-art insights into molecular systematics. A strategy that could be used in the future to decide whether or not a member of a novel genus could be considered a member of a known or a novel family and/or any

other of the defined higher ranks would include (i) generation of a high-quality, complete or almost-complete 16S rDNA sequence, (ii) proper alignment of the sequence to reference sequences of the same quality, (iii) determination of the phylogenetic position, and (iv) checking for the presence of signature nucleotides as given below for members of the taxon with which the organism groups. If the vast majority of the signature nucleotides match those previously defined for the nearest neighbors, the organism can be considered a member of this taxon. If, however, several signature nucleotides are missing, this genus most likely represents a novel family for which a novel set of signature nucleotides must be defined.

The proposal presented here does not change the current descriptions of species and genera, which are in most cases based upon morphological, chemotaxonomic, and physiological characteristics. These taxa, which provide the working basis for taxonomists, have been revised in the past 20 years to constitute phylogenetically coherent taxonomic units. In contrast, the descriptions of taxa above the genus level have a more broadly based description to incorporate the characteristics of the individual genera contained therein. The description of the family *Micromonosporaceae* should serve as an example (78), and other examples include the families *Propionibacteriaceae* and *Pseudonocardiaceae*.

Class *Actinobacteria* classis nov., Stackebrandt, Rainey, and Ward-Rainey. *Actinobacteria* (Ac.ti.no.bac.te'ri.a. Gr. n. *actis*, *actinis*, a ray, beam; Gr. dim. n. *bakterion*, a small rod; *-ia*, proposed ending to denote class; *Actinobacteria*, actinomycete group of bacteria of diverse morphological properties). The class is definable in phylogenetic terms as derived from the analysis of macromolecules of universally homologous functions. Strains of the class *Actinobacteria* can consistently be recovered as members of the same phylogenetic lineage, revealing >80% 16S rDNA/rRNA sequence similarity among each other (Fig. 1), and the presence of the following signature nucleotides in the 16S rDNA/rRNA: an A residue at position 906 and either an A or a C residue at position 955 (except for members of the subclasses *Rubrobacteridae* and *Sphaerobacteridae* [which show U residues at these positions]).

The intraclass relatedness reveals the presence of six phylogenetically distinct lineages which are consistently recovered from phylogenetic analyses (42). These lineages are described as orders (Fig. 3). The 16S rDNA/rRNA signatures defining the higher taxa are based on the available 16S rDNA/rRNA sequences of the type strains of type species of the genera. As certain taxa contain only one or two species, the pattern of signature nucleotides may need to be modified as new species are added to the respective genera.

Subclass *Acidimicrobidae* subclassis nov., Stackebrandt, Rainey, and Ward-Rainey. *Acidimicrobidae* (A.ci.di.mi.cro.bi'dae. M.L. n. *Acidimicrobium*, type genus of the subclass; *-idae*, ending to denote a subclass; M.L. fem. pl. n. *Acidimicrobidae*, the *Acidimicrobium* subclass). The subclass contains the type order *Acidimicrobiales*. The 16S rDNA/rRNA signature pattern is as that of the family *Acidimicrobiaceae*.

Order *Acidimicrobiales* ordo. nov., Stackebrandt, Rainey, and Ward-Rainey. *Acidimicrobiales* (A.ci.di.mi.cro.bi.a'les. M.L. n. *Acidimicrobium*, type genus of the order; *-ales*, ending to denote an order; M.L. fem. pl. n. *Acidimicrobiales*, the *Acidimicrobium* order). The order contains the type family *Acidimicrobiaceae*. The 16S rDNA/rRNA signature pattern is as that of the family *Acidimicrobiaceae*.

Family *Acidimicrobiaceae* fam. nov., Stackebrandt, Rainey, and Ward-Rainey. *Acidimicrobiaceae* (A.ci.di.mi.cro.bi.a'ce.ae. M.L. neut. n. *Acidimicrobium*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Acidimicrobiaceae*, the *Acidimicrobium* family). The following pattern of 16S rDNA/rRNA signature nucleotides and nucleotide pairs defines the family *Acidimicrobiaceae*: 291-309 (U-A), 294-303 (U-A), 408-434 (A-U), 670-736 (C-G), 722-733 (A-C), 955-1225 (C-G), 1118-1155 (C-G), 1311-1326 (A-U), and 1410-1490 (A-U). The family contains the type genus *Acidimicrobium* (24). Phylogenetic analyses have been published previously (17, 23, 149).

Subclass *Rubrobacteridae* subclassis nov., Rainey, Ward-Rainey, and Stackebrandt. *Rubrobacteridae* (Ru.bro.bac.te.ri'dae. M.L. masc. n. *Rubrobacter*, type genus of the subclass; *-idae*, ending to denote a subclass; M.L. fem. pl. n. *Rubrobacteridae*, the *Rubrobacter* subclass). The subclass contains the type order *Rubrobacterales*. The 16S rDNA/rRNA signature pattern is as that of the family *Rubrobacteraceae*.

Order *Rubrobacterales* ordo. nov., Rainey, Ward-Rainey, and Stackebrandt. *Rubrobacterales* (Ru.bro.bac.te.ra'les. M.L. masc. n. *Rubrobacter*, type genus of the order; *-ales*, ending to denote an order; *Rubrobacterales*, the *Rubrobacter* order). The order contains the type family *Rubrobacteraceae*. The 16S rDNA/rRNA signature pattern is as that of the family *Rubrobacteraceae*.

Family *Rubrobacteraceae* fam. nov., Rainey, Ward-Rainey, and Stackebrandt. *Rubrobacteraceae* (Ru.bro.bac.te.ra'ce.ae.

M.L. masc. n. *Rubrobacter*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Rubrobacteraceae*, the *Rubrobacter* family). The following pattern of 16S rDNA/rRNA signature nucleotides and nucleotide pairs defines the family: 127-234 (G-C), 291-309 (U-A), 657-749 (G-C), 681-709 (C-G), 941-1342 (A-U), 955-1225 (U-A), 1051-1207 (C-G), 1115-1185 (C-G), 1311-1326 (A-U), and 1410-1490 (A-U). The family contains the genus *Rubrobacter* (157). A phylogenetic analysis has been published previously (17).

Subclass *Coriobacteridae* subclassis nov., Stackebrandt, Rainey, and Ward-Rainey. *Coriobacteridae* (Co.ri.o.bac.te.ri'dae. M.L. neut. n. *Coriobacterium*, type genus of the subclass; *-idae*, ending to denote a subclass; M.L. fem. pl. n. *Coriobacteridae*, the *Coriobacterium* subclass). The subclass contains the type order *Coriobacteriales*. The 16S rDNA/rRNA signature pattern is as that of the family *Coriobacteriaceae*.

Order *Coriobacteriales* ordo. nov., Stackebrandt, Rainey, and Ward-Rainey. *Coriobacteriales* (Co.ri.o.bac.te.ri.a'les. M.L. neut. n. *Coriobacterium*, type genus of the order; *-ales*, ending to denote an order; M.L. fem. pl. n. *Coriobacteriales*, the *Coriobacterium* order). The order contains the type family *Coriobacteriaceae*. The 16S rDNA/rRNA signature pattern is as that of the family *Coriobacteriaceae*.

Family *Coriobacteriaceae* fam. nov., Stackebrandt, Rainey, and Ward-Rainey. *Coriobacteriaceae* (Co.ri.o.bac.te.ri.a'ce.ae. M.L. neut. n. *Coriobacterium*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Coriobacteriaceae*, the *Coriobacterium* family). The pattern of 16S rDNA/rRNA signature nucleotides of members of the family consists of 113-314 (C-G), 294-303 (G-C), 295-302 (U-A), 670-736 (G-C), 771-808 (U-A), 772-807 (A-U), 823-877 (A-U), 941-1342 (A-U), 950-1231 (U-G), 1120-1153 (G-C), 1148 (C), 1165-1171 (C-G), 1242-1295 (G-C), 1313-1324 (G-C), and 1410-1490 (A-U). The family contains the type genus *Coriobacterium* (61) as well as *Atopobium* (26). Phylogenetic analyses have been published previously (128, 146).

Subclass *Sphaerobacteridae* subclassis nov., Stackebrandt, Rainey, and Ward-Rainey. *Sphaerobacteridae* (Sphae.ro.bac.te.ri'dae. M.L. masc. n. *Sphaerobacter*, type genus of the subclass; *-idae*, ending to denote a subclass; M.L. fem. pl. n. *Sphaerobacteridae*, the *Sphaerobacter* subclass). The subclass contains the type order *Sphaerobacterales*. The 16S rDNA/rRNA signature pattern is as that of the family *Sphaerobacteraceae*.

Order *Sphaerobacterales* ordo. nov., Stackebrandt, Rainey, and Ward-Rainey. *Sphaerobacterales* (Sphae.ro.bac.te.ra'les. M.L. masc. n. *Sphaerobacter*, type genus of the order; *-ales*, ending to denote an order; M.L. fem. pl. n. *Sphaerobacterales*, the *Sphaerobacter* order). The order contains the type family *Sphaerobacteraceae*. The 16S rDNA/rRNA signature pattern is as that of the family *Sphaerobacteraceae*.

Family *Sphaerobacteraceae* fam. nov., Stackebrandt, Rainey, and Ward-Rainey. *Sphaerobacteraceae* (Sphae.ro.bac.te.ra'ce.ae. M.L. masc. n. *Sphaerobacter*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Sphaerobacteraceae*, the *Sphaerobacter* family). The 16S rDNA/rRNA signature pattern for the family consists of 291-309 (U-A), 294-303 (U-A), 408-434 (A-U), 417-426 (C-G), 657-749 (G-C), 670-736 (G-C), 681-709 (C-G), 941-1342 (A-U), 955-1225 (U-A), 1120-1153 (G-C), 1148 (C), and 1351-1371 (C-G). The family contains the type genus *Sphaerobacter* (41). A phylogenetic analysis has been published previously (41).

Subclass *Actinobacteridae* subclassis nov., Stackebrandt, Rainey, and Ward-Rainey. *Actinobacteridae* (Ac.ti.no.bac.te.ri'dae. M.L. masc. n. *Actinomyces*, type genus of the subclass; *-idae*, ending to denote a subclass; M.L. fem. pl. n. *Actinobacteridae*, the *Actinomyces* subclass). Members of *Actinobacteri-*

dae can consistently be recovered as members of the same phylogenetic lineage (42, 48, 133) (Fig. 3). The subclass contains two orders, *Actinomycetales* and *Bifidobacteriales*. The type order is *Actinomycetales* Buchanan 1917 (13) emend. Members of the subclass contain an insertion of about 100 bases between helices 54 and 55 within domain III of the 23S rDNA (132). This insertion has not been found in members of the subclass *Coriobacteridae* (cf. reference 42). The pattern of 16S rDNA/rRNA signatures consists of nucleotides at positions 291-309 (C-G), 294-303 (C-G), 408-434 (G-C), 670-736 (A-U), 941-1342 (G-C), 1148 (U), and 1410-1490 (G-C).

Order *Actinomycetales* Buchanan 1917 (13), emend. Stackebrandt, Rainey, and Ward-Rainey. *Actinomycetales* (Ac.ti.no.my.ce.ta'les. M.L. masc. n. *Actinomyces*, type genus of the order; *-ales*, ending to denote an order; M.L. pl. fem. n. *Actinomycetales*, the *Actinomyces* order). The 16S rDNA signature pattern consists of nucleotides at positions 122-239 (A-G), 449 (A), 450-483 (G-C), 823-877 (G-C), and 1118-1155 (U-A). The order contains the suborders *Actinomycineae*, *Corynebacterineae*, *Frankineae*, *Glycomycineae*, *Micrococcineae*, *Micromonosporineae*, *Propionibacterineae*, *Pseudonocardineae*, *Streptomycineae*, and *Streptosporangineae*. The type suborder is *Actinomycineae*.

Suborder *Actinomycineae* subordo. nov., Stackebrandt, Rainey, and Ward-Rainey. *Actinomycineae* (Ac.ti.no.my.ci'ne.ae. M.L. masc. n. *Actinomyces*, type genus of the suborder; *-ineae*, ending to denote a suborder; M.L. fem. pl. n. *Actinomycineae*, the *Actinomyces* suborder). The 16S rDNA signature pattern is as that of the type family *Actinomycetaceae*.

Family *Actinomycetaceae* Buchanan 1918 (14), emend. Stackebrandt, Rainey, and Ward-Rainey. *Actinomycetaceae* (Ac.ti.no.my.ce.ta'ce.ae. M.L. masc. n. *Actinomyces*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Actinomycetaceae*, the *Actinomyces* family). The pattern of 16S rDNA signature nucleotides consists of positions 598-640 (U-G), 1059-1198 (U-A), and 1061-1195 (G-U). Genera belonging to the family are the type genus *Actinomyces* (63), *Mobiluncus* (141), and *Arcanobacterium* (32). Phylogenetic analyses have been published previously (51, 87, 99, 142).

Suborder *Propionibacterineae* subordo. nov., Rainey, Ward-Rainey, and Stackebrandt. *Propionibacterineae* (Pro.pi.on.i.bac.te.ri'ne.ae. M.L. neut. n. *Propionibacterium*, type genus of the suborder; *-ineae*, ending to denote a suborder; M.L. fem. pl. n. *Propionibacterineae*, the *Propionibacterium* suborder). The pattern of 16S rDNA signatures consists of nucleotides at positions 127-234 (A-U), 603-635 (A-U), 657-749 (G-C), 671-735 (A-U), 986-1219 (U-A), 987-1218 (G-C), 990-1215 (U-G), and 1059-1198 (C-G). The suborder contains the type family *Propionibacteriaceae* and the family *Nocardioidaceae*.

Family *Propionibacteriaceae* Delwiche 1957 (40), emend. Rainey, Ward-Rainey, and Stackebrandt. *Propionibacteriaceae* (Pro.pi.o.ni.bac.te.ri.a'ce.ae. M.L. neut. n. *Propionibacterium*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Propionibacteriaceae*, the *Propionibacterium* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 66-103 (A-U), 328 (U), 370-391 (C-G), 407-435 (C-G), 602-636 (A-U), 658-748 (A-U), 686 (G), 780 (A), 787 (C), 819 (G), 825-875 (A-U), and 1409-1491 (A-U). Genera included in the family are the type genus *Propionibacterium* (108) as well as *Luteococcus* (163), *Micrococcus* (103), and *Propioniferax* (187). Phylogenetic analyses have been published previously (19, 20, 28, 103, 163, 187).

Family *Nocardioidaceae* Nesterenko et al. 1985 (104), emend. Rainey, Ward-Rainey, and Stackebrandt. *Nocardioidaceae* (No.car.di.o.i.da'ce.ae. M.L. masc. n. *Nocardioides*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl.

n. *Nocardioidaceae*, the *Nocardioides* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 66-103 (G-C), 328 (C), 370-391 (G-C), 407-435 (A-U), 602-636 (G-U), 658-748 (U-A), 686 (U), 780 (G), 787 (A), 819 (U), 825-875 (G-C), and 1409-1491 (C-G). Genera included in the family are the type genus *Nocardioides* (116) and *Aeromicrobium* (101). Phylogenetic analyses have been published previously (101, 161).

Suborder *Micrococcineae* (*Micrococceae* Prevot 1961) (120), emend. Stackebrandt, Rainey, and Ward-Rainey. *Micrococceae* (Mi.cro.coc.ci'ne.ae. M.L. masc. n. *Micrococcus*, type genus of the suborder; *-ineae*, ending to denote a suborder; M.L. fem. pl. n. *Micrococcineae*, the *Micrococcus* suborder). The pattern of 16S rDNA signatures consists of nucleotides at positions 66-103 (A-U), 70-98 (U-A), 82-87 (G-C), 127-234 (A-U), 449 (A), 598-640 (U-G), 600-638 (U-G), 722-733 (A-A), 952-1229 (C-G), 986-1219 (A-U), 987-1218 (A-U), and 1059-1198 (U-A). The type family is *Micrococccaceae*. Other families in the suborder include *Cellulomonadaceae*, *Promicromonosporaceae*, *Dermatophilaceae*, *Brevibacteriaceae*, *Dermabacteraceae*, *Intrasporangiaceae*, *Jonesiaceae*, and *Microbacteriaceae*.

Family *Micrococccaceae* Pribham 1929 (121), emend. Stackebrandt, Rainey, and Ward-Rainey. *Micrococccaceae* (Mi.cro.coc.ca'ce.ae. M.L. masc. n. *Micrococcus*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Micrococccaceae*, the *Micrococcus* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 293-304 (G-U), 610 (G), 598-640 (U-U), 615-625 (G-C), 839-847 (A-U), 859 (U), 1025-1036 (C-G), 1026-1035 (C-G), 1265-1270 (U-G), and 1278 (U). The family contains the type genus *Micrococcus* (25) as well as the genera *Arthrobacter* (35; emended in reference 77), *Kocuria* (150), *Nesterenkonia* (150), *Renibacterium* (137), *Rothia* (52), and *Stomatococcus* (7). Phylogenetic analyses have been published previously (76, 150).

Family *Cellulomonadaceae* Stackebrandt and Prauser 1991 (147), emend. Stackebrandt, Rainey, and Ward-Rainey. *Cellulomonadaceae* (Cel.lu.lo.mo.na.da'ce.ae. M.L. fem. n. *Cellulomonas*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Cellulomonadaceae*, the *Cellulomonas* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 30-553 (C-G), 100 (C), 183-194 (A-U), 258-268 (G-C), 610 (A), 615-625 (A-U), 630 (C), 658-748 (G-A), 659-746 (C-G), 694 (G), 747 (C), 832-854 (G-U), 859 (C), 1002-1038 (G-C), 1003-1037 (G-U), 1006-1023 (A-C), and 1256 (C). The family contains the type genus *Cellulomonas* (8; emended in references 24 and 153) as well as the genera *Oerskovia* (117; emended in reference 90) and *Rarobacter* (182). Phylogenetic analyses have been published previously (49, 129, 153).

Family *Promicromonosporaceae* fam. nov., Rainey, Ward-Rainey, and Stackebrandt. *Promicromonosporaceae* (Pro.mi.cro.mo.no.spo.ra'ce.ae. M.L. fem. n. *Promicromonospora*, the type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Promicromonosporaceae*, the *Promicromonospora* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 77-92 (G-U), 144-178 (U-G), 183-194 (C-G), 199-218 (U-U), 381 (A), 602-636 (G-U), 630 (C), 694 (G), 1002-1038 (Purine-U), 1003-1037 (G-C), 1025-1036 (U-A), and 1267 (U). The family contains the type genus *Promicromonospora* (82). Phylogenetic analyses have been published previously (49, 129).

Family *Dermatophilaceae* Austwick 1958 (4), emend. Stackebrandt, Rainey, and Ward-Rainey. *Dermatophilaceae* (Der.ma.to.phi.la'ce.ae. M.L. masc. n. *Dermatophilus*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n.

Dermatophilaceae, the *Dermatophilus* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 146-176 (G-U), 153-168 (G-U), 502-543 (G-C), 546 (G), 580-761 (U-A), 602-636 (C-G), 615-625 (G-C), 659-746 (U-A), 825-875 (G-C), 838-848 (Pyr-Pur), and 1251 (G). The family contains the type genus *Dermatophilus* (170) as well as the genera *Kytococcus* (150) and *Dermacoccus* (10). Phylogenetic analyses have been published previously (150, 151).

Family *Brevibacteriaceae* Breed 1953 (10), emend. Stackebrandt, Rainey, and Ward-Rainey. *Brevibacteriaceae* (Brev.i.bac.te.ri.a'ce.ae. M.L. neut. n. *Brevibacterium*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Brevibacteriaceae*, the *Brevibacterium* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 41-401 (U-A), 69-99 (C-U), 142-221 (U-A), 144-178 (U-G), 407-435 (C-G), 586-755 (U-A), 591-648 (G-U), 612-628 (G-C), 616-624 (C-G), 631 (G), 660-745 (A-U), 670-736 (U-A), 896-903 (U-G), 1011-1018 (U-A), 1012-1017 (G-C), 1244-1293 (U-A), 1254-1283 (A-C), 1256 (A), 1257 (G), 1262 (A), 1263-1272 (C-G), 1310-1327 (U-A), and 1442-1460 (U-G). The family contains the type genus *Brevibacterium* (10; emended in reference 31). Phylogenetic analyses have been published previously (16, 127).

Family *Dermabacteraceae* fam. nov., Stackebrandt, Rainey, and Ward-Rainey. *Dermabacteraceae* (Der.ma.bac.te.ra'ce.ae. M.L. masc. n. *Dermabacter*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Dermabacteraceae*, the *Dermabacter* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 153-168 (C-G), 248-276 (U-G), 258-268 (A-U), 280 (U), 407-435 (G-U), 580-761 (U-A), 586-755 (U-A), 589-650 (C-G), 602-636 (C-G), 615-625 (A-U), 838-848 (Pur-Pyr), and 1189 (C). The family contains the type genus *Dermabacter* (69) as well as the genus *Brachybacterium* (27). Phylogenetic analyses have been published previously (16, 139).

Family *Intrasporangiaceae* fam. nov. Rainey, Ward-Rainey, and Stackebrandt. *Intrasporangiaceae* (In.tra.spo.ran.gi.a'ce.ae. M.L. neut. n. *Intrasporangium*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Intrasporangiaceae*, the *Intrasporangium* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 30-553 (C-G), 69-99 (G-U), 140-223 (G-C), 157-164 (G-C), 258-268 (A-U), 630 (C), 658-748 (G-U), 659-746 (U-A), 660-745 (G-C), 694 (G), 838-848 (C-G), 839-847 (U-A), 859 (C), 1003-1037 (G-C), 1007-1022 (C-G), 1133-1141 (A-U), and 1134-1140 (C-G). The family contains the type genus *Intrasporangium* (71) as well as the genera *Sanguibacter* (47) and *Terrabacter* (29). Phylogenetic analyses have been published previously (29, 47).

Family *Jonesiaceae* fam. nov., Stackebrandt, Rainey, and Ward-Rainey. *Jonesiaceae* (Jone.si.a'ce.ae. M.L. fem. n. *Jonesia*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Jonesiaceae*, the *Jonesia* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 153-168 (C-G), 280 (U), 379-384 (G-C), 407-435 (G-U), 445-489 (A-U), 589-650 (U-G), 602-636 (U-G), 615-625 (A-U), 668-738 (U-A), 838-848 (Pur-Pyr), and 1189 (C). The family contains the type genus *Jonesia* (130). Phylogenetic analyses have been published previously (49, 129).

Family *Microbacteriaceae* Park et al. 1993 (113), emend. Rainey, Ward-Rainey, and Stackebrandt. *Microbacteriaceae* (Mi.cro.bac.te.ri.a'ce.ae. M.L. masc. n. *Microbacterium*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Microbacteriaceae*, the *Microbacterium* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 45-396 (U-A), 144-178 (C-G), 258-268 (A-U), 497 (A), 615-625 (A-U), 694 (G), 771-808 (G-C), 839-847 (G-U),

1256 (C), 1310-1327 (A-U), and 1414-1486 (U-A). The family contains the type genus *Microbacterium* (109) as well as the genera *Agrococcus* (58), *Agromyces* (54), *Aureobacterium* (30), *Clavibacter* (39), *Curtobacterium* (181), and *Rathayibacter* (189). Phylogenetic analyses have been published previously (58, 122, 158, 159).

Suborder *Corynebacterineae* subordo. nov., Stackebrandt, Rainey, and Ward-Rainey. *Corynebacterineae* (Co.ry.ne.bac.te.ri'ne.ae. M.L. masc. n. *Corynebacterium*, type genus of the suborder; *-ineae*, ending to denote a suborder; M.L. fem. pl. n. *Corynebacterineae*, the *Corynebacterium* suborder). The pattern of 16S rDNA signatures consists of nucleotides at positions 127-234 (G-C), 131-231 (U-Pur), 502-543 (A-U), 658-748 (A-A), 564 (C), 600-638 (G-C), 601-637 (U-G), 660-745 (U-A), 671-735 (C-G), 819 (G), 952-1229 (U-A), 986-1219 (U-A), 1116-1184 (U-G), and 1414-1486 (U-G). The suborder contains the type family *Corynebacteriaceae* as well as the families *Dietziaceae*, *Gordoniaceae*, *Mycobacteriaceae*, *Nocardiaceae*, and *Tsakamurellaceae*.

Family *Corynebacteriaceae* Lehmann and Neumann 1907 (95), emend. Stackebrandt, Rainey, and Ward-Rainey. *Corynebacteriaceae* (Co.ry.ne.bac.te.ri.a'ce.ae. M.L. neut. n. *Corynebacterium*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Corynebacteriaceae*, the *Corynebacterium* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 293-304 (G-U), 307 (A), 316-337 (U-G), 468 (U), 508 (U), 586-755 (U-G), 631 (G), 661-744 (G-C), 662-743 (U-G), 771-808 (A-U), 824-876 (C-G), 825-875 (G-C), 837-849 (G-U), 843 (C), and 1059-1198 (U-A). The family contains the type genus *Corynebacterium* (94) as well as the genus *Turicella* (50). Phylogenetic analyses have been published previously (50, 114, 135).

Family *Mycobacteriaceae* Chester 1897 (21), emend. Stackebrandt, Rainey, and Ward-Rainey. *Mycobacteriaceae* (My.co.bac.te.ri.a'ce.ae. M.L. neut. n. *Mycobacterium*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Mycobacteriaceae*, the *Mycobacterium* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 70-98 (A-U), 293-304 (G-U), 307 (C), 328 (U), 614-626 (A-U), 631 (G), 661-744 (G-C), 824-876 (U-A), 825-875 (A-U), 843 (C), and 1122-1151 (A-U). The family contains the type genus *Mycobacterium* (94). Phylogenetic analyses have been published previously (115, 131).

Family *Nocardiaceae* Castellani and Chalmers 1919 (18), emend. Rainey, Ward-Rainey, and Stackebrandt. *Nocardiaceae* (No.car.di.a'ce.ae. M.L. fem. n. *Nocardia* type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Nocardiaceae*, the *Nocardia* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 70-98 (U-A), 139-224 (G-C), 843 (C), 1008-1021 (C-G), 1189 (C), 1244-1293 (C-G), and 1308-1329 (C-G). The family contains the type genus *Nocardia* (169) as well as the genus *Rhodococcus* (190). Phylogenetic analyses have been published previously (22, 124, 134).

Family *Gordoniaceae* fam. nov., Rainey, Ward-Rainey, and Stackebrandt. *Gordoniaceae* (Gor.do.ni.a'ce.ae. M.L. fem. n. *Gordonia*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Gordoniaceae*, the *Gordonia* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 70-98 (A-U), 293-304 (A-U), 307 (U), 661-744 (A-U), 824-876 (U-A), 825-875 (A-U), 843 (U), 1002-1038 (A-U), 1007-1022 (C-G), 1122-1151 (G-C), and 1124-1149 (A-U). The family contains the type genus *Gordonia* (154). Corrigendum: The name *Gordonia*, not *Gordona*, is proposed as the correct etymology. Phylogenetic analyses have been published previously (6, 124, 134).

Family Tsukamurellaceae fam. nov., Rainey, Ward-Rainey, and Stackebrandt. *Tsukamurellaceae* (Tsu.ka.mu.rel.la'ce.ae. M.L. fem. n. *Tsukamurella*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Tsukamurellaceae*, the *Tsukamurella* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 70-98 (U-A), 293-304 (G-U), 307 (C), 631 (C), 661-744 (G-C), 824-876 (U-A), 825-875 (A-U), 843 (C), 1007-1022 (G-U), and 1122-1151 (A-U). The family contains the type genus *Tsukamurella* (33). Phylogenetic analyses have been published previously (33, 124, 183).

Family Dietziaceae fam. nov., Rainey, Ward-Rainey, and Stackebrandt. *Dietziaceae* (Diet.zi.a'ce.ae. M.L. fem. n. *Dietzia*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Dietziaceae*, the *Dietzia* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 70-98 (U-A), 293-304 (G-U), 307 (U), 418-425 (U-A), 508 (U), 614-626 (U-G), 631 (G), 661-744 (A-U), 771-808 (A-U), 824-876 (C-G), 825-875 (G-C), 843 (C), 1049-1198 (U-A), and 1122-1151 (A-U). The family contains the type genus *Dietzia* (125). A phylogenetic analysis has been published previously (124).

Suborder Pseudonocardineae subordo. nov., Stackebrandt, Rainey, and Ward-Rainey. *Pseudonocardineae* (Pseu.do.no.car'di.ne.ae. M.L. fem. n. *Pseudonocardia*, the type genus of the suborder; *-ineae*, ending to denote a suborder; M.L. fem. pl. n. *Pseudonocardineae*, the *Pseudonocardia* suborder). The pattern of 16S rDNA signatures is as that for the family. The type family is *Pseudonocardiaceae*.

Family Pseudonocardiaceae Warwick et al. 1994 (175), emend. Stackebrandt, Rainey, and Ward-Rainey. *Pseudonocardiaceae* (Pseu.do.no.car.di.a'ce.ae. M.L. fem. n. *Pseudonocardia*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Pseudonocardiaceae*, the *Pseudonocardia* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 127-234 (G-C), 183-194 (G-U), 502-543 (A-U), 603-635 (C-G), 610 (A), 747 (A), 952-1229 (U-A), 986-1219 (U-A), 987-1218 (G-C), 1001-1039 (Pyr-G), and 1308-1329 (C-G). Comment: Although in phylogenetic terms this family is rather broad, it is currently not possible to subdivide the family due to the lack of an unambiguous pattern of signature nucleotides. The family contains the type genus *Pseudonocardia* (66) as well as the genera *Actinopolyspora* (55), *Actinosynnema* (65), *Amycolatopsis* (92), *Kibdelosporangium* (140), *Kutzneria* (152), *Lentzea* (184), *Saccharomonospora* (106), *Saccharopolyspora* (86), *Saccharothrix* (84), *Streptoalloteichus* (168), and *Thermocrispum* (79). Phylogenetic analyses have been published previously (9, 43, 74, 79, 175, 184).

Suborder Streptomycineae subordo. nov., Rainey, Ward-Rainey, and Stackebrandt. *Streptomycineae* (Strep.to.my.ci'ne.ae. M.L. masc. n. *Streptomyces*, type genus of the suborder; *-ineae*, ending to denote a suborder; M.L. fem. pl. n. *Streptomycineae*, the *Streptomyces* suborder). The pattern of signature nucleotides of 16S rDNA is as that of the type family *Streptomycetaceae*.

Family Streptomycetaceae Waksman and Henrici 1943 (171), emend. Rainey, Ward-Rainey, and Stackebrandt. *Streptomycetaceae* (Strep.to.my.ce.ta'ce.ae. M.L. masc. n. *Streptomyces*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Streptomycetaceae*, the *Streptomyces* family). The family is emended to exclude the genus *Sporichthya*. The pattern of 16S rDNA signature nucleotides consists of 71 (G), 80-89 (G-C), 81-88 (C-G), 82-87 (U-G), 127-234 (G-C), 209 (C), 210 (C), 211 (G), 610 (G), 671-735 (U-A), 819 (G), 837-849 (C-G), 950-1231 (U-G), 955-1225 (C-G), 965 (C), 1254-1283 (A-U), and 1409-1491 (C-G). The family contains the type genus *Streptomyces* (171; emended in references 176 and

178). Phylogenetic analyses have been published previously (73, 155, 160, 176, 178).

Suborder Streptosporangineae subordo. nov., Ward-Rainey, Rainey, and Stackebrandt. *Streptosporangineae* (Strep.to.spo.ran.gi'ne.ae. M.L. neut. n. *Streptosporangium*, type genus of the suborder; *-ineae*, ending to denote a suborder; M.L. fem. pl. n. *Streptosporangineae*, the *Streptosporangium* suborder). The pattern of 16S rDNA signatures consists of nucleotides at positions 127-234 (A-U), 657-749 (G-Pyr), and 955-1225 (C-G). The type family is *Streptosporangiaceae*.

Family Streptosporangiaceae Goodfellow et al. 1990 (56) (validation list no. 34), emend. Ward-Rainey, Rainey, and Stackebrandt. *Streptosporangiaceae* (Strep.to.spo.ran.gi.a'ce.ae. M.L. neut. n. *Streptosporangium*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Streptosporangiaceae*, the *Streptosporangium* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 440-494 (C-G), 445-489 (G-C), 501-544 (C-G), 502-543 (G-C), no extra base between positions 453 and 479, 586-755 (U-G), 613-627 (Pyr-Pur), 681-709 (U-A), 1116-1184 (U-G), 1137 (U), 1355-1367 (A-U), 1436-1465 (GC), and 1422-1478 (G-U). The family contains the type genus *Streptosporangium* (37) as well as the genera *Herbidospira* (83), *Microbispora* (105), *Microtraspura* (167), *Planobispira* (164), and *Planomonospora* (166). Phylogenetic analyses have been published previously (172, 174).

Family Nocardiopsaceae Rainey et al. 1996 (127), emend. Rainey, Ward-Rainey, and Stackebrandt. *Nocardiopsaceae* (No.car.di.op.sa'ce.ae. M.L. fem. n. *Nocardiopsis*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Nocardiopsaceae*, the *Nocardiopsis* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 440-494 (U-G), 442-492 (C-G), 445-489 (C-G), four extra bases between positions 453 and 479, 501-544 (G-C), 502-543 (A-U), 586-755 (C-G), 603-635 (U-A), 613-627 (C-G), 658-748 (U-A), 671-735 (C-G), 681-709 (U-A), 1003-1037 (U-G), 1116-1184 (C-G), 1137 (A), 1355-1367 (G-C), 1422-1478 (G-U), and 1435-1466 (A-U). The family contains the type genus *Nocardiopsis* (100). A phylogenetic analysis has been published previously (127).

Family Thermomonosporaceae fam. nov., Rainey, Ward-Rainey, and Stackebrandt. *Thermomonosporaceae* (Ther.mo.mo.no.spo.ra'ce.ae. M.L. fem. n. *Thermomonospora*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Thermomonosporaceae*, the *Thermomonospora* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 440-494 (C-G), 442-492 (G-C), four to seven extra bases between position 453 and 479, 501-544 (C-G), 502-543 (G-C), 586-755 (C-G), 613-627 (C-G), 658-748 (C-U), 681-709 (C-G), 1003-1037 (A-G), 1116-1184 (C-G), 1355-1367 (A-U), 1422-1478 (G-C), and 1435-1466 (G-C). The family contains the type genus *Thermomonospora* (66) as well as the genera *Actinomadura* (89) and *Spirillospora* (38). Phylogenetic analyses have been published previously (127, 172).

Suborder Micromonosporineae subordo. nov., Stackebrandt, Rainey, and Ward-Rainey. *Micromonosporineae* (Mi.cro.mo.no.spo.ri'ne.ae. M.L. fem. n. *Micromonospora*, type genus of the suborder; *-ineae*, ending to denote a suborder; M.L. fem. pl. n. *Micromonosporineae*, the *Micromonospora* suborder). The pattern of 16S rDNA signature nucleotides is as indicated for the family. The suborder contains the type family *Micromonosporaceae*.

Family Micromonosporaceae Krassilnikov 1938 (80), emend. Koch et al. 1996 (78), emend. Stackebrandt, Rainey, and Ward-Rainey. *Micromonosporaceae* (Mi.cro.mo.no.spo.ra'ce.ae. M.L. fem. n. *Micromonospora*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Micromonospora-*

ceae, the *Micromonospora* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 66-103 (G-C), 127-234 (A-U), 153-168 (C-G), 502-543 (G-C), 589-650 (C-G), 747 (A), 811 (U), 840-846 (C-G), 952-1229 (C-G), 1116-1184 (C-G), and 1133-1141 (G-C). The family contains the type genus *Micromonospora* (111) as well as the genera *Actinoplanes* (36; emended in reference 145), *Catellatospora* (3), *Couchioplanes* (162), *Catenuloplanes* (185), *Dactylosporangium* (165), and *Pilimelia* (72). Phylogenetic analyses have been published previously (75, 78).

Suborder Frankineae subordo. nov., Stackebrandt, Rainey, and Ward-Rainey. *Frankineae* (Frank.i.'ne.ae. M.L. fem. n. *Frankia*, type genus of the suborder; *-ineae*, ending to denote a suborder; M.L. fem. pl. n. *Frankineae*, the *Frankia* suborder). The pattern of 16S rDNA signatures consists of nucleotides at positions 82-87 (C-G), 127-234 (G-C), 141-222 (G-C), 371-390 (G-C), 502-543 (A-U), and 1003-1037 (G-G). The suborder contains the type family *Frankiaceae* as well as the families *Acidothermaceae*, *Microsphaeraceae*, *Geodermatophilaceae*, and *Sporichthyaceae*. Phylogenetic analyses have been published previously (44, 62, 107, 123, 126).

Family Frankiaceae Becking 1970 (5), emend. Hahn et al. 1989 (62), emend. Normand et al. 1996 (107), emend. Stackebrandt, Rainey, and Ward-Rainey. *Frankiaceae* (Frank.i.a'ce.ae. M.L. fem. n. *Frankia*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Frankiaceae*, the *Frankia* family). The 16S rDNA signature nucleotide pattern consists of 139-224 (G-C), 148-174 (A-G), 155-166 (U-G), 839-847 (A-G), 987-1218 (G-C), 1059-1198 (C-G), and 1308-1329 (C-G). The family contains the type genus *Frankia* (12). Phylogenetic analyses have been published previously (62, 107).

Family Geodermatophilaceae Normand et al. 1996 (107), emend. Stackebrandt, Rainey, and Ward-Rainey. *Geodermatophilaceae* (Ge.o.der.ma.to.phi.la'ce.ae. M.L. masc. n. *Geodermatophilus*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Geodermatophilaceae*, the *Geodermatophilus* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 139-224 (C-G), 157-164 (A-U), 158-163 (A-U), 186-191 (C-G), 263 (G), 293-304 (G-U), 986-1219 (U-A), 987-1218 (A-U), 1059-1198 (U-A), and 1308-1329 (U-A). The family contains the type genus *Geodermatophilus* (98) as well as the genus *Blastococcus* (2). Phylogenetic analyses have been published previously (44, 107).

Family Microsphaeraceae fam. nov., Rainey, Ward-Rainey, and Stackebrandt. *Microsphaeraceae* (Mi.cro.sphae.ra'ce.ae. M.L. fem. n. *Microsphaera*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Microsphaeraceae*, the *Microsphaera* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 139-224 (C-G), 157-164 (G-C), 186-191 (C-G), 839-847 (U-A), 987-1218 (A-U), 1059-1198 (U-A), and 1308-1329 (U-A). The family contains the type genus *Microsphaera* (188). A phylogenetic analysis has been published previously (188).

Family Sporichthyaceae fam. nov., Rainey, Ward-Rainey, and Stackebrandt. *Sporichthyaceae* (Spo.rich.thy.a'ce.ae. M.L. fem. n. *Sporichthya*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Sporichthyaceae*, the *Sporichthya* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 139-224 (U-A), 186-191 (G-C), 600-638 (C-G), 839-847 (U-A), 987-1218 (A-U), 1059-1198 (U-A), and 1308-1329 (U-A). The family contains the type genus *Sporichthya* (91). A phylogenetic analysis has been published previously (126).

Family Acidothermaceae fam. nov., Rainey, Ward-Rainey, and Stackebrandt. *Acidothermaceae* (A.ci.do.ther.ma'ce.ae. M.L. masc. n. *Acidothermus*, type genus of the family; *-aceae*,

ending to denote a family; M.L. fem. pl. n. *Acidothermaceae*, the *Acidothermus* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 139-224 (C-G), 186-191 (G-C), 839-847 (A-U), 987-1218 (G-C), 1059-1198 (C-G), and 1308-1329 (C-G). The family contains the type genus *Acidothermus* (102). A phylogenetic analysis has been published previously (123).

Suborder Glycomycineae subordo. nov., Rainey, Ward-Rainey, and Stackebrandt. *Glycomycineae* (Gly.co.my.ci.ne'ae. M.L. masc. n. *Glycomyces*, type genus of the suborder; *-ineae*, ending to denote a suborder; M.L. fem. pl. n. *Glycomycineae*, the *Glycomyces* suborder). The pattern of signature nucleotides of 16S rDNA is as that of the type family *Glycomycetaceae*.

Family Glycomycetaceae fam. nov., Rainey, Ward-Rainey, and Stackebrandt. *Glycomycetaceae* (Gly.co.my.ce.ta'ce.ae. M.L. masc. n. *Glycomyces*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Glycomycetaceae*, the *Glycomyces* family). The 16S rDNA pattern of 16S rDNA signature nucleotides contains 70-98 (A-U), 127-234 (G-Pyr), 140-223 (A-U), 229 (G), 366 (U), 415 (C), 449 (C), 534 (G), 681-709 (A-U), 825-875 (G-C), 999-1041 (C-G), 1059-1198 (C-G), 1064-1192 (G-G), 1117-1183 (A-U), and 1309-1328 (C-G). The family contains the type genus *Glycomyces* (85). The phylogenetic position is shown in Fig. 3.

Order Bifidobacteriales ordo. nov., Stackebrandt, Rainey, and Ward-Rainey. *Bifidobacteriales* (Bi.fi.do.bac.te.ri.a'les. M.L. neut. n. *Bifidobacterium*, type genus of the order; *-ales*, ending to denote an order; M.L. fem. pl. n. *Bifidobacteriales*, the *Bifidobacterium* order). The type family of the order is *Bifidobacteriaceae*. The 16S rDNA nucleotide signature is as that of the family.

Family Bifidobacteriaceae fam. nov., Stackebrandt, Rainey, and Ward-Rainey. *Bifidobacteriaceae* (Bi.fi.do.bac.te.ri.a'ce.ae. M.L. neut. n. *Bifidobacterium*, type genus of the family; *-aceae*, ending to denote a family; M.L. fem. pl. n. *Bifidobacteriaceae*, the *Bifidobacterium* family). The pattern of 16S rDNA signatures consists of nucleotides at positions 122-239 (G-U), 128-233 (C-G), 450-483 (C-G), 602-636 (G-C), 681-709 (C-G), 688-699 (A-U), 823-877 (A-U), 1118-1155 (C-G), and 1311-1326 (A-U). The family contains the type genus *Bifidobacterium* (110) as well as *Gardnerella* (57). A phylogenetic structure of the family has been published previously (88, 99).

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