

Road map of the phyla *Bacteroidetes*, *Spirochaetes*, *Tenericutes* (*Mollicutes*), *Acidobacteria*, *Fibrobacteres*, *Fusobacteria*, *Dictyoglomi*, *Gemmatimonadetes*, *Lentisphaerae*, *Verrucomicrobia*, *Chlamydiae*, and *Planctomycetes*

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This revised road map updates previous outlines of Garrity and Holt (2001) and Garrity et al. (2005) with the description of additional taxa and new phylogenetic analyses. While the outline/road map seeks to be complete for all taxa validated prior to July 1, 2006, 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 the variable sequence positions, may differ with respect to detailed topology, especially at levels of closer relationships within and between genera. In the trees shown here, branch lengths – in 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 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, 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 phylogeny and establishing taxonomy of organisms. Although generally well established in taxonomy, the polyphasic approach cannot currently be 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 400,000 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 the definition of 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>; Pruesse et al., 2007) databases of processed small-subunit rRNA primary structures.

Data analysis

The current release of the integrated small-subunit rRNA database of the SILVA project (Pruesse et al., 2007) provides 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 18–1509 (*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 length with processed sequence

data. Unfortunately, only some 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 optimal 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

The phylogenetic conclusions were used for evaluating and modifying the taxonomic outline of the phyla "*Bacteroidetes*", "*Spirochaetes*", *Tenericutes* (*Mollicutes*), "*Acidobacteria*", "*Fibrobacteres*", "*Fusobacteria*", "*Dictyoglomi*", *Gemmatimonadetes*, *Lentisphaerae*, "*Verrucomicrobia*", "*Chlamydiae*", and "*Planctomycetes*". These include all the phyla not described in earlier volumes with the exception of the *Actinobacteria*, which will be included in the fifth and last volume of this edition. There is no particular rationale for inclusion in this volume. Although some of the phyla may be related in a kingdom or superphylum (i.e., "*Chlamydiae*", *Lentisphaerae*, "*Planctomycetes*", and "*Verrucomicrobia*") (Griffiths and Gupta, 2007; Lee et al., 2009; Pilhofer et al., 2008; Wagner and Horn, 2006), most are unrelated to each other (Figure 1). Some are major pathogens of humans, other animals, and plants. Some are exotic and only described in the last decade.

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 validly published, but phylogenetically misplaced, type strains are also generally maintained. These strains are mentioned in the context of the respective phylogenetic groups. In cases 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.

Upon the recommendation of the Judicial Commission (De Vos et al., 2005), many of the names and classifications previously proposed by Cavalier-Smith (2002) are not used in this work. The classification used categories not covered by the Rules of the Code and priority and proposed types without standing in nomenclature. For these reasons, the following phylum (or

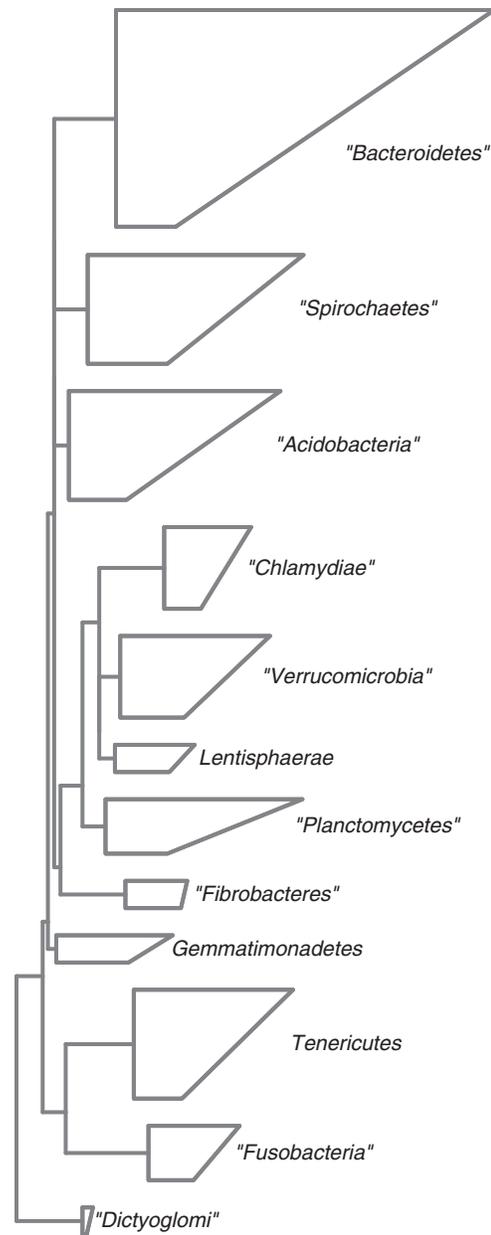


FIGURE 1. Phyla *Bacteroidetes*, *Spirochaetes*, *Tenericutes*, *Acidobacteria*, *Fibrobacteres*, *Fusobacteria*, *Dictyoglomi*, *Gemmatimonadetes*, *Lentisphaerae*, *Verrucomicrobia*, *Chlamydiae*, and *Planctomycetes*. While the phyla *Lentisphaerae*, *Verrucomicrobia*, *Chlamydiae*, and *Planctomycetes* may be specifically related to each other, the other phyla included in volume 4 are not related.

division) names are not used: *Planctobacteria*, *Sphingobacteria*, and *Spirochaetae*. Likewise, the following class names are not used: *Acidobacteria*, *Chlamydiae*, *Flavobacteria*, *Planctomycea*, and *Spirochaetes*. Lastly, priority for the order name *Acidobacteriales* is no longer attributed to Cavalier-Smith (2002).

Phylum "*Bacteroidetes*"

In previous classifications, the phylum "*Bacteroidetes*" was proposed to comprise three classes, "*Bacteroidia*", "*Flavobacteriia*", and "*Sphingobacteriia*" (Garrity et al., 2005). While the analyses performed here, which were based upon many more sequences and differ-

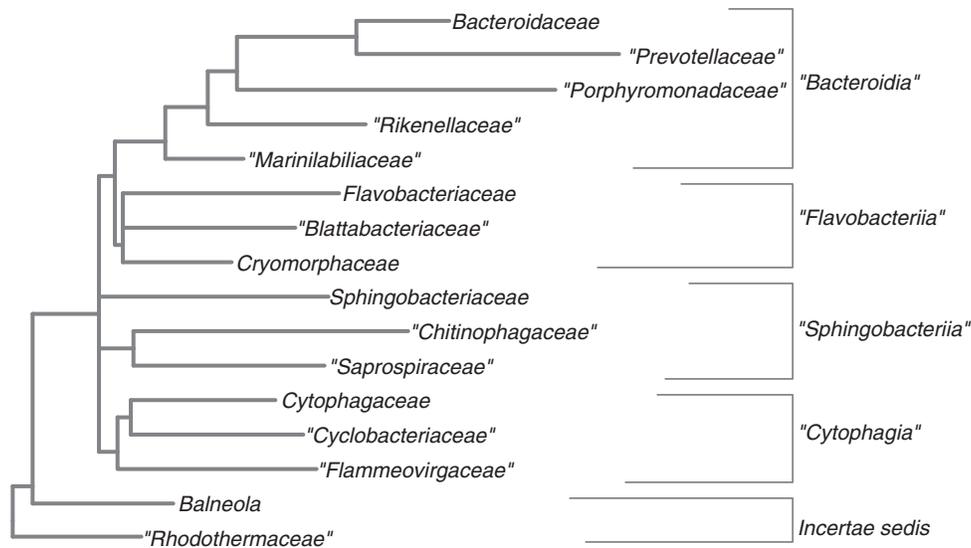


FIGURE 2. Overview of the phylum "Bacteroidetes". This phylum contains 15 families classified within four classes. Currently, the *incertae sedis* taxa *Balneola* and "*Rhodothermaceae*" are classified within the class "Cytophagia".

ent methods, generally support this conclusion, they also justify formation of a fourth class within this phylum, the "Cytophagia" (Figure 2). This new class comprises many genera previously classified within the "Flexibacteraceae", "Flammeovirgaceae", and "Crenotrichaceae" (see below). Thus, the phylum "Bacteroidetes" comprises at least four phylogenetic groups that are well delineated on the basis of their 16S rRNA gene sequences. In addition, two groups are affiliated with the phylum but could not be readily assigned to one of these classes. While additional evidence may warrant classification with one of the known or novel classes, these organisms were grouped within *Incertae sedis* of the "Cytophagia" for the present time (Figure 2).

Class "Bacteroidia" and order "Bacteroidales"

The class "Bacteroidia" contains five families, all classified within the order "Bacteroidales". These families include the four families proposed previously (Garrity et al., 2005), *Bacteroidaceae*, "*Rikenellaceae*", "*Porphyromonadaceae*", and "*Prevotellaceae*", as well as a new family proposed here, "*Marinilabiliaceae*" (Figure 3). In addition, on the basis of the dissimilarity of its 16S rRNA gene sequence to other members of the order, *Odoribacter* (*Bacteroides*) *splanchnicus* may represent an additional undescribed family or a member of the "*Marinilabiliaceae*". However, chemotaxonomic characteristics and analyses of the *fimA* gene imply a close relationship to the family "*Porphyromonadaceae*" (Hardham et al., 2008). Therefore, its reclassification is not proposed at this time. Lastly, the recently described marine organism, *Prolixibacter bellariivorans*, appears to represent a deep lineage in this class but whose affiliation with these families is ambiguous (Holmes et al., 2007).

Family *Bacteroidaceae*

In addition to the type genus, *Bacteroides*, this family comprises three monospecific genera, *Acetofilamentum*, *Acetothermus*, and *Anaerorhabdus*, and one genus, *Acetomicrobium*, comprising two species. Because complete 16S rRNA gene sequences are not available for representatives of these four genera, these assignments are tentative. Two genera previously assigned to

this family have also been reassigned. As recommended by Morotomi et al. (2007), *Megamonas* has been transferred to the *Firmicutes*. Based on its rRNA gene sequence, *Anaerophaga* has been transferred to the new family "*Marinilabiliaceae*".

The genus *Bacteroides* comprises at least six lineages or clades. The type species, *Bacteroides fragilis*, together with *Bacteroides acidifaciens*, *caccae*, *finogoldii*, *nordii*, *ovatus*, *salyersiae*, *thetaitotamicon*, and *xylanisolvans*, represent a cluster slightly separated from the other members of the genus. If supported by other evidence, each of the other lineages could be classified as new genera within this family. The other lineages are represented by *Bacteroides cellulolyticus* and *intestinalis*; *Bacteroides coprosus* and *propionifaciens*; *Bacteroides pyogenes*, *suis*, and *tectus*; *Bacteroides barnesiae*, *coprocola*, *coprophilus*, *dorei*, *helicogenes*, *massiliensis*, *plebeius*, *salanitronis*, *uniformis*, and *vulgatus*. The species *Bacteroides eggerthii*, *gallinarum*, and *stercoris* cannot clearly be assigned to one of the lineages.

In addition to these clades within the genus, the following validly published species are probably misclassified. *Bacteroides splanchnicus* was recently reclassified as *Odoribacter splanchnicus* (Hardham et al., 2008); this genus may represent a novel member of family "*Porphyromonadaceae*" (see above). *Bacteroides capillosus* and *cellulosolvans* are probably members of the phylum *Firmicutes*. In addition, rRNA gene sequences are not available for *Bacteroides capillus*, *forsythus*, *furcosus*, *polypragmatus*, and *salivovus*, so their assignment is uncertain.

Lastly, the family *Bacteroidaceae* appears to be paraphyletic, and the family "*Prevotellaceae*" falls within the radiation of *Bacteroides* clades. Because the members of the "*Prevotellaceae*" are generally closely related and the branch length to the *Bacteroidaceae* is fairly long, this conclusion is tentative. While these families were not combined at this time, this classification may warrant further investigation.

Family "*Marinilabiliaceae*"

This family represents a group of sister but not clearly monophyletic branches within the "Bacteroidales" and comprises three genera.

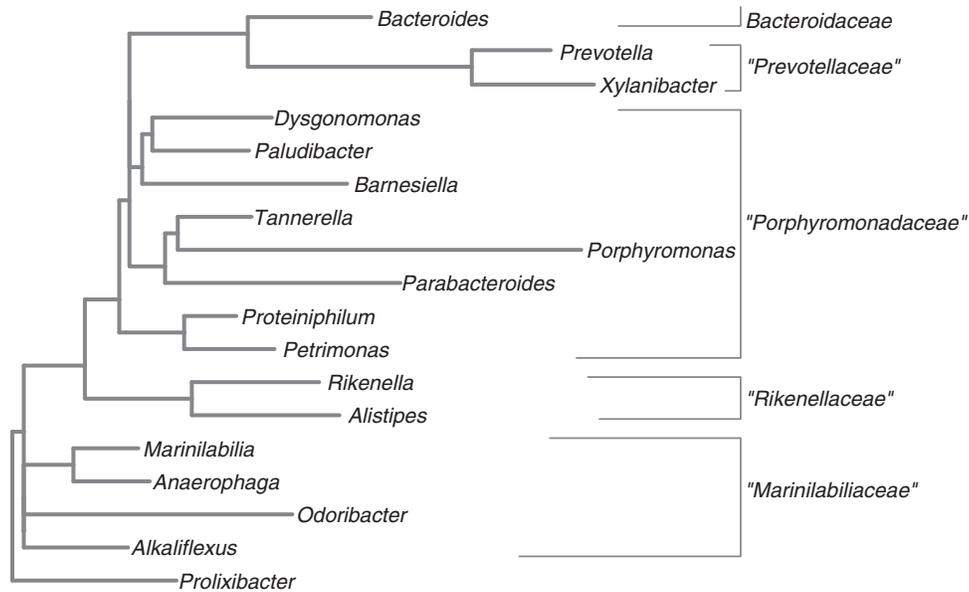


FIGURE 3. Genera of the class "Bacteroidia". This class comprises five families and the genus *Prolixibacter*, which has not yet been assigned to a family.

The type genus, *Marinilabilia*, contains two species, *Marinilabilia salmonicolor* and *agarovorans*, and was previously classified within the "Rikenellaceae" (Garrity et al., 2005). The remaining taxa include *Alkaliflexus imshenetskii* and *Anaerophaga thermohalophila*, the latter of which was formerly classified within the *Bacteroidaceae* (Garrity et al., 2005). The current analysis suggests that *Cytophaga fermentans* should be reclassified as a novel genus that is associated with this family. Lastly, rRNA analyses suggest that *Odoribacter* (*Bacteroides*) *splanchnicus*, which was proposed after the deadline for inclusion in this volume, may represent an additional member of the "Marinilabiliaceae". However, chemotaxonomic characteristics and analyses of the *fimA* gene imply a close relationship to the family "Porphyromonadaceae" (Hardham et al., 2008), so this classification is not proposed at this time.

Family "Rikenellaceae"

The family comprises the monospecific genus *Rikenella microfus* and the closely related genus *Alistipes*. The latter genus comprises the type species *Alistipes putredinis* and *Alistipes finegoldii*, *onderdonkii*, and *shahii*. *Marinilabilia*, which was classified within this family by Garrity et al. (2005), is now classified within the family "Marinilabiliaceae".

Family "Porphyromonadaceae"

The genus *Porphyromonas*, which was formed by reclassification of various species of *Bacteroides* (Shah and Collins, 1988), is the type for this family. Originally, this family comprised the genera *Porphyromonas*, *Dysgonomonas*, and *Tannerella* (Garrity et al., 2005).

The genus *Porphyromonas* comprises five subclusters: (1) the type species *Porphyromonas asaccharolytica* and *Porphyromonas circumdentaria*, *endodontalis*, *gingivicanis*, and *uenonis*; (2) *Porphyromonas cangingivalis*, *canoris*, *levii*, and *somerae*; (3) *Porphyromonas crevioricanis*, *gingivalis*, and *gulae*; (4) *Porphyromonas catoniae* and *macacae*; and (5) *Porphyromonas cansulci*.

The genus *Dysgonomonas* comprises the type *Dysgonomonas gadei* and the closely related species *Dysgonomonas capnocytophagoides* and *mossii*.

The last genus is monospecific, *Tannerella forsythia*.

The current analyses add five other genera to this family. These include three monospecific genera represented by *Paludibacter propionisigenes*, *Petrimonas sulfuriphila*, and *Proteiniphilum acetatigenes*. Also included is the recently described genus comprising *Barnesiella viscericola* and *intestinihominis* (Morotomi et al., 2008; Sakamoto et al., 2007). Lastly, the genus *Parabacteroides* comprises the type species *Parabacteroides distasonis* and three closely related species *Parabacteroides goldsteinii*, *johnsonii*, and *merdae* (Sakamoto and Benno, 2006). This last genus was also described after the deadline for inclusion in this volume.

Family "Prevotellaceae"

Although the family "Prevotellaceae" appears within the cluster of species of the family *Bacteroidaceae*, the genera representing the "Prevotellaceae" are well separated from the *Bacteroidaceae*. Therefore, both families are continued in the current classification. The genus *Prevotella*, which was formed by reclassification of various species of *Bacteroides* (Shah and Collins, 1990), is the type for this family. It comprises a number of phylogenetic groups, each of which may warrant reclassification into one or more genera if supported by additional evidence: (1) the type species *Prevotella melaninogenica* and *Prevotella histolytica* and *veroralis*; (2) *Prevotella denticola* and *multiformis*; (3) *Prevotella corporis*, *disiens*, *falsenii*, *intermedia*, *nigrescens*, and *pallens*; (4) *Prevotella maculosa*, *oris*, and *salivae*; (5) *Prevotella bryantii*, and *multisaccharivorax*; (6) *Prevotella baroniae*, *buccae* and *dentalis*; (7) *Prevotella enoeca* and *pleuritidis*; (8) *Prevotella buccalis* and *timonensis*; (9) *Prevotella loescheii* and *shahii*; (10) *Prevotella brevis* and *ruminicola*; and (11) *Prevotella amnii* and *bivia*.

The species *Prevotella albensis*, *bergensis*, *copri*, *marshii*, *oralis*, *oulorum*, *paludivivens*, and *stercorea* cannot be clearly assigned to one of the lineages. *Xylanibacter oryzae* is also found within the radiation of the described *Prevotella* clusters. *Prevotella tanneriae* represents a more distant branch of the family. In contrast, *Prevotella heparinolytica* and *zooglyphiformans* are clearly separated from the other members of this family and may warrant reclassification. Lastly, *Hallella serogens* is closely related to *Prevotella dentalis*, which has priority (Willems and Collins, 1995). Therefore, *Hallella serogens* is not used.

Class “Flavobacteriia” and order “Flavobacteriales”

This class comprises a single order, “Flavobacteriales”, and is essentially unchanged from the original proposal of Garrity et al. (2005). The order comprises three families, *Flavobacteriaceae*, “*Blattabacteriaceae*”, and *Cryomorphaceae* (Figures 4 and 5) (Bowman et al., 2003). The family “*Myroidaceae*” proposed by

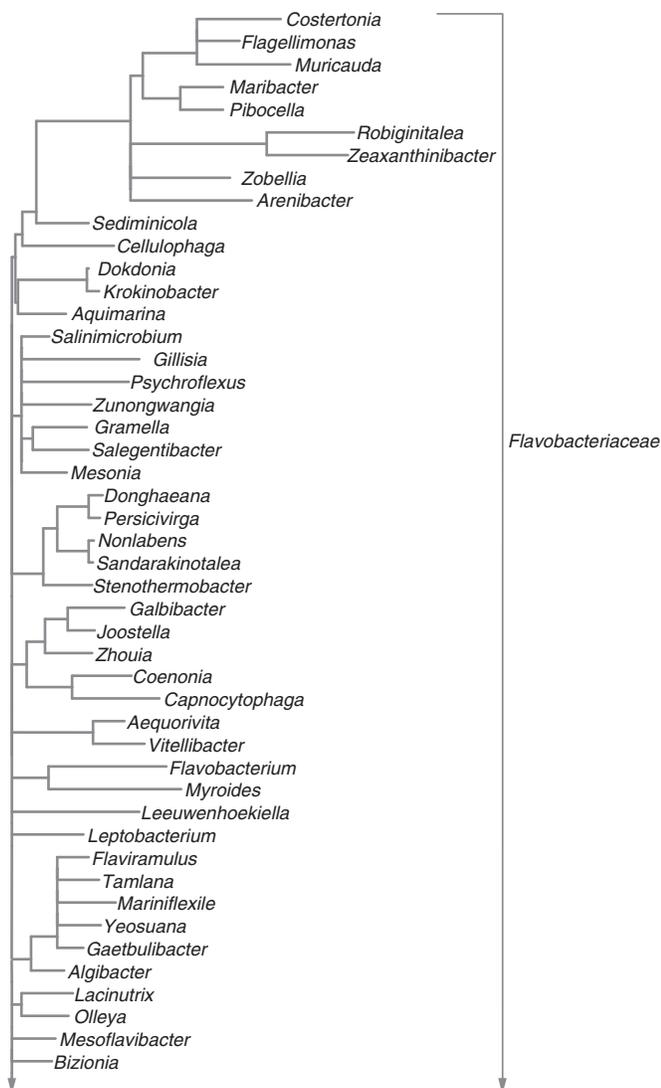


FIGURE 4. Genera of the class “Flavobacteriia”. This class comprises three families. The first part of the family *Flavobacteriaceae* is shown here.

Garrity et al. (2005) was judged to be insufficiently resolved from the *Flavobacteriaceae* and was not used.

Family *Flavobacteriaceae*

This extraordinarily diverse family comprises over 70 genera. The rRNA analyses indicate the presence of many phylogenetic clusters that may warrant separation into novel families if supported by additional evidence. Many of the clusters described here are identical to those found by Bernardet and Nakagawa (2006) or include mostly taxa described after their work. Cluster (1) includes the type genus *Flavobacterium* and *Myroides*. This latter genus includes three closely related species, *Myroides odoratus*, *odoratimimus*, and *pelagicus*. Although the genus *Flavobacterium* is very diverse, the rRNA phylogeny lacks clear indication of clades that might serve as the basis for further subdivision. Species included in this genus include the type species *Flavobacterium aquatile* and, in alphabetical order, *Flavobacterium antarcticum*, *aquidurense*, *branchiophilum*, *columnare*, *croceum*, *cucumis*, *daejeonense*, *defluvi*, *degerlachei*, *denitrificans*, *flevense*, *frigidarium*, *frigidimaris*, *frigoris*, *fryxelicola*, *gelidilacus*, *gillisiae*, *granuli*, *hercynium*, *hibernum*, *hydatis*, *johnsoniae*, *limicola*, *micromati*, *omnivorum*, *pectinovorum*, *psychrolimnae*, *psychrophilum*, *saccharophilum*, *saliperosum*, *segetis*, *sol*, *succinicans*, *suncheonense*, *tegetincola*, *terrae*, *terrigena*, *weaverense*, *xanthum*, and *xinjiangense*. In addition, there are some species for which sequences are not available, including *Flavobacterium acidificum*, *acidurans*, *oceanosedimentum*, and *thermophilum*.

(2) *Capnocytophaga ochracea* (type species), *canimorsus*, *cynodegmi*, *gingivalis*, *granulosa*, *haemolytica*, *ochracea*, and *sputigena*; and *Coenonia anatina*. Although *Galbibacter mesophilus* (Khan et al., 2007c), *Joostella marina* (Quan et al., 2008), and *Zhouia amylobytica* are associated with this cluster, this relationship is not strong.

(3) *Actibacter sediminis* (Kim et al., 2008a); *Aestuariicola saemankumensis* (Yoon et al., 2008d); *Lutibacter litoralis*; *Lutimonas vernicola* (Yang et al., 2007); *Polaribacter filamentus* (type species), *butkevichii*, *franzmannii*, and *glomeratus*; *Polaribacter dokdonensis* (which forms a separate clade from the other species of this genus); *Tenacibaculum maritimum* (type species), *adriaticum*, *aestuarii*, *aiptasiae*, *amylobyticum*, *galleicum*, *litopenaei*, *litoreum*, *lutimaris*, *mesophilum*, *ovolyticum*, *skagerrakense*, and *soleae*.

(4) *Chryseobacterium gleum* (type species), *aquaticum*, *aquifrigidense*, *arothri*, *balustinum*, *bovis*, *caeni*, *daecheongense*, *daeguense*, *defluvi*, *flavum*, *formosense*, *gambrini*, *gregarium*, *haifense*, *hispanicum*, *hominis*, *hungaricum*, *indologenes*, *indoltheticum*, *jejuense*, *joostei*, *luteum*, *marina*, *molle*, *oranimense*, *pallidum*, *pisicum*, *scophthalmum*, *shigense*, *soldanellicola*, *sol*, *taeanense*, *taichungense*, *taiwanense*, *ureilyticum*, *vrystaatense*, and *wanjuense*. In addition to these species, the following taxa appear within the radiation of *Chryseobacterium*, including *Epilithonimonas tenax*, *Kaistella koreensis*, *Sejongia antarctica* (type species) and *jeonii*. Other taxa within this cluster include *Bergeyella zoohelcum*, *Cloacibacterium normanense*, *Elizabethkingia meningoseptica* (type species) and *miricola*, *Empedobacter brevis*, *Ornithobacterium rhinotracheale*, *Riemerella anatipestifer* (type species) and *columbina*, *Wautersiella falsenii*, and *Weeksella virosa*.

(5) *Arenibacter latericius* (type species), *certesii*, *echinorum*, *pal-ladensis*, and *troitsensis*; *Cellulophaga algicola*, *baltica*, and *pacifica* (a clade which does not include the type species); *Costertonia aggregata*, *Flagellimonas eckloniae* (Bae et al., 2007); *Maribacter*

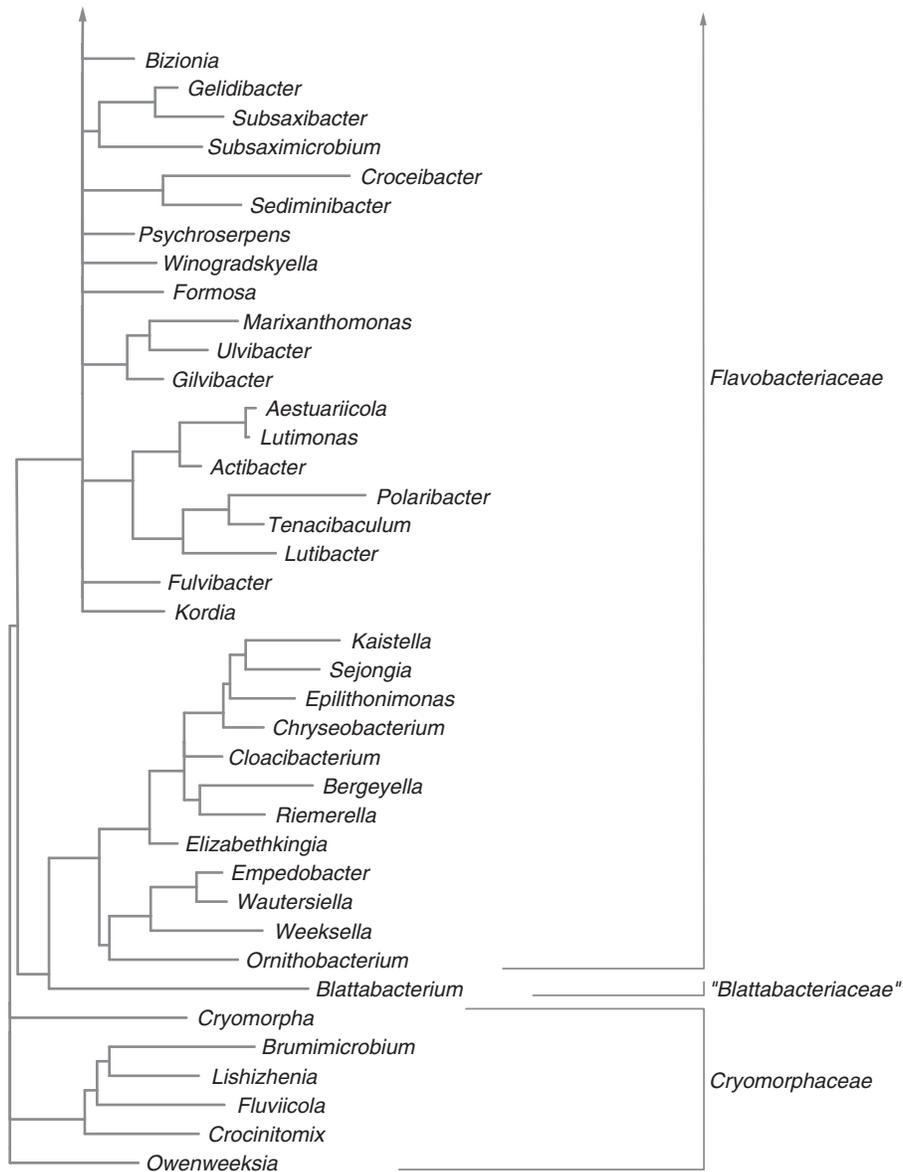


FIGURE 5. Genera of the class "Flavobacteriia". This class comprises three families. The second part of the family *Flavobacteriaceae* and the remaining two families are shown here.

sedimenticola (type species), *aquivivus*, *arcticus*, *dokdonensis*, *forsetii*, *orientalis*, *polysiphoniae*, and *ulvicola*; *Muricauda ruestringensis* (type species), *aquimarina*, *lutimaris*, and *flavescens*; *Pibocella ponti* (which appears within the cluster of *Maribacter* species); *Robiginitalea biformata* and *myxolifaciens*; *Sediminicola luteus*; *Zeaxanthinibacter enoshimensis* (Asker et al., 2007); and *Zobellia galactanivorans* (type species), *amurskyensis*, *laminariae*, *russellii*, and *uliginosa*. In addition, *Cellulophaga lytica* (the type species of this genus) and *fucicola* appear as either a deep branch of this cluster (Bernardet and Nakagawa, 2006) or as an associated but independent group (this analysis). In either case, the reclassification of *Cellulophaga algicola*, *baltica*, and *pacifica* to a new genus would appear to be warranted. Lastly, the type strain of *Pibocella ponti* has been lost.

If available, this strain would be reclassified within *Maribacter*. For that reason, this genus is not included in the outline.

(6) *Algibacter lectus* and *mikhailovii*; *Flaviramulus basaltis*; *Gaetbulibacter saemankumensis* and *marinus*; *Mariniflexile gromovii* and *fucanivorans*; *Tamlana crocina* (Lee, 2007); and *Yeosuana aromativorans*.

(7) *Croceibacter atlanticus* and *Sediminibacter furfurosus* (Khan et al., 2007a).

(8) *Gelidibacter algens* (type species), *gilvus*, *mesophilus*, and *salicanalis*; *Subsaxibacter broadyi*; *Subsaximicrobium wynnwilliamsii* (type species) and *saxinquilinus*.

(9) *Lacinutrix copepodicola*, *algicola*, and *mariniflava*; and *Olleya marilimosa*.

(10) *Gilvibacter sediminis* (Khan et al., 2007a); *Marixanthomonas ophiuræ* (Romanenko et al., 2007). *Ulvibacter litoralis* and *antarcticus*.

(11) *Dokdonia donghaensis*; *Krokinobacter genikus* (type species), *diaphorus*, *eikastus*, and *genicus*.

(12) *Donghaena dokdonensis*; *Nonlabens tegetincola*; *Persicivirga xylanidelens*; *Sandarakinotalea sediminis*; and *Stenothermobacter spongiae*.

(13) *Gillisia limnaea* (type species), *hiemivivida*, *illustrilutea*, *mitskevichiae*, *myxillae*, and *sandarakina*; *Gramella echinicola* (type species) and *portivictoriae*; *Mesonina algae* (type species) and *mobilis*; *Psychroflexus torques* (type species), *gondwanensis*, and *tropicus*; *Salegentibacter salegens* (type species), *agarivorans*, *flavus*, *holothuriorum*, *mishustinae*, *salaries*, and *salinarum*; *Salinimicrobium catena*, *terrae*, and *xinjiangense* (Chen et al., 2008; Lim et al., 2008); and *Zunongwangia profunda* (Qin et al., 2007). Among these taxa, *Salinimicrobium catena* was previously classified as *Salegentibacter catena* (Lim et al., 2008).

(14) *Aequorivita antarctica* (type species), *crocea*, *lipolytica*, and *sublithincola* and *Vitellibacter vladivostokensis*.

In addition to these well delineated clusters, a large number of taxa were not closely associated with any of these clusters or each other. These include: *Aquimarina muelleri* (type species), *brevivita*, *intermedia*, and *latercula*; *Bizionia paragorgiae* (type species), *gelidisalsuginis*, and *saleffrena*; a second clade of *Bizionia* species including *Bizionia algorithergicola* and *myxarmorum*; *Formosa algae* (type species) and *agariphila*; *Fulvibacter tottoriensis*; *Kordia algicida*; *Leeuwenhoekella marinoflava* (type species), *aequorea*, and *blandensis*; *Leptobacterium flavescens*; *Mesoflavibacter zeaxanthinifaciens*; *Psychroserpens burtonensis* (type species) and *mesophilus*; and *Winogradskyella thalassocola* (type species), *epiphytica*, *eximia*, and *poriferorum*. The rRNA gene sequences of the following pairs of genera are closely related, which may justify combining them: *Sandarakinotalea*–*Nonlabens*; *Dokdonia*–*Krokinobacter*.

Family “*Blattabacteriaceae*”

This family comprises *Blattabacterium cuenoti*, which is an endosymbiont of insects that has not been grown in pure culture.

Family *Cryomorpaceae*

Proposed by Bowman et al. (2003) to include novel genera of cold-tolerant marine bacteria isolated from sea ice and other polar environments, this family comprises six monospecific genera: *Cryomorpha ignava*, *Brumimicrobium glaciale*, *Crocinitomix catalasitica*, *Fluviicola taffensis*, *Lishizhenia caseimilytica*, and *Owenweeksia hongkongensis*. The phylogenetic analyses conducted here suggest that this family is polyphenetic and contains three lineages that cluster together at the base of the phylogenetic tree for the *Flavobacteriales*. *Cryomorpha* and *Owenweeksia* each comprise one monogeneric lineage, with the remaining four genera comprising the third lineage. However, in the absence of additional evidence, these lineages were not separated at this time.

Class “*Sphingobacteriia*” and order “*Sphingobacteriales*”

This class comprises a single order, the “*Sphingobacteriales*”. It is more circumscribed than the original proposal (2005) and excludes many taxa previously classified within the “*Flexibacteraceae*”. The order comprises three families: *Sphingobacteriaceae*, “*Chitinophagaceae*”, and “*Saprosiraceae*” (Figure 6). The family *Crenotrichaceae* was removed because the type genus *Crenothrix* was transferred to the *Proteobacteria* (Stoecker et al., 2006). The genus *Chitinophaga* then became the type for a new family within the order. Based upon their rRNA gene sequence similarities, the genera *Rhodothermus* and *Salinibacter*, which were also previously classified within the *Crenotrichaceae*, were transferred to the class “*Cytophagia*” as an order *incertae sedis* (see below). Similarly, *Balneola*, which was described after the deadline for

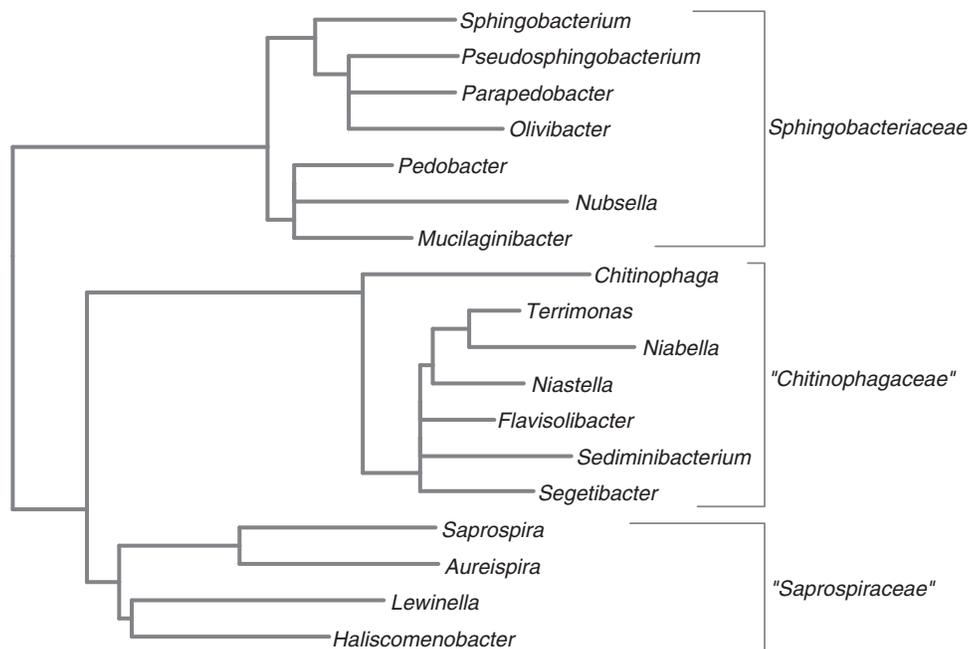


FIGURE 6. Genera of the class “*Sphingobacteriia*”.

inclusion in this volume, was classified within the *Crenotrichaceae* based in part upon its similarity to *Rhodothermus* (Urios et al., 2006). Analyses performed here suggest that it may also be a deep lineage of the “*Cytophagia*”. Lastly, the sequence of the 16S rRNA gene for *Toxothrix trichogenes* is not available, so this genus was transferred to *incertae sedis*. Even with these changes, this class is not clearly monophyletic (Figure 2). The families “*Chitinophagaceae*” and “*Saprosiraceae*” may represent a sister lineage to the family *Sphingobacteriaceae*. However, in the absence of confirmatory evidence, the grouping of the three families into one class was retained in the current outline.

Family *Sphingobacteriaceae*

At the time these analyses were performed, seven genera were identified within this family. The genera *Sphingobacterium*, *Olivibacter*, *Parapedobacter*, and *Pseudosphingobacterium* form one phylogenetic cluster. The genera *Pedobacter*, *Mucilaginibacter*, and *Nubsella* form a second cluster. In addition, the species *Flexibacter canadensis* represents an additional deep phylogenetic group within this family that may warrant classification as a novel genus.

The genus *Sphingobacterium* comprises *Sphingobacterium spiritorum* (type species), *anhuiense*, *canadense*, *composti*, *daejeonense*, *faecium*, *kitahiroshimense*, *mizutaii*, *multivorum*, *siyangense*, and *thalpophilum*. Interestingly, the species epithet *Sphingobacterium composti* was independently proposed for two different organisms by Ten et al. (2006, 2007) and Yoo et al. (2007). Because *Sphingobacterium composti* Ten et al. (2007) has priority, the species of Yoo et al. (2007) warrants renaming. In addition, this genus contains *Sphingobacterium antarcticum*, whose rRNA gene sequence is not available. Related to the genus *Sphingobacterium* are the taxa *Olivibacter sitiensis* (type species), *ginsengisoli*, *solii*, and *terrae* (Ntougiaris et al., 2007; Wang et al., 2008), *Parapedobacter koreensis* (type species) and *solii* (Kim et al., 2007b, 2008b), and *Pseudosphingobacterium domesticum* (Kim et al., 2007b; Vaz-Moreira et al., 2007). These genera were described after the deadline for inclusion in this volume.

The second cluster is composed of *Pedobacter* species, which itself comprises four subclusters. The first subcluster contains *Pedobacter heparinus* (type species), *africanus*, *caeni*, *cryconitis*, *duraquae*, *ginsengisoli*, *himalayensis*, *metabolipaupe*, *panaciterrae*, *pisicum*, *steynii*, and *westerhofensis*. The second subcluster comprises *Pedobacter insulae* and *koreensis*. The third subcluster comprises *Pedobacter daechungensis*, *lentus*, *saltans*, and *terricola*, which may warrant reclassification into a novel genus if supported by additional evidence. A fourth subcluster is represented by *Mucilaginibacter gracilis*, *kameinonesis*, and *paludis* (Pankratov et al., 2007; Urai et al., 2008). A number of species were not closely associated with any of these clusters or each other: *Nubsella zeaxanthinifaciens* (Asker et al., 2008); *Pedobacter agri*, *aquatilis*, *composti*, *roseus*, *sandarokinus*, *suwonensis*, and *terrae*.

Family “*Chitinophagaceae*”

This family contains two phylogenetic clusters. The first cluster includes the genus *Chitinophaga*. This genus comprises *Chitinophaga pinensis* (type species), *arvensicola*, *filiformis*, *ginsengisegetis*, *ginsengisoli*, *japonensis*, *sancti*, *skermani*, and *terraei*. The second cluster includes six related genera with ten species: *Flavisolibacter ginsengisoli* and *ginsengiterrae* (Yoon and Im, 2007); *Niabella aurantiaca* and *solii* (Kim et al., 2007a; Weon et al.,

2008a); *Niastella koreensis* (type species) and *yeongjuensis* (Weon et al., 2006); *Sediminibacterium salmonicum* (Qu and Yuan, 2008); *Segetibacter koreensis* (An et al., 2007); and *Terrimonas ferruginea* (type species) and *lutea*. *Flavisolibacter*, *Niabella*, *Niastella*, *Sediminibacterium*, and *Segetibacter* were described after the deadline for inclusion in this volume (Weon et al., 2006).

Family “*Saprosiraceae*”

As originally proposed by Garrity et al. (2005), the family comprises three related genera and nine species. These include: *Saprosira grandis*; *Haliscomenobacter hydrossis*, and *Lewinella cohaerens* (type species), *agarilytica*, *antarctica*, *lutea*, *marina*, *nigricans*, and *persica*. Recently, the newly discovered genus *Aureispira (marina and maritime)* has also been classified within this family (Hosoya et al., 2006, 2007).

Class “*Cytophagia*” and order *Cytophagales*

Analyses performed here of the rRNA genes indicate that many of the genera previously classified within the families “*Flexibacteraceae*” and “*Flammeovirgaceae*” are not closely related to the “*Sphingobacteriia*” and should be transferred to a novel class (Figure 7). The order *Cytophagales* is designated the type for the new class. The genus *Cytophaga* is the type for the order and family *Cytophagaceae*. Because the family *Cytophagaceae* includes the type genera of the families “*Flexibacteraceae*” and *Spirosomaceae*, these classifications are not used.

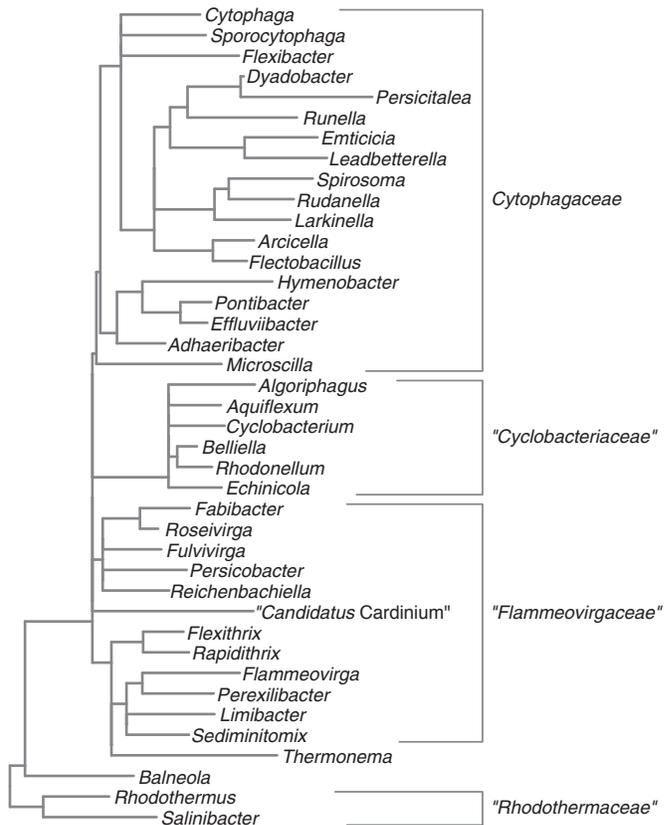


FIGURE 7. Genera of the class “*Cytophagia*”. This class comprises three families and four orders *incertae sedis*.

Family *Cytophagaceae*

This family comprises 19 genera distributed within seven phylogenetic clusters: the first cluster includes *Cytophaga hutchinsonii* (type species) and *aurantiaca*; the second cluster includes *Sporocytophaga myxococcoides* (type and only species); the third cluster includes *Effluviibacter roseus*; *Hymenobacter roseosalivarius* (type species), *actinosclerus*, *aerophilus*, *chitinivorans*, *deserti*, *gelipurpurascens*, *norwichensis*, *ocellatus*, *psychrotolerans*, *rigui*, *solii*, and *xinjiangensis*; and *Pontibacter actiniarum* (type species), *akesuensis*, and *korlensis*. In addition, *Adhaeribacter aquaticus* appears to represent a deep lineage in this cluster.

The fourth cluster includes *Arcicella aquatica* and *rosea*; *Dyadobacter fermentans* (type species), *alkalitolerans*, *beijingensis*, *crusticola*, *ginsengisoli*, *hamtensis*, and *korensis*; *Emticicia ginsengisoli* and *oligotrophica*; *Flectobacillus major* (type species) and *lacus*; *Larkinella insperata*; *Leadbetterella byssophila*; *Persicitalea jodogahamensis* (Yoon et al., 2007b); *Rudanella lutea* (Weon et al., 2008b); *Runella slithyiformis* (type species), *defluvi*, *limosa*, and *zeae*; and *Spirosoma linguale*, *panaciterrae*, and *rigui*. The fifth cluster includes *Flexibacter roseolus*, *elegans*, and *Microscilla marina*. The sixth cluster comprises *Flexibacter flexilis* (type species). The seventh cluster comprises *Flexibacter ruber*.

Cyclobacterium and *Reichenbachiella*, two genera previously classified with this group (Garrity et al., 2005), have been transferred to the “*Cyclobacteriaceae*” and “*Flammeovirgaceae*”, respectively. In addition, *Meniscus glaucopsis* is retained within the *Cytophagaceae* even though the sequence of its rRNA gene is not available.

Family “*Cyclobacteriaceae*”

This family includes the genus *Cyclobacterium*, which was previously classified within the “*Flexibacteraceae*”, and five related genera: *Cyclobacterium marinum* (type species), *amurskyense*, and *lianum*; *Aquiflexum balticum*; *Algoriphagus ratkowskyi* (type species), *alkaliphilus*, *antarcticus*, *aquimarinus*, *boritolerans*, *chordae*, *halophilus*, *localis*, *mannitolivorans*, *marincola*, *ornithinivorans*, *terrigena*, *vanfongensis*, *winogradskyi*, and *yeomjeoni*. This cluster includes *Chimaericella* and *Hongiella* species that were transferred to *Algoriphagus* (Nedashkovskaya et al., 2007b); *Belliella baltica*; *Echinicola pacifica* (type species) and *vietnamensis*; and *Rhodonellum psychrophilum* represent further genera.

Family “*Flammeovirgaceae*”

This family includes the genus *Flammeovirga* and at least seven related genera and one *Candidatus* taxon. This family comprises two phylogenetic groups which are neighbors in all trees but not clearly monophyletic. In addition, *Thermonema*, which was previously classified in this family (Garrity et al., 2005), possesses only low similarity to the other genera and was reclassified to an order *incertae sedis*. Subsequently, it was found that this reassignment was equivocal, and analyses with more representatives of this family are ambiguous (Figure 7). For the purposes of this road map, this genus was retained in an order *incertae sedis*. As a result, this family comprises two phylogenetic groups: *Flammeovirga aprica* (type species), *arenaria*, *kamogawensis*, and *yaeyamensis*; *Flexibacter aggregans*, *litoralis*, and *polymorphus*, which appear to be misclassified; *Flexithrix dorotheae*, *Limibacter armeniacum* (Yoon et al., 2008b); *Perexilbacter aurantiacus* (Yoon et al., 2007a); *Rapidithrix thailandica*

(Srisukchayakul et al., 2007); and *Sediminitomix flava* (Khan et al., 2007b).

The second group comprises *Fabibacter halotolerans*; *Fulvirvirga kasyanovii* (Nedashkovskaya et al., 2007a); *Reichenbachiella agariperforans*; *Roseovirga ehrenbergii* (type species), *echinicomitans*, *seohaensis*, and *spongicola*; and *Persicobacter diffluens*.

In addition, *Flexibacter tractuosus*, which appears to be misclassified, and “*Candidatus Cardinium hertigii*”, a symbiont of parasitoid wasps (Zchori-Fein et al., 2004), are neighboring lineages.

Class “*Cytophagia*” orders *incertae sedis*

In addition to the members of these families whose taxonomic position is relatively well defined, three deep lineages are classified within “*Cytophagia*” as separate orders *incertae sedis*. These lineages include (1) the family “*Rhodothermaceae*”, comprising *Rhodothermus marinus* and *Salinibacter ruber*; (2) the genus *Balneola*, with species *Balneola vulgaris* (type) and *alkaliphila*, which were described after the deadline for inclusion in the volume (Urios et al., 2006, 2008); and (3) *Thermonema lapsum* (type species) and *rossianum* (which may also be assigned to the “*Flammeovirgaceae*”).

The assignment of the first two lineages to this class is ambiguous, and their reclassification may be warranted with additional evidence. *Toxothrix trichogenes*, for which the rRNA gene sequence is not available, is also included as *incertae sedis* within this class.

Phylum “*Spirochaetes*”

As a result of the current analyses of 16S rRNA gene sequences, a single class and order are recognized within the phylum “*Spirochaetes*”. Members of the “*Spirochaetes*” possess a cellular ultrastructure unique to bacteria with internal organelles of motility, namely periplasmic flagella.

Class “*Spirochaetia*” and order *Spirochaetales*

The class comprises a single order. The order *Spirochaetales* comprises four families that are well delineated by 16S rRNA gene sequences (Figure 8). Compared to the previous outline (Garrity et al., 2005), the families *Spirochaetaceae* and *Leptospiraceae* are retained in the current classification. However, the genus *Serpulina* was judged to be a subjective synonym of *Brachyspira* (Ochiai et al., 1997). As a consequence, the family “*Serpulinaceae*” was replaced with “*Brachyspiraceae*”. The genus *Brevinema* was also transferred from the family *Spirochaetaceae* to a novel family “*Brevinemataceae*” in recognition of the differences in 16S rRNA gene sequences. Lastly, four genera of arthropod symbionts for which no sequences are available were transferred from the *Spirochaetaceae* to a fifth family, *incertae sedis*.

Family *Spirochaetaceae*

This family comprises four genera that are well delineated on the basis of their 16S rRNA gene sequences. Compared to previous classifications, the genus *Brevinema* was transferred to a new family on the basis of substantial differences in its 16S rRNA gene sequence. Likewise, the genera *Clevelandina*, *Diplocalyx*, *Hollandina*, and *Pillotina* were transferred to a family *incertae sedis* in the absence of rRNA gene sequences.

The culture for the type species of the genus *Spirochaeta*, *Spirochaeta plicatilis*, is not available, and its rRNA gene has not

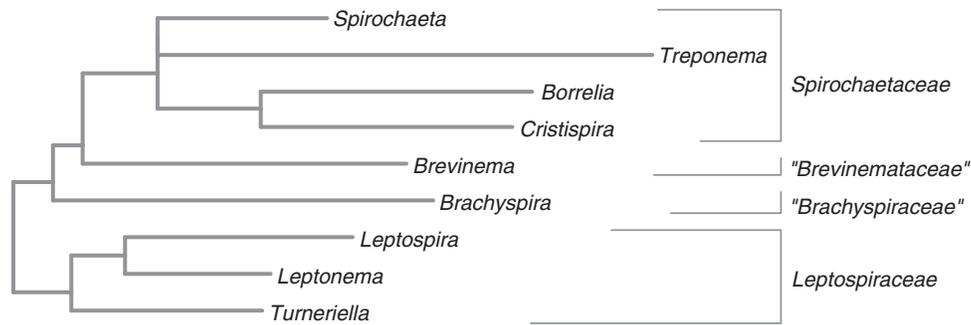


FIGURE 8. Genera of the phylum "Spirochaetes".

been sequenced. Of the remaining species, three are more closely related to *Treponema* and should probably be reclassified within that group (see below). The remaining species of the genus *Spirochaeta* comprise at least seven phylogenetic groups: (1) *Spirochaeta africana* and *asiatica*; (2) *Spirochaeta alkalica*, *americana*, and *halophila*; (3) *Spirochaeta aurantia*; (4) *Spirochaeta bajacaliforniensis* and *smaragdinae*; (5) *Spirochaeta coccooides*; (6) *Spirochaeta isovalerica* and *litoralis*; and (7) *Spirochaeta thermophila*.

The genus *Borrelia* comprises three phylogenetic groups. One group contains the type species, *Borrelia anserina*, and the causative agents of relapsing fever, *Borrelia coriaceae*, *crocidurae*, *duttonii*, *hermsii*, *hispanica*, *miyamotoi*, *parkeri*, *persica*, *recurrentis*, *theileri*, and *turicatae*. Many of these species are transmitted by soft-bodied ticks. The second group includes the causative agent of Lyme disease, *Borrelia burgdorferi*, and species transmitted by hard-bodied ticks, *Borrelia afzelii*, *burgdorferi*, *garinii*, *japonica*, *lusitaniae*, *sinica*, *spielmanii*, *tanukii*, *turdi*, and *valaisiana*. The third group consists solely of *Borrelia turcica*.

In addition, sequences are not available for some named species, including *Borrelia baltazardii*, *brasiliensis*, *caucasica*, *dugesii*, *graingeri*, *harveyi*, *latschewii*, *mazzottii*, *tillae*, and *venezuelensis*.

The genus *Cristispira* is represented by a single species, *Cristispira pectinis*, which is related to *Borrelia*. This microorganism has been identified in the crystalline styles of oysters (Paster et al., 1996).

The genus *Treponema* comprises three phylogenetic groups: *Treponema pallidum* (type species), "*calligyrum*", *denticola*, *medium*, *phagedenis*, *putidum*, "*refringens*", and "*vincentii*"; in addition, *Spirochaeta zuelzeri* is associated with this group. The second group comprises *Treponema amylovorum*, *berlinense*, *bryantii*, *brennaborensis*, *lecithinolyticum*, *maltophilum*, *parvum*, *pectinovorum*, *porcinum*, *saccharophilum*, *socranskii*, and *succinifaciens*. The third group comprises *Treponema azotonutricium* and *primita*; in addition, *Spirochaeta caldaria* and *stenostrepta* are associated with this group. Lastly, no sequence is available for *Treponema minutum*, so its placement is ambiguous.

Family "Brachyspiraceae"

This family comprises a single genus of closely related species: *Brachyspira aalborgi* (type species), *alvinipulli*, *hyodysenteriae*, *innocens*, *intermedia*, *murdochii*, and *pilosicoli*. Many of the species in this genus were previously classified in the genus *Serpulina*, which is not used in the current classification (Ochiai et al., 1997).

Family "Brevinemataceae"

This family is represented by a single genus and species, *Brevinema andersonii*, isolated from rodents.

Family Leptospiraceae

This family comprises the large genus *Leptospira* and two monospecies genera, *Leptonema illini* and *Turneriella parva*. These latter genera were previously classified within the *Leptospira*. However, on the basis of differences in their 16S rRNA gene sequences, they were transferred to novel genera.

The genus *Leptospira* comprises three phylogenetic groups: (1) *Leptospira interrogans* (type species), *alexanderi*, *borgpetersenii*, *kirschneri*, *noguchii*, *santarosai*, and *weilii*; (2) *Leptospira broomii*, *fainei*, *inadai*, *licerasiae*, and *wolffii*; and (3) *Leptospira biflexa*, *meyeri*, and *wolbachii*.

Spirochaetales family incertae sedis

This family includes four genera of symbionts of arthropod invertebrates. Although their morphologies have been described in detail (Bermudes et al., 1988), their 16S rRNA genes have not been sequenced, and their phylogenetic placements are unknown. They are *Clevelandina reticulitermitidis*, *Diplocalyx calotermitidis*, *Hollandina pterotermitidis*, and *Pillotina calotermitidis*.

Phylum Tenericutes

This phylum comprises a single class, *Mollicutes*, which was previously classified within the *Firmicutes* (Garrity et al., 2005). Elevation of these organisms to a separate phylum is justified in part by analyses of a number of conserved phylogenetic markers such as the elongation factor Tu and RNA polymerase (Ludwig and Schleifer, 2005). This classification is further supported by the presence of a wall-less cytoplasmic membrane which is a distinctive cellular structure of this group.

Class Mollicutes

This class comprises four orders, *Mycoplasmatales*, *Entomoplasmatales*, *Acholeplasmatales*, and *Anaeroplasmatales*. While these orders do not agree well with the 16S rRNA gene phylogeny, efforts to reorganize the taxonomy are confounded by the presence of many human and animal pathogens within the group and the priority of some genus names that are seldom used (Brown et al., 2010). A major difficulty is the polyphyletic nature of the genus *Mycoplasma*, species of which are found in 13 distinct clusters distributed over three deep lineages. A fuller

discussion of the complexities of this group along with rRNA gene trees is found in the chapter on *Mycoplasmatales*.

Order *Mycoplasmatales*

This order is the type for the class and comprises two families and four genera. The genera *Mycoplasma* and *Ureaplasma* are classified within the family *Mycoplasmataceae*. The other two genera, *Eperythrozoon* and *Haemobartonella*, contain many blood parasites that have not been cultivated. Although some of the species have been transferred to the genus *Mycoplasma*, the genera are classified within a family *incertae sedis* in recognition of the remaining uncertainties in their classification.

Family *Mycoplasmataceae*

This family contains the genera *Mycoplasma* and *Ureaplasma*. While *Ureaplasma* is well defined on the basis of its rRNA gene sequence phylogeny, *Mycoplasma* is found in at least three deep phylogenetic lineages or groups. The first group contains the type species, *Mycoplasma mycoides*, which is actually more closely related to *Entomoplasma*, the type genus of the order *Entomoplasmatales*, than to most other species of *Mycoplasma* and *Ureaplasma*. A second lineage, called the “*pneumoniae* group”, includes the genus *Ureaplasma* as well as four *Mycoplasma* clusters. The third lineage, called the “*hominis* group”, includes the remaining eight *Mycoplasma* clusters.

The group containing the type species includes: *Mycoplasma mycoides* (type species), *capricolum*, *cottewii*, *putrefaciens*, and *yeatsii*.

The “*hominis* group” includes eight clusters of *Mycoplasma* species. (1) The “*bovis*” cluster comprises *Mycoplasma adleri*, *agalactiae*, *bovigenitalium*, *bovis*, *californicum*, *caviae*, *columbinasale*, *columbinum*, *felifaucium*, *fermentans*, *gallinarum*, *iners*, *leopharyngis*, *lipofaciens*, *maculosum*, *meleagridis*, *opalescens*, *phocirhinis*, *primum*, *simbae*, and *spermatophilum*. (2) The “*equigenitalium*” cluster comprises *Mycoplasma elephantis* and *equigenitalium*. (3) The “*hominis*” cluster comprises *Mycoplasma alkalescens*, *anseris*, *arginini*, *arthritidis*, *auris*, *buccale*, *canadense*, *cloacale*, *equirhinis*, *falconis*, *faucium*, *gateae*, *gypis*, *hominis*, *hyosynoviae*, *indiense*, *orale*, *phocicebrale*, *phocidae*, *salivarium*, *spumans*, and *subdotum*. (4) The “*lipophilum*” cluster comprises *Mycoplasma hyopharyngis* and *lipophilum*. (5) The “*neurolyticum*” cluster comprises *Mycoplasma bovoculi*, *collis*, *cricetuli*, *conjunctivae*, *dispar*, *flocculare*, *hypopneumoniae*, *hyorhinis*, *iguanae*, *lagogenitalium*, *molare*, *neurolyticum*, and *ovipneumoniae*. (6) The “*pulmonis*” cluster comprises *Mycoplasma agassizii*, *pulmonis*, and *testudineum*. (7) The “*sualvi*” cluster comprises *Mycoplasma moatsii*, *mobile*, and *sualvi*. (8) The “*synoviae*” cluster comprises *Mycoplasma alligatoris*, *anatis*, *bovirhinis*, *buteonis*, *canis*, *citelli*, *columborale*, *corogypsi*, *crocydylis*, *cynos*, *edwardii*, *felis*, *gallinaceum*, *gallopavonis*, *glycophilum*, *leonicaptivi*, *mustelae*, *oxoniensis*, *pullorum*, *sturni*, *synoviae*, and *verecundum*.

The “*pneumoniae* group” includes four clusters of *Mycoplasma* species and *Ureaplasma*. (1) The “*fastidiosum*” cluster comprises *Mycoplasma cavipharyngis* and *fastidiosum*. (2) The “hemotropic” cluster comprises many species that were formerly classified within the genera *Eperythrozoon* and *Haemobartonella* (see below), including *Mycoplasma coccoides*, *haemocanis*, *haemofelis*, *haemomuris*, *ovis*, *suis*, and *wenyonii*. (3) The “*muris*” cluster comprises *Mycoplasma iowae*, *microti*, *muris*, and *penetrans*. (4) The “*pneumoniae*” cluster comprises *Mycoplasma alvi*, *amphoriforme*, *gallisepticum*, *genitalium*, *imitans*, *pirum*, *pneumoniae*, and *testudinis*. The genus *Ureaplasma* comprises *Ureaplasma urealyticum* (type species), *canigenitalium*, *cati*, *diversum*, *felinum*, *gallorale*, and *parvum*.

Mycoplasmatales family *incertae sedis*

This family includes the genera of blood parasites *Eperythrozoon* and *Haemobartonella*. Species whose 16S rRNA genes have been sequenced are also classified within the *Mycoplasma* hemotropic cluster. On the basis of their 16S rRNA gene sequences, the species of these genera are intermixed in two groups. The first group comprises *Eperythrozoon coccoides* (type species) and *Haemobartonella canis* and *felis*. *Haemobartonella muris*, which is the type species of its genus, is a deep lineage in this group. Upon reclassification to *Mycoplasma*, the *Haemobartonella* species were renamed *haemocanis*, *haemofelis*, and *haemomuris*, respectively, to distinguish them from previously named *Mycoplasma* species. The second group comprises *Eperythrozoon ovis*, *suis*, and *wenyonii*.

Order *Entomoplasmatales*

This order contains two families, *Entomoplasmataceae* and *Spiroplasmataceae*. The order is paraphyletic because it includes the type species of the genus *Mycoplasma*, most species of which are classified in the *Mycoplasmatales*.

Family *Entomoplasmataceae*

This family comprises the genera *Entomoplasma* and *Mesoplasma*. However, on the basis of their 16S rRNA gene sequences, some species of *Acholeplasma* appear to be misclassified within this group. The family comprises four phylogenetic lineages: (1) *Entomoplasma ellychniae* (type species), *Mesoplasma florum* (type species), and *Mesoplasma chauliocola*, *coleopterae*, *corruscae*, *entomophilum*, *grammopterae*, and *tabanidae*; (2) *Mesoplasma photuris*, *seiffertii*, and *syrphidae*, *Entomoplasma lucivorax*, *luminosum*, and *somnilux*; and *Acholeplasma multilocale*; (3) *Mesoplasma lactucae*, and (4) the group containing the type species of *Mycoplasma*, *Mycoplasma mycoides* (see above).

Family *Spiroplasmataceae*

This family comprises the single genus *Spiroplasma*, which itself comprises three relatively deep phylogenetic lineages. In fact, these lineages are no more closely related to each other than to some *Mycoplasma* species. These lineages include (1) *Spiroplasma citri* (type species), *chrysopicola*, *insolitum*, *melliferum*, *penaei*, *phoeniceum*, *poulsonii*, and *syrphidicola*; (2) *Spiroplasma alleghenense*, *cantharicola*, *chinense*, *corruscae*, *culicicola*, *diabroticae*, *diminutum*, *gladiatoris*, *helicoides*, *lampyridicola*, *leptinotarsae*, *lineolae*, *litorale*, *montanense*, *sabaudiense*, *turonicum*, and *velocitescens*; and (3) *Spiroplasma ixodetis* and *platyhelix*.

Order *Acholeplasmatales* and family *Acholeplasmataceae*

This order comprises the family *Acholeplasmataceae* and a family *incertae sedis* of uncultured plant pathogens classified within “*Candidatus* Phytoplasma”. On the basis of their 16S rRNA gene sequences, both of these groups are well defined phylogenetically. The family *Acholeplasmataceae* comprises four closely related lineages that are all classified with the genus *Acholeplasma*: (1) *Acholeplasma laidlawii* (type species), *equifetale*, *granularum*, *oculi*, and *pleciae*; (2) *Acholeplasma axanthum*, *cavigenitalium*, and *modicum*; *Mycoplasma feliminutum*; (3) *Acholeplasma brassicae*, *morum*, and *vituli*; and (4) *Acholeplasma palmae* and *parvum*.

Order *Anaeroplasmatales* and family *Anaeroplasmataceae*

This order and family comprises two genera which, on the basis of 16S rRNA gene sequence similarity, are not closely related. *Anaeroplasma* is related to members of the order *Acholeplasmatales*. The second genus, *Asteroleplasma*, appears to represent a very deep lineage within the phylum. The genus *Anaeroplasma* comprises three closely related species: *Anaeroplasma abactoclasticum* (type species), *bactoclasticum*, and *varium*. In addition, the species *Anaeroplasma intermedium* has been described for which no sequence is available. *Asteroleplasma anaerobium* is the sole species in the genus *Asteroleplasma*.

Phylum “*Acidobacteria*”

With only seven species, this phylum of mostly oligotrophic heterotrophs comprises two classes of validly published bacteria (Figure 9). However, surveys of environmental DNA indicate that this is one of the most abundant groups of bacteria in soil and many other habitats.

Class “*Acidobacteriia*”, order “*Acidobacteriales*”, and family “*Acidobacteriaceae*”

These taxa comprise two monospecific genera, represented by *Acidobacterium capsulatum* and *Terriglobus roseus*, and *Edaphobacter modestus* (type species) and *aggregans*.

Class *Holophagae*, order *Holophagales*, family *Holophagaceae*, order *Acanthopleuribacterales*, and family *Acanthopleuribacteraceae*

The family *Holophagaceae* comprises two monospecific genera, represented by *Holophaga foetida* and *Geothrix fermentans*. The family *Acanthopleuribacteraceae* comprises one monospecific genus, *Acanthopleuribacter*.

Phylum “*Fibrobacteres*”

This phylum comprises the class “*Fibrobacteria*”, the order “*Fibrobacterales*”, the family “*Fibrobacteraceae*”, and the genus *Fibrobacter*. This genus contains two species, *Fibrobacter succinogenes* (type species) and *intestinalis*.

Phylum “*Fusobacteria*”

This phylum comprises a single class, “*Fusobacteriia*”, and order “*Fusobacteriales*”. Two families are currently described (Figure 10). While the family “*Leptotrichiaceae*” is well defined on the basis of 16S rRNA gene sequences, the family “*Fusobacteriaceae*” is more complicated. It comprises five genera. The genus *Fusobacterium* is paraphyletic and includes the lineage containing the genus *Cetobacterium*. The genera *Ilyobacter* and *Propionigenium* are also intermixed. If additional evidence supports these conclusions, reclassification within this family would be warranted.

The phylogenetic groups within the family “*Fusobacteriaceae*” are (1) *Fusobacterium nucleatum* (type species), *canifelinum*, *equinum*, *gonidiaformans*, *mortiferum*, *necrogenes*, *necrophorum*, *perfoetens*, *periodonticum*, *russii*, *simiae*, *ulcerans*, and *varium*; and *Cetobacterium ceti* (type species) and *somerae*, representing a deeper branch; (2) *Ilyobacter polytropus* (type species), *insuetus*, and *tartaricus*; *Propionigenium modestum* (type species) and *maris*; and (3) *Psychrilyobacter atlanticus*, which was described after the deadline for inclusion in this volume, but it appears to be a deep lineage of this family (Zhao et al., 2009).

The phylogenetic groups within the family “*Leptotrichiaceae*” are (1) *Leptotrichia buccalis* (type species), *hofstadii*, *shahii*, *trevisanii*, and *wadei*; (2) *Leptotrichia goodfellowii*; (3) *Sebaldella termitidis*; (4) *Sneathia sanguinegens*; and (5) *Streptobacillus moniliformis*.

Phylum “*Dictyoglomi*”

This phylum comprises the class “*Dictyoglomia*”, the order “*Dictyoglomales*”, the family “*Dictyoglomaceae*”, and the genus

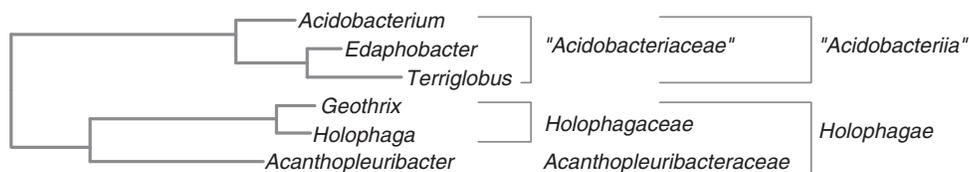


FIGURE 9. Genera of the phylum “*Acidobacteria*”.

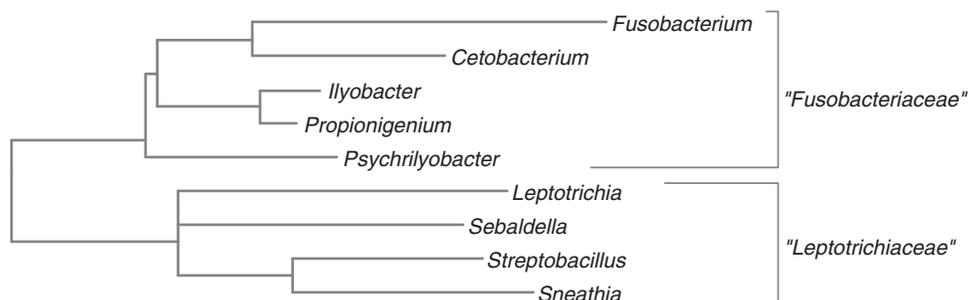


FIGURE 10. Genera of the phylum “*Fusobacteria*”.

Dictyoglossus. This genus contains two species, *Dictyoglossus thermophilum* (type species) and *turgidum*.

Phylum Gemmatimonadetes

This phylum comprises the class *Gemmatimonadetes*, the order *Gemmatimonadales*, the family *Gemmatimonadaceae*, and the genus *Gemmatimonas*. This genus contains one species, *Gemmatimonas aurantiaca*.

Phylum Lentisphaerae

On the basis of their 16S rRNA gene sequences and other molecular markers, this phylum is related to the phyla "*Verrucomicrobia*", "*Chlamydiae*", and "*Planctomycetes*", which form a deep group within the *Bacteria*. The phylum *Lentisphaerae* comprises the class "*Lentisphaeria*" and two orders. The order *Lentisphaerales* comprises the family "*Lentisphaeraceae*" and the monospecific genus *Lentisphaera*, the type of which is *Lentisphaera araneosa*. The order *Victivallales* comprises the family "*Victivallaceae*" and the monospecific genus *Victivallis*, the type of which is *Victivallis vadensis*.

Phylum "Verrucomicrobia"

On the basis of their 16S rRNA gene sequences and other molecular markers, this phylum is related to the phyla "*Chlamydiae*", "*Lentisphaerae*", and "*Planctomycetes*", which form a deep group within the bacteria. "*Verrucomicrobia*" comprises three classes, *Verrucomicrobiae*, *Opiritae*, and "*Spartobacteria*" (Figure 11).

Currently, the class *Verrucomicrobiae* comprises the order *Verrucomicrobiales*, which comprises the families *Verrucomicrobiaceae*, "*Akkermansiaceae*", and "*Rubritaleaceae*". The family *Verrucomicrobiaceae* comprises *Verrucomicrobium spinosum*, *Prostheco bacter fusiformis* (type species), *debonii*, *dejongei*, and *vanneervenii*. In addition, *Prostheco bacter fluviatilis*, which was described after the deadline for inclusion in this volume, is a member of this family (Takeda et al., 2008). The family "*Akkermansiaceae*" comprises the monospecific genus *Akkermansia*, the type of which is *Akkermansia muciniphila*. The family "*Rubritaleaceae*" comprises *Rubritalea marina* (type species), *sabuli*, *spongiae*, *squalenifaciens*, and *tangerina*.

In addition to these genera, four genera were described after the deadline for inclusion in this volume. *Persicirhabdus sediminis*; and *Roseibacillus ishigakijimensis* (type species), *persicicus*, and *ponti* (Yoon et al., 2008a), are affiliated with the family "*Rubritaleaceae*". The remaining two genera, *Haloferula rosea* (type species), *harenae*, *helveola*, *phyci*, *rosea*, and *sargassicola* (Yoon et al., 2008c) and *Luteolibacter pohnppeiensis* (type species) and *algae* (Yoon et al., 2008a), appear to be members of the order *Verrucomicrobiales*, but their affiliation with a particular family is more ambiguous. For this reason, they have not been included in the Taxonomic Outline.

The class *Opiritae* comprises the orders *Opiritales* and *Puniceococcales*. The order *Opiritales* comprises a single family, *Opiritaceae*, and two monospecific genera, the type species of which are *Opiritus terrae* and *Alterococcus agarolyticus*. The order *Puniceococcales* comprises a single family, *Puniceococcaceae*, and four genera. The genera form two clusters. The first cluster includes three monospecific genera, the type species of which are *Puniceococcus vermicola*, *Cerasiococcus arenae*, and *Coraliomargarita akajimensis*. The second cluster includes *Pelagicoccus mobilis* (type species),

albus, *croceus*, and *litoralis*. In addition, the genus "*Fucophilus*", which has been described but whose name has never been validly published, is a member of this family.

The class "*Spartobacteria*" comprises the order "*Chthoniobacteriales*", which includes the family "*Chthoniobacteraceae*". This family comprises "*Chthoniobacter flavus*" and the nematode symbionts "*Candidatus Xiphinematobacter brevicolli*" (type species), "*americani*", and "*rivesi*".

Phylum "Chlamydiae"

On the basis of their 16S rRNA gene sequences and other molecular markers, this phylum is related to the phyla *Lentisphaerae*, "*Planctomycetes*", and "*Verrucomicrobia*", which form a deep group within the bacteria. All known members of the phylum "*Chlamydiae*" are obligate intracellular bacteria and multiply in eukaryotic hosts, including humans and other animals and protozoa. They also possess a developmental cycle that is characterized by morphologically and physiologically distinct stages. The intracellular lifestyle of chlamydiae is thus thought to be an ancient trait of this phylum (Everett et al., 1999). As a consequence of the intracellular lifestyle, no species has ever been grown in axenic culture. Because of changes to the Bacteriological Code beginning in 1997, only the species described before that time have been validly published, and many of the newer taxa are limited to *Candidatus* status (Labeleda, 1997; Murray and Stackebrandt, 1995). In addition, even though some species have been cultivated in the free-living amoebae *Acanthamoeba castellanii* and *Acanthamoeba polyphaga*, they have not been deposited in two public culture collections, and thus their names have not been validly published (Heyrman et al., 2005).

The phylum "*Chlamydiae*" comprises a single class, "*Chlamydiai*", and order, *Chlamydiales*. The order comprises eight families of varying relatedness based upon 16S rRNA gene sequence similarities (Figure 12). The family *Chlamydiaceae* contains the type genus for the order. Two taxonomies are in widespread use for this family. One taxonomy assigns all species within this family to the genus *Chlamydia*. The second taxonomy classifies many of these species within a second genus, *Chlamydo philia*, in recognition of their differences in a variety of molecular markers including the 16S rRNA gene and some phenotypic markers (Everett et al., 1999). The merits of these approaches have been discussed (Everett and Andersen, 2001; Schachter et al., 2001). While this taxonomic outline uses the taxonomy of Everett et al. (1999), the first taxonomy is used by the authors of the chapter *Chlamydiaceae* (Kuo and Stephens, 2010). On the basis of the taxonomy of Everett et al. (1999), the genus *Chlamydia* comprises *Chlamydia trachomatis* (type species), *muridarum*, and *suis*. The genus *Chlamydo philia* comprises *Chlamydo philia psittaci* (type species), *abortus*, *caviae*, *felis*, *pecorum*, and *pneumoniae*.

The remaining families in the order are: "*Candidatus Clavichlamydiaceae*" comprising "*Candidatus Clavichlamydia salmonicola*"; "*Criblamydiaceae*" comprising "*Criblamydia sequanensis*"; *Parachlamydiaceae* comprising *Parachlamydia acanthamoebae* (type species and genus), *Neochlamydia hartmannellae*, and "*Protochlamydia amoebophila*"; "*Candidatus Piscichlamydiaceae*" comprising "*Candidatus Piscichlamydia salmonis*"; "*Rhabdochlamydiaceae*" comprising "*Candidatus Rhabdochlamydia porcellionis*" and "*Candidatus Rhabdochlamydia crassificans*"; *Simkaniaceae* comprising *Simkania negevensis* (type species and genus) and "*Candidatus Fritschea*

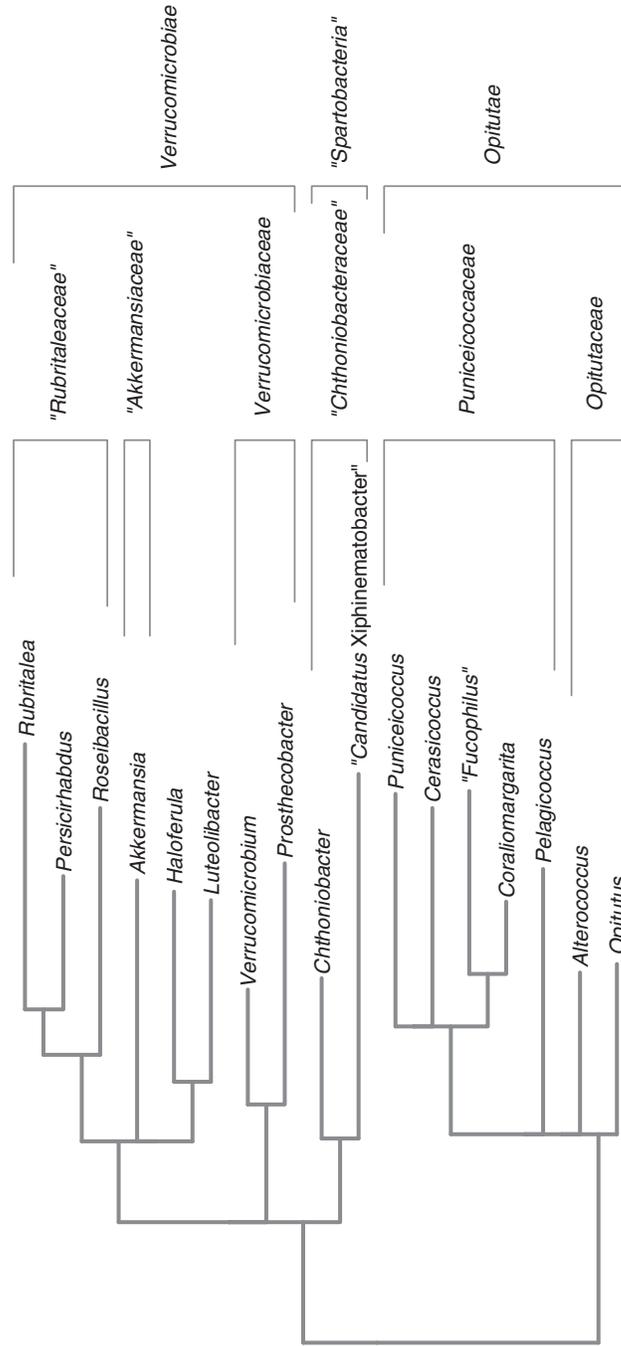


FIGURE 11. Genera of the phylum "Verrucomicrobia".

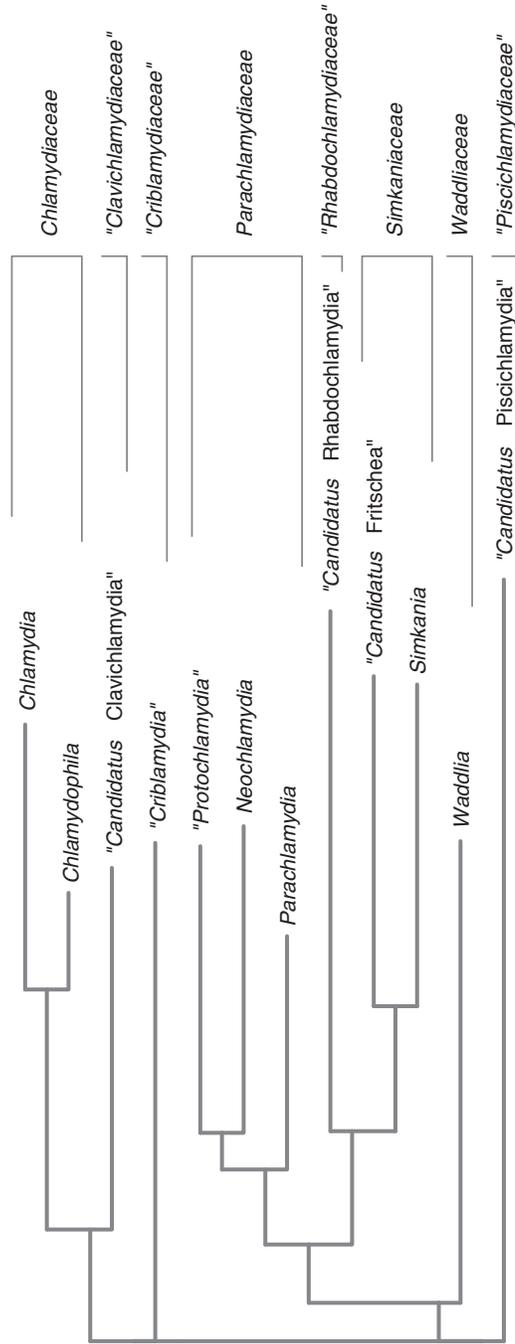


FIGURE 12. Genera of the phylum "Chlamydiae".

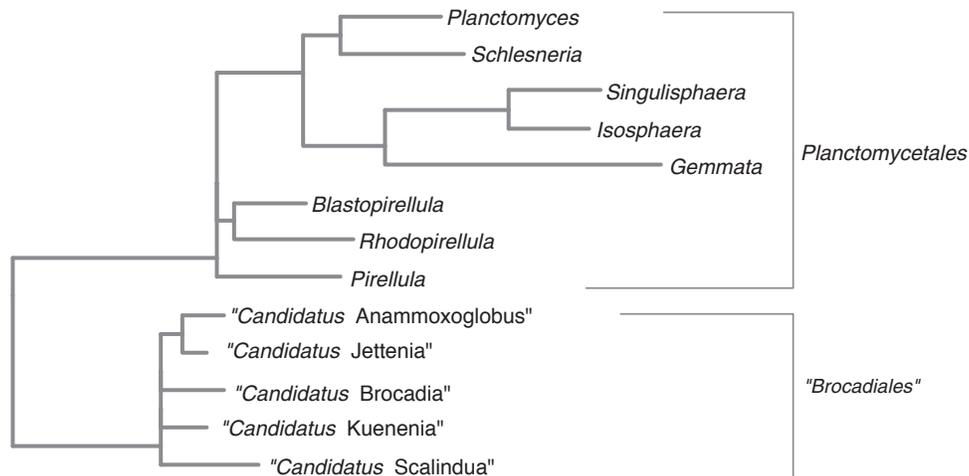


FIGURE 13. Genera of the phylum “Planctomycetes”.

bemisiae” and “*Candidatus Fritschea eriococci*”; and *Waddliaceae* comprising *Waddlia chondrophila* and “*Waddlia malaysiensis*” (Chua et al., 2005).

Phylum “Planctomycetes”

This phylum comprises a single class, “Planctomycetia”, and two orders, Planctomycetales and “Brocadiales” (Figure 13). The order Planctomycetales comprises the family Planctomycetaceae, containing eight diverse genera. The type genus is *Planctomyces*. However, a strain and 16S rRNA gene sequence are not available for the type species, *Planctomyces bekefi*, or for two other validly published species in this genus, *Planctomyces guttaeformis* and *stranskae*. Therefore, the taxonomy of this group is based upon the properties of the species that are available: *Planctomyces brasiliensis*, *limnophilus*, and *maris*. Most of the other genera in this family are monospecific and represented by *Blastopirellula marina*, *Gemmata obscuriglobus*, *Isosphaera pallida*, *Pirellula staleyi* (type species) and *marina*, *Rhodopirellula baltica*, *Schlesneria paludicola*, and *Singulisphaera acidiphila*. In addition to these, *Zavarzinella formosa* was described after the deadline for this volume but could be classified within this family (Kulichovskaya et al., 2009).

The order “Brocadiales” and family “Brocadiaaceae” comprises *Candidatus* species. They include “*Candidatus Brocadia anammoxidans*” and “fulgida”, “*Candidatus Anammoxoglobus propionicus*”, “*Candidatus Jettenia asiatica*”, “*Candidatus Kuenenia stuttgartiensis*”, and “*Candidatus Scalindua brodiae*”, “sorokinii”, and “wagneri”.

References

- An, D.S., H.G. Lee, W.T. Im, Q.M. Liu and S.T. Lee. 2007. *Segetibacter koreensis* gen. nov., sp. nov., a novel member of the phylum Bacteroidetes, isolated from the soil of a ginseng field in South Korea. *Int. J. Syst. Evol. Microbiol.* 57: 1828–1833.
- Asker, D., T. Beppu and K. Ueda. 2007. *Zeaxanthinibacter enoshimensis* gen. nov., sp. nov., a novel zeaxanthin-producing marine bacterium of the family Flavobacteriaceae, isolated from seawater off Enoshima Island, Japan. *Int. J. Syst. Evol. Microbiol.* 57: 837–843.
- Asker, D., T. Beppu and K. Ueda. 2008. *Nubsella zeaxanthinifaciens* gen. nov., sp. nov., a zeaxanthin-producing bacterium of the family Sphingobacteriaceae isolated from freshwater. *Int. J. Syst. Evol. Microbiol.* 58: 601–606.
- Bae, S.S., K.K. Kwon, S.H. Yang, H.S. Lee, S.J. Kim and J.H. Lee. 2007. *Flagellimonas eckloniae* gen. nov., sp. nov., a mesophilic marine bacterium of the family Flavobacteriaceae, isolated from the rhizosphere of *Ecklonia kurome*. *Int. J. Syst. Evol. Microbiol.* 57: 1050–1054.
- Bermudes, D., D. Chase and L. Margulis. 1988. Morphology as a basis for taxonomy of large spirochetes symbiotic in wood-eating cockroaches and termites: *Pillotina* gen. nov., nom. rev., *Pillotina calotermitidis* sp. nov., nom. rev., *Diplocalyx* gen. nov., nom. rev., *Diplocalyx calotermitidis* sp. nov., nom. rev., *Hollandina* gen. nov., nom. rev., *Hollandina pterotermitidis* sp. nov., nom. rev., and *Clevelandina reticulitermitidis* gen. nov., sp. nov. *Int. J. Syst. Bacteriol.* 38: 291–302.
- Bernardet, J.F. and Y. Nakagawa. 2006. An introduction to the family Flavobacteriaceae. In *The Prokaryotes: a Handbook on the Biology of Bacteria*, 3rd edn, vol. 7, Proteobacteria: Delta and Epsilon Subclasses. *Deeply Rooting Bacteria* (edited by Dworkin, Falkow, Rosenberg, Schleifer and Stackebrandt). Springer, New York, pp. 455–480.
- Bowman, J.P., C. Mancuso, C.M. Nichols and J.A.E. Gibson. 2003. *Algoriphagus ratkowskyi* gen. nov., sp. nov., *Brumimicrobium glaciale* gen. nov., sp. nov., *Cryomorpha ignava* gen. nov., sp. nov. and *Crocinitomix catalasitica* gen. nov., sp. nov., novel flavobacteria isolated from various polar habitats. *Int. J. Syst. Evol. Microbiol.* 53: 1343–1355.
- Brown, D.R., M. May, J.M. Bradbury, K.-E. Johansson and H. Neimark. 2010. Order I. *Mycoplasmatales*. In *Bergey's Manual of Systematic Bacteriology*, 2nd edn, vol. 4, The Bacteroidetes, Spirochaetes, Tenericutes (Mollicutes), Acidobacteria, Fibrobacteres, Fusobacteria, Dictyoglomi, Gemmatimonadetes, Lentisphaerae, Verrucomicrobia, Chlamydiae, and Planctomycetes (edited by Krieg, Staley, Brown, Hedlund, Paster, Ward, Ludwig and Whitman). Springer, New York, pp. 574–644.
- Cavalier-Smith, T. 2002. The neomuran origin of archaeobacteria, the negibacterial root of the universal tree and bacterial megaclassification. *Int. J. Syst. Evol. Microbiol.* 52: 7–76.
- Chen, Y.G., X.L. Cui, Y.Q. Zhang, W.J. Li, Y.X. Wang, C.J. Kim, J.M. Lim, L.H. Xu and C.L. Jiang. 2008. *Salinimicrobium terrae* sp. nov., isolated from saline soil, and emended description of the genus *Salinimicrobium*. *Int. J. Syst. Evol. Microbiol.* 58: 2501–2504.
- Chua, P.K., J.E. Corkill, P.S. Hooi, S.C. Cheng, C. Winstanley and C.A. Hart. 2005. Isolation of *Waddlia malaysiensis*, a novel intracellular bacterium, from fruit bat (*Eonycteris spelaea*). *Emerg. Infect. Dis.* 11: 271–277.
- Cicarelli, F.D., T. Doerks, C. von Mering, C.J. Creevey, B. Snel and P. Bork. 2006. Toward automatic reconstruction of a highly resolved tree of life. *Science* 311: 1283–1287.

- Cole, J.R., B. Chai, R.J. Farris, Q. Wang, A.S. Kulam-Syed-Mohideen, D.M. McGarrell, A.M. Bandela, E. Cardenas, G.M. Garrity and J.M. Tiedje. 2007. The ribosomal database project (RDP-II): introducing myRDP space and quality controlled public data. *Nucleic Acids Res.* 35: D169–D172.
- De Vos, P., H.G. Truper and B.J. Tindall. 2005. Judicial Commission of the International Committee on Systematics of Prokaryotes Minutes. Xth International (IUMS) Congress of Bacteriology and Applied Microbiology. *Int. J. Syst. Bacteriol.* 55: 525–532.
- Everett, K.D., R.M. Bush and A.A. Andersen. 1999. Emended description of the order *Chlamydiales*, proposal of *Parachlamydiaceae* fam. nov. and *Simkaniaceae* fam. nov., each containing one monotypic genus, revised taxonomy of the family *Chlamydiaceae*, including a new genus and five new species, and standards for the identification of organisms. *Int. J. Syst. Bacteriol.* 49: 415–440.
- Everett, K.D.E. and A.A. Andersen. 2001. Radical changes to chlamydial taxonomy are not necessary just yet: reply. *Int. J. Syst. Evol. Microbiol.* 51: 251–253.
- Garrity, G.M. and J.G. Holt. 2001. The road map to the manual. In *Bergey's Manual of Systematic Bacteriology*, 2nd edn, vol. 1, *The Archaea and the Deeply Branching and Phototrophic Bacteria* (edited by Boone, Castenholz and Garrity). Springer, New York, pp. 119–166.
- Garrity, G.M., J.A. Bell and T. Lilburn. 2005. The revised road map to the manual. In *Bergey's Manual of Systematic Bacteriology*, 2nd edn, vol. 2, *The Proteobacteria, Part A, Introductory Essays* (edited by Brenner, Krieg, Staley and Garrity). Springer, New York, pp. 159–206.
- Griffiths, E. and R.S. Gupta. 2007. Phylogeny and shared conserved inserts in proteins provide evidence that *Verrucomicrobia* are the closest known free-living relatives of chlamydiae. *Microbiology* 153: 2648–2654.
- Hardham, J.M., K.W. King, K. Dreier, J. Wong, C. Strietzel, R.R. Eversole, C. Sfintescu and R.T. Evans. 2008. Transfer of *Bacteroides splanchnicus* to *Odoribacter* gen. nov. as *Odoribacter splanchnicus* comb. nov., and description of *Odoribacter denticanis* sp. nov., isolated from the crevicular spaces of canine periodontitis patients. *Int. J. Syst. Evol. Microbiol.* 58: 103–109.
- Heyrman, J., M. Rodriguez-Diaz, J. Devos, A. Felske, N.A. Logan and P. De Vos. 2005. *Bacillus arenosi* sp. nov., *Bacillus arvi* sp. nov. and *Bacillus humi* sp. nov., isolated from soil. *Int. J. Syst. Evol. Microbiol.* 55: 111–117.
- Holmes, D.E., K.P. Nevin, T.L. Woodard, A.D. Peacock and D.R. Lovley. 2007. *Prolixibacter bellariivorans* gen. nov., sp. nov., a sugar-fermenting, psychrotolerant anaerobe of the phylum *Bacteroidetes*, isolated from a marine-sediment fuel cell. *Int. J. Syst. Evol. Microbiol.* 57: 701–707.
- Hosoya, S., V. Arunpairojana, C. Suwannachart, A. Kanjana-Opas and A. Yokota. 2006. *Aureispira marina* gen. nov., sp. nov., a gliding, arachidonic acid-containing bacterium isolated from the southern coastline of Thailand. *Int. J. Syst. Evol. Microbiol.* 56: 2931–2935.
- Hosoya, S., V. Arunpairojana, C. Suwannachart, A. Kanjana-Opas and A. Yokota. 2007. *Aureispira maritima* sp. nov., isolated from marine barnacle debris. *Int. J. Syst. Evol. Microbiol.* 57: 1948–1951.
- Khan, S.T., Y. Nakagawa and S. Harayama. 2007a. *Sedimibacter furfurosus* gen. nov., sp. nov. and *Gilvibacter sediminis* gen. nov., sp. nov., novel members of the family *Flavobacteriaceae*. *Int. J. Syst. Evol. Microbiol.* 57: 265–269.
- Khan, S.T., Y. Nakagawa and S. Harayama. 2007b. *Sediminitomix flava* gen. nov., sp. nov., of the phylum *Bacteroidetes*, isolated from marine sediment. *Int. J. Syst. Evol. Microbiol.* 57: 1689–1693.
- Khan, S.T., Y. Nakagawa and S. Harayama. 2007c. *Galbibacter mesophilus* gen. nov., sp. nov., a novel member of the family *Flavobacteriaceae*. *Int. J. Syst. Evol. Microbiol.* 57: 969–973.
- Kim, B.Y., H.Y. Weon, S.H. Yoo, S.B. Hong, S.W. Kwon, E. Stackebrandt and S.J. Go. 2007a. *Niabella aurantiaca* gen. nov., sp. nov., isolated from a greenhouse soil in Korea. *Int. J. Syst. Evol. Microbiol.* 57: 538–541.
- Kim, J.H., K.Y. Kim, Y.T. Hahm, B.S. Kim, J. Chun and C.J. Cha. 2008a. *Actibacter sediminis* gen. nov., sp. nov., a marine bacterium of the family *Flavobacteriaceae* isolated from tidal flat sediment. *Int. J. Syst. Evol. Microbiol.* 58: 139–143.
- Kim, M.K., J.R. Na, D.H. Cho, N.K. Soung and D.C. Yang. 2007b. *Parapedobacter koreensis* gen. nov., sp. nov. *Int. J. Syst. Evol. Microbiol.* 57: 1336–1341.
- Kim, M.K., Y.A. Kim, Y.J. Kim, N.K. Soung, T.H. Yi, S.Y. Kim and D.C. Yang. 2008b. *Parapedobacter soli* sp. nov., isolated from soil of a ginseng field. *Int. J. Syst. Evol. Microbiol.* 58: 337–340.
- Kulichevskaya, I.S., O.I. Baulina, P.L. Bodelier, W.I. Rijpstra, J.S. Damste and S.N. Dedysh. 2009. *Zavarzinella formosa* gen. nov., sp. nov., a novel stalked, Gemmata-like planctomycete from a Siberian peat bog. *Int. J. Syst. Evol. Microbiol.* 59: 357–364.
- Kuo, C.C. and R.S. Stephens. 2010. Family I. *Chlamydiaceae*. In *Bergey's Manual of Systematic Bacteriology*, 2nd edn, vol. 4, *The Bacteroidetes, Spirochaetes, Tenericutes (Mollicutes), Acidobacteria, Fibrobacteres, Fusobacteria, Dictyoglomi, Gemmatimonadetes, Lentisphaerae, Verrucomicrobia, Chlamydiae, and Planctomycetes* (edited by Krieg, Staley, Brown, Hedlund, Paster, Ward, Ludwig and Whitman). Springer, New York, p. 845.
- Labeled, D.P. 1997. International Committee on Systematic Bacteriology, VIIIth International Congress of Microbiology and Applied Bacteriology Minutes. *Int. J. Syst. Bacteriol.* 47: 597–600.
- Lee, K.C., R.I. Webb, P.H. Janssen, P. Sangwan, T. Romeo, J.T. Staley and J.A. Fuerst. 2009. Phylum *Verrucomicrobia* representatives share a compartmentalized cell plan with members of bacterial phylum *Planctomycetes*. *BMC Microbiol.* 9: 5.
- Lee, S.D. 2007. *Tamlana crocina* gen. nov., sp. nov., a marine bacterium of the family *Flavobacteriaceae*, isolated from beach sediment in Korea. *Int. J. Syst. Evol. Microbiol.* 57: 764–769.
- Lim, J.M., C.O. Jeon, S.S. Lee, D.J. Park, L.H. Xu, C.L. Jiang and C.J. Kim. 2008. Reclassification of *Saligentibacter catena* Ying *et al.* 2007 as *Salinimicrobium catena* gen. nov., comb. nov. and description of *Salinimicrobium xinjiangense* sp. nov., a halophilic bacterium isolated from Xinjiang province in China. *Int. J. Syst. Evol. Microbiol.* 58: 438–442.
- Ludwig, W., O. Strunk, R. Westram, L. Richter, H. Meier, Yadhukumar, A. Buchner, T. Lai, S. Steppi, G. Jobb, W. Forster, I. Brettske, S. Gerber, A.W. Ginhart, O. Gross, S. Grumann, S. Hermann, R. Jost, A. Konig, T. Liss, R. Lussmann, M. May, B. Nonhoff, B. Reichel, R. Strehlow, A. Stamatakis, N. Stuckmann, A. Vilbig, M. Lenke, T. Ludwig, A. Bode and K.H. Schleifer. 2004. ARB: a software environment for sequence data. *Nucleic Acids Res.* 32: 1363–1371.
- Ludwig, W. and H.P. Klenk. 2005. Overview: a phylogenetic backbone and taxonomic framework for prokaryotic systematics. In *Bergey's Manual of Systematic Bacteriology*, 2nd edn, vol. 2, *The Proteobacteria, Part A, Introductory Essays* (edited by Brenner, Krieg, Staley and Garrity). Springer, New York, pp. 49–65.
- Ludwig, W. and K.H. Schleifer. 2005. Molecular phylogeny of bacteria based on comparative sequence analysis of conserved genes. In *Microbial Phylogeny and Evolution, Concepts and Controversies* (edited by Sapp). Oxford University Press, New York, pp. 70–98.
- Morotomi, M., F. Nagai and H. Sakon. 2007. Genus *Megamonas* should be placed in the lineage of *Firmicutes; Clostridia; Clostridiales; 'Acidaminococaceae'; Megamonas*. *Int. J. Syst. Evol. Microbiol.* 57: 1673–1674.
- Morotomi, M., F. Nagai, H. Sakon and R. Tanaka. 2008. *Dialister succinatiphilus* sp. nov. and *Barnesiella intestinihominis* sp. nov., isolated from human faeces. *Int. J. Syst. Evol. Microbiol.* 58: 2716–2720.
- Murray, R.G. and E. Stackebrandt. 1995. Taxonomic note: implementation of the provisional status *Candidatus* for incompletely described prokaryotes. *Int. J. Syst. Bacteriol.* 45: 186–187.
- Nedashkovskaya, O.I., S.B. Kim, D.S. Shin, I.A. Beleneva and V.V. Mikhailov. 2007a. *Fulvivirga kasyanovii* gen. nov., sp. nov., a novel member of the phylum *Bacteroidetes* isolated from seawater in a mussel farm. *Int. J. Syst. Evol. Microbiol.* 57: 1046–1049.

- Nedashkovskaya, O.I., M. Vancanneyt, S.B. Kim, B. Hoste and K.S. Bae. 2007b. *Algibacter mikhailovii* sp. nov., a novel marine bacterium of the family *Flavobacteriaceae*, and emended description of the genus *Algibacter*. *Int. J. Syst. Evol. Microbiol.* 57: 2147–2150.
- Ntoutogias, S., C. Fasseas and G.I. Zervakis. 2007. *Olivibacter sitiensis* gen. nov., sp. nov., isolated from alkaline olive-oil mill wastes in the region of Sitia, Crete. *Int. J. Syst. Evol. Microbiol.* 57: 398–404.
- Ochiai, S., Y. Adachi and K. Mori. 1997. Unification of the genera *Serpulina* and *Brachyspira*, and proposals of *Brachyspira hyodysenteriae* comb. nov., *Brachyspira innocens* comb. nov. and *Brachyspira pilosicoli* comb. nov. *Microbiol. Immunol.* 41: 445–452.
- Pankratov, T.A., B.J. Tindall, W. Liesack and S.N. Dedysh. 2007. *Mucilagibacter paludis* gen. nov., sp. nov. and *Mucilagibacter gracilis* sp. nov., pectin-, xylan- and laminarin-degrading members of the family *Sphingobacteriaceae* from acidic Sphagnum peat bog. *Int. J. Syst. Evol. Microbiol.* 57: 2349–2354.
- Paster, B.J., D.A. Pelletier, F.E. Dewhirst, W.G. Weisburg, V. Fusing, L.K. Poulsen, S. Dannenberg and I. Schroeder. 1996. Phylogenetic position of the spirochetal genus *Cristispira*. *Appl. Environ. Microbiol.* 62: 942–946.
- Pilhofer, M., K. Rappl, C. Eckl, A.P. Bauer, W. Ludwig, K.H. Schleifer and G. Petroni. 2008. Characterization and evolution of cell division and cell wall synthesis genes in the bacterial phyla *Verrucomicrobia*, *Lentisphaerae*, *Chlamydiae*, and *Planctomycetes* and phylogenetic comparison with rRNA genes. *J. Bacteriol.* 190: 3192–3202.
- Pruesse, E., C. Quast, K. Knittel, B. Fuchs, W. Ludwig, J. Peplies and F.O. Glöckner. 2007. SILVA: a comprehensive online resource for quality checked and aligned rRNA sequence data compatible with ARB. *Nucleic Acids Res.* 35: 7188–7196.
- Qin, Q.L., D.L. Zhao, J. Wang, X.L. Chen, H.Y. Dang, T.G. Li, Y.Z. Zhang and P.J. Gao. 2007. *Wangia profunda* gen. nov., sp. nov., a novel marine bacterium of the family *Flavobacteriaceae* isolated from southern Okinawa Trough deep-sea sediment. *FEMS Microbiol. Lett.* 271: 53–58.
- Qu, J.H. and H.L. Yuan. 2008. *Sediminibacterium salmoneum* gen. nov., sp. nov., a member of the phylum *Bacteroidetes* isolated from sediment of a eutrophic reservoir. *Int. J. Syst. Evol. Microbiol.* 58: 2191–2194.
- Quan, Z.X., Y.P. Xiao, S.W. Roh, Y.D. Nam, H.W. Chang, K.S. Shin, S.K. Rhee, Y.H. Park and J.W. Bae. 2008. *Joostella marina* gen. nov., sp. nov., a novel member of the family *Flavobacteriaceae* isolated from the East Sea. *Int. J. Syst. Evol. Microbiol.* 58: 1388–1392.
- Romanenko, L.A., M. Uchino, G.M. Frolova and V.V. Mikhailov. 2007. *Marixanthomonas ophiuræ* gen. nov., sp. nov., a marine bacterium of the family *Flavobacteriaceae* isolated from a deep-sea brittle star. *Int. J. Syst. Evol. Microbiol.* 57: 457–462.
- Sakamoto, M. and Y. Benno. 2006. Reclassification of *Bacteroides distasonis*, *Bacteroides goldsteinii* and *Bacteroides merdae* as *Parabacteroides distasonis* gen. nov., comb. nov., *Parabacteroides goldsteinii* comb. nov. and *Parabacteroides merdae* comb. nov. *Int. J. Syst. Evol. Microbiol.* 56: 1599–1605.
- Sakamoto, M., P.T. Lan and Y. Benno. 2007. *Barnesiella viscericola* gen. nov., sp. nov., a novel member of the family *Porphyromonadaceae* isolated from chicken caecum. *Int. J. Syst. Evol. Microbiol.* 57: 342–346.
- Schachter, J., R.S. Stephens, P. Timms, C. Kuo, P.M. Bavoil, S. Birkelund, J. Boman, H. Caldwell, L.A. Campbell, M. Chernesky, G. Christiansen, I.N. Clarke, C. Gaydos, J.T. Grayston, T. Hackstadt, R. Hsia, B. Kaltenboeck, M. Leinonen, D. Ojcius, G. McClarty, J. Orfila, R. Peeling, M. Puolakkainen, T.C. Quinn, R.G. Rank, J. Raulston, G.L. Ridgeway, P. Saikku, W.E. Stamm, D.T. Taylor-Robinson, S.P. Wang and P.B. Wyrick. 2001. Radical changes to chlamydial taxonomy are not necessary just yet. *Int. J. Syst. Evol. Microbiol.* 51: 249; author reply 251–253.
- Shah, H.N. and M.D. Collins. 1988. Proposal for reclassification of *Bacteroides asaccharolyticus*, *Bacteroides gingivalis*, and *Bacteroides endodontalis* in a new genus, *Porphyromonas*. *Int. J. Syst. Bacteriol.* 38: 128–131.
- Shah, H.N. and D.M. Collins. 1990. *Prevotella*, a new genus to include *Bacteroides melaninogenicus* and related species formerly classified in the genus *Bacteroides*. *Int. J. Syst. Bacteriol.* 40: 205–208.
- Srisukchayakul, P., C. Suwanachart, Y. Sangnoi, A. Kanjana-Opas, S. Hosoya, A. Yokota and V. Arunpairojana. 2007. *Rapidithrix thailandica* gen. nov., sp. nov., a marine gliding bacterium isolated from samples collected from the Andaman sea, along the southern coastline of Thailand. *Int. J. Syst. Evol. Microbiol.* 57: 2275–2279.
- Stamatakis, A.P., T. Ludwig and H. Meier. 2005. RAxML-II: a program for sequential, parallel & distributed inference of large phylogenetic trees. *Concurrency Comput. Pract. Exp.* 17: 1705–1723.
- Stoecker, K., B. Bendinger, B. Schoning, P.H. Nielsen, J.L. Nielsen, C. Baranyi, E.R. Toenshoff, H. Daims and M. Wagner. 2006. Cohn's *Crenothrix* is a filamentous methane oxidizer with an unusual methane monooxygenase. *Proc. Natl. Acad. Sci. U.S.A.* 103: 2363–2367.
- Takeda, M., A. Yoneya, Y. Miyazaki, K. Kondo, H. Makita, M. Kondoh, I. Suzuki and J. Koizumi. 2008. *Prostheco bacter fluvialis* sp. nov., which lacks the bacterial tubulin *btubA* and *btubB* genes. *Int. J. Syst. Evol. Microbiol.* 58: 1561–1565.
- Ten, L.N., O.M. Liu, W.T. Im, Z. Aslam and S.T. Lee. 2006. *Sphingobacterium composti* sp. nov., a novel DNase-producing bacterium isolated from compost. *J. Microbiol. Biotechnol.* 16: 1728–1733.
- Ten, L.N., Q.-M. Liu, W.-T. Im, Z. Aslam and S.-T. Lee. 2007. List of new names and new combinations previously effectively, but not validly published. Validation List no. 116 *Int. J. Syst. Evol. Microbiol.* 57: 1372.
- Urai, M., T. Aizawa, Y. Nakagawa, M. Nakajima and M. Sunairi. 2008. *Mucilagibacter kameinonensis* sp. nov., isolated from garden soil. *Int. J. Syst. Evol. Microbiol.* 58: 2046–2050.
- Urios, L., H. Agogue, F. Lesongeur, E. Stackebrandt and P. Lebaron. 2006. *Balneola vulgaris* gen. nov., sp. nov., a member of the phylum *Bacteroidetes* from the north-western Mediterranean Sea. *Int. J. Syst. Evol. Microbiol.* 56: 1883–1887.
- Urios, L., L. Intertaglia, F. Lesongeur and P. Lebaron. 2008. *Balneola alkaliphila* sp. nov., a marine bacterium isolated from the Mediterranean Sea. *Int. J. Syst. Evol. Microbiol.* 58: 1288–1291.
- Vaz-Moreira, I., M.F. Nobre, O.C. Nunes and C.M. Manaia. 2007. *Pseudosphingobacterium domesticum* gen. nov., sp. nov., isolated from home-made compost. *Int. J. Syst. Evol. Microbiol.* 57: 1535–1538.
- Wagner, M. and M. Horn. 2006. The *Planctomycetes*, *Verrucomicrobia*, *Chlamydiae* and sister phyla comprise a superphylum with biotechnological and medical relevance. *Curr. Opin. Biotechnol.* 17: 241–249.
- Wang, L., L.N. Ten, H.G. Lee, W.T. Im and S.T. Lee. 2008. *Olivibacter soli* sp. nov., *Olivibacter ginsengisoli* sp. nov. and *Olivibacter terrae* sp. nov., from soil of a ginseng field and compost in South Korea. *Int. J. Syst. Evol. Microbiol.* 58: 1123–1127.
- Weon, H.Y., B.Y. Kim, S.H. Yoo, S.Y. Lee, S.W. Kwon, S.J. Go and E. Stackebrandt. 2006. *Niastella korensis* gen. nov., sp. nov. and *Niastella yeongjuensis* sp. nov., novel members of the phylum *Bacteroidetes*, isolated from soil cultivated with Korean ginseng. *Int. J. Syst. Evol. Microbiol.* 56: 1777–1782.
- Weon, H.Y., B.Y. Kim, J.H. Joa, S.W. Kwon, W.G. Kim and B.S. Koo. 2008a. *Niabella soli* sp. nov., isolated from soil from Jeju Island, Korea. *Int. J. Syst. Evol. Microbiol.* 58: 467–469.
- Weon, H.Y., H.J. Noh, J.A. Son, H.B. Jang, B.Y. Kim, S.W. Kwon and E. Stackebrandt. 2008b. *Rudanella lutea* gen. nov., sp. nov., isolated from an air sample in Korea. *Int. J. Syst. Evol. Microbiol.* 58: 474–478.
- Willems, A. and M.D. Collins. 1995. 16S ribosomal RNA gene similarities indicate that *Hallella sergens* (Moore and Moore) and *Mitsuohella dentalis* (Haapasalo *et al.*) are genealogically highly related and are members of the genus *Prevotella*: emended description of the genus *Prevotella* (Shah and Collins) and description of *Prevotella dentalis* comb. nov. *Int. J. Syst. Bacteriol.* 45: 832–836.
- Yang, S.J., Y.J. Choo and J.C. Cho. 2007. *Lutimonas vermicola* gen. nov., sp. nov., a member of the family *Flavobacteriaceae* isolated from the marine polychaete *Periserrula leucophryna*. *Int. J. Syst. Evol. Microbiol.* 57: 1679–1684.
- Yoo, S.H., H.Y. Weon, H.B. Jang, B.Y. Kim, S.W. Kwon, S.J. Go and E. Stackebrandt. 2007. *Sphingobacterium composti* sp. nov., isolated from cotton-waste composts. *Int. J. Syst. Evol. Microbiol.* 57: 1590–1593.

- Yoon, J., S. Ishikawa, H. Kasai and A. Yokota. 2007a. *Perexilibacter aurantiacus* gen. nov., sp. nov., a novel member of the family 'Flammeovirgaceae' isolated from sediment. *Int. J. Syst. Evol. Microbiol.* 57: 964–968.
- Yoon, J., S. Ishikawa, H. Kasai and A. Yokota. 2007b. *Persicitalea jodogahamensis* gen. nov., sp. nov., a marine bacterium of the family 'Flexibacteraceae', isolated from seawater in Japan. *Int. J. Syst. Evol. Microbiol.* 57: 1014–1017.
- Yoon, J., Y. Matsuo, K. Adachi, M. Nozawa, S. Matsuda, H. Kasai and A. Yokota. 2008a. Description of *Persicirhabdus sediminis* gen. nov., sp. nov., *Roseibacillus ishigakijimensis* gen. nov., sp. nov., *Roseibacillus ponti* sp. nov., *Roseibacillus persicus* sp. nov., *Luteolibacter pohlnpeiensis* gen. nov., sp. nov. and *Luteolibacter algae* sp. nov., six marine members of the phylum 'Verrucomicrobia', and emended descriptions of the class Verrucomicrobiae, the order Verrucomicrobiales and the family Verrucomicrobiaceae. *Int. J. Syst. Evol. Microbiol.* 58: 998–1007.
- Yoon, J., Y. Matsuo, H. Kasai and A. Yokota. 2008b. *Limibacter armeniacum* gen. nov., sp. nov., a novel representative of the family 'Flammeovirgaceae' isolated from marine sediment. *Int. J. Syst. Evol. Microbiol.* 58: 982–986.
- Yoon, J., Y. Matsuo, A. Katsuta, J.H. Jang, S. Matsuda, K. Adachi, H. Kasai and A. Yokota. 2008c. *Haloferula rosea* gen. nov., sp. nov., *Haloferula harenae* sp. nov., *Haloferula phyci* sp. nov., *Haloferula helveola* sp. nov. and *Haloferula sargassicola* sp. nov., five marine representatives of the family Verrucomicrobiaceae within the phylum 'Verrucomicrobia'. *Int. J. Syst. Evol. Microbiol.* 58: 2491–2500.
- Yoon, J.H., S.J. Kang, Y.T. Jung and T.K. Oh. 2008d. *Aestuariaicola saemankumensis* gen. nov., sp. nov., a member of the family Flavobacteriaceae, isolated from tidal flat sediment. *Int. J. Syst. Evol. Microbiol.* 58: 2126–2131.
- Yoon, M.H. and W.T. Im. 2007. *Flavisolibacter ginsengiterrae* gen. nov., sp. nov. and *Flavisolibacter ginsengisoli* sp. nov., isolated from ginseng cultivating soil. *Int. J. Syst. Evol. Microbiol.* 57: 1834–1839.
- Zchori-Fein, E., S.J. Perlman, S.E. Kelly, N. Katzir and M.S. Hunter. 2004. Characterization of a 'Bacteroidetes' symbiont in *Encarsia* wasps (Hymenoptera: Aphelinidae): proposal of 'Candidatus Cardinium hertigii'. *Int. J. Syst. Evol. Microbiol.* 54: 961–968.
- Zhao, J.S., D. Manno and J. Hawari. 2009. *Psychrobacter atlanticus* gen. nov., sp. nov., a marine member of the phylum Fusobacteria that produces H₂ and degrades nitramine explosives under low temperature conditions. *Int. J. Syst. Evol. Microbiol.* 59: 491–497.

Taxonomic outlines of the phyla *Bacteroidetes*, *Spirochaetes*, *Tenericutes* (*Mollicutes*), *Acidobacteria*, *Fibrobacteres*, *Fusobacteria*, *Dictyoglomi*, *Gemmatimonadetes*, *Lentisphaerae*, *Verrucomicrobia*, *Chlamydiae*, and *Planctomycetes*

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 described after the deadline of July 1, 2006, and are therefore not included in this volume are indicated by an asterisk (*).

Phylum XIV. “*Bacteroidetes*”

Class I. “*Bacteroidia*”

Order I. “*Bacteroidales*”

Family I. *Bacteroidaceae*^{AL}

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

Genus II. *Acetofilamentum*^{VP}

Genus III. *Acetomicrobium*^{VP}

Genus IV. *Acetothermus*^{VP}

Genus V. *Anaerorhabdus*^{VP}

Family II. “*Marinilabiliaceae*”

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

Genus II. *Alkaliflexus*^{VP}

Genus III. *Anaerophaga*^{VP}

Family III. “*Rikenellaceae*”

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

Genus II. *Alistipes*^{VP}

Family IV. “*Porphyromonadaceae*”

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

Genus II. *Barnesiella*^{VP}

Genus III. *Dysgonomonas*^{VP}

Genus IV. *Paludibacter*^{VP}

Genus V. *Parabacteroides*^{VP*}

Genus VI. *Petrimonas*^{VP}

Genus VII. *Proteiniphilum*^{VP}

Genus VIII. *Tannerella*^{VP}

Family V. “*Prevotellaceae*”

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

Genus II. *Xylanibacter*^{VP}

Class II. “*Flavobacteriia*”

Order I. “*Flavobacteriales*”

Family I. *Flavobacteriaceae*^{VP}

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

Genus II. *Actibacter*^{VP*}

Genus III. *Aequorivita*^{VP}

Genus IV. *Aestuariaicola*^{VP*}

Genus V. *Algibacter*^{VP}

Genus VI. *Aquimarina*^{VP}

Genus VII. *Arenibacter*^{VP}

Genus VIII. *Bergeyella*^{VP}

Genus IX. *Bizionia*^{VP}

Genus X. *Capnocytophaga*^{VP}

Genus XI. *Cellulophaga*^{VP}

Genus XII. *Chryseobacterium*^{VP}

Genus XIII. *Cloacibacterium*^{VP}

Genus XIV. *Coenonia*^{VP}

Genus XV. *Costertonia*^{VP}

Genus XVI. *Croceibacter*^{VP}

Genus XVII. *Dokdonia*^{VP}

Genus XVIII. *Donghaeana*^{VP}

Genus XIX. *Elizabethkingia*^{VP}

Genus XX. *Empedobacter*^{VP}

Genus XXI. *Epilithonimonas*^{VP}

Genus XXII. *Flagellimonas*^{VP*}

Genus XXIII. *Flaviramulus*^{VP}

Genus XXIV. *Formosa*^{VP}

Genus XXV. *Fulvibacter*^{VP*}

Genus XXVI. *Gaetbulibacter*^{VP}

Genus XXVII. *Galbibacter*^{VP*}

Genus XXVIII. *Gelidibacter*^{VP}

Genus XXIX. *Gillisia*^{VP}

Genus XXX. *Gilvibacter*^{VP*}

Genus XXXI. *Gramella*^{VP}

Genus XXXII. *Joostella*^{VP*}

Genus XXXIII. *Kaistella*^{VP}

Genus XXXIV. *Kordia*^{VP}

Genus XXXV. *Krokinobacter*^{VP}

Genus XXXVI. *Lacinutrix*^{VP}

Genus XXXVII. *Leeuwenhoekella*^{VP}

Genus XXXVIII. *Leptobacterium*^{VP*}

Genus XXXIX. *Lutibacter*^{VP}

- Genus XL. *Lutimonas*^{VP*}
 Genus XLI. *Maribacter*^{VP}
 Genus XLII. *Mariniflexile*^{VP}
 Genus XLIII. *Marixanthomonas*^{VP*}
 Genus XLIV. *Mesoflavibacter*^{VP*}
 Genus XLV. *Mesonina*^{VP}
 Genus XLVI. *Muricauda*^{VP}
 Genus XLVII. *Myroides*^{VP}
 Genus XLVIII. *Nonlabens*^{VP}
 Genus XLIX. *Olleya*^{VP}
 Genus L. *Ornithobacterium*^{VP}
 Genus LI. *Persicivirga*^{VP}
 Genus LII. *Polaribacter*^{VP}
 Genus LIII. *Psychroflexus*^{VP}
 Genus LIV. *Psychroserpens*^{VP}
 Genus LV. *Riemerella*^{VP}
 Genus LVI. *Robiginitalea*^{VP}
 Genus LVII. *Salegentibacter*^{VP}
 Genus LVIII. *Salinimicrobium*^{VP*}
 Genus LIX. *Sandarakinotalea*^{VP}
 Genus LX. *Sediminibacter*^{VP*}
 Genus LXI. *Sediminicola*^{VP}
 Genus LXII. *Sejongia*^{VP}
 Genus LXIII. *Stenothermobacter*^{VP}
 Genus LXIV. *Subsaxibacter*^{VP}
 Genus LXV. *Subsaximicrobium*^{VP}
 Genus LXVI. *Tamiana*^{VP*}
 Genus LXVII. *Tenacibaculum*^{VP}
 Genus LXVIII. *Ulvibacter*^{VP}
 Genus LXIX. *Vitellibacter*^{VP}
 Genus LXX. *Wautersiella*^{VP}
 Genus LXXI. *Weeksella*^{VP}
 Genus LXXII. *Winogradskyella*^{VP}
 Genus LXXIII. *Yeosuana*^{VP}
 Genus LXXIV. *Zeaxanthinibacter*^{VP*}
 Genus LXXV. *Zhouia*^{VP}
 Genus LXXVI. *Zobellia*^{VP}
 Genus LXXVII. *Zunongwangia*^{VP*}
- Family II. “*Blattabacteriaceae*”
 Genus I. *Blattabacterium*^{AL(T)}
- Family III. “*Cryomorphaceae*”
 Genus I. *Cryomorpha*^{VP(T)}
 Genus II. *Brumimicrobium*^{VP}
 Genus III. *Crocinitomix*^{VP}
 Genus IV. *Fluviicola*^{VP}
 Genus V. *Lishizhenia*^{VP}
 Genus VI. *Owenweeksia*^{VP}
- Class III. “*Sphingobacteriia*”
 Order I. “*Sphingobacteriales*”
 Family I. “*Sphingobacteriaceae*”^{VP}
 Genus I. *Sphingobacterium*^{VP(T)}
 Genus II. *Mucilagibacter*^{VP*}
 Genus III. *Nubsella*^{VP*}
 Genus IV. *Olivibacter*^{VP*}
 Genus V. *Parapedobacter*^{VP*}
 Genus VI. *Pedobacter*^{VP}
 Genus VII. *Pseudosphingobacterium*^{VP*}
- Family II. “*Chitinophagaceae*”
 Genus I. *Chitinophaga*^{VP(T)}
- Genus II. *Flavisolibacter*^{VP*}
 Genus III. *Niabella*^{VP*}
 Genus IV. *Niastella*^{VP*}
 Genus V. *Sediminibacterium*^{VP*}
 Genus VI. *Segetibacter*^{VP*}
 Genus VII. *Terrimonas*^{VP}
- Family III. “*Saprosiraceae*”
 Genus I. *Saprosira*^{AL(T)}
 Genus II. *Aureispira*^{VP}
 Genus III. *Haliscomenobacter*^{AL}
 Genus IV. *Lewinella*^{VP}
- Class IV. “*Cytophagia*”
 Order I. “*Cytophagales*”^{AL(T)}
 Family I. “*Cytophagaceae*”^{AL}
 Genus I. *Cytophaga*^{AL(T)}
 Genus II. *Adhaeribacter*^{VP}
 Genus III. *Arcicella*^{VP}
 Genus IV. *Dyadobacter*^{VP}
 Genus V. *Effluviibacter*^{VP}
 Genus VI. *Emticicia*^{VP}
 Genus VII. *Flectobacillus*^{AL}
 Genus VIII. *Flexibacter*^{AL}
 Genus IX. *Hymenobacter*^{VP}
 Genus X. *Larkinella*^{VP}
 Genus XI. *Leadbetterella*^{VP}
 Genus XII. *Meniscus*^{AL}
 Genus XIII. *Microscilla*^{AL}
 Genus XIV. *Persicitalea*^{VP*}
 Genus XV. *Pontibacter*^{VP}
 Genus XVI. *Rudanella*^{VP*}
 Genus XVII. *Runella*^{AL}
 Genus XVIII. *Spirosoma*^{AL}
 Genus XIX. *Sporocytophaga*^{AL}
- Family II. “*Cyclobacteriaceae*”
 Genus I. *Cyclobacterium*^{VP(T)}
 Genus II. *Algoriphagus*^{VP}
 Genus III. *Aquiflexum*^{VP}
 Genus IV. *Belliella*^{VP}
 Genus V. *Echinicola*^{VP}
 Genus VI. *Rhodonellum*^{VP}
- Family III. “*Flammeovirgaceae*”
 Genus I. *Flammeovirga*^{VP(T)}
 Genus II. *Fabibacter*^{VP}
 Genus III. *Flexithrix*^{AL}
 Genus IV. *Fulvivirga*^{VP*}
 Genus V. *Limibacter*^{VP*}
 Genus VI. *Perexilibacter*^{VP*}
 Genus VII. *Persicobacter*^{VP}
 Genus VIII. *Rapidithrix*^{VP*}
 Genus IX. *Reichenbachiella*^{VP}
 Genus X. *Roseivirga*^{VP}
 Genus XI. *Sedimitomix*^{VP*}
- Order II. *Incertae sedis*
 Family I. “*Rhodothermaceae*”
 Genus I. *Rhodothermus*^{VP(T)}
 Genus II. *Salinibacter*^{VP}
- Order III. *Incertae sedis*
 Genus I. *Balneola*^{VP*}
- Order IV. *Incertae sedis*

- Genus I. *Thermonema*^{VP}
 Order V. *Incertae sedis*
 Genus I. *Toxothrix*^{AL}
- Phylum XV. "*Spirochaetes*"
 Class I. "*Spirochaetia*"
 Order I. *Spirochaetales*^{AL(T)}
 Family I. *Spirochaetaceae*^{AL}
 Genus I. *Spirochaeta*^{AL(T)}
 Genus II. *Borrelia*^{AL}
 Genus III. *Cristispira*^{AL}
 Genus IV. *Treponema*^{AL}
 Family II. "*Brachyspiraceae*"
 Genus I. *Brachyspira*^{VP(T)}
 Family III. "*Brevinemataceae*"
 Genus I. *Brevinema*^{VP(T)}
 Family IV. *Leptospiraceae*^{AL}
 Genus I. *Leptospira*^{AL(T)}
 Genus II. *Leptonema*^{VP}
 Genus III. *Turneriella*^{VP}
 Family V. *Incertae sedis*
 Genus I. *Clevelandina*^{VP}
 Genus II. *Diplocalyx*^{VP}
 Genus III. *Hollandina*^{VP}
 Genus IV. *Pillotina*^{VP}
- Phylum XVI. *Tenericutes*^{VP}
 Class I. *Mollicutes*^{AL}
 Order I. *Mycoplasmatales*^{AL(T)}
 Family I. *Mycoplasmataceae*^{AL}
 Genus I. *Mycoplasma*^{AL(T)}
 Genus II. *Ureaplasma*^{VP}
 Family II. *Incertae sedis*
 Genus I. *Eperythrozoon*^{AL}
 Genus II. *Haemobartonella*^{AL}
 Order II. *Entomoplasmatales*^{VP}
 Family I. *Entomoplasmataceae*^{VP}
 Genus I. *Entomoplasma*^{VP(T)}
 Genus II. *Mesoplasma*^{VP}
 Family II. *Spiroplasmataceae*^{VP}
 Genus I. *Spiroplasma*^{AL(T)}
 Order III. *Acholeplasmatales*^{VP}
 Family I. *Acholeplasmataceae*^{AL}
 Genus I. *Acholeplasma*^{AL(T)}
 Family II. *Incertae sedis*
 Genus I. "*Candidatus Phytoplasma*"
 Order IV. *Anaeroplasmatales*^{VP}
 Family I. *Anaeroplasmataceae*^{VP}
 Genus I. *Anaeroplasma*^{AL(T)}
 Genus II. *Asteroleplasma*^{VP}
- Phylum XVII. "*Acidobacteria*"
 Class I. "*Acidobacteriia*"
 Order I. "*Acidobacteriales*"^(T)
 Family I. "*Acidobacteriaceae*"
 Genus I. *Acidobacterium*^{VP(T)}
 Genus II. *Edaphobacter*^{VP}
 Genus III. *Terriglobus*^{VP}
 Class II. *Holophagae*^{VP}
 Order I. *Holophagales*^{VP(T)}
 Family I. *Holophagaceae*^{VP}
 Genus I. *Holophaga*^{VP(T)}
- Genus II. *Geothrix*^{VP}
 Order II. *Acanthopleuribacterales*^{VP}
 Family I. *Acanthopleuribacteraceae*^{VP}
 Genus I. *Acanthopleuribacter*^{VP(T)}
- Phylum XVIII. "*Fibrobacteres*"
 Class I. "*Fibrobacteriia*"
 Order I. "*Fibrobacteriales*"^(T)
 Family I. "*Fibrobacteraceae*"
 Genus I. *Fibrobacter*^{VP(T)}
- Phylum XIX. "*Fusobacteria*"
 Class I. "*Fusobacteriia*"
 Order I. "*Fusobacteriales*"^(T)
 Family I. "*Fusobacteriaceae*"
 Genus I. *Fusobacterium*^{AL(T)}
 Genus II. *Cetobacterium*^{VP}
 Genus III. *Ityobacter*^{VP}
 Genus IV. *Propionigenium*^{VP}
 Genus V. *Psychrilyobacter*^{VP*}
 Family II. "*Leptotrichiaceae*"
 Genus I. *Leptotrichia*^{AL(T)}
 Genus II. *Sebaldella*^{VP}
 Genus III. *Sneathia*^{VP}
 Genus IV. *Streptobacillus*^{AL}
- Phylum XX. "*Dictyoglomi*"
 Class I. "*Dictyoglossia*"
 Order I. "*Dictyoglossales*"^(T)
 Family I. "*Dictyoglossaceae*"
 Genus I. *Dictyoglossus*^{VP(T)}
- Phylum XXI. *Gemmatimonadetes*
 Class I. *Gemmatimonadetes*^{VP}
 Order I. *Gemmatimonadales*^{VP(T)}
 Family I. *Gemmatimonadaceae*^{VP}
 Genus I. *Gemmatimonas*^{VP(T)}
- Phylum XXII. *Lentisphaerae*
 Class I. "*Lentisphaeria*"
 Order I. *Lentisphaerales*^{VP(T)}
 Family I. "*Lentisphaeraceae*"
 Genus I. *Lentisphaera*^{VP(T)}
 Order II. *Victivallales*^{VP}
 Family I. "*Victivallaceae*"
 Genus I. *Victivallis*^{VP(T)}
- Phylum XXIII. "*Verrucomicrobia*"
 Class I. *Verrucomicrobiae*^{VP}
 Order I. *Verrucomicrobiales*^{VP(T)}
 Family I. *Verrucomicrobiaceae*^{VP}
 Genus I. *Verrucomicrobium*^{VP(T)}
 Genus II. *Prostheco bacter*^{VP}
 Family II. "*Akkermansiaceae*"
 Genus I. *Akkermansia*^{VP(T)}
 Family III. "*Rubritaleaceae*"
 Genus I. *Rubritalea*^{VP(T)}
 Genus II. *Persicirhabdus*^{VP*}
 Genus III. *Roseibacillus*^{VP*}
 Class II. *Opiritutae*^{VP}
 Order I. *Opiritutales*^{VP(T)}
 Family I. *Opiritutaceae*^{VP}
 Genus I. *Opiritutus*^{VP(T)}
 Genus II. *Alterococcus*^{VP}

- Order II. *Puniceococcales*^{VP}
 Family I. *Puniceococcaceae*^{VP}
 Genus I. *Puniceicoccus*^{VP(T)}
 Genus II. *Cerasicoccus*^{VP}
 Genus III. *Coraliomargarita*^{VP}
 Genus IV. *Pelagicoccus*^{VP}
- Class III. “*Spartobacteria*”
 Order I. “*Chthoniobacterales*”^(T)
 Family I. “*Chthoniobacteraceae*”
 Genus I. “*Chthoniobacter*”^(T)
 Genus II. “*Candidatus Xiphinematobacter*”
- Phylum XXIV. “*Chlamydiae*”
 Class I. “*Chlamydiia*”
 Order I. *Chlamydiales*^{AL(T)}
 Family I. *Chlamydiaceae*^{AL}
 Genus I. *Chlamydia*^{AL(T)}
 Genus II. *Chlamydomphila*^{VP}
 Family II. “*Clavichlamydiaceae*”
 Genus I. “*Candidatus Clavichlamydia*”
 Family III. “*Criblamydiaceae*”
 Genus I. “*Criblamydia*”^(T)
 Family IV. *Parachlamydiaceae*^{VP}
 Genus I. *Parachlamydia*^{VP(T)}
 Genus II. *Neochlamydia*^{VP}
 Genus III. “*Protochlamydia*”
 Family V. “*Piscichlamydiaceae*”
 Genus I. “*Candidatus Piscichlamydia*”^(T)
 Family VI. “*Rhabdochlamydiaceae*”
 Genus I. “*Candidatus Rhabdochlamydia*”^{VP(T)}
- Family VII. *Simkaniaceae*^{VP}
 Genus I. *Simkania*^{VP(T)}
 Genus II. “*Candidatus Fritschea*”^{VP}
- Family VIII. *Waddliaceae*^{VP}
 Genus I. *Waddlia*^{VP(T)}
- Phylum XXV. “*Planctomycetes*”
 Class I. “*Planctomycetia*”
 Order I. *Planctomycetales*^{VP(T)}
 Family I. *Planctomycetaceae*^{VP}
 Genus I. *Planctomyces*^{AL(T)}
 Genus II. *Blastopirellula*^{VP}
 Genus III. *Gemmata*^{VP}
 Genus IV. *Isosphaera*^{VP}
 Genus V. *Pirellula*^{VP}
 Genus VI. *Rhodopirellula*^{VP}
 Genus VII. *Schlesneria*^{VP}
 Genus VIII. *Singulisphaera*^{VP}
- Order II. “*Brocadiales*”
 Family I. “*Brocadiaceae*”
 Genus I. “*Candidatus Brocadia*”^{VP(T)}
 Genus II. “*Candidatus Anammoxoglobus*”
 Genus III. “*Candidatus Jettenia*”
 Genus IV. “*Candidatus Kuenenia*”
 Genus V. “*Candidatus Scalindua*”

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