

Road map of the phylum *Actinobacteria*

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This revised road map and the resulting taxonomic outline update the previous versions of Garrity and Holt (2001) and Garrity et al. (2005) with the description of additional taxa and new phylogenetic analyses. While the road map seeks to be complete for all taxa validly named prior to 1 January 2008, some taxa described after that date are included.

The new phylogenetic trees are strict consensus trees based on various maximum-likelihood and maximum-parsimony analyses and corrected according to results obtained when applying alternative treeing methods. Multifurcations indicate that a common branching order was not significantly supported after applying alternative treeing approaches. Detailed branching orders are shown if supported by at least 50% of the “treeings” performed in addition to the maximum-likelihood approach.

Given that the focus is on the higher (taxonomic) ranks, rather restrictive variability filters were applied. Consequently, resolution power is lost for lower levels. Of special importance, relationships within genera lack the resolution that would be obtained with genus/family level analyses. Furthermore, the type strain tree, which is available online at www.bergeys.org, is an extract of comprehensive trees comprising some thousand sequences. Thus, trees for the specific groups in subsequent chapters, which are based upon smaller datasets and include variable sequence positions, may differ with respect to detailed topology, especially at levels of closer relationship within and between genera. In the trees shown here, branch lengths – in the first instance – indicate significance and only approximate estimated number of substitutions.

Starting with the second edition of *Bergey's Manual of Systematic Bacteriology*, the arrangement of content follows a phylogenetic framework or road map based largely on analyses of nucleotide sequences of the ribosomal small subunit RNA rather than on phenotypic data (Garrity et al., 2005). Implicit in the use of the road map are the convictions that prokaryotes have a phylogeny and that phylogeny matters. However, phylogenies, like other experimentally derived hypotheses, are not static but may change whenever new data and/or improved methods of analysis become available (Ludwig and Klenk, 2005). Thus, the large increases in data since the publication of the taxonomic outlines in the preceding volumes have led to a re-evaluation of the road map. Not surprisingly, the taxonomic hierarchy has been modified or newly interpreted for a number of taxonomic units. These changes are described in the following paragraphs.

The taxonomic road map proposed in volume 1 and updated and emended in volume 2 was derived from phylogenetic and principal component analyses of comprehensive datasets of small-subunit rRNA gene sequences. A similar approach is continued here. Since the introduction of comparative rRNA sequencing (Ludwig and Klenk, 2005; Ludwig and Schleifer, 2005), there

has been a continuous debate concerning the justification and power of a single marker molecule for elucidating and establishing the phylogeny and taxonomy of organisms, respectively. Although generally well established in taxonomy, comparable analyses of multiple genes cannot currently be applied because of the lack of comprehensive datasets for other marker molecules. Even in the age of genomics, the datasets for non-rRNA markers are poor in comparison to more than 400,000 rRNA primary structures available in general and specialized databases (Cole et al., 2007; Pruesse et al., 2007). Nevertheless, the data provided by full genome sequencing projects have identified a small set of genes representing the conserved core of prokaryotic genomes (Cicarelli et al., 2006; Ludwig and Schleifer, 2005). Furthermore, comparative analyses of core gene sequences globally support the small-subunit rRNA-derived view of prokaryotic evolution. Although the tree topologies reconstructed from alternative markers differ in detail, the major groups (and taxa) are verified or at least not disproved (Ludwig and Schleifer, 2005). Consequently, this volume is organized on the basis of updated and curated databases of processed small-subunit rRNA primary structures (<http://www.arb-silva.de>; Ludwig et al., 2004).

Data analysis

The current release of the integrated small-subunit rRNA database of the SILVA project (Pruesse et al., 2007) provided the basis for these phylogenetic analyses. The tools of the ARB software package (Ludwig et al., 2004) were used for data evaluation, optimization, and phylogenetic inference. A subset of about 33,000 high-quality sequences from *Bacteria* was extracted from the current SILVA SSU Ref database. Among the criteria for restrictive quality analyses and data selection were: coverage of at least positions 18 to 1509 (*Escherichia coli* 16S rRNA numbering), no ambiguities or missing sequence stretches, no chimeric primary structures, low deviation from overall and group-specific consensus and conservation profiles, and good agreement of tree topologies and branch lengths with processed sequence data. Unfortunately, not all of the type strain sequences successfully passed this restrictive quality check. The alignment of the sequences of this subset, as well as all type strain sequences initially excluded given incompleteness or lower quality, was manually evaluated and optimized. Phylogenetic treeing was first based on the high quality dataset and performed applying phylum-specific position filters (50% positional identity). The partial or lower quality type strain sequences were subsequently added using a special ARB-tool allowing the optimally positioning of branches to the reference tree without admitting topology changes (Ludwig and Klenk, 2005). The consensus trees used for evaluating or modifying the taxonomic outline

were based on maximum-likelihood analyses (RAXML, implemented in the ARB package; Stamatakis et al., 2005) and further evaluated by maximum-parsimony and distance matrix analyses with the respective ARB tools (Ludwig et al., 2004).

Taxonomic interpretation

In order to ensure applicability and promote acceptance, the proposed taxonomic modifications were made following a conservative procedure. The overall organization follows the type “taxon” principle as applied in the previous volumes. Taxa defined in the outline of the preceding volumes were only unified, dissected, or transferred in the cases of strong phylogenetic support. This approach is justified by the well-known low significance of local tree topologies (also called “range of unsharpness” around the nodes; Ludwig and Klenk, 2005). Thus, many of the cases of paraphyletic taxa found were maintained in the current road map if the respective (sub)-clusters rooted closely together, even if they were separated by intervening clusters representing other taxa. While reorganization of these taxa may be warranted, it was not performed in the absence of confirmatory evidence. The names of type strains of species with validly published names that are phylogenetically misplaced are also generally maintained. These strains are mentioned in the context of the respective phylogenetic groups. In case of paraphyly, all concerned species or higher taxa are assigned to the respective (sub)-groups. New higher taxonomic ranks are only proposed if species or genera – previously assigned to different higher taxonomic units – are significantly unified in a monophyletic branch.

Phylum “*Actinobacteria*”

The phylum “*Actinobacteria*” is well supported by analyses of the 16S and 23S rRNA genes, presence of conserved insertions and deletions (or indels) in certain proteins, and characteristic gene rearrangements (as reviewed by Goodfellow and Fiedler, 2010). The current road map builds upon the thorough taxonomic analyses of Zhi et al. (2009) and Stackebrandt et al. (1997). However, in the classification proposed herein, the taxonomic ranks of subclass and suborder are not used, and the clades previously represented by these ranks are mostly elevated to the ranks of class and order, respectively. This modification makes the taxonomy of the “*Actinobacteria*” more consistent with that of other prokaryotes and thereby facilitates comparisons between phyla and the development of a unified classification across all bacteria and archaea. Moreover, it reduces the number of subdivisions within the higher ranks from six (class, subclass, order, suborder, family, and genus) to four. The lower number of higher ranks is more realistic given the limited ability to distinguish phylogenetic relationships among this large and complex group. This change has a number of important consequences. The class “*Actinobacteria*” now excludes the subclasses *Acidimicrobiales*, *Coriobacteriales*, *Nitriliruptoriales*, and *Rubrobacteriales*, with the elevation of these subclasses to classes. In addition, with the elevation of suborders to orders, the order *Actinomycetales* is now restricted to members of the family *Actinomycetaceae* and many suborders that are well established in the literature, such as *Micrococccineae* and *Pseudonocardineae*, are not used. Nevertheless, the possible confusion that might result from these changes is out-weighed by the advantages of a simpler classification which more closely resembles that found in other prokaryotic phyla.

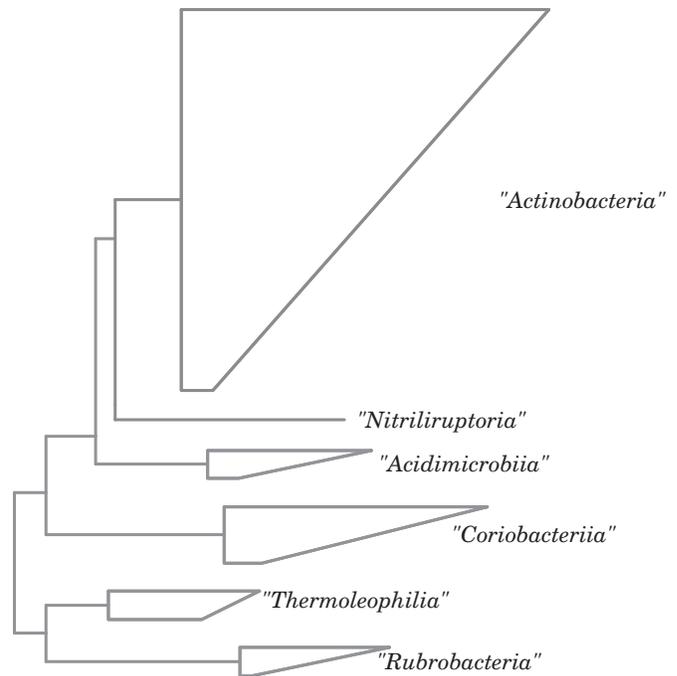


FIGURE 1. Overview of the classes within the phylum *Actinobacteria*. Consensus dendrogram of the phylogenetic relationships of the 16S rRNA genes based on various maximum-likelihood and maximum-parsimony analyses and corrected according to results obtained when applying alternative treeing methods. Multifurcations indicate that a common branching order was not significantly supported after applying alternative treeing approaches. Detailed branching orders are shown if supported by at least 50% of the “treeings” performed in addition to the maximum-likelihood approach. For additional methods, please see the text.

The proposed classification does not preclude the use of the term “actinomycetales” in its conventional sense. This practice is common in other prokaryotic groups where the implementation of a natural classification based upon phylogeny made the earlier terminology inappropriate. Thus, “bacillus” refers to a member of a large number of genera that encompass aerobic, endospore-forming rods and not the genus *Bacillus*.

With the class “*Actinobacteria*” defined in this manner, six classes are proposed (Figure 1). In addition to the class “*Actinobacteria*”, which is now restricted to the clades formerly classified within the subclass *Actinobacteridae*, the classes “*Acidimicrobiia*”, “*Coriobacteriia*”, “*Nitriliruptoria*”, “*Rubrobacteria*”, and “*Thermoleophilia*” are proposed. This last class includes many of the genera formerly classified within the *Rubrobacteria* that were not closely related to it (see below).

Class “*Actinobacteria*”

As shown in Figure 2, the class “*Actinobacteria*” comprises the orders previously classified as suborders within the order *Actinomycetales* by Zhi et al. (2009), as well as *Bifidobacteriales*, which was previously classified as an order, and the new order *Jiangellales* (Tang et al., 2011). Upon publication of the class “*Actinobacteria*”, a type order was not designated. Hence, this name is not validly published under Rule 27 of the *International Code of Nomenclature of Bacteria* (Euzéby and Tindall, 2001; Lapage

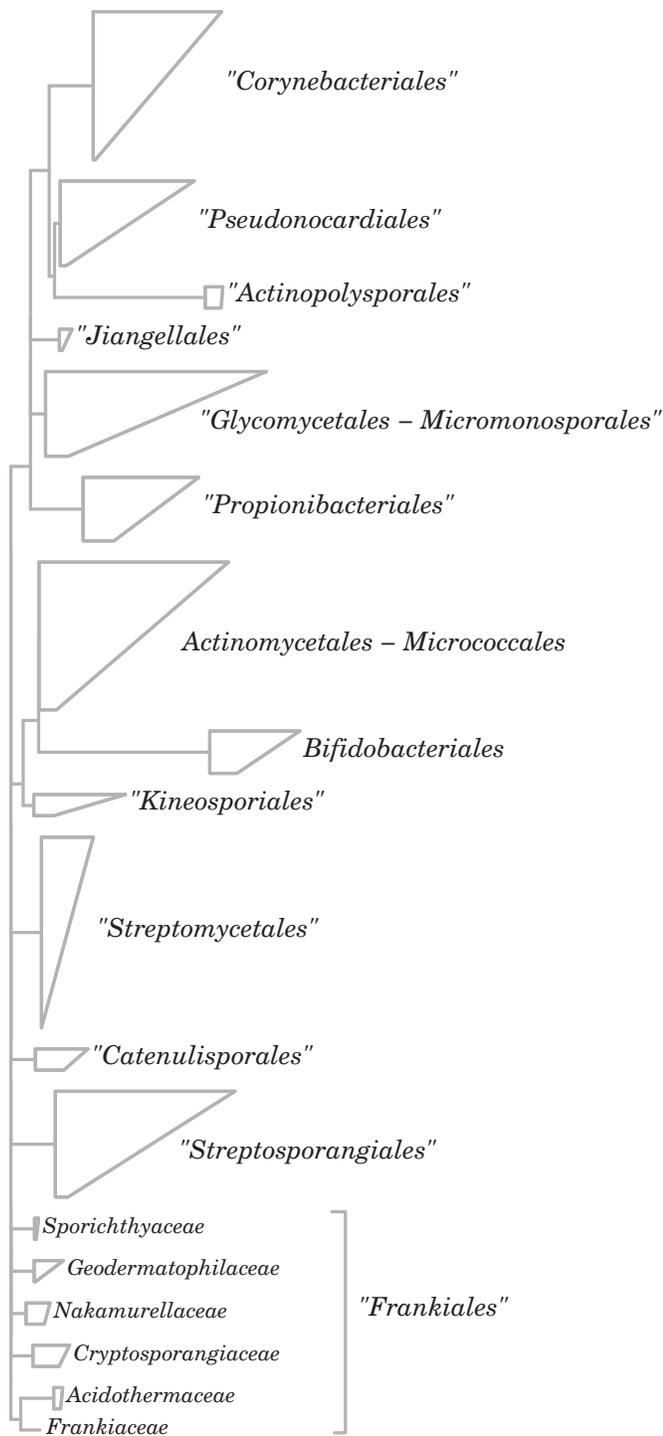


FIGURE 2. Orders of the class *Actinobacteria*. Analyses were performed as described for Figure 1.

et al., 1992). Nevertheless, because of its wide use, the name is adopted for this volume. If so designated by the Judicial Commission, the type order is likely to be *Actinomycetales*, which is the convention followed herein.

Within the class, two large clades are observed in the rRNA gene trees prepared for this volume (Figure 2). The first clade includes the orders “*Actinopolysporales*”, “*Corynebacteriales*”,

“*Glycomycetales*”, “*Jiangellales*”, “*Micromonosporales*”, “*Propionibacteriales*”, and “*Pseudonocardiales*”. The second clade includes the orders *Actinomycetales*, *Bifidobacteriales*, “*Kineosporiales*”, and *Micrococcales*. The orders “*Catenulisporales*”, “*Streptomycetales*”, and “*Streptosporangiales*” form deep lineages radiating from the base of the class. Lastly, the families of the order “*Frankiales*” do not form a clade, but appear as independent lineages at the base of the tree. However, these relationships were not observed in rRNA gene trees of Zhi et al. (2009). Thus, in the absence of confirmatory evidence, they were not used to make taxonomic decisions in the road map.

Order *Actinomycetales* and family *Actinomycetaceae*

With the elevation of the suborders of Zhi et al. (2009) to orders, this order now comprises only the family *Actinomycetaceae*. Thus, the taxonomic designation is no longer congruent with the common term “actinomycetales”. The family appears as an independent clade somewhat related to the family *Jonesiaceae* of the order *Micrococcales* (Figure 3). It comprises the diffuse type genus *Actinomyces* and the four well-defined genera *Actinobaculum*, *Arcanobacterium*, *Mobiluncus*, and *Varibaculum*.

The genus *Actinomyces* is represented by five clades within the family. The largest clade includes the type species *Actinomyces bovis* and *Actinomyces bowdenii*, *catuli*, *dentalis*, *denticolens*, *gerencseriae*, *graevenitzii*, *howellii*, *israelii*, *johnsonii*, *massiliensis*, *naeslundii*, *oricola*, *oris*, *radicidentis*, *ruminicola*, *slackii*, *urogenitalis*, and *viscosus*. The remaining clades are no more closely related to the type species than to the members of other genera within the family, which might be grounds for their reclassification in the future. The second largest clade includes the species *Actinomyces canis*, *cardiffensis*, *funkei*, *georgiae*, *hyovaginalis*, *meyeri*, *odontolyticus*, *radinae*, *suimastitidis*, *turicensis*, and *vaccimaxillae*. It is loosely related to two additional clades, one of which includes *Actinomyces coleocanis* and *Actinomyces europaeus* and the other *Actinomyces neuii* and the monospecific genus *Varibaculum* (type species *Varibaculum cambriense*). With only 90% sequence similarity and some phenotypic differences to *Varibaculum*, *Actinomyces neuii* may warrant reclassification in a new genus (Hall et al., 2003). The last clade clusters close to the root of the family tree and includes *Actinomyces marimammalium*, *hongkongensis*, *hordeovulneris*, and *nasicola*. The taxonomic significance of these groups is discussed in further detail by Schaal and Yassin (2012).

The other genera in the family all form monophyletic clades. The genera *Actinobaculum* and *Arcanobacterium* are related to each other. *Actinobaculum* comprises the type species *Actinobaculum suis* and *Actinobaculum massiliense*, *schaalii*, and *urinale*. *Arcanobacterium* comprises the type species *Arcanobacterium haemolyticum* and *Arcanobacterium abortusuis*, *bernardiae*, *bialowiezense*, *bonasi*, *hippocoleae*, *phocae*, *pluranimalium*, and *pyogenes*. The genus *Mobiluncus* comprises the type species *Mobiluncus curtisii* and *Mobiluncus mulieris*. This genus has precedence over *Falcivibrio*, which appears to be a later heterotypic synonym (Hoyles et al., 2004).

Order “*Actinopolysporales*” and family *Actinopolysporaceae*

In the rRNA gene trees described herein, this order is related to “*Corynebacteriales*” and “*Pseudonocardiales*”. These three orders are members of a larger clade that also includes “*Glycomycetales*”,

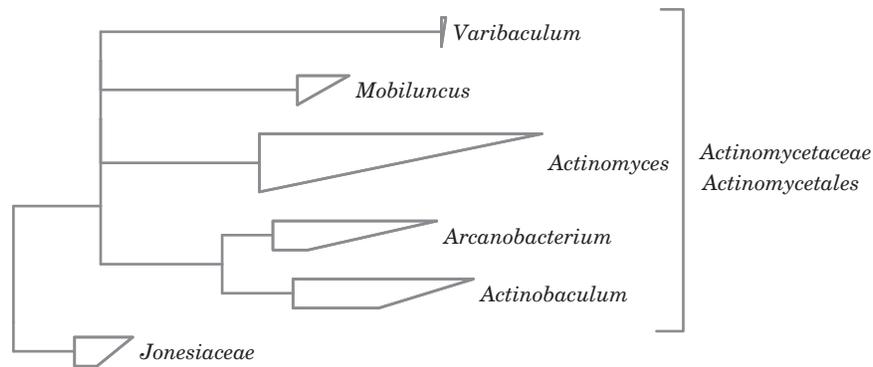


FIGURE 3. Genera of the order *Actinomycetales* and *Jonesiaceae* of the order *Micrococcales*. Analyses were performed as described for Figure 1.

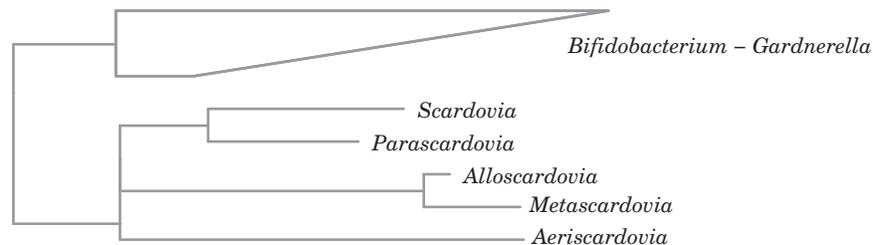


FIGURE 4. Genera of the order *Bifidobacteriales*. Analyses were performed as described for Figure 1.

“*Jiangellales*”, “*Micromonosporales*”, and “*Propionibacteriales*” (Figure 2). In the analyses of Zhi et al. (2009), only the relationship of “*Actinopolysporales*” and “*Glycomycetales*” was observed, although without bootstrap support. The monogeneric family comprises the type species *Actinopolyspora halophila* and *Actinopolyspora mortivallis*. The species *Actinopolyspora iraqiensis* was misclassified and is now classified as a heterotypic synonym of *Saccharomonospora halophila*.

Order *Bifidobacteriales* and family *Bifidobacteriaceae*

The order *Bifidobacteriales* comprises the family *Bifidobacteriaceae*, which encompasses seven closely related genera (Figure 4). In the rRNA gene trees used here, the entire group is separated by a long branch that arises within a clade formed by the *Actinomycetales*, *Micrococcales*, and “*Kineosporiales*” (Figure 2). However, the root of the order *Bifidobacteriales* is unstable and this relationship was not observed by Zhi et al. (2009). In their gene trees, based upon a different method of analysis, the order *Bifidobacteriales* appears as a deep branch of the class “*Actinobacteria*”. In either case, both methods agree that the genera assigned to this group are well separated from other orders.

The family *Bifidobacteriaceae* comprises two clades. One clade includes the genus *Bifidobacterium* and the monospecific genus *Gardnerella* (type species *Gardnerella vaginalis*). The second clade comprises five additional monospecific genera with type species *Aeriscardovia aeriphila*, *Alloscardovia omnicoles*, *Metascardovia criceti*, *Parascardovia denticolens*, and *Scardovia inopinata*. The genus *Bifidobacterium* encompasses nine subclades, each about as related to one another as they are to *Gardnerella vaginalis*. These subclades include the type species *Bifidobacterium*

bifidum; *Bifidobacterium adolescentis*, *angulatum*, *catenulatum*, *dentium*, *merycicum*, *pseudocatenulatum*, and *ruminantium*; *Bifidobacterium animalis*, *choerinum*, *cuniculi*, *gallicum*, *magnum*, and *pseudolongum*; *Bifidobacterium asteroides*, *bombi*, *coryneforme*, *indicum*, *minimum*, *mongoliense*, *psychraerophilum*, and *thermophilum*; *Bifidobacterium boum* and *thermacidophilum*; *Bifidobacterium breve*, *longum*, and *subtile*; *Bifidobacterium gallinarum*, *pullorum*, and *saeculare*; *Bifidobacterium scardovii*; and *Bifidobacterium tsurumense*. The significance of these subclades is not certain and they only correspond imperfectly to similarities in cell-wall composition and in 16S–23S intergenic spacer regions (Biavati and Mattarelli, 2012; Leblond-Bourget et al., 1996).

Order “*Catenulisporales*” and families *Catenulisporaceae* and *Actinospicaceae*

This order represents a deep clade within the class “*Actinobacteria*” and comprises two monogeneric families (Figure 5). The family *Catenulisporaceae* contains the type species *Catenulispora acidiphila* and three related species, *Catenulispora rubra*, *subtropica*, and *yoronensis*. The family *Actinospicaceae* includes the type species *Actinospica robiniae* and *Actinospica acidiphila*.

Order “*Corynebacteriales*”

In the rRNA gene trees described herein, this order is related to the orders “*Actinopolysporales*” and “*Pseudonocardiales*”. In the analyses of Zhi et al. (2009), only the relationship between “*Corynebacteriales*” and “*Pseudonocardiales*” was observed, albeit without bootstrap support. All three orders have the cell-wall chemotype IV, which includes the presence of *meso*-diaminopimelate, arabinose, and galactose. However, their quinones

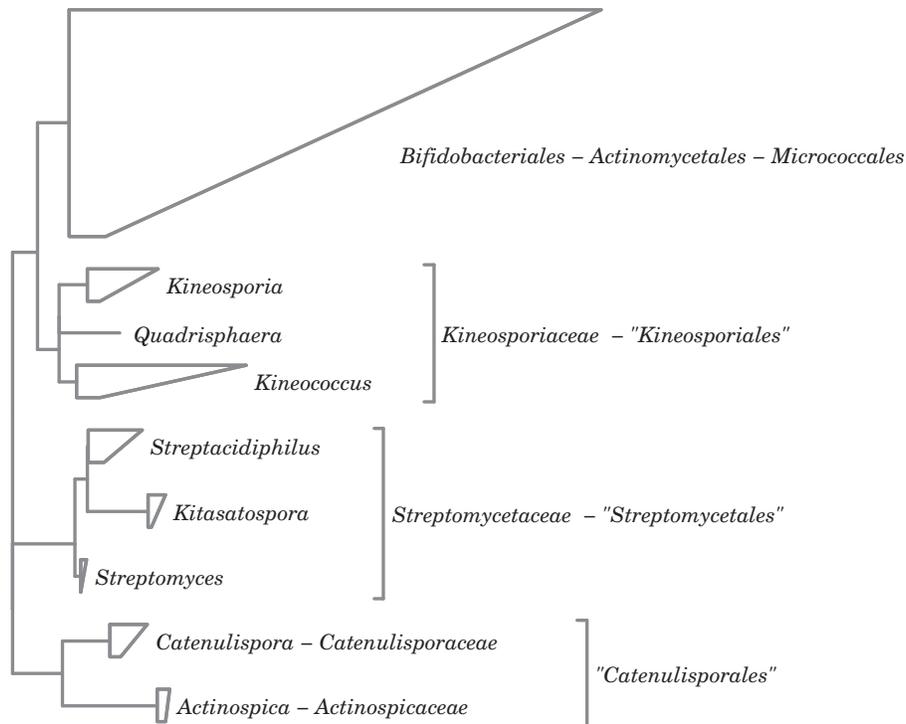


FIGURE 5. Genera and families of the orders “*Catenulesporales*”, “*Kineosporiales*”, and “*Streptomycetales*”. Analyses were performed as described for Figure 1.

and major fatty acids are different, and species belonging to the “*Pseudonocardiales*” lack mycolic acids. Therefore, the biological importance of this deep relationship requires further examination. These orders are also members of the larger clade that also includes “*Glycomycetales*”, “*Jiangellales*”, “*Micromonosporales*”, and “*Propionibacteriales*”, whose biological significance is also not known (Figure 2).

Six suprageneric taxa can be recognized in the current 16S rRNA gene tree, the families *Corynebacteriaceae*, *Dietziaceae*, *Mycobacteriaceae*, *Nocardiaceae*, *Segniliparaceae*, and *Tsukamurellaceae* (Figure 6). While most of these families are monophyletic, many of the genera of the *Nocardiaceae* appear as deep lineages in the rRNA gene tree, no more closely related to the type genus *Nocardia* than members of other families (see below). For that reason, this family appears to be paraphyletic. While the status of some of the families, notably the *Mycobacteriaceae* and *Tsukamurellaceae*, is strongly supported by chemotaxonomic data, others such as the family *Nocardiaceae* are markedly heterogeneous in this respect. Indeed, a case can be made for the recognition of the family *Gordoniaceae* to encompass the genera *Gordonia*, *Millisia*, *Williamsia*, and *Skermania* (Goodfellow and Jones, 2012). The assignment of the recently described, mycolateless genera *Amycolicococcus* (Wang et al., 2010), *Hoyosella* (Jurado et al., 2009), and *Tomitella* (Katayama et al., 2010) further complicates the delineation of families classified in the order *Corynebacteriales* (Goodfellow and Jones, 2012). Consequently, the biological significance of several families within this order requires further study.

Family *Corynebacteriaceae*

This family comprises the large and complex genus *Corynebacterium* and the monospecific genus *Turicella* (type species *Turicella otitidis*). On the basis of the rRNA gene tree, many of the species of the genus appear equally related to the type species *Corynebacterium diphtheriae* and *Turicella otitidis* and, on this basis, the genus is paraphyletic. However, most *Corynebacterium* species possess mycolic acids and the menaquinones MK-8(H₂), MK-9(H₂), or a mixture of both. *Turicella* and some *Corynebacterium* species, such as *Corynebacterium amycolatum*, lack mycolic acids. *Turicella* also possesses the menaquinones MK-10 and MK-11 (Goodfellow and Jones, 2012). It appears that these species have lost the capacity to produce mycolic acids, so the significance of this chemotaxonomic marker is ambiguous. Given the uncertainties in the relationships within this group, the current taxonomy is retained at this time.

In addition to the type species, the genus *Corynebacterium* comprises a large number of species which, while related to *Corynebacterium diphtheriae*, do not form specific associations with other species of the genus. These include *Corynebacterium accolens*, *aquilae*, *argentoratense*, *atypicum*, *auris*, *camporealensis*, *capitovis*, *caspium*, *confusum*, *doosanense*, *felinum*, *flavescens*, *freiburgense*, *halotolerans*, *kutscheri*, *lipophiloflavum*, *lubricantis*, *macginleyi*, *maris*, *massiliense*, *mastitidis*, *mycetoides*, *renale*, *spheniscorum*, *testudinoris*, *timonense*, *tuberculostearicum*, and *vitaeruminis*. In addition, the rRNA gene tree identifies nine small clades of species, including: *Corynebacterium afermentans*, *appendicis*, *coyleae*,

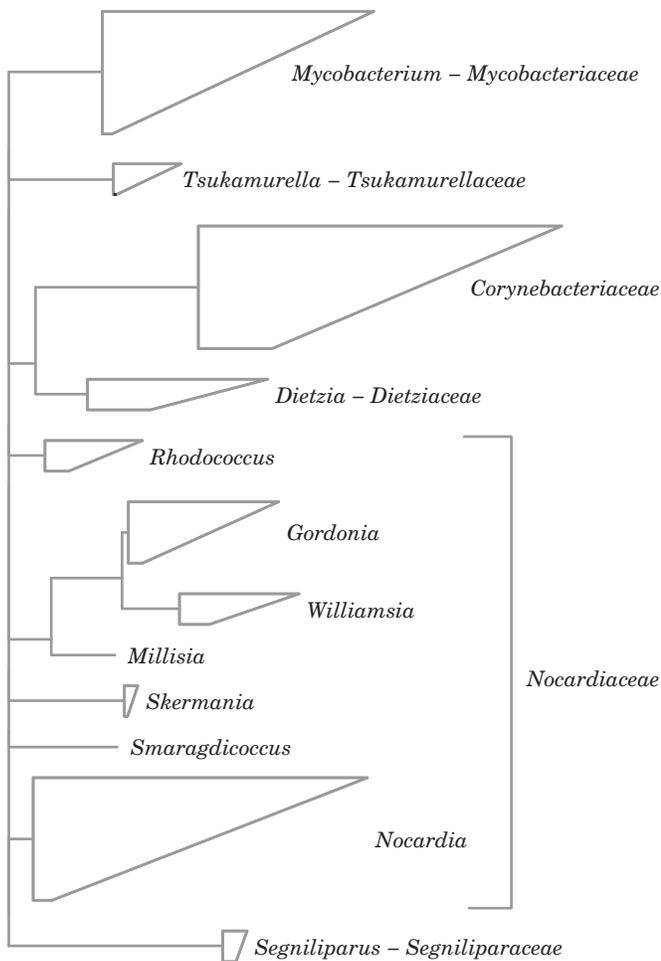


FIGURE 6. Genera and families of the order “Corynebacteriales”. Analyses were performed as described for Figure 1.

glaucum, *imitans*, *mucifaciens*, *riegelii*, *sundsvallense*, *thomsseni*, *tuscaniense*, and *ureicelerivorans*; *Corynebacterium ammoniagenes*, *casei*, and *stationis*; *Corynebacterium amycolatum*, *frenyi*, *hanseni*, *sphenisci*, *sputi*, *ulceribovis*, and *xerosis*; *Corynebacterium aurimucosum*, *minutissimum*, *phocae*, *simulans*, and *singulare*; *Corynebacterium auriscanis*, *bovis*, *falsenii*, *jeikeium*, *kroppenstedtii*, *resistens*, *suicordis*, *terpenotabidum*, *urealyticum*, and *variabile*; *Corynebacterium callunae*, *efficiens*, and *glutamicum*; *Corynebacterium ciconiae*, *propinquum*, and *pseudodiphtheriticum*; *Corynebacterium cystitidis*, *glucuronolyticum*, and *pilosum*; and *Corynebacterium durum*, *matruchothii*, *pseudotuberculosis*, and *ulcerans*.

The affiliations of some additional species of the genus are uncertain. *Corynebacterium ilicis* was originally thought to be a homotypic synonym of *Arthrobacter ilicis*. However, this appears not to be the case and the rRNA gene sequence of *Corynebacterium ilicis* is not known (Judicial Commission of the International Committee on Systematics of Bacteria, 2008). The type strain of *Corynebacterium striatum* has been lost and this species might be declared *nomen dubium* (Coyle et al., 1993). Lastly, *Corynebacterium beticola* appears to be more properly classified as a strain of *Erwinia herbicola* (Collins and Jones, 1982).

Family Dietziaceae

This monogeneric family comprises the type species *Dietzia maris* and the closely related species *Dietzia aerolata*, *cercidiphylli*, *cinnamea*, *kunjamensis*, *natronolimnaea*, *papillomatosi*, *psychralcaliphila*, *schimae*, and *timorensis*.

Family Mycobacteriaceae

This monogeneric family is well-defined in the 16S rRNA gene tree and also characterized by the presence of mycolic acids with large numbers of carbon atoms and the predominance of dihydrogenated menaquinones with nine isoprene units (Magee and Ward, 2012). It comprises the type species *Mycobacterium tuberculosis* and over 140 other species with validly published names. In the 16S rRNA gene tree, a major clade is easily recognized that corresponds to most of the “slow-growing species” (Magee and Ward, 2012). This clade is of special importance because it includes many dangerous pathogens, as well as the type species *Mycobacterium tuberculosis*. Other species include *Mycobacterium africanum*, *arosiense*, *asiaticum*, *avium*, *bohemicum*, *botniense*, *bouchedurhonense*, *bovis*, *branderi*, *caprae*, *celatum*, *chimaera*, *colombiense*, *conspicuum*, *cooki*, *florentinum*, *gastri*, *genavense*, *gordonae*, *haemophilum*, *heckeshornense*, *heidelbergense*, *interjectum*, *intermedium*, *intracellulare*, *kansasii*, *kubicae*, *kyorinense*, *lacus*, *lentiflavum*, *leprae*, *malmoense*, *mantenii*, *marinum*, *marseillense*, *microti*, *montefiorensense*, *nebraskense*, *noviomagense*, *palustre*, *parascrofulaceum*, *paraseoulense*, *parmense*, *pinnipedii*, *pseudoshottsii*, *riyadhense*, *saskatchewanense*, *scrofulaceum*, *seoulense*, *shimoidi*, *shottsii*, *simiae*, *stomatepiae*, *szulgai*, *triplex*, *ulcerans*, *vulneris*, and *xenopi*. A second, unrelated clade is composed of other “slow-growing species”: *Mycobacterium arupense*, *hiberniae*, *kumamotoense*, *nonchromogenicum*, and *terrae*. Most of the remaining species, including most of the “rapid-growing species”, are poorly differentiated from each other in the 16S rRNA gene tree.

Family Nocardiaceae

In the current rRNA gene tree, the family *Nocardiaceae* is paraphyletic and is represented by seven genera comprising five deep lineages, none of which are more closely related to each other than to other members of the order “Corynebacteriales”. In the previous road map, the family contained only the genera *Nocardia* and *Rhodococcus* (Garrity et al., 2005). *Gordonia* and *Skermania* were classified within the family *Gordoniaceae* and *Williamsia* was classified within the family “*Williamsiaceae*”. Zhi et al. (2009) subsequently proposed combining all these genera and *Millisia* into a single family *Nocardiaceae* based upon the rRNA gene signature nucleotides. With the addition of *Smaragdicoccus* (Adachi et al., 2007), this taxonomy was used here.

Chemotaxonomic criteria provide some modest support for combining these genera in a single family. *Smaragdicoccus* possesses cyclic menaquinones, MK-8(H₄, ω-methylenecycl) and MK-8(H₄, dicycl), which are similar in structure to those of the genera *Nocardia* and *Skermania*, which are dominated by MK-8(H₄, ω-cycl). This feature is distinctive enough to suggest a close relationship between these genera. Likewise, both *Gordonia* and *Williamsia* contain the menaquinone MK-9(H₂), which is consistent with their close relationship in the rRNA gene tree. In contrast, *Rhodococcus* and *Millisia* both possess MK-8(H₂) even though the rRNA gene trees do not indicate a special affinity between them. Therefore, while the menaquinone composition supports the hypothesis that some members of this

group are related to each other, it does not provide strong support that they represent a single family. Somewhat clearer evidence for the placement of these seven genera in a single family comes from similarities in their mycolic acids. *Nocardia* species contain mycolic acids with 46–64 C-atoms, and *Rhodococcus* species contain mycolic acids with 30–54 C-atoms. The other five genera all have mycolic acids with numbers of C-atoms within these ranges. Lastly, all genera within this family possess meso-diaminopimelate, but this feature is also common to other families of the “*Corynebacteriales*” and to other orders, such as the “*Pseudonocardiales*”. In conclusion, the chemotaxonomic markers are evidence of additional phylogenetic relatedness not apparent in the rRNA gene tree and offer some support for the current classification. Nevertheless, the composition of the family *Nocardiaceae* should be considered tentative until a time when conclusive evidence is available.

In the rRNA gene tree, the genus *Nocardia* forms a deep, monophyletic lineage near the base of the “*Corynebacteriales*”. The *Nocardia* tree itself exhibits a complicated branching pattern with many very short branches. Three clusters can be recognized. The first cluster contains the type species *Nocardia asteroides* and a large number of species whose relatedness is not well differentiated: *Nocardia abscessus*, *acidivorans*, *alba*, *altamirensis*, *anemiae*, *blacklockiae*, *brasiliensis*, *caishijiensis*, *concava*, *crasostreae*, *cyriacigeorgica*, *exalbida*, *gamkensis*, *harenae*, *inohanensis*, *iowensis*, *jejuensis*, *jiangxiensis*, *lijiangensis*, *mexicana*, *miyunensis*, *neocaledoniensis*, *niigatensis*, *ninae*, *nova*, *polyresistens*, *pseudobrasilensis*, *pseudovaccinii*, *seriolae*, *takedensis*, *tenerifensis*, *terpenica*, *thailandica*, *transvalensis*, *uniformis*, *vinacea*, *wallacei*, *xishanensis*, and *yamanashiensis*. This cluster also contains three subclades that are well differentiated from the other species: *Nocardia brevicatena* and *paucivorans*; *Nocardia carnea*, *flavorosea*, *jinanensis*, *pigrifrangens*, *sienata*, *speluncae*, and *testacea*; and *Nocardia coubleae*, *cummidelens*, *fluminea*, *ignorata*, *salmonicida*, and *solii*. The second cluster includes *Nocardia africana*, *amamiensis*, *aobensis*, *araoensis*, *arthritidis*, *beijingensis*, *cerradoensis*, *elegans*, *kruzcakiae*, *pneumoniae*, *vaccinii*, *vermiculata*, and *veterana*. The third cluster is at the base of the *Nocardia* lineage and includes the species *Nocardia asiatica*, *farcinica*, *higoensis*, *otitiscaviarum*, *puris*, and *shimofusensis*.

The genus *Gordonia* is represented by a well-defined clade comprising the type species *Gordonia bronchialis* and *Gordonia aichiensis*, *alkanivorans*, *amarae*, *amicalis*, *araii*, *cholesterolivorans*, *defluvii*, *desulfuricans*, *effusa*, *hankookensis*, *hirsuta*, *hydrophobica*, *kroppenstedtii*, *lacunae*, *malaquae*, *namibiensis*, *otitidis*, *paraffinivorans*, *polyisoprenivorans*, *rhizosphaera*, *rubripertincta*, *shandongensis*, *sihwensis*, *sinesedis*, *solii*, *sputi*, *terrae*, and *westfalica*. It is closely related to the genus *Williamsia*, a relationship that is also supported by similarities in menaquinone content and other chemotaxonomic markers (Goodfellow and Jones, 2012).

In the rRNA gene tree, the monospecific genus *Millisia* (type species *Millisia brevis*) is related to the genera *Gordonia* and *Williamsia*. This relationship is also consistent with similarities in the chain lengths of their mycolic acids.

The genus *Rhodococcus* is represented by a number of deep, paraphyletic lineages with short branch lengths at the base of the radiation including the family *Nocardiaceae* and order “*Corynebacteriales*”. One clade comprises the type species *Rhodococcus rhodochrous* and *Rhodococcus aetherivorans*, *coprophilus*, *gordoniae*, *phenolicus*, *pyridinivorans*, *ruber*, and *zopfii*. A second, poorly resolved clade encompasses *Rhodococcus baikonurensis*,

erythropolis, *fascians*, *globerulus*, *imtechensis*, *jialingiae*, *jostii*, *koreensis*, *kyotomensis*, *maanshanensis*, *marinonascens*, *opacus*, *percolatus*, *qingshengii*, *tukisamuensis*, *wratislaviensis*, and *yunnanensis*. Lastly, a number of species are not resolved into clades and may represent new genera. These include *Rhodococcus corynebacterioides*, *equi*, *kroppenstedtii*, *kunmingensis*, *rhodnii*, and *triatomae*. The case for the recognition of a new genus for *Rhodococcus equi* is especially strong (Jones and Goodfellow, 2012).

The monospecific genera *Skermania* (type species *Skermania piniformis*) and *Smaragdicosoccus* (type species *Smaragdicosoccus niigatensis*) represent two deep lineages at the base of the rRNA gene tree of the family *Nocardiaceae* (Figure 6).

The genus *Williamsia* forms a well-defined clade that is closely related *Gordonia*. It is represented by the type species *Williamsia muralis* and *Williamsia deligens*, *marianensis*, *maris*, and *serinedens*.

Family *Segniliparaceae*

This monogeneric family is represented by the type species *Segniliparus rotundus* and *Segniliparus rugosus*. These species form a deep lineage at the base of the radiation including the *Nocardiaceae* and “*Corynebacteriales*” (Figure 6).

Family *Tsakamurellaceae*

This monogeneric family comprises the type species *Tsakamurella paurometabola* and the closely related species *Tsakamurella carboxydivorans*, *inchonensis*, *pseudospumae*, *pulmonis*, *spongiae*, *spumae*, *strandjordii*, *sunchonensis*, and *tyrosinosolvans*. The presence of a completely unsaturated menaquinone MK-9 detected in all species of this group supports placement in a single genus.

Order “*Frankiales*”

This order is formed by elevation of the suborder of *Frankineae* (Stackebrandt et al., 1997; Zhi et al., 2009) and comprises the families *Frankiaceae*, *Acidothermaceae*, *Cryptosporangiaceae*, *Geodermatophilaceae*, *Nakamurellaceae*, and *Sporichthyaceae* (Figure 7). The major difference between this order and the corresponding group described in the previous road map (Garrity et al., 2005) is the reclassification of the genera *Kineosporia* and *Kineococcus* to the novel order “*Kineosporiales*” (Zhi et al., 2009). In addition, the family *Cryptosporangiaceae* was proposed to include the genus *Cryptosporangium*, which had previously been classified within the family *Kineosporiaceae* but was retained in the “*Frankiales*”. Lastly, the previous road map included the monogeneric family *Microsphaeraceae*. However, this genus name was ruled illegitimate because of precedence of a fungal genus, and the bacterial species was reclassified to the new family *Nakamurellaceae* (Tao et al., 2004).

Although the group “*Frankiales*” was observed in early studies of the phylogeny of the 16S rRNA gene in *Actinobacteria* (Normand et al., 1996; Stackebrandt et al., 1997), more recent studies with different selections of outgroups and other methods of phylogenetic analyses do not provide strong support for this classification. For instance, although 16S rRNA gene signatures have been proposed for the order, there is little bootstrap support for this group in the 16S rRNA gene tree of Zhi et al. (2009). In the gene trees prepared for this volume, only the families *Frankiaceae* and *Acidothermaceae* are closely related (Figures 2 and 7), a relationship also observed by Zhi et al.

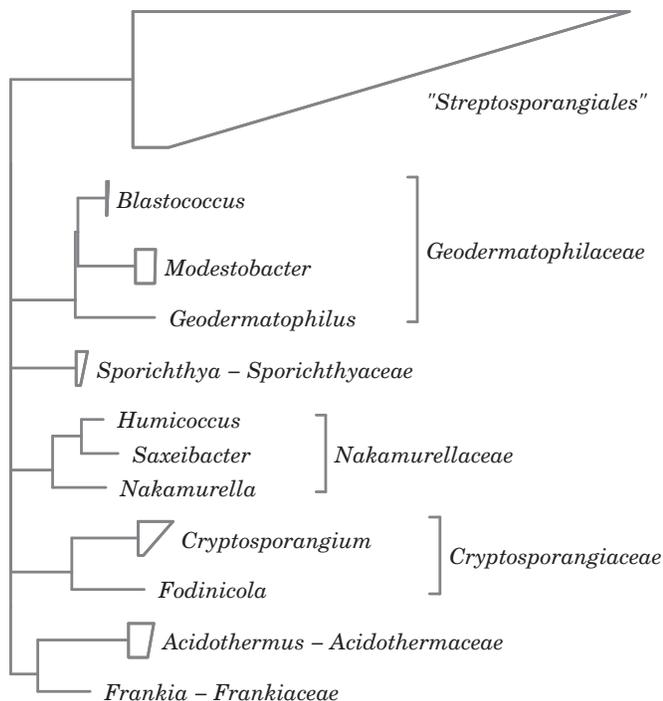


FIGURE 7. Genera and families of the order “Frankiales”. Analyses were performed as described for Figure 1.

(2009) and supported by similarities in *recA* genes (Marechal et al., 2000). The remaining families appear as deep lineages of the class *Actinobacteria* but are not specifically related to the family *Frankiaceae*. Chemotaxonomic evidence does not fully resolve this issue (Normand and Benson, 2012). The cell-wall diamino acid is *meso*-diaminopimelate in all families tested except for the family *Sporichthyaceae*, which contains LL-diaminopimelate. In the families *Frankiaceae*, *Cryptosporangiaceae*, and *Sporichthyaceae*, the abundant menaquinones are MK-9(H₄), MK-9(H₆), and MK-9(H₈). However, *Geodermatophilaceae* contains MK-9(H₄) and MK-8(H₄); and *Nakamurellaceae* contains mostly MK-8(H₄). The menaquinones of the *Acidothermaceae* have not been determined. Lastly, the fatty acid composition is also diverse. Members of all families contain mostly saturated fatty acids in the range of 15–18 carbons, some or all of which are branched. Thus, while the chemotaxonomic evidence identifies some unifying features, it does not provide strong evidence for the order “*Frankiales*”. Hence, its composition should be considered tentative until conclusive evidence is available.

Family *Frankiaceae*

This monogeneric family comprises the type genus *Frankia* (type and only species *Frankia alni*). Common nitrogen-fixing symbionts of dicotyledonous plants, at least 12 genospecies have been isolated but their names have not been validly published. Hence, the diversity of the genus is certainly larger than represented by the nomenclature.

Family *Acidothermaceae*

This monogeneric family comprises the type genus *Acidothermus* (type and only species *Acidothermus cellulolyticus*). Its growth temperature range of 37–70°C, inability to fix N₂, and rapid

growth distinguish this moderately thermophilic taxon from the *Frankiaceae*.

Family *Cryptosporangiaceae*

This family comprises the genus *Cryptosporangium*. It contains the type species *Cryptosporangium arvum* and three closely related species *Cryptosporangium aurantiacum*, *japonicum*, and *minutisporangium*. Based upon similarities in its 16S rRNA gene sequence, the monospecific genus *Fodinicola* (type species *Fodinicola feengrottensis*) is tentatively classified in this family as a genus *incertae sedis*.

Family *Geodermatophilaceae*

The type for this family is the monospecific genus *Geodermatophilus* (type species *Geodermatophilus obscurus*). Other genera and species include *Blastococcus aggregatus* (type species), *jejuensis*, and *saxobidens*, as well as *Modestobacter multiseptatus* (type species) and *versicolor*.

Family *Nakamurellaceae*

This family comprises three monospecific genera: *Nakamurella* (type species *Nakamurella multipartita*), *Humicoccus* (type species *Humicoccus flavidus*), and *Saxeibacter* (type species *Saxeibacter lacteus*). This latter is a recently described genus which is not described further in this volume (Lee et al., 2008).

Family *Sporichthyaceae*

This monogeneric family encompasses two closely related species: *Sporichthya polymorpha* (type species) and *Sporichthya brevicatena*.

Order “*Glycomycetales*” and family *Glycomycetaceae*

This order is formed by elevation of the suborder *Glycomycineae* (Stackebrandt et al., 1997; Zhi et al., 2009) and comprises the single family *Glycomycetaceae*. In the 16S rRNA gene trees prepared for this volume, the “*Glycomycetales*” appears as a long branch specifically related to the genus *Actinocatenispora* within the order “*Micromonosporales*” (Figure 8). Some chemotaxonomic and phenotypic properties tend to support this association (Labeda, 2012; Matsumoto et al., 2007; Seo and Lee, 2009; Thawai et al., 2006). The family *Glycomycetaceae* and *Actinocatenispora* each have type II cell walls which contain *meso*-diaminopimelic acid and glycine as well as N-glycolylmuramic acid. They also produce chains of spores on aerial hyphae. However, some differences also exist. *Glycomycetaceae* and *Actinocatenispora* possess phospholipid types I and II, respectively. Moreover, in the *Glycomycetaceae*, MK-10, MK-11, and MK-12 menaquinones are abundant, whereas in the *Actinocatenispora*, MK-9 (H₄, H₆) menaquinones predominate. For these reasons, the association between these two taxa is considered tentative at this time.

The family *Glycomycetaceae* contains three genera. The genus *Glycomyces* encompasses the type species *Glycomyces harbinensis* and nine other species: *Glycomyces algeriensis*, *arizonensis*, *endophyticus*, *lechevalierae*, *mayteni*, *rutgersensis*, *sambucus*, *scopariae*, and *tenuis*. Closely related is the recently described monospecific genus *Haloglycomyces* (type species *Haloglycomyces albus*), which is not described in this volume (Guan et al., 2009). Lastly, the genus *Stackebrandtia* contains the type species *Stackebrandtia nassauensis* and *Stackebrandtia albiflava*.

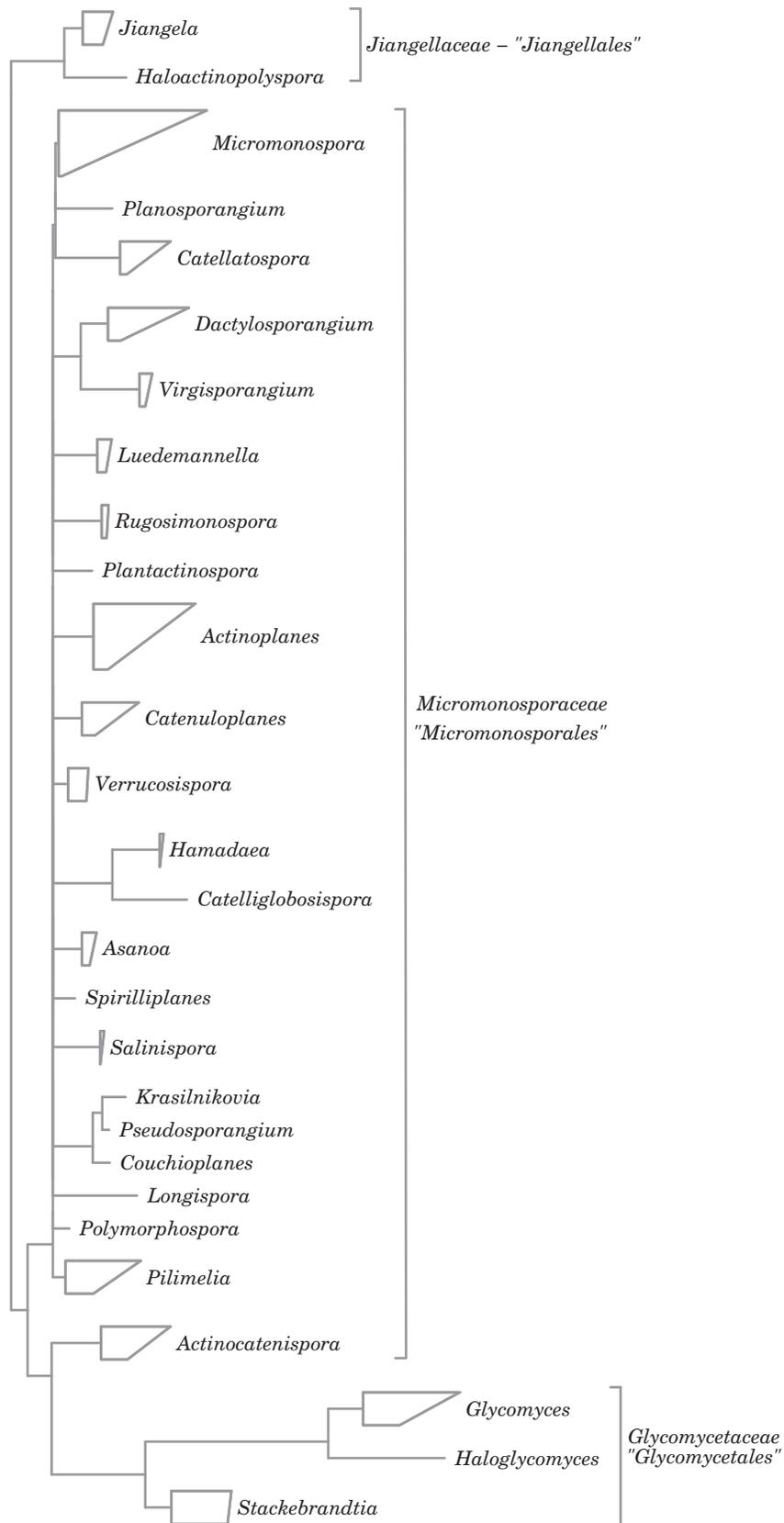


FIGURE 8. Genera of the orders “*Glycomycetales*”, “*Jiangellales*”, and “*Micromonosporales*”. Analyses were performed as described for Figure 1.

Order “*Jiangellales*” and family *Jiangellaceae*

In the rRNA gene trees described herein, this order is a member of a larger clade which also includes the orders “*Corynebacteriales*”, “*Glycomycetales*”, “*Micromonosporales*”, “*Propionibacteriales*”, and “*Pseudonocardiales*” (Figure 2). However, this clade was not observed in the analyses of Zhi et al. (2009) and is also not supported by chemotaxonomic markers. While these latter results are not surprising given the depth of this relationship, the biological importance of this clade should be considered tentative at this time.

The order “*Jiangellales*” was formed by elevation of the suborder *Jiangellineae*. This classification was proposed following the description of a novel genus *Haloactinopolyspora*, which is closely related to the genus *Jiangella* (Tang et al., 2011). Previously, *Jiangella* was classified within the family *Nocardioideaceae* based upon polyphasic evidence (Song et al., 2005). Currently, the order comprises the family *Jiangellaceae* and two genera (Figure 8). The genus *Jiangella* comprises the type species *Jiangella gansuensis* and *Jiangella alba* and *alkaliphila*. The monospecific genus *Haloactinopolyspora* (type species *Haloactinopolyspora alba*) is also classified in the family.

Order “*Kineosporiales*” and family *Kineosporiaceae*

This order is formed by elevation of the suborder *Kineosporiineae*, which was proposed to include some of the genera previously classified in the suborder *Frankineae* (Garrity et al., 2005; Zhi et al., 2009). In the rRNA gene trees used here, this order is within a clade that also includes the orders *Actinomycetales*, *Bifidobacteriales*, and *Micrococcales* (Figure 2). This clade is not observed in the analyses of Zhi et al. (2009) and is considered tentative at this time. The order comprises the family *Kineosporiaceae*, which is composed of three genera (Figure 5). The genus *Kineosporia* includes the type species *Kineosporia aurantiaca* and the closely related species *Kineosporia babensis*, *mesophila*, *mikuniensis*, *rhamnosa*, *rhizophila*, and *succinea*. The genus *Kineococcus* encompasses the type species *Kineococcus aurantiacus* and four closely related species *Kineococcus gynurae*, *radiotolerans*, *rhizosphaerae*, and *xinjiangensis*. In addition, *Kineococcus marinus*, which in rRNA trees appears equally related to the type species of all three genera in the family, is also classified in the *Kineococcus*. Lastly, the monospecific genus *Quadrisphaera* (type species *Quadrisphaera granulorum*) is also a member of the order *Kineosporiales*.

Order *Micrococcales*

This order is formed by elevation of the suborder *Micrococcineae* (Zhi et al., 2009). In the rRNA gene tree used here, the order lies within a clade that also includes the orders *Actinomycetales* and *Bifidobacteriales* (Figure 2). The order “*Kineosporiales*” also appears as an ancestral lineage to this clade. The order *Actinomycetales* forms a subclade along with the *Micrococcales* families *Brevibacteriaceae*, *Dermabacteraceae*, *Jonesiaceae*, and *Micrococcaceae* (Figure 9). The family *Yaniellaceae* has been transferred to the *Micrococcaceae* and is not used here (Yassin et al., 2011). A second subclade encompasses the families *Beutenbergiaceae*, *Bogoriellaceae*, *Cellulomonadaceae*, *Promicromonosporaceae*, *Rarobacteraceae*, *Ruaniaceae*, and *Sanguibacteraceae*. The third subclade comprises the families *Dermacoccaceae*, *Dermatophilaceae*, and *Intrasporangiaceae*, which appears to be paraphyletic (Figure 12).

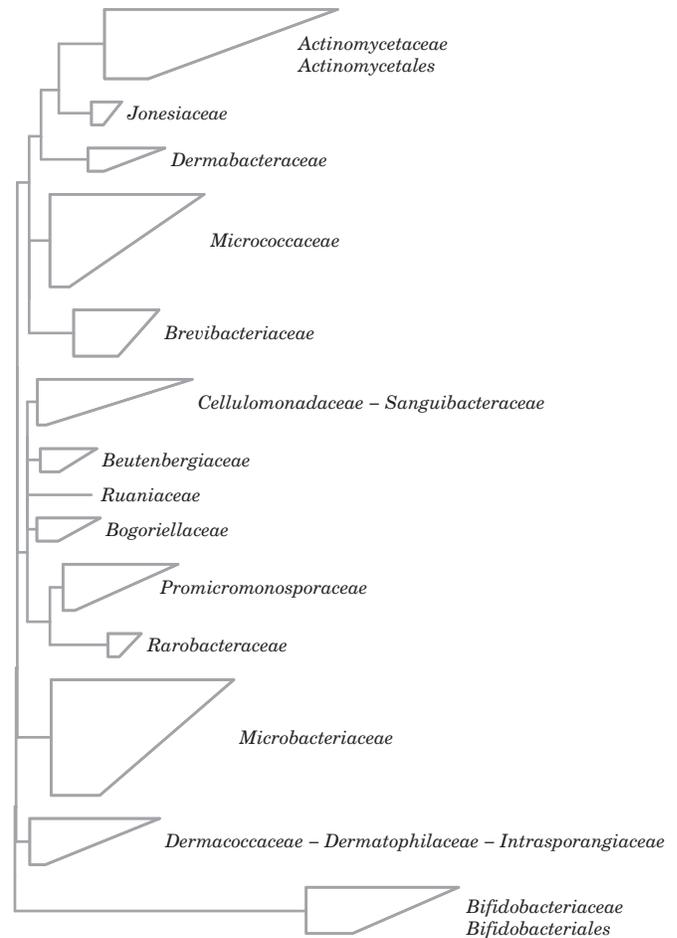


FIGURE 9. Overview of the families of the order *Micrococcales*. Analyses were performed as described for Figure 1.

The family *Microbacteriaceae* and the order *Bifidobacteriales* represent the two remaining subclades. Zhi et al. (2009) also found evidence for the first three subclades, albeit without bootstrap support. However, the associations with *Actinomycetales* and *Bifidobacteriales* were not reproduced. Thus, in the absence of additional evidence, the biological significance of this clade and its constituent subclades remain uncertain.

Family *Micrococcaceae*

Regardless of the complex phylogeny between the families in the order, the family *Micrococcaceae* is well-defined in rRNA gene trees (Figure 10). It includes all the genera that were classified within this family in the previous road map except for *Stomatococcus*, which has since been reclassified to the genus *Rothia* (Collins et al., 2000; Garrity et al., 2005). In addition, four genera have been added, including *Acaricomes*, *Yaniella*, *Zhihengliuella*, and the recently described *Sinomonas* (Zhou et al., 2009).

The genus *Micrococcus* forms a subclade within the family that is closely related to the genus *Citricoccus*. This relationship is supported by similarities in the cell-wall composition, major fatty acids, and polar lipids, although significant differences are present in the menaquinone composition (Busse, 2012). The genus *Micrococcus* comprises the type species *Micrococcus*

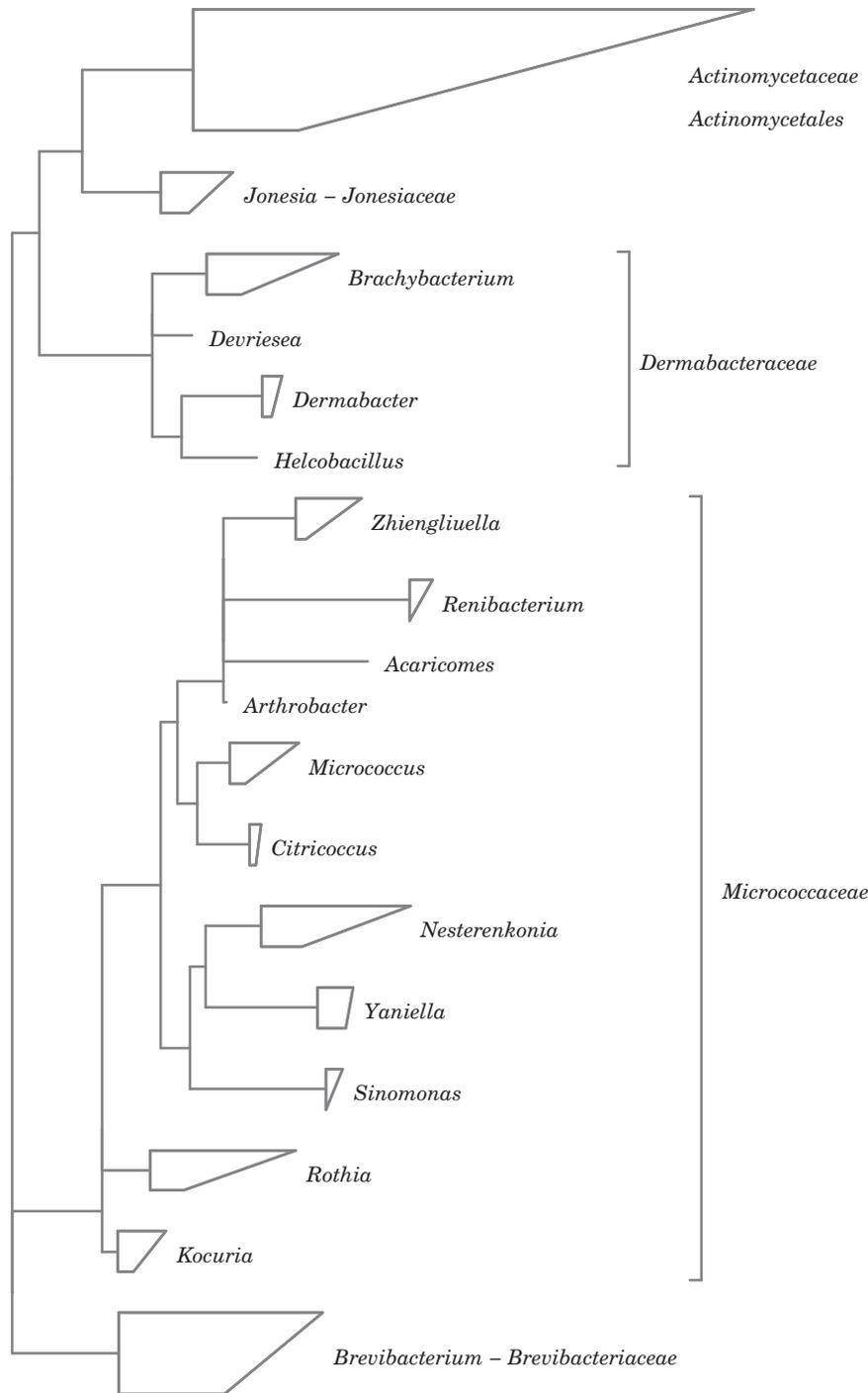


FIGURE 10. Genera of the families *Brevibacteriaceae*, *Dermabacteraceae*, *Jonesiaceae*, and *Micrococcaceae* of the order *Micrococcales*. Analyses were performed as described for Figure 1.

luteus and five closely related species *Micrococcus antarcticus*, *endophyticus*, *flavus*, *lylae*, and *yunnanensis*.

In rRNA gene trees, the monospecific genus *Acaricomus* (type species *Acaricomus phytoseiuli*) is closely related to *Arthrobacter sanguinis* within the large radiation of *Arthrobacter* species (see below). However, chemotaxonomic data which might support this relationship are not available, and it remains unproven (Busse et al., 2012).

The rRNA gene tree of the genus *Arthrobacter* is complex with many short branches and multifurcations that are difficult to resolve. Moreover, the genera *Acaricomus*, *Renibacterium*, and *Zhiengliuella* appear within the radiation that includes the type species *Arthrobacter globiformis*, making the genus *Arthrobacter* paraphyletic (Figure 10). Reclassification of many *Arthrobacter* species may be necessary in the future to reduce the diversity of the genus. In addition, some species are more closely affiliated

with type species of other genera in the family *Micrococcaceae* and should be reclassified on those grounds.

A combination of rRNA gene sequence similarity and chemotaxonomic features have been used to further classify *Arthrobacter* species into four “rRNA clusters”, five “subclades” and two “groups” (Busse et al., 2012). The rRNA clusters comprise species with similar chemotaxonomic features and high rRNA gene sequence similarity that do not form a discrete clade in the phylogenetic trees. rRNA cluster 1 includes the type species *Arthrobacter globiformis* and *Arthrobacter humicola*, *oryzae*, and *pascens*. rRNA cluster 2 includes *Arthrobacter aureus*, *histidinovorans*, *ilicis*, *nicotinovorans*, *nitroguajacolicus*, and *ureafaciens*. rRNA cluster 3 includes *Arthrobacter chlorophenolicus*, *defluvi*, *niigatensis*, *oxydans*, *phenanthrenivorans*, *polychromogenes*, *scleromae*, and *sulfonivorans*. rRNA cluster 4 includes *Arthrobacter ardleyensis*, *arilaitensis*, *bergerei*, *creatinolyticus*, *mysorens*, *nicotianae*, *protophormiae*, *rhombi*, *solii*, and *uratoxydans*.

The rRNA subclades comprise species with similar chemotaxonomic features that form discrete clades in the rRNA gene phylogenetic trees. Subclade I comprises *Arthrobacter antarcticus*, *gangotriensis*, *keruelensis*, *psychrophenicus*, and *sulfureus*. Subclade II comprises *Arthrobacter agilis*, *flavus*, *parietis*, *subterraneus*, *tecti*, and *tumbae*. Subclade III comprises *Arthrobacter citreus*, *gandavensis*, *korensis*, and *luteolus*. Subclade IV comprises *Arthrobacter alpinus*, *psychrochitiniphilus*, *psychrolactophilus*, and *stackebrandtii*. Subclade V comprises *Arthrobacter albidus* and *echigonensis* as well as *Sinomonas atrocyanea* and *flava*. This subclade is unrelated to the other species of *Arthrobacter* (Figure 10). Thus, reclassification of *Arthrobacter albidus* and *echigonensis* within the genus *Sinomonas* appears warranted.

The groups encompass species with similar chemotaxonomic properties that do not necessarily possess high rRNA gene sequence similarity. Group 1 comprises *Arthrobacter castelli*, *monumenti*, and *pigmenti*. Group 2 comprises *Arthrobacter albus* and *cumminsii*. In rRNA gene trees, this latter group is affiliated with the clade containing the genera *Nesterenkonia*, *Sinomonas*, and *Yaniella*. Possibly, they represent a novel genus within this clade. Lastly, not all described species could be classified within this scheme, including *Arthrobacter alcaliphilus*, *crystallopoietes*, *methylotrophus*, *nasiphocae*, *ramosus*, *roseus*, *russicus*, *sanguinis*, and *woluwensis*. In addition, the sequence of the rRNA gene of *Arthrobacter viscosus* suggests that it is closely related to *Rhizobium* and misclassified within *Arthrobacter* (Heyrman et al., 2005).

The genus *Citricoccus* is closely related to the genus *Micrococcus* in rRNA gene trees. It comprises the type species *Citricoccus muralis* and the closely related species *Citricoccus alkalitolerans*, *parietis*, and *zhacaiensis*.

The genus *Kocuria* represents one of the deepest lineages in the family *Micrococcaceae*. The genus comprises four clades. The first contains the type species *Kocuria rosea* as well as *Kocuria aegyptia*, *flava*, *himachalensis*, *polaris*, and *turfanensis*. The second clade is closely related and comprises *Kocuria halotolerans*, *korensis*, and *kristinae*, as well as the genus *Rothia*. The third clade includes only *Kocuria palustris*. The last clade appears as the deepest lineage in the family and comprises *Kocuria atrinae*, *cariphila*, *gwangalliensis*, *marina*, *rhizophila*, and *varians*. However, the biological significance of these clades is not currently supported by chemotaxonomic or other evidence, so their importance is not yet certain.

The genus *Nesterenkonia* is in a clade containing the genera *Sinomonas* and *Yaniella* and the *Arthrobacter* species *Arthrobacter albus* and *cumminsii*. The genus contains two subclades. The first comprises the type species *Nesterenkonia halobia* and *Nesterenkonia aethiopica*, *alba*, *flava*, *halophila*, *lacusekhoensis*, and *xinjiangensis*. The second, closely related subclade comprises *Nesterenkonia halotolerans*, *jeotgali*, *lutea*, and *sandarakina*. Although the chemotaxonomic and physiological properties of the two subclades are very similar, only members of this second subclade possess peptidoglycan containing L-Lys–Gly–D-Asp (Stackebrandt, 2012b). In the first subclade, the peptidoglycan contains L-Lys–Gly–D-Glu or L-Lys–D-Glu.

The monospecific genus *Renibacterium* (type species *Renibacterium salmoninarum*) is related to *Arthrobacter russicus* and *Arthrobacter* Subclade IV, which includes *Arthrobacter psychrolactophilus*, *stackebrandtii*, and *psychrochitiniphilus*. Differences in the menaquinone and peptidoglycan composition of *Renibacterium* and the *Arthrobacter* species do not provide support for this affiliation, although it is possible that *Renibacterium* was derived from an *Arthrobacter* ancestor by changes in these and other characters.

The genus *Rothia* includes a well-defined clade composed of the type species *Rothia dentocariosa* and *Rothia aerea*, *amarae*, *mucilaginoso*, *nasimurium*, and *terrae*. These taxa are also related to some species of *Kocuria*.

The genus *Sinomonas* comprises the type species *Sinomonas flava* and *Sinomonas atrocyanea*. In rRNA gene trees, it is affiliated with the clade containing the genera *Nesterenkonia*, *Yaniella*, and the *Arthrobacter* group 2 species *Arthrobacter albus* and *cumminsii*.

The genus *Yaniella* contains the type species *Yaniella halotolerans* and *Yaniella flava*. Although originally classified in its own family (Li et al., 2008), the rRNA gene trees calculated here suggest it is closely related to *Nesterenkonia*, *Sinomonas*, and *Arthrobacter* group 2 species *Arthrobacter albus* and *cumminsii*. This conclusion is consistent with similarities in cell wall, menaquinone and phospholipid compositions (Yassin et al., 2011). However, the DNA G+C content is quite different, 53–58 mol% in *Yaniella* and 64–72 mol% in *Nesterenkonia*.

The genus *Zhihengliuella* comprises the type species *Zhihengliuella halotolerans* and *Zhihengliuella alba* and is closely related to the subclades of *Arthrobacter*. Presumably, this relationship reflects the heterogeneity of the genus *Arthrobacter* rather than the need for reclassification of the genus *Zhihengliuella*.

Family *Beutenbergiaceae*

This family comprises the monospecific genera *Beutenbergia* (type species *Beutenbergia cavernae*), *Miniimonas* (type species *Miniimonas arenae*), *Salana* (type species *Salana multivorans*), and *Serinibacter* (type species *Serinibacter salmoneus*) (Figure 11). When initially proposed, the family also included the genus *Georgenia* (Zhi et al., 2009). However, subsequent analyses led to the reclassification of this genus into the family *Bogoriellaceae* (Hamada et al., 2009).

Family *Bogoriellaceae*

Initially a monogeneric family, this taxon has been emended to include the genus *Georgenia* (Hamada et al., 2009; Stackebrandt and Schumann, 2000). Currently, it comprises the monospecific

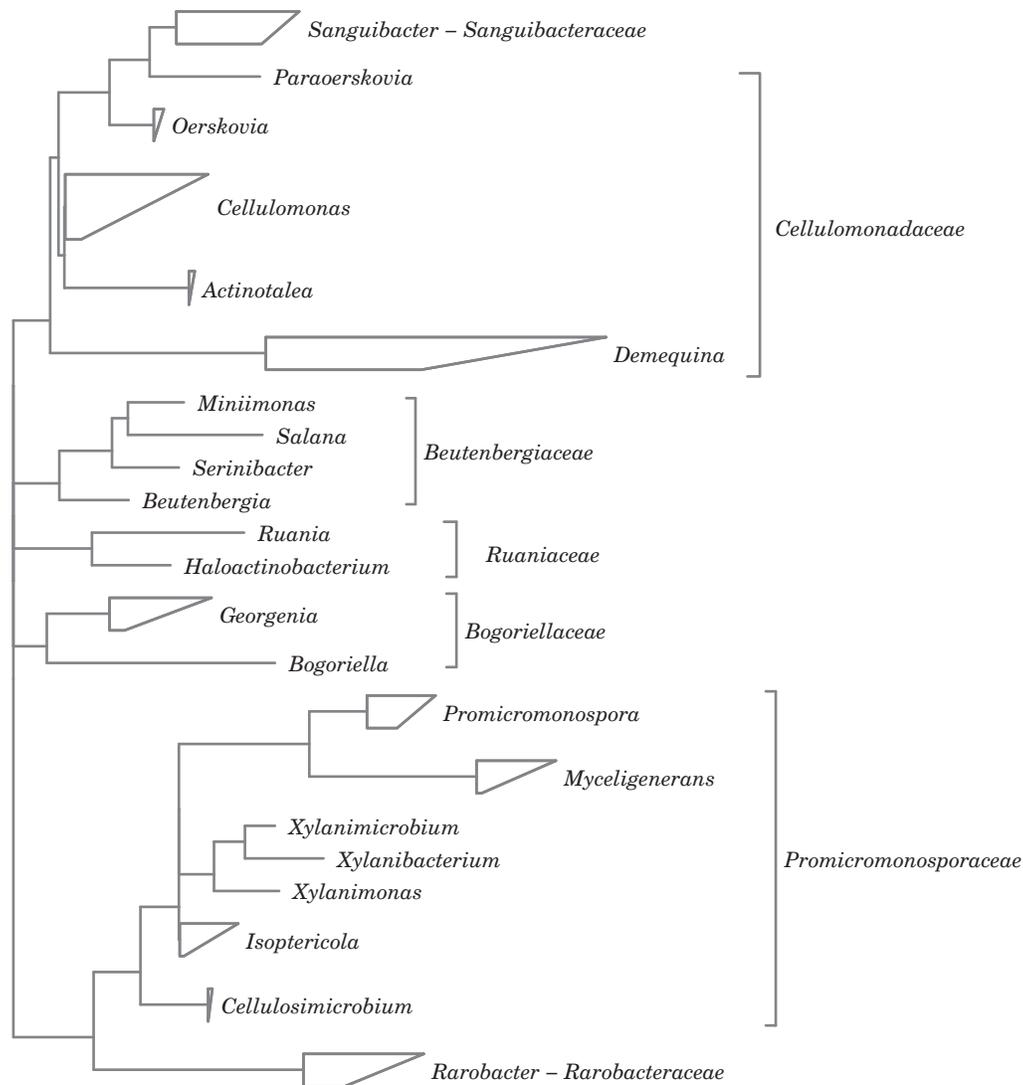


FIGURE 11. Genera of the Beutenbergiaceae, Bogoriellaceae, Cellulomonadaceae, Promicromonosporaceae, Rarobacteraceae, Ruaniaceae, and Sanguibacteraceae of the order Micrococcales. Analyses were performed as described for Figure 1.

genus *Bogoriella* (type species *Bogoriella caseilytica*) and *Georgenia muralis* (type species), *ruanii*, and *thermotolerans*.

Family Brevibacteriaceae

This monogeneric family is well separated from other members of the order *Micrococcales* in rRNA gene trees (Figure 9). The genus *Brevibacterium* contains four clades. The first clade comprises the type species *Brevibacterium linens* and *Brevibacterium antiquum*, *aurantiacum*, *avium*, *casei*, *celere*, *epidermidis*, *iodinum*, *marinum*, *oceanii*, *permense*, *picturae*, *sandarakinum*, and *sanguinis*. The second clade comprises *Brevibacterium luteolum* and *otitidis*. The third clade comprises *Brevibacterium massiliense*, *mcbrillneri*, *paucivorans*, and *ravenspurghense*. The fourth clade comprises *Brevibacterium album*, *pityocampae*, and *samyangense*. Lastly, on the basis of unpublished rRNA gene sequences, the species *Brevibacterium halotolerans* and *frigoritolerans* appear to be misclassified and represent strains of *Bacillus*.

Family Cellulomonadaceae

The family *Cellulomonadaceae* was proposed by Stackebrandt and Prauser (1991) to include the genera *Cellulomonas*, *Jonesia*, *Oerskovia*, and *Promicromonospora*. Subsequent proposals elevated the genera *Jonesia* and *Promicromonospora* to the family level (Rainey et al., 1995; Stackebrandt et al., 1997). Thus, in the previous road map (Garrity et al., 2005), the family *Cellulomonadaceae* comprised the genera *Cellulomonas*, *Oerskovia*, and *Tropheryma*. Since that time, three subsequently described genera have been added (see below). In the current rRNA gene analyses, this family is paraphyletic, and the family *Sanguibacteraceae* appears as a specific relative of *Oerskovia* (Figure 11). This relationship is consistent with similarities in cell-wall composition and in the menaquinone and fatty acid profiles of these groups (Stackebrandt and Schumann, 2012). In addition, *Tropheryma* is not closely related to the other genera classified in the family and

appears as a deep lineage related to the family *Microbacteriaceae* (Figure 13). However, because of the low sequence similarities to *Microbacteriaceae* and differences in DNA G+C content (nothing else is known of its chemotaxonomic properties), the genus *Tropheryma* may warrant reclassification into a novel family.

The genus *Cellulomonas* appears as multiple short branches at the base of the family tree and hence is not well resolved into clades. It comprises the type species *Cellulomonas flavigena* and *Cellulomonas aerilata*, *biazotea*, *bogoriensis*, *cellulasea*, *chitinilytica*, *compoti*, *denverensis*, *fimi*, *gelida*, *hominis*, *humilata*, *iranensis*, *persica*, *terrae*, *uda*, and *xylanilytica*.

The monospecific genus *Actinotalea* (type species *Actinotalea fermentans*) was formed by reclassification of the *Cellulomonas* species based upon its unusual menaquinone composition [MK-10(H₂)] and low rRNA gene sequence similarities.

In rRNA gene trees, the genus *Demequina* is clearly separated from other members of the family (Figure 11). It comprises the type species *Demequina aestuarii* and *Demequina lutea*.

The genus *Oerskovia* forms a subclade within the family *Cellulomonadaceae* that includes the genus *Paraoerskovia* and the family *Sanguibacteraceae*. It comprises the type species *Oerskovia turbata* and three closely related species *Oerskovia enterophila*, *jenensis*, and *paurometabola*.

The monospecific genus *Paraoerskovia* (type species *Paraoerskovia marina*) is related to the genus *Oerskovia* and the family *Sanguibacteraceae*.

Although still currently classified within the family *Cellulomonadaceae*, the monospecific genus *Tropheryma* (type species *Tropheryma whipplei*) appears to warrant reclassification.

Family *Dermabacteraceae*

This family was proposed by Stackebrandt et al. (1997) to include the genera *Dermabacter* and *Brachybacterium* (Stackebrandt et al., 1997). This classification is unchanged apart for the addition of two monospecific genera, *Devriesea* (type species *Devriesea agamarum*) (Martel et al., 2008) and *Helcobacillus* (type species *Helcobacillus massiliensis*) (Renvoise et al., 2009), which were described after the deadline for inclusion in this volume. The members of this family that have been tested possess an unusual peptidoglycan type (A4γ), which contains *meso*-diaminopimelate and an interpeptide bridge of *D*-dicarboxylic amino acids. The family also contains the monospecific genus *Dermabacter* (type species *Dermabacter hominis*) and *Brachybacterium facium* (type species), *alimentarium*, *conglomeratum*, *fresconis*, *muris*, *nesterenkovi*, *paraconglomeratum*, *phenoliresistens*, *rhamnosum*, *sacelli*, *tyrofermentans*, and *zhongshanense*. These four genera form a well-defined clade that clusters with the families *Actinomycetaceae* and *Jonesiaceae* in the rRNA gene trees (Figure 10).

Family *Dermacoccaceae*

This family was proposed by Stackebrandt and Schumann (2000) to include the genera *Dermacoccus*, *Demetria*, and *Kytococcus* based upon analyses of rRNA genes. This classification was unchanged in the previous road map (Garrity et al., 2005) and subsequent analyses (Zhi et al., 2009). However, in the rRNA gene trees prepared for this volume, *Kytococcus* appears to be unrelated to the other members of the family and clusters instead with some genera from the family *Intrasporangiaceae*, which is also paraphyletic (Figure 12). However, comparison of chemotaxonomic markers does not support the reclassification of *Kytococcus*, which possesses completely unsaturated menaquinones and an

interpeptide bridge composed of L-Lys-D-Glu₂ (Stackebrandt, 2012a). While these features are not found elsewhere within the family *Dermacoccaceae*, they are also absent from the family *Intrasporangiaceae* (Kämpfer and Groth, 2012). Thus, the classification of *Kytococcus* has not been changed here.

The genus *Dermacoccus* comprises the type species *Dermacoccus nishinomiyaensis* and *Dermacoccus abyssi*, *barathri*, and *profundi*. It is closely related to the monospecific genus *Demetria* (type species *Demetria terrigena*). The species of *Kytococcus* form a separate and well-defined clade comprising the type species *Kytococcus sedentarius* and *Kytococcus aerolatus* and *schroeteri*.

Family *Dermatophilaceae*

The current family was proposed by Stackebrandt et al. (1997) and retained in the previous road map (Garrity et al., 2005). However, in the rRNA gene trees prepared for this volume, the relationship between *Dermatophilus* and *Kineosphaera*, the two genera in the family, is not well supported (Figure 12). Similarly, the physiological and chemotaxonomic properties of these genera are quite different, suggesting that this family may warrant re-examination (Stackebrandt, 2012c). The genus *Dermatophilus* comprises the type species *Dermatophilus congolensis* and *Dermatophilus chelonae*. The genus *Kineosphaera* comprises only the type species *Kineosphaera limosa*.

Family *Intrasporangiaceae*

In the original proposal, this family comprised the genera *Intrasporangium*, *Sanguibacter*, and *Terrabacter* (Stackebrandt et al., 1997). Subsequently, the genera *Janibacter* and *Terracoccus* were added, and *Sanguibacter* was moved to a new family (Stackebrandt and Schumann, 2000). The genera *Knoellia*, *Ornithinicoccus*, *Ornithinimicrobium*, “*Candidatus* Nostocoida”, and *Tetrasphaera* were then added in the previous version of the road map (Garrity et al., 2005). “*Candidatus* Nostocoida” was subsequently united with the genus *Tetrasphaera* (McKenzie et al., 2006). In the current road map, the family includes the remaining genera plus the genera *Arsenicicoccus*, *Fodinibacter*, *Humibacillus*, *Humihabitans*, *Kribbia*, *Lapillicoccus*, *Marihabitans*, *Oryzihumus*, *Phycoccus*, and *Serinicoccus*.

However, in the rRNA gene trees prepared for this volume, the family *Intrasporangiaceae* appears to be paraphyletic and comprises a major clade of genera closely related to the type genus *Intrasporangium*; a second clade consisting of the genera *Janibacter*, *Knoellia*, *Marihabitans*, and *Kytococcus* of the family *Dermacoccaceae*; a third clade composed of the genera *Ornithinicoccus*, *Ornithinimicrobium*, and *Serinicoccus*; and the genera *Arsenicicoccus* and *Kribbia*, each of which represent deep lineages unaffiliated with other genera (Figure 12). However, this alternative phylogeny is not strongly supported by other taxonomic evidence. As discussed above, chemotaxonomic data does not provide support for the reclassification of the genus *Kytococcus* with the *Intrasporangiaceae* genera in this clade. Moreover, the chemotaxonomic properties of most genera in the family appear relatively uniform. In contrast, while most of the family possesses diaminopimelate as the cell-wall diamino acid, the genera *Ornithinicoccus*, *Ornithinimicrobium*, and *Serinicoccus* possess ornithine (Kämpfer and Groth, 2012), providing some support for the biological significance of the third clade. Nevertheless, in the absence of additional evidence, the genera of the family *Intrasporangiaceae* have not been reclassified at this time.

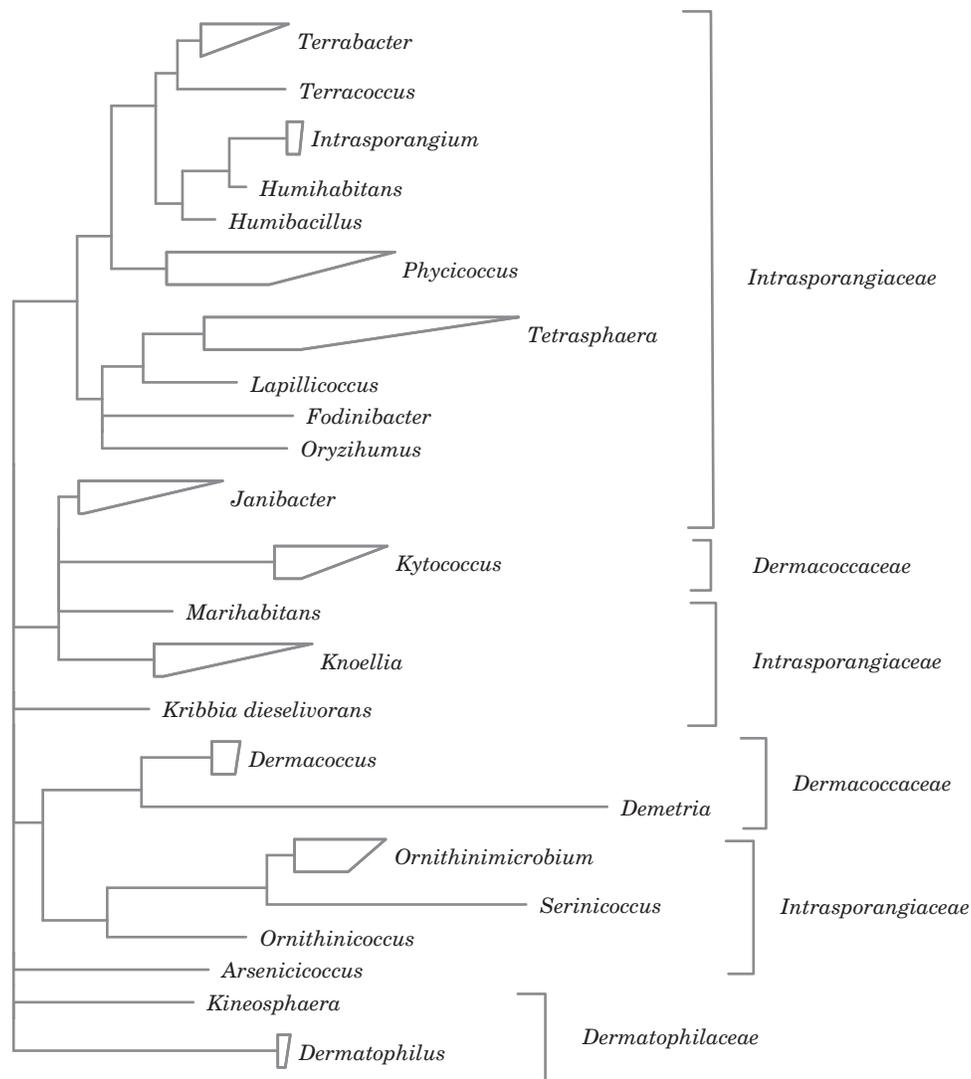


FIGURE 12. Genera of the families *Dermacoccaceae*, *Dermatophilaceae*, and *Intrasporangiaceae* of the order *Micrococcales*. Analyses were performed as described for Figure 1.

The first clade observed in the rRNA gene trees comprises *Intrasporangium calvum*; *Fodinibacter luteus*; *Humibacillus xanthopallidus*; *Humihabitans oryzae*; *Lapillicoccus jejuensis*; *Oryzihumus leptocrescens*; *Phycococcus jejuensis* (type species), *aerophilus*, *big-eumensis*, and *dokdonensis*; *Terrabacter tumescens* (type species), *aerolatus*, *lapilli*, *terrae*, and *terrigena*; *Terracoccus luteus*; and *Tetrasphaera japonica* (type species), *australiensis*, *duodecadis*, *elongata*, *jenkinsii*, *remsis*, *vanveenii*, and *veronensis*. The second clade encompasses *Janibacter limosus* (type species), *anophelis*, *corallicola*, *hoylei*, *melonis*, and *terrae*; *Knoellia sinensis* (type species), *aerolata*, and *subterranea*; and *Marihabitans asiaticum*. The third clade consists of *Ornithinococcus hortensis*; *Ornithinimicrobium humiphilum* (type species), *kibberense*, and *pekingense*, and *Serinicoccus marinus*. Lastly, *Arsenicococcus bolidensis* (type species) and *Arsenicococcus piscis* and *Kribbia dieselivorans* do not appear to be affiliated with other genera.

Family *Jonesiaceae*

This family was proposed by Stackebrandt et al. (1997) to recognize the distinctiveness of the genus *Jonesia* (Rainey et al., 1995). This genus comprises the type species *Jonesia denitrificans* and *Jonesia quinghaiensis*. In the rRNA gene trees prepared for this volume, this taxon appears as a deep lineage specifically related to the order *Actinomycetales* (Figure 9).

Family *Microbacteriaceae*

This large family represents a distinct lineage within the order *Micrococcales* (Figure 9). In rRNA gene trees, the family contains some well-defined clades, as well as a number of genera which are not specifically related to any other genus (Figure 13). The clades include: *Microbacterium*, *Mycetocola*, *Okibacterium*, and *Plantibacter*; *Clavibacter*, *Cryobacterium*, and *Klugiella*; *Agromyces*

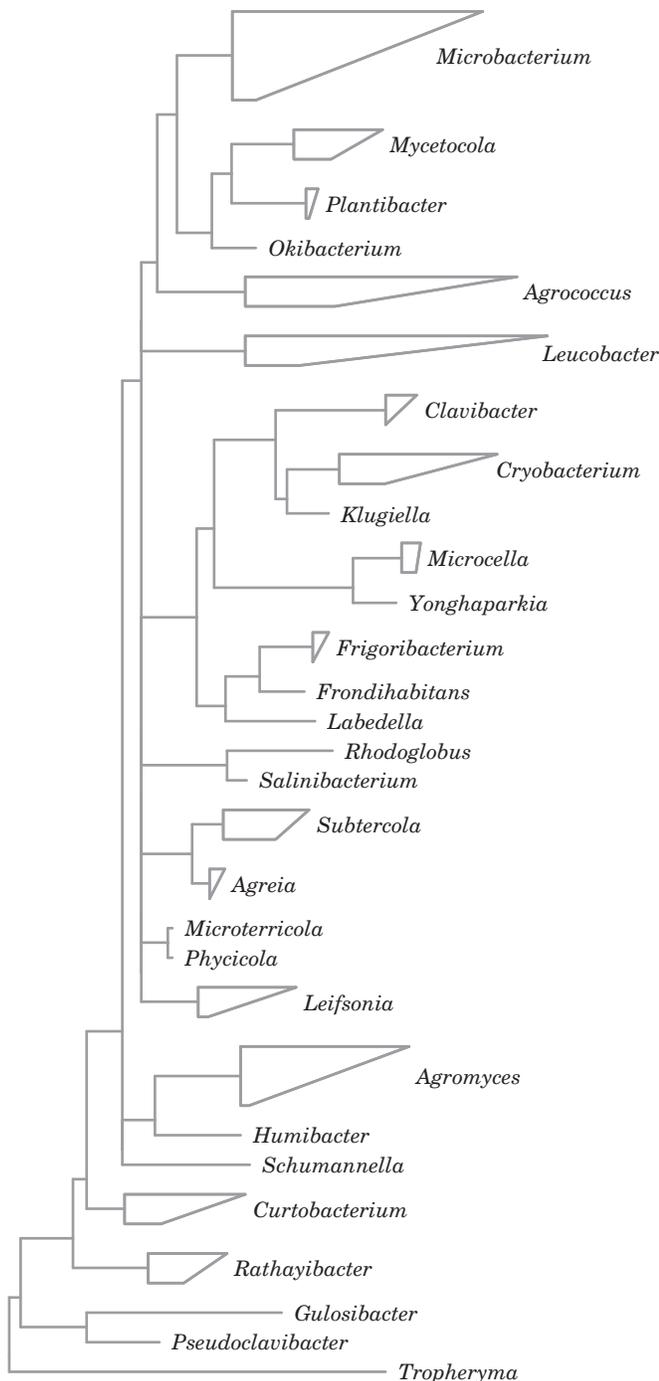


FIGURE 13. Genera of the family *Microbacteriaceae* and *Tropheryma* of the family *Cellulomonadaceae* from the order *Micrococcales*. Analyses were performed as described for Figure 1.

and *Humibacter*; *Agreia* and *Subtercola*; *Gulosibacter* and *Pseudoclavibacter*; *Microcella* and *Yonghaparkia*; *Microterricola* and *Phycicola*; and *Rhodoglobus* and *Salinibacterium*. Although assigned to the family *Cellulomonadaceae*, the genus *Tropheryma* appears as a deep lineage related to this family.

The large genus of *Microbacterium* comprises many closely related species. The type species *Microbacterium lacticum* forms a well-defined clade with *Microbacterium aoyamense*, *aurum*,

awajiense, *deminutum*, *flavum*, *fluvii*, *hatanonis*, *invictum*, *koreense*, *lacus*, *pumilum*, *pygmaeum*, *schleiferi*, *terregens*, and *terricola*. In addition, specific clusters of the following species are formed: *Microbacterium gubbeenense*, *indicum*, and *luticocti*; *Microbacterium aurantiacum*, *chocolatum*, and *kitamiense*; *Microbacterium arborescens* and *imperiale*; and *Microbacterium aquimaris* and *halophilum*. However, the remaining species do not appear specifically related to any other species in rRNA gene trees. These taxa include *Microbacterium aerolatum*, *agarici*, *arabinogalactanolyticum*, *barkeri*, *binotii*, *dextranolyticum*, *esteraromaticum*, *flavescens*, *foliorum*, *ginsengisoli*, *halotolerans*, *hominis*, *humi*, *hydrocarbonoxydans*, *insulae*, *keratanolyticum*, *ketosireducens*, *kribbense*, *laevaniformans*, *liquefaciens*, *luteolum*, *marinilacus*, *maritypicum*, *natoriense*, *oleivorans*, *oxydans*, *paludicola*, *paraoxydans*, *phyllosphaerae*, *profundi*, *pseudoresistens*, *resistens*, *saperdae*, *sediminicola*, *solis*, *terrae*, *testaceum*, *thalassium*, *trichothecenolyticum*, *ulmi*, and *xylanilyticum*.

The genus *Agreia* comprises the type species *Agreia bicolorata* and *Agreia pratensis*. It appears to be related to the genus *Subtercola*.

The genus *Agrococcus* includes the type species *Agrococcus jenkinsii* and three closely related species of *Agrococcus baldri*, *citreus*, and *lahaulensis*. The genus also contains three more distantly related species, *Agrococcus casei*, *jejuensis*, and *versicolor*.

The genus *Agromyces* encompasses the type species *Agromyces ramosus* and the closely related species *Agromyces albus*, *allii*, *aurantiacus*, *brachium*, *cerinus*, *fucosus*, *hippuratus*, *humatus*, *italicus*, *lapidis*, *luteolus*, *mediolanus*, *neolithicus*, *rhizosphaerae*, *salentinus*, *subbeticus*, *terreus*, and *ulmi*. It also appears to be related to the genus *Humibacter*.

The monospecific genus of *Clavibacter* (type species *Clavibacter michiganensis*) appears to be related to the genera *Cryobacterium* and *Klugiella*.

The genus *Cryobacterium* is formed by the type species *Cryobacterium psychrophilum* and the closely related psychrophilic species *Cryobacterium psychrotolerans* and *roopkundense*. The mesophilic species *Cryobacterium mesophilum* forms a deeper lineage related to *Klugiella xanthotipulae*.

The genus *Curtobacterium* represents a deep lineage in the family *Microbacteriaceae* and comprises the type species *Curtobacterium citreum* and the closely related species *Curtobacterium ammoniigenes*, *flaccumfaciens*, *herbarum*, *luteum*, *plantarum*, and *pusillum*. The species *Curtobacterium ginsengisoli* represents a deeper lineage in this genus.

The genus *Frigoribacterium* comprises the type species *Frigoribacterium faeni* and *Frigoribacterium mesophilum*. Although the rRNA gene sequences are similar, these species do not form a distinct clade independent of closely related genera. The conclusion that *Frigoribacterium mesophilum* may represent a new genus is supported by differences in the cell-wall amino acids. *Frigoribacterium mesophilum* peptidoglycan contains 2,4-diaminobutyric acid, alanine, glycine, glutamate, and lysine (Dastager et al., 2008), whereas that of *Frigoribacterium faeni* contains alanine, glycine, homoserine, and D-lysine (Kämpfer et al., 2000). Likewise, *Frigoribacterium mesophilum* lacks the fatty acid C_{15:0} anteiso dimethylacetal, which is characteristic of *Frigoribacterium faeni*.

The monospecific genus *Frondihabitans* (type species *Frondihabitans australicus*) is related to *Frigoribacterium faeni*.

The monospecific genus *Gulosibacter* (type species *Gulosibacter molinativorax*) represents a deep lineage in the family along with the genus *Pseudoclavibacter*.

The monospecific genus *Humibacter* (type species *Humibacter albus*) is related to the genus *Agromyces*.

The monospecific genus *Klugiella* (type species *Klugiella xanthotipulae*) is related to the genera *Cryobacterium* and *Clavibacter* and was described after the deadline for inclusion in this volume (Cook et al., 2008).

The monospecific genus *Labeledella* (type species *Labeledella gwakjiensis*) represents a distinct lineage within the family *Microbacteriaceae*.

The genus *Leifsonia* includes the type species *Leifsonia aquatica* and some closely related species: *Leifsonia lichenia*, *naganoensis*, *poae*, *shinshuensis*, and *xyl*. In addition, other species are included in this genus, each of which appear to represent a distinct lineage within the family and may thereby warrant reclassification (Evtushenko, 2012b). These include *Leifsonia antarctica*, *bigeumensis*, *ginsengi*, *kafniensis*, *kribbensis*, and *pindariensis*. Lastly, two species, *Leifsonia aurea* and *rubra* appear to be closely related to the genus *Rhodoglobus*.

The genus *Leucobacter* comprises the type species *Leucobacter komagatae* and the closely related species *Leucobacter albus*, *alluvii*, *aridicollis*, *chironomi*, *chromiireducens*, *iarisus*, *luti*, and *tardus*. This genus represents a distinct lineage within the family *Microbacteriaceae*.

The genus *Microcella* comprises the type species *Microcella putealis* and *Microcella alkaliphila* and forms a clade with *Yonghaparkia*.

The monospecific genus *Microterricola* (type species *Microterricola viridarii*) is closely related to *Phycicola gilvus*.

The genus *Mycetocola* comprises the type species *Mycetocola saprophilus* and the closely related *Mycetocola lacteus* and *tolaasinivorans*. The remaining species, *Mycetocola reblochoni*, forms a deeper lineage of the genus. This genus also forms a larger clade with the genera *Okibacterium* and *Plantibacter* (Figure 12).

The monospecific genus *Okibacterium* (type species *Okibacterium fritillariae*) forms a larger clade with the genera *Mycetocola* and *Plantibacter*.

The monospecific genus *Phycicola* (type species *Phycicola gilvus*) is closely related to *Microterricola viridarii*.

The genus *Plantibacter*, which contains the type species *Plantibacter flavus* and the closely related *Plantibacter auratus*, forms a larger clade with the genera *Mycetocola* and *Okibacterium*.

The genus *Pseudoclavibacter* comprises the type species *Pseudoclavibacter helvolus* and *Pseudoclavibacter soli*. This lineage represents one of the deepest in the family *Microbacteriaceae* along with the genus *Gulosibacter*. Moreover, species of the genus *Zimmermannella*, *Zimmermannella alba*, *bifida*, and *faecalis*, are also in this clade. However, the genus *Zimmermannella* is a later homotypic synonym of *Pseudoclavibacter*, and is not used in this volume. Therefore, these remaining species should be reclassified.

The genus *Rathayibacter* comprises the type species *Rathayibacter rathayi* and the closely related species *Rathayibacter caricis*, *festucae*, *iranicus*, *toxicus*, and *tritici*. The genus forms a distinct and deep clade in the family *Microbacteriaceae*.

The monospecific genus *Rhodoglobus* (type species *Rhodoglobus vestalii*) is closely related to *Leifsonia aurea* and *rubra*.

The genus *Salinibacterium* includes the type species *Salinibacterium amurskyense* and *Salinibacterium xinjiangense*, both of which are closely related to *Rhodoglobus vestalii*.

The monospecific genus *Schumannella* (type species *Schumannella luteola*) represents a deep lineage in the family *Microbacteriaceae* but was described after the deadline for inclusion in this volume (An et al., 2008).

The genus *Subtercola*, which comprises the type species *Subtercola boreus* and *Subtercola frigoramans*, is closely related to the genus *Agreia*.

The monospecific genus *Yonghaparkia* (type species *Yonghaparkia alkaliphila*) is closely related to *Microcella*.

Family *Promicromonosporaceae*

In rRNA gene trees, this family appears as a well-defined clade related to the family *Rarobacteraceae* (Figure 11). While this relationship is not observed in other analyses of the rRNA gene (Stackebrandt and Schumann, 2000; Zhi et al., 2009), similarities in the cell walls, fatty acids, and menaquinones provide some support. For instance, the *Promicromonosporaceae* possess cell-wall type A4 α composed of L-Lys, D-Glu or D-Asp, L-Ala or L-Ser or L-Thr (Schumann and Stackebrandt, 2012), whereas the *Rarobacteraceae* have the A4 β chemotype composed of L-Orn, D-Glu, L-Ala, and D-Ala (and D-Ser) (Kämpfer, 2012b). Members of each family are rich in iso- and anteiso-branching fatty acids with C_{15:0} anteiso predominating and have MK-9 (H₄) as a major, if not predominant, menaquinone. Thus, this relationship warrants further investigation.

Currently, the family *Promicromonosporaceae* comprises seven genera. The genus *Promicromonospora* contains the type species *Promicromonospora citrea* and the closely related *Promicromonospora aerolata*, *kroppenstedtii*, *sukumoe*, *umidemergens*, and *vindobonensis*. In rRNA gene trees, *Promicromonospora flava* represents a deep branch of this lineage. However, phenotypic similarities between it and the other species do not provide strong support for reclassification as a novel genus (Jiang et al., 2009).

The genus *Cellulosimicrobium* comprises the type species *Cellulosimicrobium cellulans* and two closely related species *Cellulosimicrobium funkei* and *terreum*.

In rRNA gene trees, the genus *Isoptericola* is represented by a cluster of very similar sequences which do not form a distinct clade within the tree. Nevertheless, in the absence of additional evidence, phenotypic properties support classification within a single genus. The genus comprises the type species *Isoptericola variabilis* and *Isoptericola dokdomensis*, *halotolerans*, *hypogeous*, and *jiangsuensis*.

The genus *Myceligenans*, which contains the type species *Myceligenans xiligouense* and *Myceligenans crystallogenes*, is closely related to the genus *Promicromonospora*.

The monospecific genus *Xylanibacterium* (type species *Xylanibacterium ulmi*) forms a clade with the monospecific genera *Xylanimicrobium* (type species *Xylanimicrobium pachnodae*) and *Xylanimonas* (type species *Xylanimonas cellulolytica*) (Figure 11).

Family *Rarobacteraceae*

This family comprises the type species *Rarobacter faecitabidus* and *Rarobacter incanus*. It appears to be closely related to the family *Promicromonosporaceae* (Figure 11).

Family *Ruaniaceae*

This family comprises two monospecific genera, *Ruania* (type species *Ruania albidiflava*) and *Haloactinobacterium* (type species

Haloactinobacterium album) which form a distinct clade within the order *Micrococcales* (Figure 11).

Family *Sanguibacteraceae*

Although it forms a distinct clade in some analyses (Stackebrandt and Schumann, 2000; Zhi et al., 2009) this family is closely related to the family *Cellulomonadaceae* in rRNA gene trees prepared here, especially the genera *Oerskovia* and *Paraoerskovia* (Figure 11). This relationship is consistent with similarities in the cell-wall composition and menaquinone and fatty acid profiles (Stackebrandt and Schumann, 2012). If supported by additional evidence, reclassification of these genera might be warranted. The family comprises the type genus and species *Sanguibacter keddiei* and the closely related species *Sanguibacter antarcticus*, *inulinus*, *marinus*, *solii*, and *suarezii*.

Order “*Micromonosporales*” and family *Micromonosporaceae*

This order is formed by elevation of the suborder *Micromonosporineae* (Stackebrandt et al., 1997) and encompasses a single family *Micromonosporaceae*. In the 16S rRNA gene trees prepared for this volume, the order “*Glycomycetales*” appears as a long branch specifically related to the genus *Actinocatenispora*, which itself is a deep branch within the order “*Micromonosporales*” (Figure 8). While some chemotaxonomic and other phenotypic properties tend to support this association, the relationship is considered tentative at this time (see above). In addition, while most genera appear as deep branches radiating from the base of the family tree, four clades are observed. These include the genera *Micromonospora*, *Catellatospora*, and *Planosporangium*; *Catelliglobospora* and *Hamadaea*; *Couchioplanes*, *Krasilnikovia*, and *Pseudosporangium*; and *Dactylosporangium* and *Virgisporangium*. However, in the absence of additional evidence, the biological significance of these clades is uncertain.

In the rRNA gene trees prepared for this volume, the genus *Micromonospora* is represented by many short branches that appear throughout the family tree. The genus does not form a distinct clade and other genera are interspersed within the *Micromonospora* sequences. The type species *Micromonospora chalcea* appears in the clade containing *Actinoplanes*, *Catellatospora*, *Longispora*, and *Planosporangium* species (Figure 8). Other *Micromonospora* species in this clade include *Micromonospora aurantiaca*, *carbonacea*, *chokoriensis*, *coxensis*, *halophytica*, *kraibensis*, *lupini*, *matsumotoense*, *mirobragensis*, *purpureochromogenes*, *rifamycinica*, *saelicesensis*, and *siamensis*. A second large group of *Micromonospora* species form a multifurcation at the base of the family tree. These include *Micromonospora auratinigra*, *chaiyaphumensis*, *chersina*, *citrea*, *coerulea*, *coriariae*, *eburnea*, *echinaurantiaca*, *echinofusca*, *echinospora*, *endolithica*, *fulvivivida*, *inositola*, *inyonensis*, *narathiwatensis*, *nigra*, *pallida*, *peucetia*, *rosaria*, *sagamiensis*, and *viridifaciens*. Three additional species are also at the base of the family tree but outside this cluster: *Micromonospora olivasterospora*, *pattaloongensis*, and *pisi*. In spite of the ambiguities of the rRNA gene trees, *gyrB*, *rpoB*, or *atpD* gene trees suggests *Micromonospora olivasterospora* is related to *Micromonospora carbonacea*. Likewise, in *gyrB* gene trees, *Micromonospora pattaloongensis*, *Micromonospora pisi* and *Polymorphospora rubra* form a group related to other *Micromonospora* species, a classification which is supported by similarities in their chemotaxonomy. Lastly, for the species *Micromonospora gallica*, the rRNA gene sequence

is not available and the type strain appears to have been lost. In contrast, most of the other genera in this family form well-defined clades.

The genus *Actinocatenispora* comprises the type species *Actinocatenispora thailandica* and *Actinocatenispora rupis* and *sera*. The genus represents a deep lineage in the family phylogenetic tree that is specifically related to the order “*Glycomycetales*” (Figure 8). Although these taxa share some similarities in cell-wall composition, this association is considered tentative at this time (see above).

The genus *Actinoplanes* comprises the type species *Actinoplanes philippinensis* and the closely related species *Actinoplanes auranticolor*, *campanulatus*, *capillaceus*, *conssettensis*, *couchii*, *cyaneus*, *deccanensis*, *derwentensis*, *digitatis*, *humidus*, *italicus*, *liguriensis*, *lobatus*, *missouriensis*, *palleronii*, *rectilineatus*, *regularis*, *sichuanensis*, *utahensis*, and *xinjiangensis*. This clade represents a deep lineage in the family. In the rRNA gene trees prepared for this volume, a second clade is also present that includes *Actinoplanes brasiliensis*, *durhamensis*, *ferrugineus*, *teichomyceticus*, *tereljensis*, and *toevenensis* and the monospecific genus *Planosporangium* (type species *Planosporangium flavigriseum*). This clade is specifically related to *Micromonospora chalcea*, the type species of the genus. *Actinoplanes globisporus* forms a third clade, which is a deep lineage in the family. Similar rRNA gene trees were generated by Ara et al. (2010), but not by Wiese et al. (2008) and Vobis et al. (2012). Although high levels of DNA hybridization between members of the second clade and *Actinoplanes globisporus* tend to support the significance of this clade (Ara et al., 2010), it is not strongly supported by chemotaxonomic or phenotypic markers and awaits confirmation by other methods (Vobis et al., 2012). Lastly, the rRNA gene sequence is unavailable for *Actinoplanes friuliensis*.

The genus *Asanoa* comprises the type species *Asanoa ferruginea* and *Asanoa iniomotensis* and *ishikariensis*. These closely related species represent a basal lineage in the family.

The genus *Catellatospora* comprises the type species *Catellatospora citrea* and *Catellatospora bangladeshensis*, *chokoriensis*, *coxensis*, and *methionotrophica*. These closely related species are specifically related to *Micromonospora chalcea*, the type species of the genus, in rRNA gene trees and possess similar chemotaxonomic features. However, their morphologies are very different.

The monospecific genus *Catelliglobospora* (type species *Catelliglobospora koreensis*) is related to the monospecific genus *Hamadaea* (type species *Hamadaea tsunoensis*) (Figure 8). These taxa were described after the deadline for inclusion in this volume and are not described further.

The genus *Catenuloplanes* forms a deep lineage in this family. It comprises the type species *Catenuloplanes japonicas* and *Catenuloplanes atrovinosus*, *castaneus*, *crispus*, *indicus*, *nepalensis*, and *niger*.

The monospecific genus *Couchioplanes* (type species *Couchioplanes caeruleus*) forms a clade with the monospecific genera *Krasilnikovia* (type species *Krasilnikovia cinnamomea*) and *Pseudosporangium* (type species *Pseudosporangium ferrugineum*) (Figure 8).

The genus *Dactylosporangium* comprises the type species *Dactylosporangium aurantiacum* and the closely related species *Dactylosporangium fulvum*, *matsuzakiense*, *roseum*, *thailandense*, and *vinaceum*. This genus forms a clade with *Virgisporangium ochraceum* (type species) and *Virgisporangium aurantiacum*.

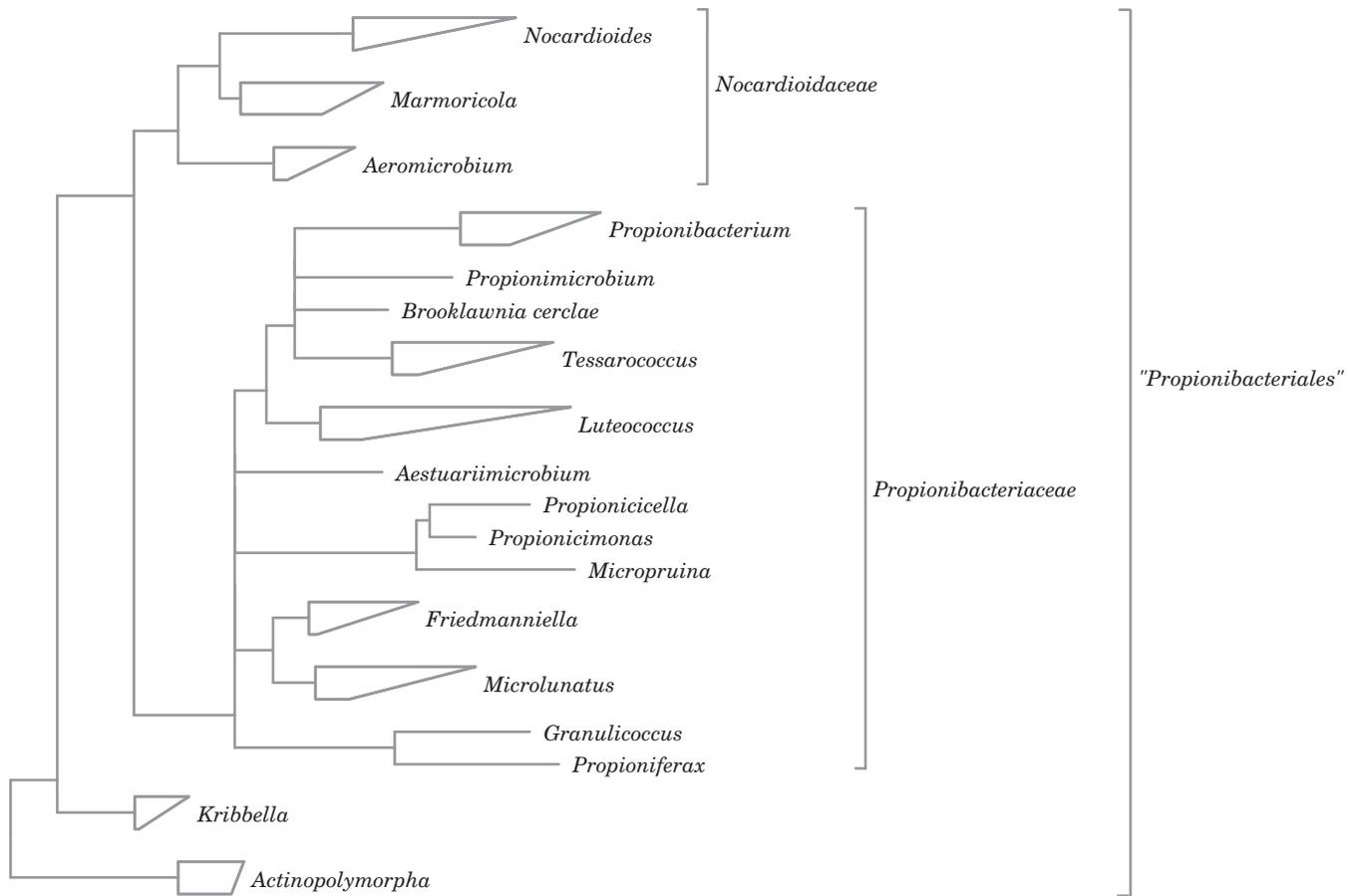


FIGURE 14. Genera and families of the order "Propionibacteriales". Analyses were performed as described for Figure 1.

The following genera represent additional deep lineages in the family tree: the monospecific genus *Longispora* (type species *Longispora albida*); *Luedemannella*, comprising the type species *Luedemannella helvata* and *Luedemannella flava*; *Pilimelia*, containing the type species *Pilimelia terevasa* and *Pilimelia anulata* and *columellifera*; the monospecific genus *Plantactinospora* (type species *Plantactinospora mayteni*); the monospecific genus *Polymorphospora* (type species *Polymorphospora rubra*); *Rugosimonospora*, encompassing the type species *Rugosimonospora acidiphila* and *Rugosimonospora africana*; *Salinispora*, comprising the type species *Salinispora arenicola* and *Salinispora tropica*; the monospecific genus *Spirilliplanes* (type species *Spirilliplanes yamanashiensis*); and *Verrucosispora*, comprising the type species *Verrucosispora gifhornensis* and *Verrucosispora lutea* and *sediminis*.

Order "Propionibacteriales"

This order is formed by elevation of the suborder *Propionibacteriineae* (Zhi et al., 2009). It forms a well-defined clade comprising the families *Propionibacteriaceae* and *Nocardioideae* (Figure 14). However, two genera currently classified within the family *Nocardioideae* appear as deep lineages outside of that family but still within the order (see below). The current taxonomy closely resembles that of the previous road map (Garrity et al., 2005) except that the genera *Friedmanniella* and *Micropruina*

have been transferred from the family *Nocardioideae* to the family *Propionibacteriaceae*. This reclassification is well supported by rRNA gene trees (Figure 14; Zhi et al., 2009) and chemotaxonomic markers (Schumann and Pukall, 2012).

Family *Propionibacteriaceae*

This family comprises 13 genera grouped within five clades (Figure 14). The first clade includes the genus *Propionibacterium*, which forms two of the five subclades recognizable in this clade. The first subclade comprises the type species *Propionibacterium freudenreichii* and *Propionibacterium acidifaciens*, *australiense*, and *cyclohexanicum*. The second subclade comprises *Propionibacterium acidipropionici*, *acnes*, *avidum*, *granulosum*, *jensenii*, *microaerophilum*, *propionicum*, and *thoenii*. While the 'classical' and 'dairy' *Propionibacterium* species are found in both subclades, the 'cutaneous' species *Propionibacterium acnes*, *avidum*, and *granulosum* are all in the second subclade (Patrick and McDowell, 2012). Moreover, *meso*-diaminopimelic acid is the dominant cell-wall diamino acid only in members of the first subclade, while *LL*-diaminopimelic acid is the dominant diamino acid in all tested species of the second subclade, observations which provide further support for the significance of these subclades. The third and fourth subclades comprise the monospecific genera *Brooklawnia cerclae* and *Propionimicrobium lymphophilum*,

respectively. The genus *Tessaracoccus* forms the fifth subclade and encompasses the type species *Tessaracoccus bendigoensis* and closely related species *Tessaracoccus flavescens* and *lubricantis*. The genus *Luteococcus* forms a deep branch of first clade and includes the type species *Luteococcus japonicus* and the closely related species *Luteococcus peritonei* and *sanguinis*.

The second clade comprises the genera *Friedmanniella* and *Microhynatus*. The genus *Friedmanniella* is composed of the type species *Friedmanniella antarctica* and the closely related species *Friedmanniella capsulata*, *lacustris*, *lucida*, *luteola*, *okinawensis*, *sagamiharensis*, and *spumicola*. The genus *Microhynatus* comprises the type species *Microhynatus phosphovorius* and the closely related species *Microhynatus aurantiacus*, *ginsengisoli*, *panaciterae*, and *soli*.

The monospecific genera *Granulicoccus* (type species *Granulicoccus phenolivorans*) and *Propioniferax* (type species *Propioniferax innocua*) form the third clade.

The monospecific genera *Micropruina* (type species *Micropruina glycogenica*), *Propionicicella* (type species *Propionicicella superfundia*), and *Propionicimonas* (type species *Propionicimonas paludicola*) form the fourth clade.

The monospecific genus *Aestuariimicrobium* (type species *Aestuariimicrobium kwangyangense*) represents an independent lineage within this family and the fifth clade.

Family Nocardioideaceae

In the previous road map (Garrity et al., 2005) and in the analyses of Zhi et al. (2009), this family included the genera *Nocardioideae*, *Actinopolymorpha*, *Aeromicrobium*, *Kribbella*, and *Marmoricola*. However, in the rRNA gene trees prepared for this volume, the family is paraphyletic with the genera *Actinopolymorpha* and *Kribbella*, appearing outside the taxon as deep lineages within the order “*Propionibacteriales*” (Figure 14). This relationship is quite robust and independent of whether phylum- or order-specific filters (or nucleotide positions) are used during tree construction and might suggest that these genera warrant reclassification. However, chemotaxonomic evidence does not provide strong support for either the current classification or a new one. On one hand, all five genera possess similar cell walls characterized by the tetrapeptide L-Ala-D-Glu-LL-diaminopimelate-D-Ala, a single glycine residue in the interpeptide bridge and similar fatty acids (Evtushenko, 2012a). On the other hand, teichoic acids have been found in all species of the genera *Nocardioideae* and *Aeromicrobium* that have been analyzed. In contrast, some *Kribbella* strains possess unusual phosphate-less acidic glycopolymers called teichulosonic acids and lack teichoic acids. Moreover, unlike the other genera, *Actinopolymorpha* forms branched fragmenting mycelia. Thus, in the absence of strong support for the reclassification of the genera *Actinopolymorpha* and *Kribbella*, these taxa are retained in this family at this time.

The genus *Nocardioideae* comprises a large clade of species closely related to the type species, as well as a smaller number of more distantly related species. The species closely related to the type species *Nocardioideae albus* include *Nocardioideae aestuarii*, *agariphilus*, *aquaticus*, *aquiterae*, *aromaticivorans*, *biguumensis*, *caeni*, *exalbidus*, *fonticola*, *furvisabuli*, *ganghwensis*, *ginsengisoli*, *hankookensis*, *humi*, *hwusunensis*, *insulae*, *islandensis*, *kongjuensis*, *kribbensis*, *lentus*, *luteus*, *marinus*, *nitrophenolicus*, *oleivorans*, *panacihumi*, *panacisoli*, *plantarum*, *pyridinolyticus*, *sediminis*, *simplex*,

terrae, *terrigena*, and *tritolerans*. The more distantly related species form seven clades: *Nocardioideae alkalitolerans*; *Nocardioideae basal-tis*, *dokdonensis*, *marinisabuli*, and *salarius*; *Nocardioideae daphniae*; *Nocardioideae dilutus* and *halotolerans*; *Nocardioideae dubius*; *Nocardioideae jensenii*; and *Nocardioideae koreensis*. These species appear to be about equally related to *Nocardioideae albus* and the genus *Marmoricola* (Figure 12).

The genus *Actinopolymorpha* is composed of the type species *Actinopolymorpha singaporensis* and the closely related species *Actinopolymorpha alba*, *cephalotaxi*, and *rutila*.

The genus *Aeromicrobium* comprises the type species *Aeromicrobium erythreum* and the closely related species *Aeromicrobium alkaliterrae*, *fastidiosum*, *flavum*, *ginsengisoli*, *marinum*, *panaciterae*, *ponti*, and *tamlense*.

The genus *Kribbella* comprises the type species *Kribbella flavida* and the closely related species *Kribbella alba*, *aluminosa*, *antibiotica*, *catacumbae*, *ginsengisoli*, *hippodromi*, *jejuensis*, *karoonsensis*, *koreensis*, *lupini*, *sancticalisti*, *sandramycini*, *solani*, *swartbergensis*, and *yunnanensis*.

The genus *Marmoricola* encompasses the type species *Marmoricola aurantiacus* and the closely related species *Marmoricola aequoreus* and *biguumensis*.

Order “*Pseudonocardiales*” and family *Pseudonocardia*ceae

This order is formed by elevation of the suborder *Pseudonocardineae* (Zhi et al., 2009). In the previous road map (Garrity et al., 2005) and the analyses of Zhi et al. (2009), the suborder comprised two families, *Pseudonocardia*ceae and *Actinosynnemataceae*. However, the taxonomic status of these families was recently re-examined (Labeda et al., 2011). Based on the rRNA gene trees, chemotaxonomic evidence, and morphology, it was concluded that the retention of the family *Actinosynnemataceae* was not warranted and that the genera it contained should be united into the family *Pseudonocardia*ceae. In the rRNA gene trees prepared for this volume, this enlarged family contains two clades which correspond to some of the genera assigned to the each of the original families, as well as numerous lineages that arise from the base of the family tree (Figure 15). The first clade includes only genera previously assigned to the *Pseudonocardia*ceae and comprises the genera *Pseudonocardia*, *Actinomycesospora*, *Amycolatopsis*, *Kibdelosporangium*, *Prauserella*, *Saccharomonospora*, *Saccharopolyspora*, *Sciscionella*, and *Thermocrispum*. The second clade includes only genera previously assigned to the family *Actinosynnemataceae* and contains the genera *Actinosynnema*, *Lechevalieria*, *Lentzea*, *Saccharothrix*, and *Umezawaea*. Although not readily distinguished by most chemotaxonomic criteria, the whole-cell sugars of these clades are different. The first clade possesses arabinose and galactose, and the second clade possesses galactose, mannose, and sometimes either rhamnose or ribose.

Previously, *Thermobispora* was also assigned to the *Pseudonocardia*ceae (Garrity et al., 2005). Re-examination of this relationship suggested that this genus was more closely related to the order “*Streptosporangiales*” (Figure 16; Zhi et al., 2009). However, because of the absence of corroborating evidence for this affiliation, this genus is classified as an order *incertae sedis* in the current road map.

Four subclades are apparent in the clade comprised exclusively of genera from the original family *Pseudonocardia*ceae (Figure 15). The first subclade includes the genus *Pseudonocardia*

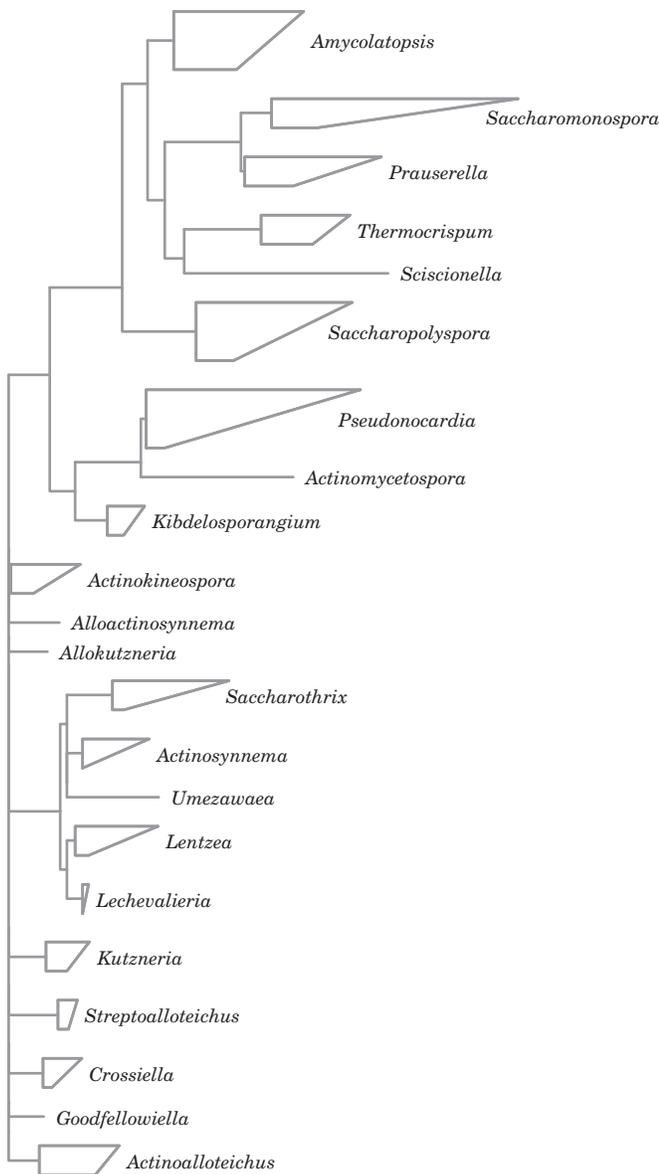


FIGURE 15. Genera of the order “Pseudonocardiales”. Analyses were performed as described for Figure 1.

and forms two further groups. The first group comprises the type species *Pseudonocardia thermophila* and *Pseudonocardia aca-ciae*, *alaniniphila*, *alni*, *ammonioxydans*, *antarctica*, *asaccharolytica*, *aurantiaca*, *autotrophica*, *carboxydivorans*, *chloroethenivorans*, *compacta*, *endophytica*, *kongjuensis*, *nitrificans*, *parietis*, *petroleophila*, *saturnea*, *spinosa*, *spinosispora*, *xinjiangensis*, *yunnanensis*, and *zijingensis*. The second group comprises *Pseudonocardia ailaonen-sis*, *benzenivorans*, *dioxanivorans*, *halophobica*, *hydrocarbonoxydans*, *oroxyli*, *sulfidoxydans*, and *tetrahydrofuranoxydans*. This latter group also includes the monospecific genus *Actinomycetospora* (type species *Actinomycetospora chiangmaiensis*) and *Kibdelosporan-gium aridum* (type species) and *Kibdelosporangium philippinense*.

The second subclade includes two groups of *Amycolatopsis* species. The largest group comprises a number of subgroups, including the type species *Amycolatopsis orientalis* and closely

related species *Amycolatopsis alba*, *azurea*, *coloradensis*, *decaplanina*, *japonica*, *keratiniphila*, *lurida*, and *regifaucium*; *Amycolatopsis albi-doflavus*, *australiensis*, *balhimycina*, *benzoatilytica*, *echigonensis*, *halotolerans*, *kentuckyensis*, *lexingtonensis*, *mediterranei*, *niigatensis*, *plumensis*, *pretoriensis*, *rifamycinica*, *rubida*, *tolypomycina*, and *van-coresmycina*; *Amycolatopsis ultimotia*; *Amycolatopsis jejuensis* and *sulfurea*; *Amycolatopsis marina* and *palatopharyngis*; *Amycolatopsis minnesotensis*, *nigrescens*, and *saalfeldensis*; and *Amycolatopsis sac-chari*. The second group of *Amycolatopsis* species includes *Amy-colatopsis eurytherma methanolica*, *tucumanensis*, *taiwanensis*, and *thermoflava*. It is unrelated to the type species, but closely related to *Thermocrispum municipale* (type species), *Thermocrispum agreste* and the monospecific genus *Sciscionella* (type species *Sciscionella marina*). In contrast to the *Amycolatopsis orientalis* group, most members of the second group of *Amycolatopsis* species are ther-motolerant. However, other phenotypic characteristics are simi-lar between the two groups and additional comparative studies are necessary to determine if the second group warrants reclas-sification as a novel genus (Tan and Goodfellow, 2011).

A third subclade includes the genera *Prauserella* and *Saccha-romonospora*. *Prauserella* comprises the type species *Prauserella rugosa* and the closely related species *Prauserella aidingensis*, *alba*, *flava*, *halophila*, *marina*, *muralis*, *salsuginis*, and *sediminis*. *Saccha-romonospora* is composed of the type species *Saccharomonospora viridis* and *Saccharomonospora azurea*, *cyanea*, *glauca*, *halophila*, *paurometabolica*, *saliphila*, and *xinjiangensis*.

The last subclade includes the genus *Saccharopolyspora*, which comprises a number of subgroups, including the type species *Saccharopolyspora hirsuta* and the closely related species *Sac-charopolyspora antimicrobica*, *hordei*, *jiangxiensis*, *qijiaojiangensis*, *rectivirgula*, *rosea*, *shandongensis*, *spinosa*, and *thermophila*; *Saccharopolyspora flava*, *halophila*, and *tripterygii*; *Saccharopolyspora eryth-raea*, *spinosporotrichia*, and *taberi*; *Saccharopolyspora gregorii*; and *Saccharopolyspora cebuensis*.

The clade composed exclusively of former members of the family *Actinosynnemataceae* comprises two subclades. The first includes the genus *Actinosynnema*, which contains the type spe-cies *Actinosynnema mirum* and the closely related species *Actinosyn-nema pretiosum*. This taxon is closely related to the monospecific genus *Umezawaea* (type species *Umezawaea tangerina*), *Lentzea albida*, and some species of the genera *Lechevalieria*: *Lechevalieria atacamensis*, *fradiae*, and *roselyniae* (Figure 15). The genus *Saccha-rothrix* is also a near neighbor and forms a well-defined group within this subclade. It comprises the type species *Saccharothrix australiensis* and the closely related species *Saccharothrix algerien-sis*, *coeruleofusca*, *espanaensis*, *longispora*, *mutabilis*, *syringae*, *texas-ensis*, *violaceirubra*, and *xinjiangensis*.

The second subclade includes the type species *Lechevalieria aerocolonigenes* and the closely related species *Lechevalieria deserti*, *flava*, and *xinjiangensis*. The type species *Lentzea albidocapillata* and the closely related species *Lentzea californiensis*, *flaviverrucosa*, *kentuckyensis*, *violacea*, and *waywayandensis* are also in this group.

The remaining genera all appear to arise from the base of the family rRNA gene tree. The genus *Actinoalloteichus* com-prises the type species *Actinoalloteichus cyanogriseus* and the closely related species *Actinoalloteichus hymeniacidonis* and *spiti-ensis*. *Streptomyces caeruleus* is closely related and is a heterotypic synonym (Tamura et al., 2008).

The genus *Actinokineospora* comprises the type species *Acti-nokineospora riparia* and the closely related species *Actinokineo-*

spora auranticolor, *diospyrosa*, *enzanensis*, *globoicata*, *inagensis*, and *terrae*. In the rRNA gene tree, each species forms a short branch at the base of the family tree but not a clade with other species. The monospecific genera *Allokutzneria* (type species *Allokutzneria albata*) and *Alloactinosynnema* (type species *Alloactinosynnema album*), as well as *Amycolatopsis* (type species *Amycolatopsis alba*), also appear to be closely related.

Other genera arising from the base of the family tree include the genus *Crossiella* comprised of the type species *Crossiella cryphila* and *Crossiella equi*, the monospecific genus *Goodfellowiella* (type species *Goodfellowiella coeruleoviolacea*), the genus *Kutzneria* comprised of the type species *Kutzneria viridogrisea* and *Kutzneria albida* and *kofuensis*, and the genus *Streptoalloteichus* comprised of the type species *Streptoalloteichus hindustanus* and *Streptoalloteichus tenebrarius*.

Order “Streptomycetales” and family Streptomycetaceae

This order is formed by elevation of the suborder *Streptomycineae* (Zhi et al., 2009) and includes only the family *Streptomycetaceae*. In the previous road map, the genera *Kitasatospora* and *Streptoverticillium* were assigned to this family in addition to *Streptomyces* (Garrity et al., 2005; Zhi et al., 2009). However, species in the genus *Streptoverticillium* have been transferred to the genus *Streptomyces* on the basis of phenotypic and rRNA gene sequence similarities (Kämpfer, 2012a; Witt and Stackebrandt, 1990). More recently, *Streptacidiphilus* was added to the family to include a clade of closely related acidophilic actinomycetes isolated from soil (Kim et al., 2003). Thus, the family included three genera *Streptomyces*, *Kitasatospora*, and *Streptacidiphilus* in the description of Zhi et al. (2009).

The current volume includes descriptions of more than 550 species of *Streptomyces* (Kämpfer, 2012c). Given the enormous diversity of this genus, it is difficult to identify meaningful phenotypic criteria that distinguish it from the other genera of the family or serve as a basis for its subdivision into genera of lower diversity. Likewise, although both *Kitasatospora* and *Streptacidiphilus* form stable clades in rRNA gene trees, they also possess high sequence similarity to many *Streptomyces* species. For these reasons, the status of these genera is questionable and they are classified as *genera incertae sedis* in this volume (Kämpfer, 2012c).

It is likely that *Streptomyces* presages the future of prokaryotic taxonomy. For whatever reason, ease of isolation, abundance of identifiable characters, or commercial and ecological interest, *Streptomyces* is currently much better represented in culture collections than most genera. However, surveys of environmental rRNA genes indicate that many more genera possess comparable diversity whose species await isolation. If bacteriologists are successful in capturing even a small fraction of nature’s diversity, we can expect many more groups of enormous complexity to become available in culture collections. What we learn from the classification of *Streptomyces* will determine the approaches necessary for these future classifications.

Order “Streptosporangiales”

This order is formed by elevation of the suborder *Streptosporangineae* (Zhi et al., 2009). It comprises the families *Streptosporangiaceae*, *Nocardiopsaceae*, and *Thermomonosporaceae*, all of which form distinct clades in the rRNA gene tree (Figure 16). In addition, *Thermobispora* arises as a long branch from the family *Streptosporangiaceae*, but it is classified as order *incertae sedis* (see below).

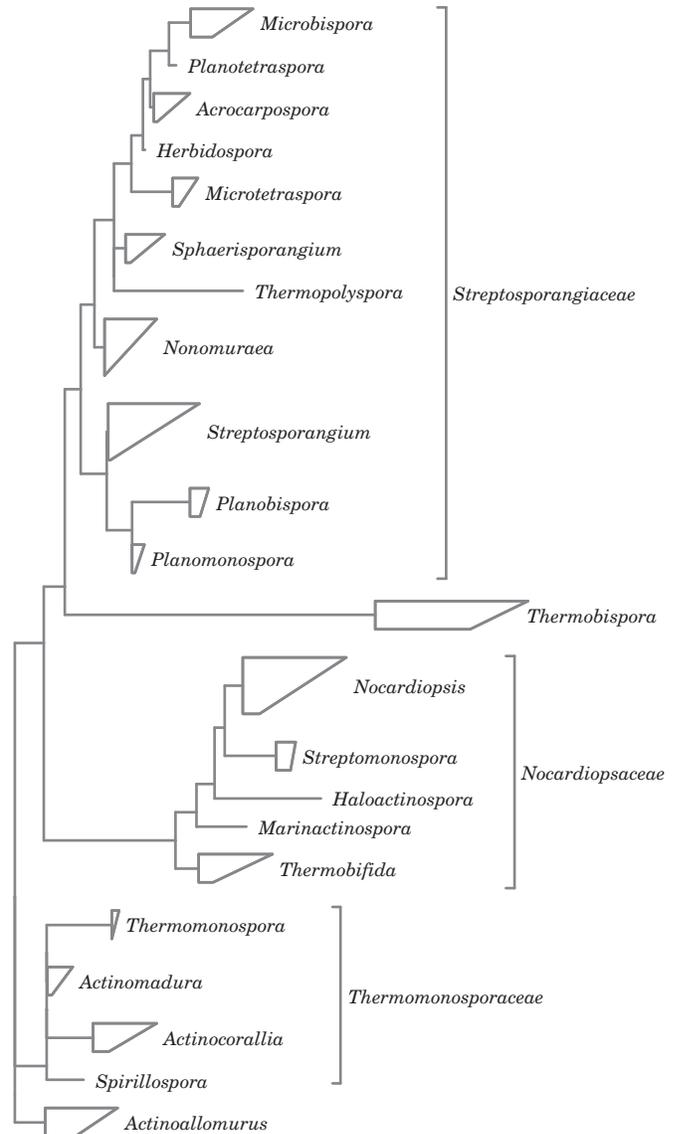


FIGURE 16. Genera and families of the order “Streptosporangiales”. Analyses were performed as described for Figure 1.

Family Streptosporangiaceae

This family is composed of 11 genera. Nine of these genera were classified in this family in the previous road map (Garrity et al., 2005), and the genera *Sphaerisporangium* and *Thermopolyspora* were subsequently added (Zhi et al., 2009). However, the genus *Planopolyspora*, which was previously classified in this family (Garrity et al., 2005), has been reassigned to the genus *Catenuloplanes* (Kudo et al., 1999). The family comprises three clades (Figure 16). The first clade comprises species of the genera *Planobispora*, *Planomonospora*, and *Streptosporangium*. The genus *Streptosporangium* is composed of three groups: the type species *Streptosporangium roseum* and *Streptosporangium album*, *amethystogenes*, *canum*, *longisporum*, *purpuratum*, *subroseum*, *vulgare*, and *yunnanense*; *Streptosporangium fragile*, *nondiastaticum*, and *pseudovulgare*; and *Streptosporangium violaceochromogenes*. In addition, *Streptosporangium carneum* lies at the base of the genus tree and outside the other groups. Lastly, *Streptosporangium claviforme* belongs to another clade and appears to be misclassified

(Petrolini et al., 1992). The other members of the first clade include *Planobispora*, which is composed of the type species *Planobispora longispora* and *Planobispora rosea* and *Planomonospora* comprised of the type species *Planomonospora parontospora* and *Planomonospora alba*, *sphaerica*, and *venezuelensis*.

The second clade encompasses the genus *Nonomuraea*, including the type species *Nonomuraea pusilla* and the closely related species *Nonomuraea angiospora*, *antimicrobica*, *bangladeshensis*, *candida*, *coxensis*, *fastidiosa*, *ferruginea*, *helvata*, *kuesteri*, *longicatena*, *maheshkhaliensis*, *polychroma*, *roseoviolacea*, *rubra*, *salmonea*, *spiralis*, and *turkmeniaca*. In addition, four species, *Nonomuraea africana*, *dietziae*, *recticatena*, and *roseola*, appear outside the clade at the base of the family tree.

The third clade contains the remaining genera clustered into a number of subclades. The first subclade includes the genus *Acrocarpospora* comprising the type species *Acrocarpospora pleiomorpha* and *Acrocarpospora corrugata* and *macrocephala*; *Herbidospora* containing the type species *Herbidospora cretacea* and *Herbidospora osyris*; *Microbispora* encompassing the type species *Microbispora rosea* and *Microbispora amethystogenes*, *corallina*, *mesophilica*, and *siamensis*; and *Planotetraspora* comprising the type species *Planotetraspora mira* and *Planotetraspora silvatica* and *thailandica*. Lastly, this subclade contains the misclassified species *Streptosporangium claviforme*.

The second subclade corresponds to the genus *Microtetraspora*, which contains the type species *Microtetraspora glauca* and *Microtetraspora fusca*, *malaysiensis*, and *niveoalba*. In addition, the species *Microtetraspora tyrrhenii* appears to have been lost and no rRNA gene sequence is available.

Species of the genus *Sphaerisporangium* form the third and fourth subclades. The third subclade comprises the type species *Sphaerisporangium melleum* and *Sphaerisporangium viridialbum*. The fourth subclade comprises the remaining species, *Sphaerisporangium album*, *cinnabarinum*, *flaviroseum*, and *rubeum*.

The last subclade is composed of the monospecific genus *Thermopolyspora* (type species *Thermopolyspora flexuosa*).

Family *Nocardiopsaceae*

This family comprises five genera. Species of the genus *Nocardiopsis* are widely distributed throughout the family and some of them are closely related to the type strains of other genera and hence may warrant reclassification. The largest group includes the type species *Nocardiopsis dassonvillei* and *Nocardiopsis aegyptia*, *alba*, *alkaliphila*, *exhalans*, *ganjiahensis*, *halotolerans*, *listeri*, *lucentensis*, *metallicus*, *prasina*, *quinghaiensis*, *synnemataformans*, *tropica*, *umidischolae*, and *valliformis*. Two related groups include the species *Nocardiopsis kunsanensis*, *litoralis*, *salina*, and *xinjiangensis* and the species *Nocardiopsis baichengensis*, *chromatogenes*, *composta*, *halophila*, and *potens*. The last group includes the species *Nocardiopsis gilva*, *rhodophaea*, *rosea*, and *trehalosi*. It is closely related to the monospecific genus *Haloactinospora* (type species *Haloactinospora alba*). Lastly, *Nocardiopsis arabia* appears within the genus *Streptomonospora*, which is comprised of the type species *Streptomonospora salina* and *Streptomonospora alba*, *amylolytica*, *flavalba*, and *halophila*. The remaining genera in the family *Nocardiopsaceae* include the monospecific genus *Marinactinospora* (type species *Marinactinospora thermotolerans*) and the genus *Thermobifida*, which is composed of the type species *Thermobifida alba* and *Thermobifida cellulolytica*, *fusca*, and *halotolerans*.

Family *Thermomonosporaceae*

This family encompasses five genera, but only two are well-defined in the rRNA gene trees prepared for this volume. The type species *Thermomonospora curvata* is found at the base of the family tree (Figure 16). The only other species in the genus, *Thermomonospora chromogena*, is more closely related to the order *incertae sedis* of *Thermobispora* and should be reclassified.

The genus *Actinoallomurus* forms a well-defined clade in the family (Tamura et al., 2009). In the gene tree prepared for this volume, this clade is found at the base of the order tree and outside of the family (Figure 16). However, this classification is not supported by other evidence. For instance, the presence of the diagnostic sugar madurose and similarities in menaquinone and cell-wall amino acid contents support its assignment to the family *Thermomonosporaceae* (Goodfellow and Trujillo, 2012). The genus comprises the type species *Actinoallomurus spadix* and *Actinoallomurus acaciae*, *amamiensis*, *caesius*, *coprocola*, *fulvus*, *iriomotensis*, *lividus*, *purpureus*, and *yoronensis*.

The genus *Actinocorallia* also forms a well-defined clade composed of the type species *Actinocorallia herbida* and *Actinocorallia aurantiaca*, *aurea*, *cavernae*, *glomerata*, *libanotica*, and *longicatena*.

In contrast, the remaining genera *Actinomadura* and *Spirillospora* are represented by many short lineages at the base of the rRNA gene tree. Presumably, other markers will be necessary to fully understand the relationships between the species assigned to these genera. The genus *Actinomadura* comprises the type species *Actinomadura madurae* and *Actinomadura atramentaria*, *bangladeshensis*, *catellatispora*, *chibensis*, *chokoriensis*, *citrea*, *coerulea*, *cremea*, *echinospora*, *fibrosa*, *flavalba*, *formosensis*, *fulvescens*, *glauciflava*, *hallensis*, *hibisca*, *keratimilytica*, *kijaniata*, *latina*, *livida*, *luteofluorescens*, *macra*, *mexicana*, *meyerae*, *miaoliensis*, *namibiensis*, *napiensis*, *nitritigenes*, *oligospora*, *pelletieri*, *rubrobrunea*, *rudentiformis*, *rugatobispora*, *sputi*, *umbrina*, *verrucosospora*, *vinacea*, *viridilutea*, *viridis*, and *yumaensis*. In addition, *Actinomadura alba* forms a distinct lineage in the family separated from the other species in the genus. Similarly, the type species of *Spirillospora albida* and *Spirillospora rubra* do not appear more closely related to each other than to species of the genus *Actinomadura*.

Order *incertae sedis* and the genus *Thermobispora*

In the previous road map, the monospecific genus *Thermobispora* (type species *Thermobispora bispora*) was assigned to the family *Pseudonocardiaceae* (Garrity et al., 2005). Re-examination of this relationship suggested that this genus was more closely related to the order “*Streptosporangiales*” (Figure 16; Wang et al., 1996; Zhi et al., 2009). However, this affiliation is not strongly supported by other evidence. For instance, while both the genus *Thermobispora* and the family *Streptosporangiaceae* have type IV polar lipids, the dominant menaquinone in *Thermobispora* is MK-9 with a saturated side-chain, whereas in the “*Streptosporangiales*” the side-chains are predominantly unsaturated or consist of more complex mixtures of menaquinones. Thus, in the absence of clear evidence for assignment of this genus to one of the existing orders, it is classified as an order *incertae sedis* in the current road map.

In the rRNA gene tree prepared for this volume, *Thermomonospora chromogena* forms a clade with the genus *Thermobispora*. This species possesses multiple rRNA operons, one of which was proposed to have been acquired from *Thermobispora* by horizontal gene transfer (Yap et al., 1999). However, both the presumed

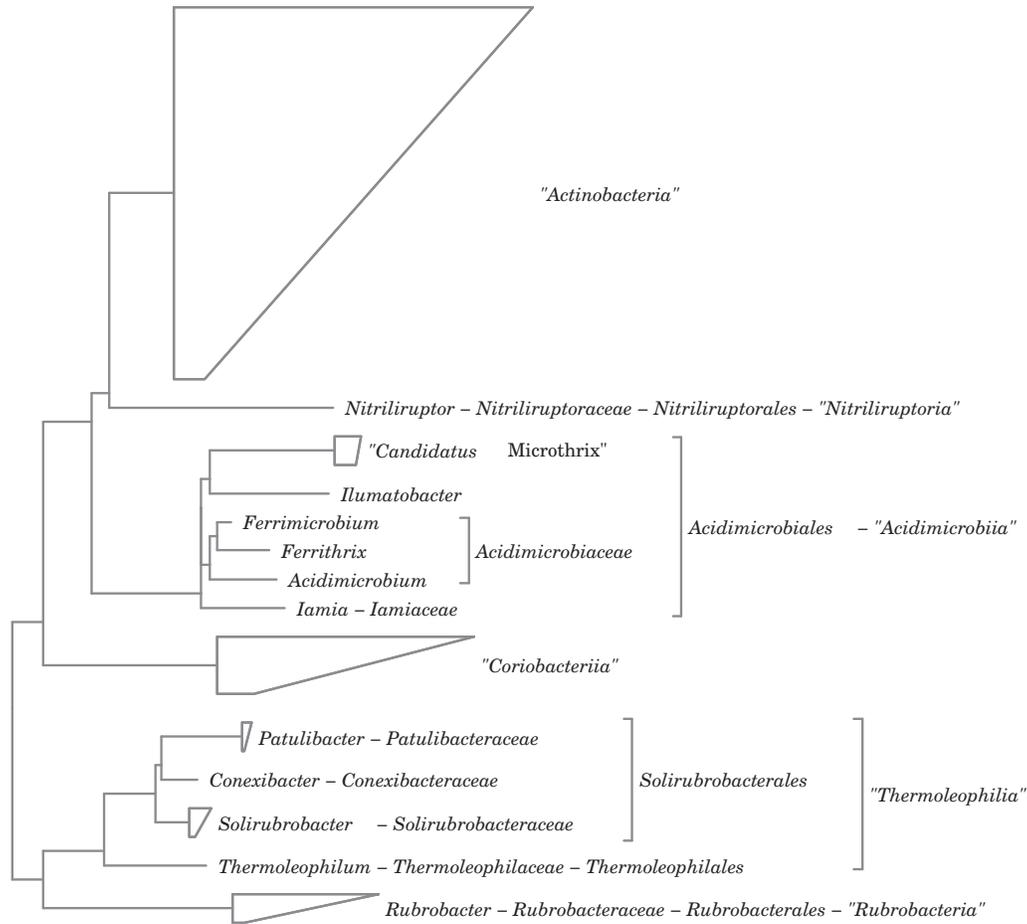


FIGURE 17. Genera and other higher taxa of the classes “Acidimicrobiia”, “Nitriliruptorales”, “Rubrobacteria”, and “Thermoleophila”. Analyses were performed as described for Figure 1.

ancestral, as well as horizontally transferred genes, form a clade with the *Thermobispora* gene. While there are numerous phenotypic differences between *Thermomonospora chromogena* and *Thermomonospora curvata* (McCarthy and Cross, 1984), their chemotaxonomic markers are fairly similar and different from *Thermobispora* (Trujillo and Goodfellow, 2012). Thus, further examination of these species will be necessary to resolve their classification.

Class “Acidimicrobiia” and order Acidimicrobiales

This class is formed by elevation of the subclass *Acidimicrobidae* (Garrity et al., 2005; Zhi et al., 2009). It comprises two families (Figure 17). The family *Acidimicrobiaceae* is composed of four monospecific genera, namely *Acidimicrobium* (type species *Acidimicrobium ferrooxidans*), *Ferrimicrobium* (type species *Ferrimicrobium acidiphilum*), *Ferrithrix* (type species *Ferrithrix thermotolerans*), and *Ilumatobacter* (type species *Ilumatobacter fluminis*). This latter forms a clade with “*Candidatus Microthrix*” and may warrant classification into a novel family. The family *Iamiaceae* comprises the monospecific genus *Iamia* (type species *Iamia majanohamensis*).

Class “Coriobacteriia” and order Coriobacteriales

This class is formed by elevation of the subclass *Coriobacteridae* (Garrity et al., 2005; Zhi et al., 2009). It contains one order and one family, *Coriobacteriaceae* (Figure 18). The family comprises six clades which arise from a multifurcation at the base of the family tree. The monospecific genus *Coriobacterium* (type species *Coriobacterium glomerans*) and *Collinsella aerofaciens* (type species), *intestinalis*, and *stercoris* form one clade. Additional clades are composed of *Adlercreutzia equolifaciens*, *Asaccharobacter celatus*, *Denitrobacterium detoxificans*, and *Enterorhabdus mucosicola*; *Atopobium minutum* (type species), *fossor*, *parvulum*, *rimae*, and *vaginae*, and *Olsenella uli* (type species) and *profusa*; *Cryptobacterium curtum*; *Eggerthella lenta* (type species) and *sinensis*, *Gordonibacter pamelaeeae*, and *Paraeggerthella hongkongensis*; and *Slackia exigua* (type species), *jaecicanis*, *heliotrinitireducens*, and *isoflavonicvertens*.

Class “Nitriliruptoria”

This class is formed by elevation of the subclass *Nitriliruptoridae*, which was described after the deadline for inclusion into

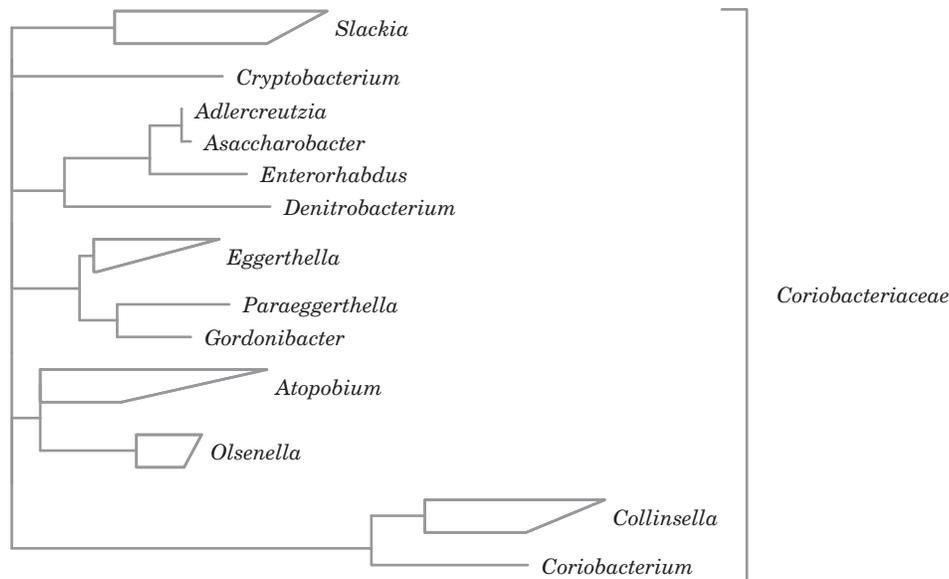


FIGURE 18. Genera and other higher taxa of the class “*Coriobacteriia*”. Analyses were performed as described for Figure 1.

this volume (Kurahashi et al., 2010). The taxon comprises two monospecific genera, which are classified in their own family and order. Thus, *Nitiliruptor alkaliphilus* is assigned to the family *Nitiliruptoraceae* of the order *Nitiliruptorales* (Sorokin et al., 2009). *Euzebya tangerina* is assigned to the family *Euzebyaceae* of the order *Euzebyales* (Kurahashi et al., 2010). Although not well represented in culture collections, numerous environmental clones have been identified with high similarity to each of these genera, suggesting that these organisms are quite abundant in nature.

Class “*Rubrobacteria*” and order *Rubrobacteriales*

This class is formed by elevation of the subclass *Rubrobacteridae* (Stackebrandt et al., 1997). At the time it was proposed, only the genus *Rubrobacter* was known and the subclass contained a single order *Rubrobacteriales*, which was represented by the family *Rubrobacteraceae* and the genus *Rubrobacter*. Later, the genus *Thermoleophilum* was reported to be a member of the subclass (Yakimov et al., 2003), and the new genera *Conexibacter* (Monciardini et al., 2003) and *Solirubrobacter* (Singleton et al., 2003) were described. In the previous road map, all of these genera were assigned to the family *Rubrobacteraceae*. Stackebrandt (2004, 2005) re-analyzed the relationship of these genera to the subclass *Rubrobacteridae* and proposed the new families *Conexibacteraceae*, *Solirubrobacteraceae*, and *Thermoleophilaceae*. Subsequently, Reddy and Garcia-Pichel (2009) proposed the orders *Thermoleophilales* and *Solirubrobacteriales*, which reflected the low sequence similarity of the 16S rRNA genes between these families and *Rubrobacter* spp. In the rRNA gene trees prepared for this volume, little phylogenetic or phenotypic evidence was found for an association between *Rubrobacter* and the orders *Thermoleophilales* and *Solirubrobacteriales* (Figure 17). For this reason, the current classification places these groups into the novel classes “*Rubrobacteria*” and “*Thermoleophilia*”. Thus, the class “*Rubrobacteria*” comprises a single order *Rubrobacteriales*, family *Rubrobacteraceae*, and genus *Rubrobacter*. On the basis of rRNA gene sequence similarity, the type species *Rubrobacter radiotolerans* is not closely related to the

other species in the genus, namely *Rubrobacter taiwanensis* and *xylanophilus*.

Class “*Thermoleophilia*”

This class was formed to distinguish the orders *Thermoleophilales* and *Solirubrobacteriales* from the order *Rubrobacteriales*, with which they are distantly related (Figure 17). The order *Thermoleophilales* comprises the family *Thermoleophilaceae* and genus *Thermoleophilum*, composed of *Thermoleophilum album* (type species) and *Thermoleophilum minutum*. The order *Solirubrobacteriales* consists of the families *Solirubrobacteraceae*, *Conexibacteraceae*, and *Patulibacteraceae*. Each family contains a single genus: *Solirubrobacter pauli* (type species) and *Solirubrobacter soli*; *Conexibacter woesei*; and *Patulibacter minatonensis* (type species) and *Patulibacter americanus*. Although not well represented in culture collections, numerous environmental clones have been identified with high similarity to each of these genera suggesting that these organisms are quite abundant in nature (Suzuki and Whitman, 2012).

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Taxonomic outline of the phylum *Actinobacteria*

WOLFGANG LUDWIG, JEAN EUZÉBY AND WILLIAM B. WHITMAN

All taxa recognized within this volume of the rank of genus and above are listed below. Within each classification, the nomenclatural type is listed first followed by the remaining taxa in alphabetical order. Taxa appearing on the Approved Lists are denoted by the superscript ^{AL}. Taxa that were otherwise validly published are denoted by the superscript ^{VP}. Taxa that have not been validly published are presented in quotations. Taxa which were not included in this volume because they were described after the deadline of 1 January 2008 are indicated by an asterick*.

Phylum XXVI. “*Actinobacteria*”

Class I. “*Actinobacteria*”

Order I. *Actinomycetales*^{AL(T)}

Family I. *Actinomycetaceae*^{AL}

Genus I. *Actinomyces*^{AL(T)}

Genus II. *Actinobaculum*^{VP}

Genus III. *Arcanobacterium*^{VP}

Genus IV. *Mobiluncus*^{VP}

Genus V. *Varibaculum*^{VP}

Order II. “*Actinopolysporales*”

Family I. *Actinopolysporaceae*^{VP}

Genus I. *Actinopolyspora*^{AL}

Order III. *Bifidobacteriales*^{VP}

Family I. *Bifidobacteriaceae*^{VP}

Genus I. *Bifidobacterium*^{AL(T)}

Genus II. *Aeriscardovia*^{VP}

Genus III. *Alloiscardovia*^{VP}

Genus IV. *Gardnerella*^{VP}

Genus V. *Metiscardovia*^{VP}

Genus VI. *Parascardovia*^{VP}

Genus VII. *Scardovia*^{VP}

Order IV. “*Catenulisporales*”

Family I. *Catenulisporaceae*^{VP}

Genus I. *Catenulispora*^{VP(T)}

Family II. *Actinospicaceae*^{VP}

Genus I. *Actinospica*^{VP(T)}

Order V. “*Corynebacteriales*”

Family I. *Corynebacteriaceae*^{AL}

Genus I. *Corynebacterium*^{AL(T)}

Genus II. *Turicella*^{VP}

Family II. *Dietziaceae*^{VP}

Genus I. *Dietzia*^{VP(T)}

Family III. *Mycobacteriaceae*^{AL}

Genus I. *Mycobacterium*^{AL(T)}

Family IV. *Nocardiaceae*^{AL}

Genus I. *Nocardia*^{AL(T)}

Genus II. *Gordonia*^{VP}

Genus III. *Millisia*^{VP}

Genus IV. *Rhodococcus*^{AL}

Genus V. *Skermania*^{VP}

Genus VI. *Smaragdicoccus*^{VP}

Genus VII. *Williamsia*^{VP}

Family V. *Segniliparaceae*^{VP}

Genus I. *Segniliparus*^{VP(T)}

Family VI. *Tsukamurellaceae*^{VP}

Genus I. *Tsukamurella*^{VP(T)}

Order VI. “*Frankiales*”

Family I. *Frankiaceae*^{AL}

Genus I. *Frankia*^{AL(T)}

Family II. *Acidothermaceae*^{VP}

Genus I. *Acidothermus*^{VP(T)}

Family III. *Cryptosporangiaceae*^{VP}

Genus I. *Cryptosporangium*^{VP(T)}

Genus *Incerta sedis Fodinicola*^{VP}

Family IV. *Geodermatophilaceae*^{VP}

Genus I. *Geodermatophilus*^{AL(T)}

Genus II. *Blastococcus*^{AL}

Genus III. *Modestobacter*^{VP}

Family V. *Nakamurellaceae*^{VP}

Genus I. *Nakamurella*^{VP(T)}

Genus II. *Humicoccus*^{VP}

Genus III. *Saxeibacter*^{VP*}

Family VI. *Sporichthyaceae*^{VP}

Genus I. *Sporichthya*^{AL(T)}

Order VII. “*Glycomycetales*”

Family I. *Glycomycetaceae*^{VP}

Genus I. *Glycomyces*^{VP(T)}

Genus II. *Haloglycomyces*^{VP*}

Genus III. *Stackebrandtia*^{VP}

Order VIII. “*Jiangellales*”

Family I. *Jiangellaceae*^{VP}

Genus I. *Jiangella*^{VP(T)}

Genus II. *Haloactinopolyspora*^{VP}

Order IX. “*Kineosporiales*”

Family I. *Kineosporiaceae*^{VP}

Genus I. *Kineosporia*^{AL(T)}

Genus II. *Kineococcus*^{VP}

Genus III. *Quadrisphaera*^{VP}

Order X. *Micrococcales*^{AL}

Family I. *Micrococcaceae*^{AL}

Genus I. *Micrococcus*^{AL(T)}

Genus II. *Acaricomes*^{VP}

Genus III. *Arthrobacter*^{AL}

Genus IV. *Citricoccus*^{VP}

Genus V. *Kocuria*^{VP}

Genus VI. *Nesterenkonia*^{VP}

Genus VII. *Renibacterium*^{VP}

Genus VIII. *Rothia*^{VP}

Genus IX. *Sinomonas*^{VP*}
 Genus X. *Yaniella*^{VP}
 Genus XI. *Zhihengliuella*^{VP}
 Family II. *Beutenbergiaceae*^{VP}
 Genus I. *Beutenbergia*^{VP(T)}
 Genus II. *Miniimonas*^{VP}
 Genus III. *Salana*^{VP}
 Genus IV. *Serinibacter*^{VP}
 Family III. *Bogoriellaceae*^{VP}
 Genus I. *Bogoriella*^{VP(T)}
 Genus II. *Georgenia*^{VP}
 Family IV. *Brevibacteriaceae*^{AL}
 Genus I. *Brevibacterium*^{AL(T)}
 Family V. *Cellulomonadaceae*^{VP}
 Genus I. *Cellulomonas*^{AL(T)}
 Genus II. *Actinotalea*^{VP}
 Genus III. *Demequina*^{VP}
 Genus IV. *Oerskovia*^{AL}
 Genus V. *Paraoerskovia*^{VP*}
 Genus VI. *Tropheryma*^{VP}
 Family VI. *Dermabacteraceae*^{VP}
 Genus I. *Dermabacter*^{VP(T)}
 Genus II. *Brachybacterium*^{VP}
 Genus III. *Devriesea*^{VP*}
 Genus IV. *Helcobacillus*^{VP*}
 Family VII. *Dermacoccaceae*^{VP}
 Genus I. *Dermacoccus*^{VP(T)}
 Genus II. *Demetria*^{VP}
 Genus III. *Kytococcus*^{VP}
 Family VIII. *Dermatophilaceae*^{AL}
 Genus I. *Dermatophilus*^{AL(T)}
 Genus II. *Kineosphaera*^{VP}
 Family IX. *Intrasporangiaceae*^{VP}
 Genus I. *Intrasporangium*^{AL(T)}
 Genus II. *Arsenicococcus*^{VP}
 Genus III. *Fodinibacter*^{VP*}
 Genus IV. *Humibacillus*^{VP*}
 Genus V. *Humihabitan*^{VP}
 Genus VI. *Janibacter*^{VP}
 Genus VII. *Knoellia*^{VP}
 Genus VIII. *Kribbia*^{VP}
 Genus IX. *Lapillicoccus*^{VP}
 Genus X. *Marihabitans*^{VP*}
 Genus XI. *Ornithinimicrobium*^{VP}
 Genus XII. *Ornithinimicrobium*^{VP}
 Genus XIII. *Oryzihumus*^{VP}
 Genus XIV. *Phycococcus*^{VP}
 Genus XV. *Serinicoccus*^{VP}
 Genus XVI. *Terrabacter*^{VP}
 Genus XVII. *Terracoccus*^{VP}
 Genus XVIII. *Tetrasphaera*^{VP}
 Family X. *Jonesiaceae*^{VP}
 Genus I. *Jonesia*^{VP(T)}
 Family XI. *Microbacteriaceae*^{VP}
 Genus I. *Microbacterium*^{AL(T)}
 Genus II. *Agreia*^{VP}
 Genus III. *Agrococcus*^{VP}
 Genus IV. *Agromyces*^{AL}
 Genus V. *Clavibacter*^{VP}
 Genus VI. *Cryobacterium*^{VP}
 Genus VII. *Curtobacterium*^{AL}
 Genus VIII. *Frigoribacterium*^{VP}

Genus IX. *Fron dih abitan*^{sVP}
 Genus X. *Glaciibacter*^{VP*}
 Genus XI. *Gulosibacter*^{VP}
 Genus XII. *Humibacter*^{VP}
 Genus XIII. *Klugiella*^{VP*}
 Genus XIV. *Labeledella*^{VP}
 Genus XV. *Leifsonia*^{VP}
 Genus XVI. *Leucobacter*^{VP}
 Genus XVII. *Microcella*^{VP}
 Genus XVIII. *Microterricola*^{VP}
 Genus XIX. *Mycetocola*^{VP}
 Genus XX. *Okibacterium*^{VP}
 Genus XXI. *Phycicola*^{VP}
 Genus XXII. *Plantibacter*^{VP}
 Genus XXIII. *Pseudoclavibacter*^{VP}
 Genus XXIV. *Rathayibacter*^{VP}
 Genus XXV. *Rhodoglobus*^{VP}
 Genus XXVI. *Salinibacterium*^{VP}
 Genus XXVII. *Schumannella*^{VP*}
 Genus XXVIII. *Subtercola*^{VP}
 Genus XXIX. *Yonghaparkia*^{VP}
 Family XII. *Promicromonosporaceae*^{VP}
 Genus I. *Promicromonospora*^{AL(T)}
 Genus II. *Cellulosimicrobium*^{VP}
 Genus III. *Isoptericola*^{VP}
 Genus IV. *Myceligenans*^{VP}
 Genus V. *Xylanibacterium*^{VP}
 Genus VI. *Xylanimicrobium*^{VP}
 Genus VII. *Xylanimonas*^{VP}
 Family XIII. *Rarobacteraceae*^{VP}
 Genus I. *Rarobacter*^{VP(T)}
 Family XIV. *Ruaniaceae*^{VP}
 Genus I. *Ruania*^{VP(T)}
 Genus II. *Haloactinobacterium*^{VP}
 Family XV. *Sanguibacteraceae*^{VP}
 Genus I. *Sanguibacter*^{VP(T)}
 Order XI. "Micromonosporales"
 Family I. *Micromonosporaceae*^{AL}
 Genus I. *Micromonospora*^{AL(T)}
 Genus II. *Actinocatenispora*^{VP}
 Genus III. *Actinoplanes*^{AL}
 Genus IV. *Asanoa*^{VP}
 Genus V. *Catellatospora*^{VP}
 Genus VI. *Catelliglobospora*^{VP*}
 Genus VII. *Catenuloplanes*^{VP}
 Genus VIII. *Couchioplanes*^{VP}
 Genus IX. *Dactylosporangium*^{AL}
 Genus X. *Hamadaea*^{VP*}
 Genus XI. *Krasilnikovia*^{VP}
 Genus XII. *Longispora*^{VP}
 Genus XIII. *Luedemannella*^{VP}
 Genus XIV. *Pilimelia*^{AL}
 Genus XV. *Planosporangium*^{VP*}
 Genus XVI. *Plantactinospora*^{VP*}
 Genus XVII. *Polymorphospora*^{VP}
 Genus XVIII. *Pseudosporangium*^{VP*}
 Genus XIX. *Rugosimonospora*^{VP*}
 Genus XX. *Salinispora*^{VP}
 Genus XXI. *Spirilliplanes*^{VP}
 Genus XXII. *Verrucosispora*^{VP}
 Genus XXIII. *Virigisporangium*^{VP}

Order XII. "Propionibacteriales"

- Family I. *Propionibacteriaceae*^{AL}
 Genus I. *Propionibacterium*^{AL(T)}
 Genus II. *Aestuariimicrobium*^{VP}
 Genus III. *Brooklawnia*^{VP}
 Genus IV. *Friedmanniella*^{VP}
 Genus V. *Granulicoccus*^{VP}
 Genus VI. *Luteococcus*^{VP}
 Genus VII. *Microlunatus*^{VP}
 Genus VIII. *Micropruina*^{VP}
 Genus IX. *Propionicicella*^{VP}
 Genus X. *Propionicimonas*^{VP}
 Genus XI. *Propioniferax*^{VP}
 Genus XII. *Propionimicrobium*^{VP}
 Genus XIII. *Tessaracoccus*^{VP}
- Family II. *Nocardioideaceae*^{VP}
 Genus I. *Nocardioides*^{AL(T)}
 Genus II. *Actinopolymorpha*^{VP}
 Genus III. *Aeromicrobium*^{VP}
 Genus IV. *Kribbella*^{VP}
 Genus V. *Marmoricola*^{VP}
- Order XIII. “*Pseudonocardiales*”
 Family I. *Pseudonocardiaceae*^{VP}
 Genus I. *Pseudonocardia*^{AL(T)}
 Genus II. *Actinoalloteichus*^{VP}
 Genus III. *Actinokineospora*^{VP}
 Genus IV. *Actinomycetospora*^{VP*}
 Genus V. *Actinosynnema*^{AL}
 Genus VI. *Alloactinosynnema*^{VP*}
 Genus VII. *Allokutzneria*^{VP*}
 Genus VIII. *Amycolatopsis*^{VP}
 Genus IX. *Crossiella*^{VP}
 Genus X. *Goodfellowiella*^{VP}
 Genus XI. *Kibdelosporangium*^{VP}
 Genus XII. *Kutzneria*^{VP}
 Genus XIII. *Lechevalieria*^{VP}
 Genus XIV. *Lentzea*^{VP}
 Genus XV. *Prauserella*^{VP}
 Genus XVI. *Saccharomonospora*^{AL}
 Genus XVII. *Saccharopolyspora*^{AL}
 Genus XVIII. *Saccharothrix*^{VP}
 Genus XIX. *Sciscionella*^{VP*}
 Genus XX. *Streptoalloteichus*^{VP}
 Genus XXI. *Thermocrispum*^{VP}
 Genus XXII. *Umezawaea*^{VP}
- Order XIV. “*Streptomycetales*”
 Family I. *Streptomycetaceae*^{AL}
 Genus I. *Streptomyces*^{AL(T)}
 Genus *Incertae sedis I. Kitasatospora*^{VP}
 Genus *Incertae sedis II. Streptacidiphilus*^{VP}
- Order XV. “*Streptosporangiales*”
 Family I. *Streptosporangiaceae*^{VP}
 Genus I. *Streptosporangium*^{AL(T)}
 Genus II. *Acrocarpospora*^{VP}
 Genus III. *Herbidospora*^{VP}
 Genus IV. *Microbispora*^{AL}
 Genus V. *Microtetraspora*^{AL}
 Genus VI. *Nonomuraea*^{VP}
 Genus VII. *Planobispora*^{AL}
 Genus VIII. *Planomonospora*^{AL}
 Genus IX. *Planotetraspora*^{VP}
 Genus X. *Sphaerisporangium*^{VP}
- Genus XI. *Thermopolyspora*^{VP}
- Family II. *Nocardiopsaceae*^{VP}
 Genus I. *Nocardiopsis*^{AL(T)}
 Genus II. *Haloactinospora*^{VP}
 Genus III. *Marinactinospora*^{VP*}
 Genus IV. *Streptomonospora*^{VP}
 Genus V. *Thermobifida*^{VP}
- Family III. *Thermomonosporaceae*^{VP}
 Genus I. *Thermomonospora*^{AL(T)}
 Genus II. *Actinoallomurus*^{VP*}
 Genus III. *Actinocorallia*^{VP}
 Genus IV. *Actinomadura*^{AL}
 Genus V. *Spirillospora*^{AL}
- Order *Incertae sedis*
 Genus I. *Thermobispora*^{VP}
- Class II. “*Acidimicrobiia*”
 Order I. *Acidimicrobiales*^{VP(T)}
 Family I. *Acidimicrobiaceae*^{VP}
 Genus I. *Acidimicrobium*^{VP(T)}
 Genus II. *Ferrimicrobium*^{VP}
 Genus III. *Ferrithrix*^{VP}
 Genus IV. *Ilumatobacter*^{VP*}
 Family II. *Iamiaceae*^{VP}
 Genus I. *Iamia*^{VP(T)}
- Class III. “*Coriobacteria*”
 Order I. *Coriobacteriales*^{VP(T)}
 Family I. *Coriobacteriaceae*^{VP}
 Genus I. *Coriobacterium*^{VP(T)}
 Genus II. *Adlercreutzia*^{VP*}
 Genus III. *Asaccharobacter*^{VP*}
 Genus IV. *Atopobium*^{VP}
 Genus V. *Collinsella*^{VP}
 Genus VI. *Cryptobacterium*^{VP}
 Genus VII. *Denitrobacterium*^{VP}
 Genus VIII. *Eggerthella*^{VP}
 Genus IX. *Enterorhabdus*^{VP*}
 Genus X. *Gordonibacter*^{VP*}
 Genus XI. *Olsenella*^{VP}
 Genus XII. *Paraeggerthella*^{VP*}
 Genus XIII. *Slackia*^{VP}
- Class IV. “*Nitriliruptoria*”
 Order I. *Nitriliruptorales*^{VP(T)}
 Family I. *Nitriliruptoraceae*^{VP}
 Genus I. *Nitriliruptor*^{VP(T)}
 Order II. *Euzebyales*^{VP(T)}
 Family I. *Euzebyaceae*^{VP}
 Genus I. *Euzebya*^{VP(T)}
- Class V. “*Rubrobacteria*”
 Order I. *Rubrobacterales*^{VP(T)}
 Family I. *Rubrobacteraceae*^{VP}
 Genus I. *Rubrobacter*^{VP(T)}
- Class VI. “*Thermoleophilia*”
 Order I. *Thermoleophilales*^{VP(T)}
 Family I. *Thermoleophilaceae*^{VP}
 Genus I. *Thermoleophilum*^{VP(T)}
 Order II. *Solirubrobacteriales*^{VP}
 Family I. *Solirubrobacteraceae*^{VP}
 Genus I. *Solirubrobacter*^{VP(T)}
 Family II. *Conexibacteraceae*^{VP}
 Genus I. *Conexibacter*^{VP(T)}
 Family III. *Patulibacteraceae*^{VP}
 Genus I. *Patulibacter*^{VP(T)}