Revised Road Map to the Phylum Firmicutes

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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 the 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, the reader should be aware that 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 of the *Firmicutes*. 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 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, the polyphasic approach cannot be currently applied for sequence-based analyses due to the lack of adequate comprehensive datasets for alternative marker molecules. Even in the age of genomics, the datasets for non-rRNA markers are poor in comparison to more than 300,000 rRNA primary structures available in general and special databases (Cole et al., 2007; Pruesse et al., 2007). Nevertheless, the data provided by the full genome sequencing projects allow defining a small set of genes representing the conserved core of prokaryotic genomes (Cicarelli et al., 2006; Ludwig and Schleifer, 2005). Furthermore, comparative analyses of the 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, the structuring of this volume is based on updated and curated (http://www.arb-silva.de; Ludwig et al., 2004) databases of processed smallsubunit rRNA primary structures.

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 of the *Firmicutes*. The tools of the ARB software package (Ludwig et al., 2004) were used for data evaluation, optimization and phylogenetic inference. The alignment of sequences comprising at least 1000 monomers was manually evaluated and optimized for all representatives of the phylum. Phylogenetic treeing was performed with all of the approximately 14,000

sequences from *Firmicutes* which contain at least 1400 nucleotides and an additional 1000 sequences from representatives of the other phyla and domains. For recognizing and avoiding the influences of chimeric sequences, all calculations were performed twice, once including and once excluding environmental clone data. The datasets also varied with respect to the inclusion of highly variable sequence positions, which were eliminated in some analyses (Ludwig and Klenk, 2005). The consensus tree used for evaluating or modifying the taxonomic outline was 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). In the case that type strains were only represented by partial sequences (less than 1400 nucleotides), the respective data were inserted by a special ARB-tool allowing the optimal positioning of branches to the reference tree without admitting topology changes.

Taxonomic interpretation

The phylogenetic conclusions were used for evaluating and modifying the taxonomic outline of the *Firmicutes*. In order to ensure applicability and promote acceptance, the proposed 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 validly published but phylogenetically misplaced type strains are also generally maintained. These strains are mentioned in the context of the respective (sub)-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.

The taxonomic backbone of the Firmicutes

In the current treatment, the phylum *Firmicutes* contains three classes, "*Bacilli*", "*Clostridia*" and "*Erysipelotrichi*". This organization is similar to that of Garrity et al. (2005). However, the *Mollicutes* were removed from the phylum given the general low support by alternative markers (Ludwig and Schleifer, 2005) and its unique phenotypic properties, in particular the lack of rigid cell walls (see Emended description of *Firmicutes*, this volume). The family *Erysipelotrichaceae*, which includes wall-forming Gram-positive organisms previously classified with the *Mollicutes*, was retained in the *Firmicutes* as a novel class, "*Erysipelotricha*", and order, "*Erysipelotrichales*".

While the bipartition of the classes "*Clostridia*" and "*Bacilli*" is corroborated by the new analyses, some of the taxa previously assigned to the "*Clostridia*" tend to root outside the *Firmicutes* and may represent separate phyla. These include taxa previously classified within the "*Thermoanaerobacterales*" and

Syntrophomonadaceae (Garrity et al., 2005), which may contain a number of phylogenetic clades that are distinct at the phylum level. However, given the absence of corroboration by other phylogenetic markers for many of these assignments and a clear consensus on the definition of a phylum, these taxa were retained within the *Firmicutes* for the present.

Class "Bacilli"

Compared to Garrity et al. (2005), only minor restructuring of the "*Bacilli*" is indicated by this new analysis of the rRNA data. The separation into two orders, *Bacillales* and "*Lactobacillales*", is well supported (Fig. 1). However, a number of paralogous groups are found within the "*Bacilli*", some of which have been reclassified.

Order Bacillales

The definition and taxonomic organization of the order *Bacillales* is as outlined in the previous volumes (Fig. 2). Of the ten families proposed in Garrity et al. (2005), eight are retained. Upon transfer of the type genus *Caryophanon* to the *Planococcaceae*, the family *Caryophanaceae* was removed. Although the family *Caryophanaceae* Peskoff 1939^{AL} has priority over *Planococcaceae* Krassilnikov 1949^{AL}, the former is confusing because it is a misnomer, meaning 'that which has a conspicuous nucleus', and was based upon misinterpretation of staining results (Trentini, 1986). Similarly, upon transfer of the type genus *Turicibacter* to the family *"Erysipelotrichaceae*", the family *"Turicibacteraceae*" was removed. In addition, the genus *Pasteuria* was transferred out of the family *"Alicyclobacillaceae*" to the family *Pasteuriaceae*. As described below, a number of genera were also moved to families *incertae sedis* in recognition of the ambiguity of their phylogeny and taxonomic assignments.

Family Bacillaceae

The 16S rRNA-based phylogenetic analyses indicate that the family *Bacillaceae* is paraphyletic and composed of species misassigned to the genus *Bacillus* as well as genera misassigned to the family (Fig. 2). Reclassification of some taxa is proposed to correct some of these problems. However, the complete reorganization of this old and well-abused taxon is outside the scope of this work.

Genus Bacillus

The majority of the *Bacillus* species with validly published names are phylogenetically grouped into subclusters within this genus. However, some validly named species of *Bacillus* are not phylogenetically related to the type species, *B. subtilis*, and are more closely related to other genera. The phylogenetic subclusters within the genus *Bacillus* are:

a: Bacillus subtilis, amyloliquefaciens, atrophaeus, mojavensis, licheniformis, sonorensis, vallismortis, including the very likely misclassified Paenibacillus popilliae.

b: Bacillus farraginis, fordii, fortis, lentus, galactosidilyticus

c:Bacillus asahii, bataviensis, benzoevorans, circulans, cohnii, firmus, flexus, fumarioli, infernus, jeotgali, luciferensis, megaterium, methanolicus, niacini, novalis, psychrosaccharolyticus, simplex, soli, vireti

d: Bacillus anthracis, cereus, mycoides, thuringiensis, weihenstephanensis

e: Bacillus aquimaris, marisflavi

f: Bacillus badius, coagulans, thermoamylovorans, acidicola, oleronius, sporothermodurans

g: Bacillus alcalophilus, arsenicoselenatis, clausii, gibsonii, halodurans, horikoshii, krulwichiae,

okhensis, okuhidensis, pseudoalcaliphilus, pseudofirmus

h: Bacillus arsenicus, barnaricus, gelatini, decolorationis,

i: Bacillus carboniphilus, endophyticus, smithii,

j: Bacillus pallidus,

k: Bacillus funiculus, panaciterrae

The *Bacillus* cluster contains three additional groups of related genera: *Anoxybacillus*, *Geobacillus*, and *Saccharococcus*.

In addition to these taxa, which compose the family *Bacillaceae sensu stricto*, other phylogenetic groups have been assigned to this family (Garrity et al., 2005). Although the largest group appears to warrant elevation to a novel family, it is retained within the *Bacillaceae* in the present outline. This cluster comprises the genera *Alkalibacillus* (new; Jeon et al., 2005), *Amphibacillus, Cerasibacillus* (new; Nakamura et el., 2004), *Filobacillus, Gracilibacillus, Halobacillus* (new; Spring et al., 1996), *Halolactibacillus* (new; Ishikawa et al., 2005), *Lentibacillus, Oceanobacillus, Paraliobacillus, Paucisalibacillus* (new; Nunes et al., 2006); not described in the current volume), *Pontibacillus, Salibacillus* (not described in the current volume), *Tenuibacillus, Thalassobacillus* (new; Garcia et al., 2005), and *Virgibacillus*. The type strains of other species are positioned phylogenetically among the members of this lineage and merit taxonomical emendation: *Bacillus halophilus* and *Bacillus thermocloacae, Sinococcus*, and *Marinococcus*. For this reason, *Marinococcus* was transferred from the *Sporolactobacillaceae* in the current outline.

In addition, the genera *Ureibacillus, Marinibacillus, Jeotgalibacillus*, and *Exiguobacterium* were previously assigned to the *Bacillaceae* (Garrity et al., 2005). *Ureibacillus* falls within the clade represented by *Planococcaceae*, and it was reassigned to that family. *Marinibacillus* and *Jeotgalibacillus* are closely related to each other as well as to *Bacillus aminovorans*. This group is distantly related to the *Planococcaceae*, and they are also assigned to that family. *Lastly, Exiguobacterium* is not closely related to any of the described families, and it is assigned to a families *incertae sedis* in the current road map.

Bacillus schlegelii and *Bacillus solfatarae* represent their own deeply branching lineage of the *"Bacilli"* and warrant reclassification.

Family "Alicyclobacillaceae"

Only the type genus *Alicyclobacillus* is retained in this family, and two genera previously classified with the *Alicyclobacillaceae* have been reclassified (Garrity et al., 2005). According to the new 16S rRNA sequence analyses, *Sulfobacillus* represents a deep branch of the "*Clostridia*", and it is now placed within

Family XVII *Incertae Sedis* of the *Clostridiales*. *Pasteuria*, which was also previously classified within this family, is an obligate parasite of invertebrates. While it can be cultivated within the body of its prey, it has not been cultured axenically. Because of the substantial phenotypic differences and low 16S rRNA sequence similarity with *Alicyclobacillus*, it is now classified within its own family, *Pasteuriaceae* (see below). Lastly, *Alicyclobacillus* possesses a moderate relationship to *Bacillus tusciae*, which could be reclassified to this family.

Family "Listeriaceae"

The monophyletic family "*Listeriaceae*" combines the genera *Listeria* and *Brochothrix* as in the previous outline.

Family "Paenibacillaceae"

The members of the family "*Paenibacillaceae*" are distributed between two phylogenetic clusters. *Paenibacillus, Brevibacillus, Cohnella* (new; Kämpfer et al., 2006) and *Thermobacillus* share a common origin and represent the first group. Some validly named *Bacillus* species are found among the *Paenibacillus* species: *Bacillus chitinolyticus, edaphicus, ehimensis,* and *mucilaginosus*. The second group comprises the genera *Aneurinibacillus, Ammoniphilus,* and *Oxalophagus.* Although not clearly monophyletic, these two clusters are often associated together in several types of analyses. Thus, in the absence of clear evidence for a separation, the second cluster is retained within the family. In contrast, *Thermicanus,* which was classified within this family by Garrity et al. (2005), appears to represent a novel lineage of the *Bacilli.* In recognition of its ambiguous status, it was reclassified within Family X *Incertae Sedis.*

Family Pasteuriaceae

This family contains *Pasteuria*, an obligate parasite of invertebrates which has not yet been cultivated outside of its host. Although this genus was previously classified within the "*Alicyclobacillaceae*", the current analyses suggest that it is more closely associated with the "*Thermoactinomycetaceae*". In spite of the similarities in morphology and rRNA sequences between *Pasteuria* and *Thermoactinomycetes*, these genera were not combined into a single family for two reasons. First, in the absence of an axenic culture of *Pasteuria*, additional phenotypic and genotypic evidence for combining these organisms into a single family are not available. Second, the obligately pathogenic nature of *Pasteuria* was judged to be distinctive enough to warrant a unique classification in the absence of evidence to the contrary.

Family *Planococcaceae*

The family *Planococcaceae* is a clearly monophyletic unit that contains the genera *Planococcus*, *Filibacter, Kurthia, Planomicrobium*, and *Sporosarcina* as well as three genera transferred from the *Bacillaceae* (*Jeotgalibacillus, Marinibacillus*, and *Ureibacillus*) and *Caryophanon. Caryophanon* is the only genus of the *Caryophanaceae* in the previous outline and is transferred to the *Planococcaceae* based upon its rRNA-based phylogeny. Thus, the family *Caryophanaceae* is not used in the current outline. Again, some validly named species of *Bacillus* are found in the *Planococcaceae* radiation: *Bacillus fusiformis*, *sphaericus*, *massiliensis*, *psychrodurans*, and *psychrotolerans*.

Family "Sporolactobacillaceae"

Given that *Marinococcus* is transferred to the *Bacillaceae*, the family "*Sporolactobacillaceae*" is now composed of only the genus *Sporolactobacillus*. A moderate relationship to this genus is found for some validly named *Bacillus* species: *Bacillus agaradhaerens*, *clarkii*, *selenitireducens*, and *vedderis* as well as two recently described genera, *Tuberibacillus* and *Pullulanibacillus*, which are not included in this volume (Hatayama et al., 2006).

Family "Staphylococcaceae"

The family "*Staphylococcaceae*", as defined in the taxonomic outline of the previous volumes, is paraphyletic (Garrity et al., 2005). Whereas the four genera *Staphylococcus, Jeotgalicoccus, Macrococcus*, and *Salinicoccus* are clearly monophyletic, the genus *Gemella* represents a separate unit paraphyletic to the first cluster. Moreover, *Gemella* is distinguished from "*Staphylococcaceae*" stricto sensu because it is catalase- and oxidase-negative and possesses predominantly straight-chained, saturated and monounsaturated rather than branched-chain membrane lipids (K. Bernard, personal communication). Thus, *Gemella* is transferred to Family XI *Incertae Sedis* within the *Bacillales*.

Family "Thermoactinomycetaceae"

The family now contains six newly described genera in addition to the original genus *Thermoactinomyces*. The new genera are *Laceyella*, *Mechercharimyces*, *Planifilum*, *Seinonella*, *Shimazuella*, and *Thermoflavimicrobium*.

Order "Lactobacillales"

As in the previous outline, this order is composed of six families (Fig. 3).

Family Lactobacillaceae

In agreement with the previous outlines, the *Lactobacillaceae* is a monophyletic group that harbors three genera: *Lactobacillus*, *Paralactobacillus*, and *Pediococcus*.

Family "Aerococcaceae"

Two paraphyletic groups are combined in the family "*Aerococcaceae*". The majority of the genera are unified in a phylogenetically tight group comprising *Abiotrophia*, *Dolosicoccus*, *Eremococcus*, *Facklamia*, *Globicatella*, and *Ignavigranum*. Only the type genus *Aerococcus* represents a separate lineage.

Family "Carnobacteriaceae"

The members of the family "*Carnobacteriaceae*" are found in two paraphyletic clusters. *Carnobacterium* together with *Alkalibacterium*, *Allofustis*, *Alloiococcus*, *Atopococcus* (new; (Collins et al., 2005), *Atopostipes*, *Desemzia*, *Dolosigranulum Isobaculum*, *Marinilactibacillus*, and *Trichococcus* represent the most comprehensive group. *Granulicatella* and *Atopobacter* (formerly in the "*Enterococcaceae*") are in the second group. However, the phylogenetic position of these genera remains ambiguous, and reassignment may be warranted as more information becomes available.

Family "Enterococcaceae"

Four genera remain within the family "*Enterococcaceae*": *Enterococcus, Melissococcus, Tetragenococcus,* and *Vagococcus. Atopobacter* was transferred to the "*Carnobacteriaceae*" (see above). The recently described genus *Catellicoccus*, which is not described in this volume, phylogenetically represents a sister group to the "*Enterococcaceae*".

Family "Leuconostocaceae"

No changes of the taxonomic organization are made for the "*Leuconostocaceae*", which unifies three phylogenetically related genera: *Leuconostoc, Oenococcus*, and *Weissella*.

Family Streptococcaceae

In addition to the genera *Streptococcus* and *Lactococcus* in the previous road map, the family *Streptococcaceae* comprises a third, recently discovered, genus, *Lactovum* (Matthies et al., 2004).

Families *incertae* sedis

In the current road map, *Thermicanus*, *Gemella*, and *Exiguobacterium* have been reclassified into different families *incertae sedis* in recognition of their ambiguous taxonomic assignments (see above). The genera *Oscillospira* and *Syntrophococcus*, which were classified in this category in the previous road map (Garrity et al., 2005), have been transferred to the "*Ruminococcaceae*" and "*Lachnospiraceae*" in the *Clostridiales*, respectively (see below).

Class "Clostridia"

The class "*Clostridia*" is comprised of three orders, *Clostridiales*, *Halanaerobiales*, and "*Thermoanaerobacterales*". This organization is similar to the previous roadmap (Garrity et al., 2005) and unites the orders *Clostridiales* Prevot 1953^{AL} and *Eubacteriales* Buchanan 1917^{AL}. Preference is given to *Clostridiales* because of the priority of its type genus. Moreover, because many of the species united in this group were previously classified with the genus *Clostridium*, this classification is the least likely to cause confusion. While the order *Halanaerobiales* is monophyletic, the remaining two orders are paraphyletic and each include taxa with only low similarity to the majority of the *Firmicutes* (Fig. 4).

Order Clostridiales

In the previous road map (Garrity et al., 2005), the order *Clostridiales* was composed of eight families, many of which were paraphyletic. While it was not possible to fully address this problem, the current road map increases the number of families to ten and notes nine additional families as *incertae sedis* (Figs 5 and 6). This is only a first step, and significant further reorganization is warranted, especially as new data and concepts are applied to these taxa.

Seven of the eight original families are retained in the current outline. However, the family "*Acidaminococcaceae*" was not used in recognition of the priority of *Veillonellaceae* 1971^{AL}. In addition, the family "*Ruminococcaceae*" is proposed to accommodate a large number of genera transferred from other families. A new family, "*Gracilibacteraceae*", is also proposed for a newly discovered genus, *Gracilibacter*.

Family *Clostridiaceae*

The family *Clostridiaceae* comprises 13 genera in the current outline (Fig. 5). Phylogentically, these genera are distributed among three paraphyletic clusters and a fourth clade represented by a single genus, *Caminicella*. In addition, seven genera were transferred to other families. Three genera (*Acetivibrio*, *Faecalibacterium*, and *Sporobacter*) were transferred to the newly named family "*Ruminococcaceae*" (see below), unifying phylogenetically related former members of the *Clostridiaceae* and "*Lachnospiraceae*". The genus *Coprobacillus* was transferred to the *Erysipelotrichaceae*. The genus *Dorea* was transferred to the "*Lachnospiraceae*". Lastly, the genus *Acidaminobacter* was transferred to Family XII *Incertae Sedis*.

The first clostridial cluster is composed of the genera *Clostridrium*, *Anaerobacter*, *Caloramator*, Oxobacter Sarcina, and Thermobrachium Despite intense restructuring, the genus Clostridium is still partly paraphyletic, comprising a large collection of validly published species and species groups. Species whose common ancestry with the type species *Clostridium butyricum* is highly supported by the rRNA data remain in this genus. They are (in alphabetical not phylogenetic order): Clostridium absonum, acetobutylicum, acetireducens, acidisoli, akagii, algidicarnis, argentinense, aurantibutvricum, baratii, beijerinckii, botulinum, bowmanii, butyricum, carnis, cellulovorans, chartatabidum, chauvoei, cochlearium, colicanis, collagenovorans, cylindrosporum, diolis, disporicum, estertheticum, fallax, felsineum, frigoris, frigidicarnis, gasigenes, grantii, hemolyticum, histolyticum, homopropionicum, intestinale, kluyveri, lacusfryxellense, limosum, lundense, novyi, paraputrificum, pascui, pasteurianum, peptidivorans, perfringens, proteolyticum, puniceum, putrificum, putrefaciens, quinii, roseum, saccharobutylicum, saccharoperbutylacetonicum, sardiniense, sartagoforme, scatologenes, septicum, sporogenes, subterminale, tertium, tetani, tetanomorphum, thermopalmarium, thermobutvricum, thiosulfatireducens, tyrobutvricum, uliginosum, and *vincentii*. Species which according to phylogenetic relationships should be assigned to other taxonomic units are mentioned below. Some species previously classified with *Eubacterium* also belong into the radiation of *Clostridium sensu stricto: Eubacterium budayi, combesii, moniliforme, nitritogenes, and tarantellae.*

Other genera of this clade, *Anaerobacter*, *Oxobacter*, and *Sarcina*, are partly intermixed with *Clostridium* species, indicating that further reorganization of this cluster remains to be done.

The second *Clostridiaceae* cluster comprises the genera *Alkaliphilus*, *Anoxynatronum* (new; Garnova et al., 2003), *Natronincola*, *Tindallia* as well as the *Clostridium* species *alcalibutyricum*, *felsineum*, *formicoaceticum*, and *halophilum*. The genera *Thermohalobacter–Caloranaerobacter* (Wery et al., 2001) represent the third cluster. *Caminicella*, represents a fourth paraphyletic lineage previously classified within this family. Based upon the rRNA analyses, reclassification of these groups into other families may be warranted.

Family "Eubacteriaceae"

The six genera of the family "*Eubacteriaceae*" are monophyletic. They comprise the species of *Eubacterium stricto sensu (Eubacterium limosum, aggregans, barkeri, callanderi)* as well as the genera *Acetobacterium, Alkalibacter, Anaerofustis, Garciella*, and *Pseudoramibacter*. It is noteworthy that *Garciella* is the only thermophile among this group, and its assignment is the least strongly supported by the rRNA analyses reported here. Other analyses suggest a closer affiliation for this genus to the thermophiles *Thermohalobacter* and *Caloranaerobacter (Clostridiaceae* group 3, D. Alazard, personal communication). Therefore, reclassification may be warranted in the future. The genera *Anaerovorax* and *Mogibacterium* have been transferred to Family XIII *Incertae Sedis*. Additional *Eubacterium* species (*Eubacterium infirmum, minutum, nodatum,* and *sulci*) are closely related to these other genera.

Family "Gracilibacteraceae"

The family "*Gracilibacteraceae*" is proposed to encompass the newly described genus *Gracilibacter* (Lee et al., 2006).

Family "Heliobacteriaceae"

The family "*Heliobacteriaceae*" is maintained as defined in the previous volumes. It comprises four genera: *Heliobacterium*, *Heliobacillus*, *Heliophilum*, and *Heliorestis*.

Family "Lachnospiraceae"

The family "Lachnospiraceae" currently comprises 19 genera. The family is monophyletic, although a number of subclusters can be recognized. The "Lachnospiraceae" genera are: Acetitomaculum, Anaerostipes, Bryantella, Butyrivibrio, Catonella, Coprococcus, Dorea (formerly in the Clostridiaceae), Hespellia, Johnsonella, Lachnobacterium, Lachnospira, Moryella (new; Carlier et al., 2007), Oribacterium (Carlier et al., 2004), Parasporobacterium, Pseudobutyrivibrio, Roseoburia, Shuttleworthia, Sporobacterium, and Syntrophococcus (formerly incertae sedis within the "Lactobacillales"). A number of Clostridium species are found within the radiation of "Lachnospiraceae": Clostridium aerotolerans, algidixylanolyticum, aminophilum, aminovalericum, amygdalinum, bolteae, celerecrescens, coccoides, colinum, fimetarium, glycyrrhizinilyticum, hathewayi, herbivorans, hylemonae, indolis, lactatifermentans, lentocellum, methoxybenzovorans, neopropionicum, nexile, oroticum, piliforme, polysaccharolyticum, populeti, propionicum, proteoclasticum, scindens, sphenoides, saccharolyticum, symbiosum, xylanolyticum, and *xylanovorans*. Furthermore, *Eubacterium cellulosolvens*, *eligens*, *hallii*, *ramulus*, *rectale*, *ruminantium*, *uniforme*, *ventriosum*, and *xylanophilum*; *Ruminococcus gnavus*, *hansenii*, *hydrogenotrophicus*, *obeum*, *productus*, *schinkii*, and *torques*, as well as *Desulfotomaculum guttoideum* phylogenetically belong to this group.

Family Peptococcaceae

The current members of the family *Peptococcaceae* occupy two paraphyletic groups within the radiation of the *Clostridiales* (Fig. 6). The first cluster includes the genera *Peptococcus*, *Dehalobacter*, *Desulfitibacter*, *Desulfitobacterium*, *Desulfonispora*, *Desulfosporosinus*, and *Syntrophobotulus*, which form a tight monophyletic group. The second group is not closely related and includes *Cryptanaerobacter*, *Desulfotomaculum*, and *Pelotomaculum* species. Given its significant relationship to these genera, *Sporotomaculum* was transferred from the family "*Thermoanaerobacteraceae*". Lastly, *Thermincola* is currently classified within this group even though rRNA analyses suggest only a weak relationship to the *Peptococcaceae sensu stricto*.

Family "Peptostreptococcaceae"

The family "*Peptostreptococcaceae*" comprised 12 genera distributed over a number of paraphyletic groups in the original road map (Garrity et al., 2005). Most of these genera are now transferred to Family XI *Incertae Sedis* (Fig. 5). The current family is greatly circumscribed and monophyletic. It includes the genera *Peptostreptococcus*, *Filifactor*, *Sporacetigenium*, and *Tepidibacter* together with a number of validly published *Clostridium* and *Eubacterium* species: *Clostridium bartlettii* (new; Song et al., 2004), *bifermentans*, *difficile*, *ghoni*, *glycolicum*, *hiranonis*, *irregularis*, *litorale*, *lituseburense*, *mangenotii*, *paradoxum*, *sordellii*, *sticklandii*, and *Eubacterium tenue*, and *yurii*.

Family "Ruminococcaceae"

A new family is proposed for a monophyletic lineage comprising 11 genera (Fig. 6). Concerning their assignment in the outline of the previous volumes, this group represents a mixture of former *"Acidaminococcaceae"*, *Clostridiaceae*, and *"Lachnospiraceae"* as well as newly described genera: *Acetanaerobacterium* (new; Chen and Dong, 2004), *Acetivibrio* (formerly in the *Clostridiaceae*), *Anaerofilum* (formerly in the *"Lachnospiraceae"*), *Anaerotruncus, Ethanoligenens* (new; Xing et al., 2006), *Faecalibacterium* (formerly in the *Clostridiaceae*), *Fastidiosipila*, *Oscillospira*, *Papillibacter* (formerly in the *"Lachnospiraceae"*), *the genus Ruminococcus (R. flavefaciens* and the three species *Ruminococcus albus, bromii*, and *callidus*; the other *Ruminococcus* species remain within the family *"Lachnospiraceae"*), *Sporobacter* (formerly in the *Clostridiaceae*), and *Subdoligranulum* (new; Holmstrom et al., 2004). A number of validly published *Clostridium* species belong to this lineage according to their phylogentic relationships: *Clostridium aldrichii, alkalicellulosi* (new; Zhilina et al., 2005), *cellobioparum*, *cellulolyticum*, *hungatei, josui, leptum, methylpentosum, orbiscindens, papyrosolvens, stercorarium*,

straminisolvens (new; Kato et al., 2004), *termitidis*, *thermocellum*, *thermosuccinogenes*, and *viride*. *Eubacterium siraeum* also belongs to this lineage.

Family Syntrophomonadaceae

The genera previously assigned to the family Syntrophomonadaceae are widely dispersed and not closely related (Garrity et al., 2005). On the basis of the current rRNA-based phylogenetic analyses, many of these genera may not even be members of the phylum *Firmicutes*. Despite these tendencies, these taxa are maintained in the current volume owing to their taxonomic history and the lack of additional data demanding an official description of new phyla. The four very deep groups include the following: the Syntrophomonadaceae sensu stricto comprise the genera Syntrophomonas, Pelospora, Syntrophospora, *Syntrophothermus*, and *Thermosyntropha* (Fig. 7). These five genera are retained within the family Syntrophomonadaceae in the current road map. Another lineage is represented by Aminobacterium, Aminomonas, Anaerobaculum, Dethiosulfovibrio, Thermanaerovibrio, and Thermovirga (new; Dahle et al., 2006). This group has been assigned to Family XV Incertae Sedis (Fig. 6). The genera Thermaerobacter and Sulfobacillus (formerly assigned to the family "Alicyclobacillaceae" in the class Bacilli) share a common ancestor and represent a third deep lineage, now assigned to Family XVII *Incertae Sedis*. Caldicellulosiruptor represents the final deep lineage. Because of similarities to genera already classified within the "Thermoanaerobacterales", it is reclassified to Family III Incertae Sedis within that order (Fig. 7). Lastly, two genera (Anaerobranca and Carboxydocella) appear to represent lineages of the Firmicutes, although they are not closely related to each other. They are reclassified into Family XIV Incertae Sedis and Family XVI Incertae Sedis, respectively (Figs 5 and 7).

Family Veillonellaceae

The genera previous classified within the family "*Acidaminococaceae*" were reclassified into the family *Veillonellaceae* due to the priority of this name. After the transfer of the genus *Papillibacter* to the new family "*Ruminococcaceae*", this family became monophyletic (Fig. 6). The 26 genera currently harbored by the family *Veillonellaceae* are: *Acetonema*, *Acidaminococcus*, *Allisonella*, *Anaeroarcus*, *Anaeroglobus*, *Anaeromusa*, *Anaerosinus*, *Anaerovibrio*, *Centipeda*, *Dendrosporobacter*, *Dialister*, *Megasphaera*, *Mitsuokella*, *Pectinatus*, *Phascolarctobacterium*, *Propionispira*, *Propionispora*, *Quinella*, *Schwartzia*, *Selenomonas*, *Sporomusa*, *Succiniclasticum*, *Succinispira*, *Thermosinus*, *Veillonella*, and *Zymophilus*.

Families Incertae Sedis

Nine families *incertae sedis* were created to recognize some of the ambiguities remaining in the current classification.

Family XI *Incertae Sedis* contains a tight monophyletic cluster comprised of the genera *Anaerococcus, Finegoldia, Gallicola, Helcococcus, Parvimonas,* and *Peptoniphilus* which were transferred from the family "*Peptostreptococcaceae*". *Soehngenia, Sporanaerobacter, Tepidimicrobium* (new; (Slobodkin et al., 2006) and *Tissierella* represent four additional genera associated with this group. The genus *Tissierella* is closely related to *Clostridium hastiforme* and *ultunense. Sedimentibacter*, which was also previously classified within the "*Peptostreptococcaceae*", appears to represent a separate but neighboring lineage in the phylogenetic tree. Thus, it remains classified with other genera transferred from this family in the current outline.

Family XII *Incertae Sedis* includes *Guggenheimella* (new; Wyss et al., 2005), a newly described genus that, while clearly a member of the *Clostridiales*, cannot be assigned to any of the defined families. It possesses moderate relationships to *Acidaminobacter* (previously classified with the *Clostridiaceae*) and *Fusibacter* (previously classified with the "*Peptostreptococcaceae*").

Family XIII *Incertae Sedis* contains the genera *Anaerovorax* and *Mogibacterium*, which were transferred from the "*Eubacteriaceae*". This group possesses a weak relationship with Family XII *Incertae Sedis*.

Family XIV *Incertae Sedis* is comprised of *Anaerobranca*, which was previously classified within the *Syntrophomonadaceae*; however, it is not closely related to any other previously described family.

Family XV *Incertae Sedis* is comprised of *Aminobacterium*, *Aminomonas*, *Anaerobaculum*, *Dethiosulfovibrio*, and *Thermanaerovibrio*. These genera form a monophyletic clade that was previously classified within the *Syntrophomonadaceae*; however, they possess only low relatedness to the type genus of that family and, thus, warrant reclassification.

Family XVI *Incertae Sedis* is comprised of *Carboxydocella*, which was previously classified within the *Syntrophomonadaceae*. Because it is not closely related to any other previously described family, it has been classified within its own group.

Family XVII *Incertae Sedis* is comprised of the genera *Sulfobacillus* and *Thermaerobacter*. Formerly classified with the "*Alicyclobacillaceae*" and *Syntrophomonadaceae*, respectively, these genera represent either a very deep group of the phylum *Firmicutes* or, perhaps, a novel phylum.

Family XVIII *Incertae Sedis* is comprised of *Symbiobacterium*. This genus also appears to represent either a very deep group of the Phylum *Firmicutes* or another novel phylum.

Family XIX *Incertae Sedis* includes *Acetoanaerobium*, whose rRNA has not been sequenced but whose phenotypic properties suggest an affiliation to this order.

Order Halanaerobiales

The taxonomic organization of this order remains as outlined in the previous volumes (Garrity et al., 2005). It contains two families, *Halanaerobiaceae* and *Halobacteroidaceae* (Fig. 7).

Family Halanaerobiaceae

The monophyletic family *Halanaerobiaceae* currently is comprised of three genera, *Halanaerobium*, *Halocella*, and *Halothermothrix*.

Family Halobacteroidaceae

Eight genera are unified in a tight monophyletic cluster of the family *Halobacteroidaceae*. *Halobacteroides*, *Acetohalobium*, *Halanaerobacter*, *Halonatronum*, *Natroniella*, *Orenia*, *Selenihalanaerobacter*, and *Sporohalobacter* represent this family.

Order "Thermoanaerobacterales"

The order "*Thermoanaerobacterales*" is used in preference to "*Thermoanaerobacteriales*" (Garrity et al., 2005) in recognition of the priority of *Thermoanaerobacter* over *Thermoanaerobacterium* as the type genus. As in the case of the *Syntrophomonadaceae*, the diversity within this order is very large, and some members may represent novel phyla (Mori et al., 2003); Fig. 7). Therefore, reclassification within this group is expected in the near future, and the current classification is of limited biological significance.

Family "Thermonanaerobacteraceae"

Eight genera are currently classified within this family, but they are not closely related to each other. The type genus *Thermoanaerobacter* forms part of a monophyletic cluster comprised of *Ammonifex*, *Carboxydibrachium* (now reclassified within *Caldanaerobacter*), *Caldanaerobacter*, *Carboxydothermus* (previously classified within the *Peptococcaceae*), *Thermacetogenium*, and *Thermanaeromonas*. Two additional genera, *Gelria* and *Moorella*, are neighbors of this cluster.

Family Thermodesulfobiaceae

A second family is comprised of the genera *Coprothermobacter* and *Thermodesulfobium*. Although not particularly closely related to each other, they are both much more distantly related to other members of the phylum *Firmicutes*.

Families Incertae Sedis

Family III Incertae Sedis contains a monophyletic cluster that is weakly related to both the "*Thermoanaerobacteraceae*" and *Syntrophomonadaceae* (Fig. 7). It is comprised of the genera *Caldicellulosiruptor* (from the *Syntrophomonadaceae*), *Thermosediminibacter*, and *Thermovenabulum*. While *Thermoanaerobacterium* is not a member of this cluster, it appears as a neighboring group in phylogenetic trees. Therefore, it is included in this family until additional analyses warrant a more informed reclassification.

Family IV *Incertae Sedis* includes the genus *Mahella*. While it possesses some relatedness to members of the "*Thermoanaerobacteraceae*" and Family III *Incertae Sedis* (above), its distinctive position in the rRNA gene tree, near the "*Ruminococcaceae*" within the *Clostridiales*, and phenotypic properties suggest that it represents a novel family (Fig. 6).

Class "Erysipelotrichi"

With the elevation of the *Mollicutes* to the phylum *Tenericutes*, the creation of a separate class within the *Firmicutes* was warranted for the family *Erysipelotrichaceae*. This new classification recognizes the low

similarity of the rRNA of this group with other members or the phylum as well as the similarity in cell wall and other phenotypic features. This class comprises a single order, *"Erysipelotrichales"*, and the family *Erysipelotrichaceae*.

Family Erysipelotrichaceae

In comparison to the outlines of the previous volumes, the family *Erysipelotrichaceae* was extended by the inclusion of four additional genera. Besides one newly described genus (*Allobaculum*), three genera were transferred from other families. The family is now organized in eight genera: *Erysipelothrix*, *Allobaculum* (new; Greetham et al., 2004), *Bulleidia*, *Catenibacterium* (formerly in the "*Lachnospiraceae*"), *Coprobacillus* (formerly in the *Clostridia*), *Holdemania*, *Solobacterium*, and *Turicibacter* (formerly *incertae sedis* among *Bacillales*). Furthermore, a number of type species validly published as members of genera not assigned to the *Erysipelotrichaceae* should also be classified within this family. These include *Clostridium catenaformis*, *cocleatum*, *innocuum*, *ramosum*, and *spiroforme*; *Eubacterium biforme*, *cylindroides*, *dolichum*, and *tortuosum*; *Lactobacillus catenaformis* and *vitulinus*; and *Streptococcus pleomorphus*.

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Figure legends

FIGURE 1. Consensus dendrogram reflecting the phylogenetic relationships of the classes "*Bacilli*" and "*Erysipelotrichi*" within the *Firmicutes*. The tree is based on maximum-likelihood analyses of a dataset comprising about 5000 almost full-length high-quality 16S rRNA sequences from representatives of the *Firmicutes* and another 1000 representing the major lines of decent of the three domains *Bacteria, Archaea,* and *Eucarya*. The topology was evaluated by distance matrix and maximum-parsimony analyses of the dataset. In addition, maximum-parsimony analyses of all currently available almost complete small-subunit rRNA sequences (137,400 of ARB-SILVA release 92, Prüsse et al., 2007) were performed. Only alignment positions invariant in at least 50% of the included primary structures from *Firmicutes* were included for tree reconstruction. Multifurcations indicate that a common relative branching order was not significantly supported applying alternative treeing methods. The (horizontal) branch lengths indicate the significance of the respective node separation.

FIGURE 2. Consensus dendrogram reflecting the phylogenetic relationships of the order *Bacillales* within the class "*Bacilli*". Analyses were performed as described for Fig. 1.

FIGURE 3. Consensus dendrogram reflecting the phylogenetic relationships of the order "*Lactobacillales*" within the class "*Bacilli*". Analyses were performed as described for Fig. 1.

FIGURE 4. Consensus dendrogram reflecting the phylogenetic relationships of the class "*Clostridia*" within the *Firmicutes*. Analyses were performed as described for Fig. 1.

FIGURE 5. Consensus dendrogram reflecting the phylogenetic relationships of the order *Clostridiales* (part one) within the class "*Clostridia*". Analyses were performed as described for Fig. 1.

FIGURE 6. Consensus dendrogram reflecting the phylogenetic relationships of the order *Clostridiales* (part two) within the class "*Clostridia*". Analyses were performed as described for Fig. 1. Family *Incertae Sedis* IV is from the "*Thermoanaerobacterales*".

FIGURE 7. Consensus dendrogram reflecting the phylogenetic relationships of the orders *Halanaerobiales* and "*Thermoanaerobacterales*" as well as some deep branches of the *Clostridiales* within the class "*Clostridia*". Analyses were performed as described for Fig. 1.

Figure 1.

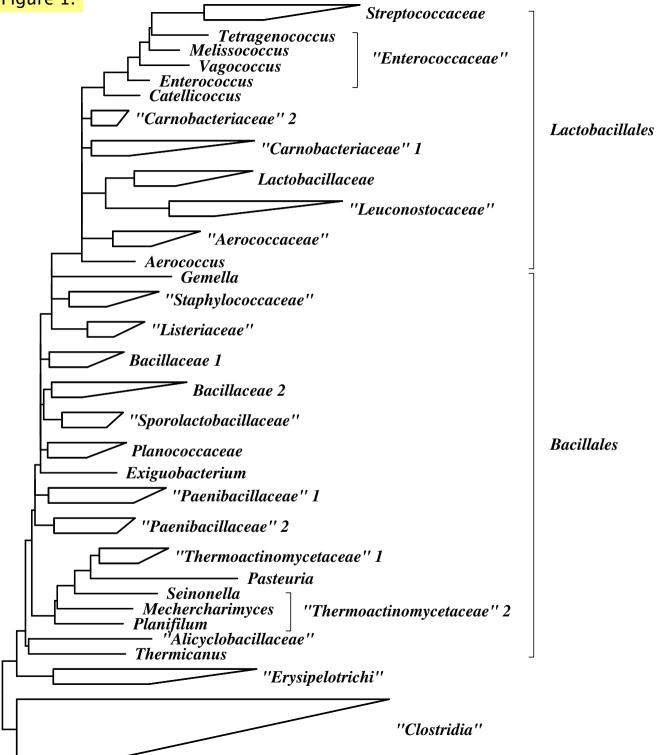


Figure 2.

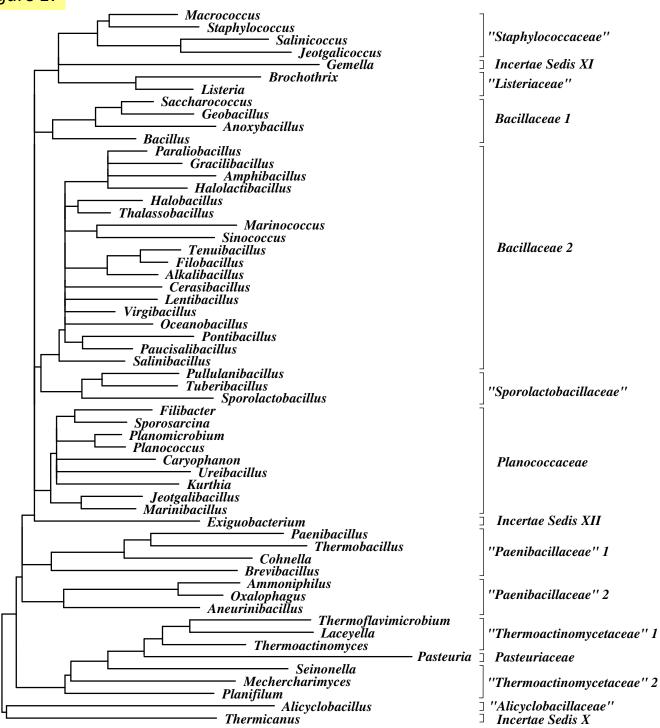


Figure 3.

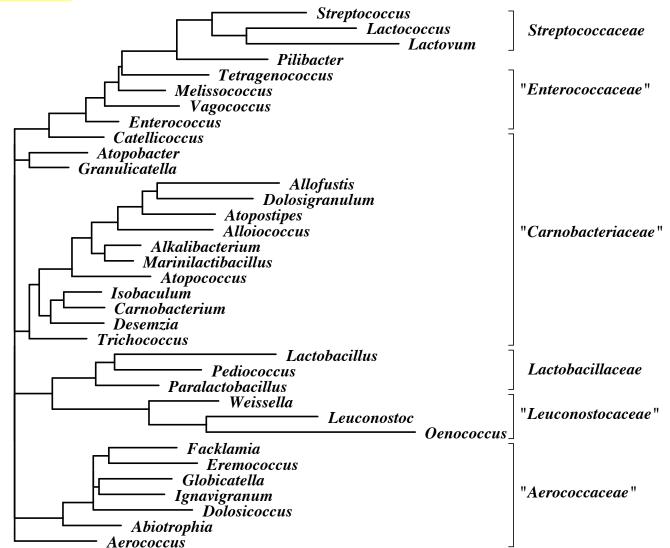


Figure 4.

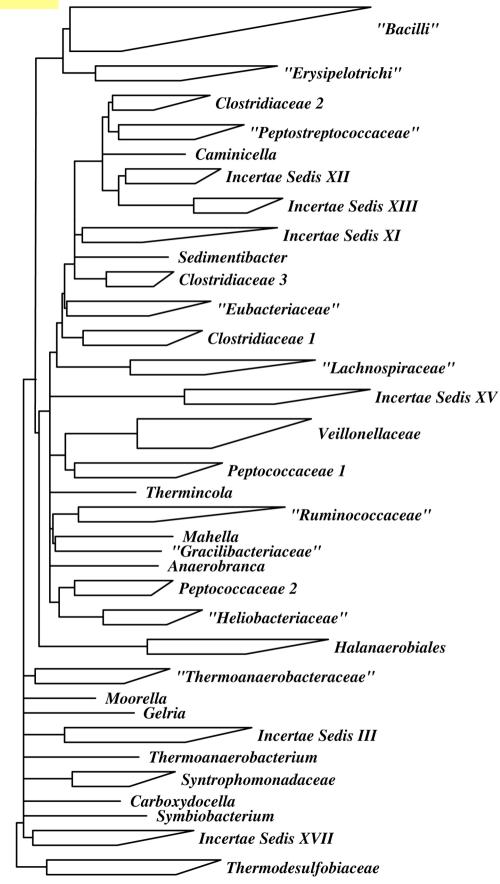
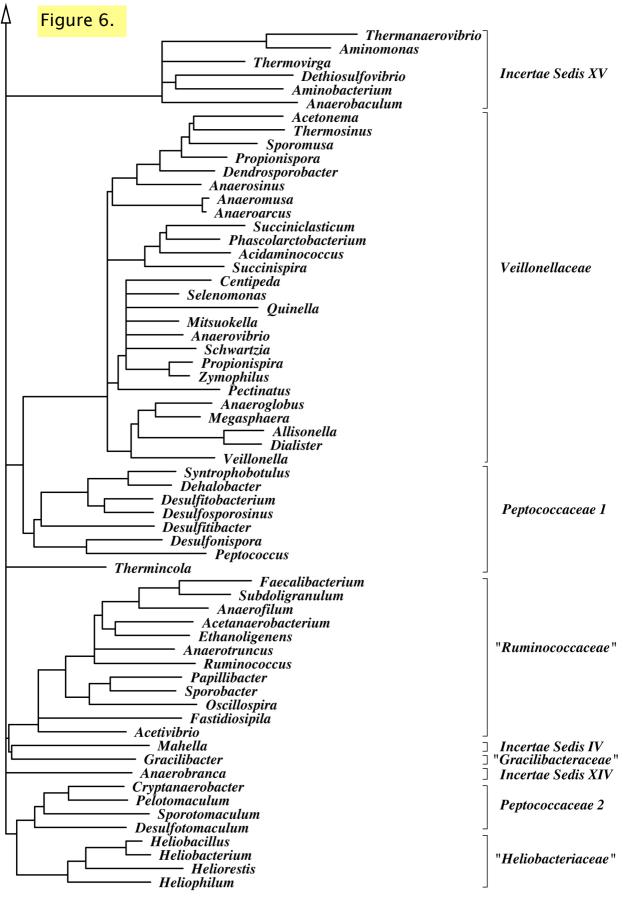
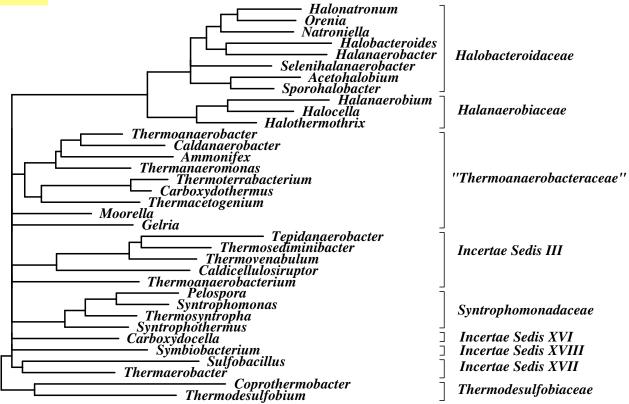


Figure 5.

	_
Anoxynatronum	
Tindallia	
Anaerovirgula	Clostridiaceae 2
Natronincola	
Alkaliphilus	
Sporacetigenium	
	"Peptostreptococcaceae"
Tepidibacter	
Filifactor	
Caminicella	Clostridiaceae 4
Acidaminobacter	
	Incertae Sedis XII
Guggenheimella	
Anaerovorax	Incertae Sedis XIII
Mogibacterium	
Anaerococcus	
Helcococcus	
Parvimonas	
Finegoldia	
Ğallicola	
Peptoniphilus	Incertae Sedis XI
Tissierella	
Soehngenia	
Sporanaerobacter	
Tepidimicrobium	
Sedimentibacter	
Caloranaerobacter	Clostridiaceae 3
Thermohalobacter	
Acetobacterium	
Eubacterium	
Pseudoramibacter	"Eubacteriaceae"
Anaerofustis	
Alkalibacter	
Garciella	
Sarcina	
Anaerobacter	
Clostridium	Clostridiaceae 1
Caloramator	Ciosirialaceae I
Thermobrachium	
Oxobacter	
Pseudobutyrivibrio	
Shuttleworthia	
Lachnobacterium	
Roseburia	
Johnsonella	
Syntrophococcus	
Bryantella	
Dorea	
Hespellia	"Lachnospiraceae"
Oribacterium	
Sporobacterium	
Parasporobacterium	
Anaerostipes	
Butyrivibrio	
Catonella	
Lachnospira	
Acetitomaculum	
Y	





Taxonomic Outline of the Phylum Firmicutes

Wolfgang Ludwig, Karl-Heinz Schleifer and William B. Whitman

All taxa recognized within this volume of the rank of genus and above are listed below. The nomenclatural type is listed first within each taxon followed by the remaining taxa in alphabetical order.

Phylum XIII. Firmicutes Class I. "Bacilli" Order I. Bacillales^{AL (T)} Family I. *Bacillaceae*^{AL} Genus I. Bacillus^{AL (T)} Genus II. Alkalibacillus^{VP} Genus III. Amphibacillus^{VP} Genus IV. Anoxybacillus^{VP} Genus V. Cerasibacillus^{VP} Genus VI. Filobacillus^{VP} Genus VII. Geobacillus^{VP} Genus VIII. Gracilibacillus^{VP} Genus IX. Halobacillus^{VP} Genus X. Halolactibacillus^{VP} Genus XI. Lentibacillus^{VP} Genus XII. Marinococcus^{VP} Genus XIII. Oceanobacillus^{VP} Genus XIV. Paraliobacillus^{VP} Genus XV. Pontibacillus^{VP} Genus XVI. Saccharococcus^{VP} Genus XVII. Tenuibacillus^{VP} Genus XVIII. Thalassobacillus^{VP} Genus XIX. Virgibacillus^{VP} Family II. "*Alicyclobacillaceae* Genus I. Alicyclobacillus^{VP (T)} Family III. "Listeriaceae" Genus I. Listeria^{AL (T)} Genus II. Brochothrix^{AL} Family IV. "Paenibacillaceae" Genus I. Paenibacillus^{VP (T)} Genus II. Ammoniphilus^{VP} Genus III. Aneurinibacillus^{VP} Genus IV. Brevibacillus^{VP} Genus V. Cohnella^{VP}

Genus VI. Oxalophagus^{VP} Genus VII. Thermobacillus^{VP} Family V. Pasteuriaceae^{AL} Genus I. Pasteuria^{AL(T)} Family VI. Planococcaceae^{AL} Genus I. Planococcus^{AL (T)} Genus II. Carvophanon^{VP} Genus III. Filibacter^{VP} Genus IV. Jeotgalibacillus^{VP} Genus V. Kurthia^{AL} Genus VI. Marinibacillus^{VP} Genus VII. Planomicrobium^{VP} Genus VIII. Sporosarcina^{AL} Genus IX. Ureibacillus^{VP} Family VII. "Sporolactobacillaceae" Genus I. Sporolactobacillus^{AL (T)} Family VIII. "Staphylococcaceae" Genus I. Staphylococcus^{AL (T)} Genus II. Jeotgalicoccus^{VP} Genus III. Macrococcus^{VP} Genus IV. Salinicoccus^{VP} Family IX. "Thermoactinomycetaceae" Genus I. Thermoactinomyces^{AL (T)} Genus II. Lacevella^{VP} Genus III. Mechercharimyces^{VP} Genus IV. Planifilum^{VP} Genus V. Seinonella^{VP} Genus VI. Shimazuella^{VP} Genus VII. Thermoflavimicrobium^{VP} Family X. Incertae Sedis Genus I. Thermicanus^{VP} Family XI. Incertae Sedis Genus I. Gemella^{AL} Family XII. Incertae Sedis Genus I. Exiguobacterium^{VP} Order II. "Lactobacillales" Family I. Lactobacillaceae^{AL} Genus I. Lactobacillus^{AL (T)} Genus II. Paralactobacillus^{VP} Genus III. Pediococcus^{AL} Family II. "Aerococcaceae"

Genus I. Aerococcus^{AL (T)} Genus II. Abiotrophia^{VP} Genus III. Dolosicoccus^{VP} Genus IV. Eremococcus^{VP} Genus V. Facklamia^{VP} Genus VI. Globicatella^{VP} Genus VII. Ignavigranum^{VP} Family III. "Carnobacteriaceae" Genus I. Carnobacterium^{VP (T)} Genus II. Alkalibacterium^{VP} Genus III. Allofustis^{VP} Genus IV. Alloiococcus^{VP} Genus V. Atopobacter^{VP} Genus VI. Atopococcus^{VP} Genus VII. Atopostipes^{VP} Genus VIII. Desemzia^{VP} Genus IX. Dolosigranulum^{VP} Genus X. Granulicatella^{VP} Genus XI. Isobaculum^{VP} Genus XII. Marinilactibacillus^{VP} Genus XIII. Trichococcus^{VP} Family IV. "Enterococcaceae" Genus I. Enterococcus^{VP (T)} Genus II. Melissococcus^{VP} Genus III. Tetragenococcus^{VP} Genus IV. Vagococcus^{VP} Family V. "Leuconostocaceae" Genus I. Leuconostoc^{AL (T)} Genus II. Oenococcus^{VP} Genus III. Weissella^{VP} Family VI. Streptococcaceae^{AL} Genus I. Streptococcus^{AL (T)} Genus II. Lactococcus^{VP} Genus III. Lactovum^{VP} Class II. "Clostridia" Order I. Clostridiales^{AL (T)} Family I. Clostridiaceae^{AL} Genus I. Clostridium^{AL (T)} Genus II. Alkaliphilus^{VP} Genus III. Anaerobacter^{VP} Genus IV. Anoxynatronum^{VP}

Genus V. Caloramator^{VP} Genus VI. Caloranaerobacter^{VP} Genus VII. Caminicella^{VP} Genus VIII. Natronincola^{VP} Genus IX. Oxobacter^{VP} Genus X. Sarcina^{AL} Genus XI. Thermobrachium^{VP} Genus XII. Thermohalobacter^{VP} Genus XIII. Tindallia^{VP} Family II. "Eubacteriaceae" Genus I. Eubacterium^{AL (T)} Genus II. Acetobacterium^{AL} Genus III. Alkalibacter^{VP} Genus IV. Anaerofustis^{VP} Genus V. Garciella^{VP} Genus VI. Pseudoramibacter^{VP} Family III. "Gracilibacteraceae" Genus I. Gracilibacter^{VP (T)} Family IV. "Heliobacteriaceae" Genus I. Heliobacterium^{VP (T)} Genus II. Heliobacillus^{VP} Genus III. Heliophilum^{VP} Genus IV. Heliorestis^{VP} Family V. "Lachnospiraceae" Genus I. Lachnospira^{AL (T)} Genus II. Acetitomaculum^{VP} Genus III. Anaerostipes^{VP} Genus IV. Bryantella^{VP} Genus V. Butyrivibrio^{AL} Genus VI. Catonella^{VP} Genus VII. Coprococcus^{AL} Genus VIII. Dorea^{VP} Genus IX. Hespellia^{VP} Genus X. Johnsonella^{VP} Genus XI. Lachnobacterium^{VP} Genus XII. Morvella^{VP} Genus XIII. Oribacterium^{VP} Genus XIV. Parasporobacterium^{VP} Genus XV. Pseudobutyrivibrio^{VP} Genus XVI. Roseburia^{VP} Genus XVII. Shuttleworthia^{VP}

Genus XVIII. Sporobacterium^{VP} Genus XIX. Syntrophococcus^{VP} Family VI. Peptococcaceae^{AL} Genus I. Peptococcus^{AL (T)} Genus II. Cryptanaerobacter^{VP} Genus III. Dehalobacter^{VP} Genus IV. Desulfitobacterium^{VP} Genus V. Desulfonispora^{VP} Genus VI. Desulfosporosinus^{VP} Genus VII. Desulfotomaculum^{AL} Genus VIII. Pelotomaculum^{VP} Genus IX. Sporotomaculum^{VP} Genus X. Syntrophobotulus^{VP} Genus XI. Thermincola^{VP} Family VII. "Peptostreptococcaceae" Genus I. Peptostreptococcus^{AL (T)} Genus II. Filifactor^{VP} Genus III. Tepidibacter^{VP} Family VIII. "Ruminococcaceae" Genus I. Ruminococcus^{AL (T)} Genus II. Acetanaerobacterium^{VP} Genus III. Acetivibrio VP Genus IV. Anaerofilum^{VP} Genus V. Anaerotruncus^{VP} Genus VI. Faecalibacterium^{VP} Genus VII. Fastidiosipila^{VP} Genus VIII. Oscillospira^{AL} Genus IX. Papillibacter^{VP} Genus X. Sporobacter^{VP} Genus XI. Subdoligranulum^{VP} Family IX. Syntrophomonadaceae^{VP} Genus I. Syntrophomonas^{VP (T)} Genus II. Pelospora^{VP} Genus III. Syntrophospora^{VP} Genus IV. Syntrophothermus^{VP} Genus V. Thermosyntropha^{VP} Family X. Veillonellaceae^{VP} Genus I. Veillonella^{AL (T)} Genus II. Acetonema^{VP} Genus III. Acidaminococcus^{AL} Genus IV. Allisonella^{VP}

Genus V. Anaeroarcus^{VP} Genus VI. Anaeroglobus^{VP} Genus VII. Anaeromusa^{VP} Genus VIII. Anaerosinus^{VP} Genus IX. Anaerovibrio^{AL} Genus X. Centipeda^{VP} Genus XI. Dendrosporobacter^{VP} Genus XII. Dialister^{VP} Genus XIII. Megasphaera^{AL} Genus XIV. Mitsuokella^{VP} Genus XV. Pectinatus^{AL} Genus XVI. Phascolarctobacterium^{VP} Genus XVII. Propionispira^{VP} Genus XVIII. Propionispora^{VP} Genus XIX. *Quinella*^{VP} Genus XX. Schwartzia^{VP} Genus XXI. Selenomonas^{AL} Genus XXII. Sporomusa^{VP} Genus XXIII. Succiniclasticum^{VP} Genus XXIV. Succinispira^{VP} Genus XXV. Thermosinus^{VP} Genus XXVI. Zymophilus^{VP} Family XI. Incertae Sedis Genus I. Anaerococcus^{VP} Genus II. Finegoldia^{VP} Genus III. Gallicola^{VP} Genus IV. Helcococcus^{VP} Genus V. Parvimonas^{VP} Genus VI. Peptoniphilus^{VP} Genus VII. Sedimentibacter^{VP} Genus VIII. Soehngenia^{VP} Genus IX. Sporanaerobacter^{VP} Genus X. Tissierella^{VP} Family XII. Incertae Sedis Genus I. Acidaminobacter^{VP} Genus II. Fusibacter^{VP} Genus III. Guggenheimella^{VP} Family XIII. Incertae Sedis Genus I. Anaerovorax^{VP} Genus II. Mogibacterium^{VP} Family XIV. Incertae Sedis

Genus I. Anaerobranca^{VP} Family XV. Incertae Sedis Genus I. Aminobacterium^{VP} Genus II. Aminomonas^{VP} Genus III. Anaerobaculum^{VP} Genus IV. Dethiosulfovibrio^{VP} Genus V. Thermanaerovibrio^{VP} Family XVI. Incertae Sedis Genus I. Carboxydocella^{VP} Family XVII. *Incertae Sedis* Genus I. Sulfobacillus^{VP} Genus II. Thermaerobacter^{VP} Family XVIII. Incertae Sedis Genus I. Symbiobacterium^{VP} Family XIX. Incertae Sedis Genus I. Acetoanaerobium^{VP} Order II. Halanaerobiales^{VP} Family I. Halanaerobiaceae^{VP} Genus I. Halanaerobium^{VP (T)} Genus II. Halocella^{VP} Genus III. Halothermothrix^{VP} Family II. Halobacteroidaceae^{VP} Genus I. Halobacteroides^{VP (T)} Genus II. Acetohalobium^{VP} Genus III. Halanaerobacter^{VP} Genus IV. Halonatronum^{VP} Genus V. Natroniella^{VP} Genus VI. Orenia^{VP} Genus VII. Selenihalanaerobacter^{VP} Genus VIII. Sporohalobacter^{VP} Order III. "Thermoanaerobacterales" Family I. "Thermoanaerobacteraceae" Genus I. Thermoanaerobacter^{VP (T)} Genus II. Ammonifex^{VP} Genus III. Caldanaerobacter^{VP} Genus IV. Carboxydothermus^{VP} Genus V. Gelria^{VP} Genus VI. Moorella^{VP} Genus VII. Thermacetogenium^{VP} Genus VIII. Thermanaeromonas^{VP} Family II. Thermodesulfobiaceae^{VP}

Genus I. Thermodesulfobium $^{VP(T)}$ Genus II. Coprothermobacter VP Family III. Incertae Sedis Genus I. Caldicellulosiruptor^{VP} Genus II. Thermoanaerobacterium^{VP} Genus III. Thermosediminibacter^{VP} Genus IV. Thermovenabulum^{VP} Family IV. Incertae Sedis Genus I. Mahella^{VP} Class III. "Erysipelotrichi" Order I. "Erysipelotrichales" (T) Family I. Erysipelotrichaceae^{VP} Genus I. Erysipelothrix^{AL (T)} Genus II. Allobaculum^{VP} Genus III. Bulleidia^{VP} Genus IV. Catenibacterium^{VP} Genus V. Coprobacillus^{VP} Genus VI. Holdemania^{VP} Genus VII. Solobacterium^{VP} Genus VIII. Turicibacter^{VP}