

UC Merced

UC Merced Previously Published Works

Title

Analysis of 1,000+ Type-Strain Genomes Substantially Improves Taxonomic Classification of Alphaproteobacteria

Permalink

<https://escholarship.org/uc/item/5xr3w8d5>

Authors

Hördt, Anton

López, Marina García

Meier-Kolthoff, Jan P

et al.

Publication Date

2020

DOI

10.3389/fmicb.2020.00468

Peer reviewed



Analysis of 1,000+ Type-Strain Genomes Substantially Improves Taxonomic Classification of *Alphaproteobacteria*

Anton Hördt¹, Marina García López¹, Jan P. Meier-Kolthoff¹, Marcel Schleuning¹, Lisa-Maria Weinhold^{1,2}, Brian J. Tindall³, Sabine Gronow³, Nikos C. Kyrpides⁴, Tanja Woyke⁴ and Markus Göker^{1*}

¹ Department of Bioinformatics, Leibniz Institute DSMZ – German Collection of Microorganisms and Cell Cultures, Brunswick, Germany, ² Institute of Organic Chemistry and Biochemistry, Czech Academy of Sciences, Prague, Czechia, ³ Department of Microorganisms, Leibniz Institute DSMZ – German Collection of Microorganisms and Cell Cultures, Brunswick, Germany, ⁴ Department of Energy, Joint Genome Institute, Berkeley, CA, United States

OPEN ACCESS

Edited by:

David W. Ussery,
University of Arkansas for Medical
Sciences, United States

Reviewed by:

Ramprasad E. V. V.,
University of Hyderabad, India
Aharon Oren,
Hebrew University of Jerusalem, Israel

*Correspondence:

Markus Göker
markus.goeker@dsMZ.de

Specialty section:

This article was submitted to
Evolutionary and Genomic
Microbiology,
a section of the journal
Frontiers in Microbiology

Received: 22 August 2019

Accepted: 04 March 2020

Published: 07 April 2020

Citation:

Hördt A, López MG,
Meier-Kolthoff JP, Schleuning M,
Weinhold L-M, Tindall BJ, Gronow S,
Kyrpides NC, Woyke T and Göker M
(2020) Analysis of 1,000+ Type-Strain
Genomes Substantially Improves
Taxonomic Classification
of *Alphaproteobacteria*.
Front. Microbiol. 11:468.
doi: 10.3389/fmicb.2020.00468

The class *Alphaproteobacteria* is comprised of a diverse assemblage of Gram-negative bacteria that includes organisms of varying morphologies, physiologies and habitat preferences many of which are of clinical and ecological importance. *Alphaproteobacteria* classification has proved to be difficult, not least when taxonomic decisions rested heavily on a limited number of phenotypic features and interpretation of poorly resolved 16S rRNA gene trees. Despite progress in recent years regarding the classification of bacteria assigned to the class, there remains a need to further clarify taxonomic relationships. Here, draft genome sequences of a collection of genomes of more than 1000 *Alphaproteobacteria* and outgroup type strains were used to infer phylogenetic trees from genome-scale data using the principles drawn from phylogenetic systematics. The majority of taxa were found to be monophyletic but several orders, families and genera, including taxa recognized as problematic long ago but also quite recent taxa, as well as a few species were shown to be in need of revision. According proposals are made for the recognition of new orders, families and genera, as well as the transfer of a variety of species to other genera and of a variety of genera to other families. In addition, emended descriptions are given for many species mainly involving information on DNA G+C content and (approximate) genome size, both of which are confirmed as valuable taxonomic markers. Similarly, analysis of the gene content was shown to provide valuable taxonomic insights in the class. Significant incongruities between 16S rRNA gene and whole genome trees were not found in the class. The incongruities that became obvious when comparing the results of the present study with existing classifications appeared to be caused mainly by insufficiently resolved 16S rRNA gene trees or incomplete taxon sampling. Another probable cause of misclassifications in the past is the partially low overall fit of phenotypic characters to the sequence-based tree. Even though a significant degree of phylogenetic conservation was detected in all characters investigated, the overall fit to the tree varied considerably.

Keywords: G+C content, genome size, Genome BLAST Distance Phylogeny, chemotaxonomy, morphology, phylogenetic systematics, phylogenomics

INTRODUCTION

The class *Alphaproteobacteria* is a diverse group of bacteria that is taxonomically assigned to the phylum *Proteobacteria* (Garrity et al., 2005a). At the time of writing the class comprises more than a dozen orders with validly published names. *Alphaproteobacteria* are cosmopolitan and colonize a wide range of habitats including soil, pelagic and benthic regions of the ocean, fresh water, and lichens. Frequently *Alphaproteobacteria* account for one of the most active and numerically dominant taxon of microbial communities (Brinkhoff et al., 2008; Bates et al., 2011; Schiaffino et al., 2016). The variety of habitats is illustrated by *Rhodobacteraceae* which is predominantly marine as for genera such as *Oceanicella* (Albuquerque et al., 2012) but also includes genera such as *Pannonibacter* (Borsodi et al., 2003; Biebl et al., 2007), which is found in lakes, and *Ketogulonigenium* (Urbance et al., 2001; Simon et al., 2017), found in soil.

Although the vast majority of *Alphaproteobacteria* are free-living, this class does include representatives associated with a broad range of hosts. *Rhizobium*, for example, establishes endosymbiotic nitrogen-fixing associations with roots of legumes (Pini et al., 2011). These bacteria are key players in the nitrogen turnover and have an important role in agriculture because they act as a natural fertilizer for plants (Fox et al., 2007) and for bioremediation and mineralization of industrial pollutants (Siddavattam et al., 2011). Other kinds of symbiosis are also established, such as the one between *Silicibacter* and marine phytoplankton (Belas et al., 2009). *Wolbachia* includes endosymbionts of arthropods (Hedges et al., 2008). Their host interactions are often complex and in some cases have evolved into a mutualistic rather than parasitic relationship (Hosokawa et al., 2010; Nikoh et al., 2014) giving their hosts resistance to viral infections (Teixeira et al., 2008). Other *Alphaproteobacteria*, such as *Bartonella* (Strong et al., 1915; Brenner et al., 1993; Birtles et al., 1995) and *Brucella* (Verger et al., 1985; Meyer and Shaw, 1920), are obligate intracellular parasites. Genera like *Rickettsia* can trigger serious diseases in plants, animals and humans (Fournier et al., 2000; Luis-Pantoja et al., 2015; Maina et al., 2016). *Alphaproteobacteria* also harbours opportunistic human pathogens such as *Roseomonas* (Rihs et al., 1993; Sánchez-Porro et al., 2009; Venkata Ramana et al., 2010).

Alphaproteobacteria are metabolically diverse, too. Most representatives of the class are chemoorganoheterotrophs but many others perform anoxygenic photosynthesis (Brinkmann et al., 2018), including the families *Rhodobacteraceae* or *Rhodospirillaceae*, the so-called purple non-sulfur bacteria (Imhoff et al., 1998). The phototrophic genera include *Porphyrobacter* (Fuerst et al., 1993; Coil et al., 2015), *Roseobacter* (Shiba, 1991; Martens et al., 2006), and *Rhodobacter* (Imhoff et al., 1984; Srinivas et al., 2007b; Wang et al., 2014). bacteriochlorophyll α and carotenoids are mostly present in phototrophic bacteria but can also be found in non-phototrophic bacteria like *Roseibium* (Zhong et al., 2014). While photoorganoheterotrophy is found in *Rhodovulum* (Hiraishi and Ueda, 1994a) and *Phaeospirillum* (Imhoff

et al., 1998), chemolithoorganotrophy is present in *Elioraea* (Albuquerque et al., 2008) and facultative methylotrophy in *Methylarcula* (Doronina et al., 2000). *Magnetospirillum* (Schleifer et al., 1991), *Magnetococcus* (Bazylnski et al., 2013a) and *Magnetovibrio* (Bazylnski et al., 2013b) contain tiny chains of magnetite which support magnetotaxis (Schleifer et al., 1991). *Alphaproteobacteria* include obligate aerobic bacteria such as *Maribius* (Choi et al., 2007) as well as facultative aerobes, facultative anaerobes like *Pannonibacter* (Borsodi et al., 2003), and obligate anaerobes such as *Phaeobacterium* (Borsodi et al., 2003; Choi et al., 2007; Nupur et al., 2015). Yet the vast majority of *Alphaproteobacteria* are aerobes and to a lesser extent facultative anaerobes.

As for chemotaxonomy, the presence of sphingolipids is remarkable within *Alphaproteobacteria* since it appears to be restricted to *Sphingomonadales* (Kosako and Yabuuchi, 2005). Morphologically, *Alphaproteobacteria* are mostly found to be rod-, coccus- or ovoid-shaped. Yet some taxa deviate from this pattern, such as the spirilla-shaped *Rhodospirillaceae* (Pfennig and Trüper, 1971) including *Magnetospirillum* (Schleifer et al., 1991) and *Thalassospira* (López-López et al., 2002; Liu et al., 2007; Tsubouchi et al., 2014). *Caulobacter* (Henrici and Johnson, 1935; Abraham et al., 1999) and *Brevundimonas* (Segers et al., 1994; Abraham et al., 1999) of *Caulobacteraceae* (Henrici and Johnson, 1935), as well as *Litorimonas* (Jung et al., 2011; Nedashkovskaya et al., 2013), *Hellea* (Alain et al., 2008) and *Oceanibulbus* (Wagner-Döbler et al., 2004) of *Rhodobacteraceae* (Garrity et al., 2005b), are also unique as they form stalks. Many *Alphaproteobacteria* are motile by means of flagella, as exemplified by *Caulobacterales* (Henrici and Johnson, 1935) which mostly display flagella. Periplasmic flagella are present in some species, particularly in *Salinispira* (Ben Hania et al., 2015). Gliding motility has rarely been reported; examples are *Pacificimonas* (Liu K. et al., 2014) and *Acuticoccus* (Hou et al., 2015).

The class *Alphaproteobacteria* was proposed relatively recently (Garrity et al., 2005a) even though the first representatives of the group were isolated as early as 1898 (Beijerinck, 1898). As in other groups of bacteria the initial classification of *Alphaproteobacteria* into orders, families and genera was based on morphological and physiological characteristics, whereas advances in molecular systematics led to the view that taxonomic classification should be based on the integrated use of genotypic and phenotypic data (Wayne et al., 1987; Stackebrandt, 1992), an approach known as polyphasic taxonomy (Colwell, 1970; Vandamme et al., 1996; Gillis et al., 2005; Kämpfer and Glaeser, 2012). In particular, 16S rRNA gene sequences have been routinely applied to infer phylogenetic trees or in conjunction with simpler approaches such as pairwise distance or similarities (Meier-Kolthoff et al., 2013b; Kim and Chun, 2014; Yarza and Munoz, 2014). The technique named Multilocus Sequence Analysis or MLSA (Glaeser and Kämpfer, 2015) has widely been used to resolve the phylogeny of different taxonomic groups of *Alphaproteobacteria* like *Ensifer* (Martens et al., 2008) and *Bradyrhizobium* (Rivas et al., 2009). However, trees based on a few thousand nucleotides

such as those based on a single phylogenetic marker (1400–1500 nucleotides in the case of the 16S rRNA gene), or even a few concatenated housekeeping genes as in the case of MLSA tend to have branches with low bootstrap values (Klenk and Göker, 2010).

Better resolved phylogenies based on the hundreds of housekeeping genes or even the core-genome has been used to elucidate the phylogenetic relationships among selected groups of closely related taxa (Williams et al., 2007; Wirth and Whitman, 2018). Given the rapid and ongoing progress in sequencing technologies (Mavromatis et al., 2012), classifications based on whole genome sequences and associated bioinformatic tools can be based on millions of characters. This provides a step change in reliability, as evidenced by high average bootstrap support in phylogenomic trees (Breider et al., 2014; Meier-Kolthoff et al., 2014a), even though the ordinary bootstrap is not necessarily the most reliable approach when dealing with supermatrices potentially comprised of genes with distinct histories (Siddall, 2010; Simon et al., 2017). Reclassifications at all levels of the taxonomic hierarchy can result from such approaches (Hahnke et al., 2016; Nouioui et al., 2018). It was also shown that DNA G+C composition values directly calculated from genome sequences have a significantly better fit to the phylogeny than the experimentally determined ones cited in many species descriptions (Hahnke et al., 2016). This is in line with the observation that within-species variation is at most 1% when G+C content is calculated from genome sequences (Meier-Kolthoff et al., 2014c) and that claims in the literature that the variation in G+C content within bacterial species is at most 3 mol% (Mesbah et al., 1989) or even 5% (Rosselló-Mora and Amann, 2001) can be attributed to experimental error in traditional methods (Mesbah et al., 1989; Moreira et al., 2011). Recent studies based on complete genomes also confirm that the distribution of the G+C content is phylogenetically conserved. While this also holds to a somewhat lesser degree for genome size (Nouioui et al., 2018), phylogenetic inertia of these features has not yet been measured for *Alphaproteobacteria*. Likewise, it is as yet unknown to which degree gene-content phylogenies (Huson and Steel, 2004) are in concordance with standard genome-scale phylogenies even though both approaches showed high agreement in subgroups of *Alphaproteobacteria* (Breider et al., 2014) and because the gene content is of relevance as it conveys phenotypic features (Zhu et al., 2015).

The aim of the present study is an improved phylogenetic framework for the classification of *Alphaproteobacteria*. Genome-scale phylogenetic trees were inferred for genome-sequenced type strains and augmented by analyses of a comprehensive collection of type-strain 16S rRNA gene sequences to address the following questions: (i) to what extent are phylogenies calculated from whole genome sequences still in conflict with the current classification of *Alphaproteobacteria* and with their 16S rRNA gene phylogenies? (ii) Which taxa need to be revised because they are evidently non-monophyletic? (iii) Which taxon descriptions should be modified because of inaccurate or missing G+C values? and (iv) How do G+C content, genome size, genomic gene content and routinely recorded phenotypic features of

Alphaproteobacteria relate to their phylogeny and to which degree can they serve as a taxonomic marker?

MATERIALS AND METHODS

The approach to taxon sampling and analysis was in almost all respects the same as previously described (Hahnke et al., 2016; Nouioui et al., 2018). A total of 1104 annotated type-strain genome sequences (**Supplementary Table S1**) for *Alphaproteobacteria* (ingroup) and *Spirochaetes* (outgroup) were collected. While some originated from GenBank the majority was obtained *de novo* in the course of the KMG projects phase II (Mukherjee et al., 2017) and phase IV and deposited in the Integrated Microbial Genomes platform (Chen et al., 2019) and in the Type-Strain Genome Server database (Meier-Kolthoff and Göker, 2019). Among *Alphaproteobacteria* KMG-II mainly targeted *Rhodobacteraceae* but also representatives of other families. All newly generated KMG sequences underwent standard quality control at DSMZ and JGI documented on the respective web pages and had < 100 contigs. All accepted genome sequences had < 500 contigs and matched the 16S rRNA gene reference database described below. Structural annotation at JGI and DSMZ was done using Prodigal v. 2.6.2 (Hyatt et al., 2010). The features of all genome sequences that entered these analyses are provided in **Supplementary Table S1**. These annotated genome sequences were processed further as in our previous study using the high-throughput version of the Genome BLAST Distance Phylogeny (GBDP) approach in conjunction with BLAST+ v2.2.30 in blastp mode (Auch et al., 2006; Camacho et al., 2009; Meier-Kolthoff et al., 2014a) and FastME version 2.1.6.1 using the improved neighbor-joining algorithm BioNJ for obtaining starting trees followed by branch swapping under the balanced minimum evolution criterion (Desper and Gascuel, 2004) using the subtree-pruning-and-regrafting algorithm (Desper and Gascuel, 2006; Lefort et al., 2015). One hundred pseudo-bootstrap replicates (Meier-Kolthoff et al., 2013a, 2014a) were used to obtain branch-support values for these genome-scale phylogenies.

Trees were visualized using Interactive Tree Of Life (Letunic and Bork, 2019) in conjunction with the script deposited at <https://github.com/mgoeker/table2itol>. Outgroup-based rooting was compared with rooting using least-squares dating as implemented in LSD version 0.2 (To et al., 2016) after removing the outgroup taxa and inferring an accordingly reduced tree with FastME. Species and subspecies boundaries were investigated using digital DNA:DNA hybridization (dDDH) as implemented in the Genome-To-Genome Distance Calculator (GGDC) version 2.1 (Meier-Kolthoff et al., 2013a) and in TYGS, the Type (Strain) Genome Server (Meier-Kolthoff and Göker, 2019).

In addition to GBDP formula d_5 , which explores sequence (dis-)similarity and is the recommended one for phylogenetic inference (Auch et al., 2006; Meier-Kolthoff et al., 2014a) we here used formula d_3 , which compares the gene content of the investigated genomes after correcting for reduction in genome size (Henz et al., 2005). While this analysis was also done using the GBDP software, for consistency with previous work

we will refer to the d_5 phylogeny as GBDP tree and to the d_3 tree as gene-content analysis. There are various reasons why a gene-content phylogeny may fail to recover the true tree, as detailed below, hence the gene-content analysis is not intended to lend phylogenetic support. However, it may nevertheless be of taxonomic interest whether or not a certain branch is supported by gene-content data, particularly since the gene content conveys metabolic capabilities (Zhu et al., 2015) and yield independent evidence for conclusions from standard genome-scale phylogenies (Breider et al., 2014).

Full-length 16S rRNA gene sequences were extracted from the genomes using RNAMmer version 1.2 (Lagesen et al., 2007) and compared with the 16S rRNA gene reference database using BLAST and phylogenetic trees to verify the taxonomic affiliation of genomes. Non-matching genome sequences were discarded from further analyses. A comprehensive sequence alignment was generated with MAFFT version 7.271 with the “localpair” option (Katoh et al., 2005) using either the sequences extracted from the genome sequences or the previously published 16S rRNA gene sequences, depending on the length and number of ambiguous bases. Trees were inferred from the alignment with RAxML (Stamatakis, 2014) under the maximum-likelihood (ML) criterion and with TNT (Goloboff et al., 2008) under the maximum-parsimony (MP). In addition to unconstrained, comprehensive 16S rRNA gene trees (UCT), constrained comprehensive trees (CCT) were inferred with ML and MP using the bipartitions of the GBDP tree with $\geq 95\%$ support as backbone constraint, as previously described (Hahnke et al., 2016; Nouioui et al., 2018).

Taxa were analyzed to determine whether they were monophyletic, paraphyletic or polyphyletic (Farris, 1974; Wood, 1994). Taxa non-monophyletic according to the GBDP tree were tested for evidence for their monophyly in the UCT and the 16S rRNA gene trees, if any, in the original publication. In the case of a significant conflict (i.e., high support values for contradicting bipartitions) between trees or low support in the GBDP tree, additional phylogenomic analyses of selected taxa were conducted. To this end, protein sequences of those taxa with the reciprocal best hits from GBDP/BLAST were clustered with MCL (Markov Chain Clustering) version 14-137 (Enright et al., 2002) under default settings and an e-value filter of 10^{-5} in analogy to OrthoMCL (Li et al., 2003). The resulting sets of orthologous proteins were aligned with MAFFT and concatenated to form a supermatrix after discarding the few clusters that still contained more than a single protein for at least one genome. Comprehensive supermatrices were compiled from all the orthologs that occurred in at least four genomes, whereas core-genome supermatrices were constructed for the orthologs that occurred in all of the genomes. Supermatrices were analyzed with TNT, and with RAxML under the “PROTCATLGF” model, in conjunction with 100 partition bootstrap replicates (Siddall, 2010; Simon et al., 2017).

Additionally, selected phenotypic features relevant for the taxonomic classification of *Alphaproteobacteria* were as comprehensively as possible collected from the taxonomic literature: motility by flagella, absence or presence of carotenoids, absence or presence of bacteriochlorophyll α , absence or presence

of sphingolipids, average number of isoprene residues of the major ubiquinones, and relationship to oxygen. To avoid circular reasoning, missing features of a species were only inferred from features of its genus when species and genus were described in the same publication or when the species description had explicitly been declared as adding to the features of the genus. For the binary chemotaxonomic characters an alternative coding was also investigated that treated all missing values as indicating absence. Ubiquinone percentages would be more informative than just statements about being “major” but mostly only the latter are provided in the literature. Oxygen conditions were coded as ordered multi-state character: (1) strictly anaerobic; (2) facultatively aerobic, facultatively anaerobic, or microaerophilic; (3) strictly aerobic. Among all nine coding options tested, this yielded the highest fit to the tree (**Supplementary Table S1**) but the differences between the coding options were not pronounced. Phylogenetic conservation of selected phenotypic and genomic characters with respect to the GBDP tree (reduced to represent each set of equivalent strains by only a single genome) was evaluated using a tip-permutation test in conjunction with the calculation of maximum-parsimony scores with TNT as previously described (Simon et al., 2017; Carro et al., 2018) and 10,000 permutations. TNT input files were generated with opm (Vaas et al., 2013). The proportion of times the score of a permuted tree was at least as low as the score of the original tree yielded the p -value. Maximum-parsimony retention indices (Farris, 1989; Wiley and Lieberman, 2011) were calculated to further differentiate between the fit of each character to the tree.

Taxa that were unambiguously non-monophyletic according to the genome-scale analyses were screened for published evidence of their monophyly. The published evidence was judged as inconclusive when based on unsupported branches in phylogenetic trees, based on probably homoplastic characters or on probable plesiomorphic character states. Plesiomorphies might well be “diagnostic” but just for paraphyletic groups (Hennig, 1965; Wiley and Lieberman, 2011; Montero-Calasanz et al., 2017) hence “diagnostic” features alone are insufficient in phylogenetic systematics.

For fixing the obviously non-monophyletic taxa taxonomic consequences were proposed if new taxon delineations could be determined that were sufficiently supported by the CCT. In these cases, the uncertain phylogenetic placement of taxa whose genome sequences were not available at the time of writing would not affect the new proposals. Where necessary taxa were tentatively placed in newly delineated groups.

RESULTS

The presentation of the results is organized as follows. After a brief overview on the figures and tables the outcome of the tests for the phylogenetic conservation are illustrated. Next, the phylogenetic results for the outgroup taxa are described and put in the context of their current taxonomic classification. Finally, the hierarchical classification of the class *Alphaproteobacteria* itself, arranged according to the orders in

which it is currently subdivided and then according to the taxonomic categories, is compared to the phylogenomic trees. These sections motivate the need for a variety of reclassifications, whereas the actual taxonomic consequences are listed at the end of the section “Discussion.” Finally, the outcome of the tests for the phylogenetic conservation are illustrated.

The GBDP tree is shown in **Figures 1–8**; **Figure 1** provides an overview and explains which specific sections of the same tree are displayed in greater detail in **Figures 2–8**. **Table 1** shows dDDH results for pairs of type strains of interest, while **Table 2** displays the results of the tests for phylogenetic inertia. Phenotypic information for groups of taxa whose taxonomic classification is treated in detail below is summarized in **Supplementary Table S1**. This **Supplementary Table S1** also contains the complete list of genome sequences used in this study, including their GenBank and IMG accession numbers. Additional phylogenetic trees, including the GBDP tree in a single figure and with phenotypic annotation and the results from the gene-content analysis, are found in **Supplementary File S2**.

Classes and Orders

The taxon sampling used in the present study was not mainly intended to provide support for or against the monophyly of the class *Alphaproteobacteria*, or of the phylum *Proteobacteria* in general. The choice of the outgroup in the present study was not intended to indicate that the phylum *Spirochaetes* represents the sister group of *Alphaproteobacteria* but was motivated by uncertainty regarding the monophyly of *Proteobacteria* (Yarza et al., 2014). Inferring the tree depicted in **Figure 1** again after removing the outgroup and rooting this reduced tree using least-squares dating yielded the same branching order for the ingroup, i.e., the root was located between the clade formed by *Magnetococcus* and *Mariprofundus* on the one hand and the remainder of the tree on the other hand. *Spirochaetes* may thus not be the ideal outgroup for *Alphaproteobacteria* phylogeny but the alternative rooting confirmed the depicted branching order.

Only a single issue regarding the classes became apparent in this study, and most of the orders of the class *Alphaproteobacteria* appeared as monophyletic in our analysis (**Figure 1**). The exceptions were mainly caused by specific genera taxonomically assigned to *Rhodospirillales* and particularly genera assigned to *Rhodobacterales* that were phylogenetically intermixed with the order currently called *Rhizobiales*.

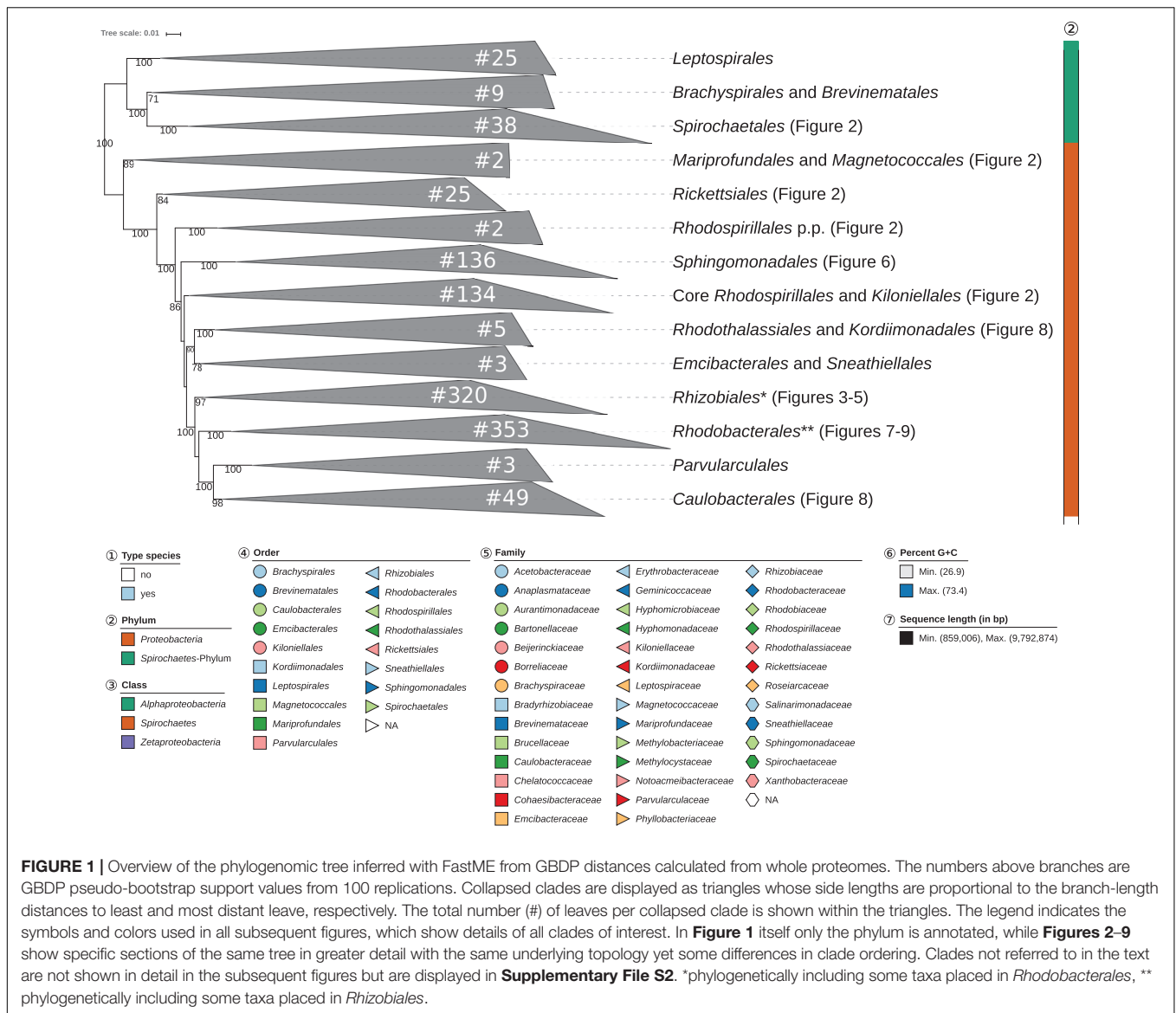
Alphaproteobacteria appeared as paraphyletic in the GBDP tree (**Figures 1, 2**) since *Mariprofundus ferrooxydans* of *Zetaproteobacteria* (Emerson et al., 2007) formed a strongly supported clade together with the alphaproteobacterium *Magnetococcus marinus* (Bazyliński et al., 2013a). The clade even obtained reasonable support in the gene-content analysis (**Supplementary File S2**) and its two representatives displayed almost the same G+C content. In the original description of *M. ferrooxydans* (Emerson et al., 2007) a new class (*Zetaproteobacteria*), order (*Mariprofundales*) and family (*Mariprofundaceae*) were proposed in the **Supplementary Material** only. None of these names became validly published so far even though a corrected name, *Mariprofundia*, was suggested for *Zetaproteobacteria* in the meantime (Oren, 2017a).

In the originally presented 16S rRNA gene trees the placement of *Mariprofundus* has no strong support and *Magnetococcus marinus* could not yet be considered. The additionally presented protein phylogenies (RecA, GyrB) only partially showed support for the placement of *M. ferrooxydans* separate from *Alphaproteobacteria*. In the CCT we did not find strong support for the placement of *M. ferrooxydans* branching first within the ingroup (**Supplementary File S2**). Phenotypically, alphaproteobacterial taxa such as *Magnetococcus marinus* are capable of forming iron oxides much like *M. ferrooxydans*. Even though the filamentous iron oxyhydroxide and branched-chain fatty acids produced by this species may differentiate it from taxa with a similar ecology, this alone provides no evidence for a separate class. It thus makes sense to again propose a separate order and family for *Mariprofundus* but to tentatively assign it to the class *Alphaproteobacteria*; an alternative arrangement is to remove *Magnetococcus* from *Alphaproteobacteria*.

Within *Alphaproteobacteria*, *Rhodospirillales* appeared as paraphyletic in the GBDP tree and in the CCT (**Figure 2** and **Supplementary File S2**) because *Kiloniella* (Wiese et al., 2009; Yang S.-H. et al., 2015) of *Kiloniellales* as well as *Roseospiillum* (Glaeser and Overmann, 1999) and *Terasakiella* (Satomi et al., 2002; Han et al., 2016) of the order currently called *Rhizobiales* were nested within *Rhodospirillales* with high support. As this also affects the monophyly of the family *Rhodospirillaceae*, we will below propose the reclassification of these three genera into *Rhodospirillales* as the preferred way to restore a monophyletic order and family. Moreover, the distant position of *Geminicoccaceae* (Proença et al., 2018) also conflicts with the monophyly of *Rhodospirillales*. Because this conflict was only poorly supported, we do not propose taxonomic changes for *Geminicoccaceae* based on the here examined data.

Rhodobacterales were shown as non-monophyletic in various ways, most of which also affect families and will thus be treated below. *Rhizobiales* (Kuykendall, 2005) appeared as paraphyletic in GBDP tree (**Figures 3–5** and **Supplementary File S2**) because *Acuticoccus* (Hou et al., 2015) *Ahrensia* (Uchino et al., 1998; Liu J. et al., 2016) *Labrenzia* (Biebl et al., 2007; Bibi et al., 2014) *Nesiotobacter* (Donachie et al., 2006) *Pannonibacter* (Borsodi et al., 2003; Biebl et al., 2007) *Pseudovibrio* (Shieh et al., 2004) *Roseibium* (Suzuki et al., 2000) and *Stappia* (Uchino et al., 1998; Biebl et al., 2007) all of which are currently classified in *Rhodobacterales*, were nested within *Rhizobiales*. According taxonomic solutions are suggested below for the affected families. *Hartmannibacter* (Suarez et al., 2014) which was not explicitly assigned to an order in its original description, is also treated below.

It should also be noted that *Rhizobiales* (Kuykendall, 2005) is validly published but illegitimate (i.e., not in accordance with the rules of the *International Code of Nomenclature of Prokaryotes*) as this order includes *Hyphomicrobium* of *Hyphomonadaceae*, type genus of *Hyphomicrobiales* (Douglas, 1957) which has priority. Our analyses do not call for placing *Rhizobium* and *Hyphomicrobium* in distinct orders (**Figure 4** and **Supplementary File S2**), hence we will below propose an emended description of *Hyphomicrobiales* to replace the illegitimate *Rhizobiales*. The following description of the results



will nevertheless use the name *Rhizobiales* throughout because this is the name used in our taxonomic input data although the name will be marked as in need of a replacement.

Neomegalonema (Oren, 2017b) of *Rhizobiales* (*Hyphomicrobiales*) was phylogenetically placed as sister group of *Rhodobacteraceae* with strong support to the exclusion of *Rhizobiales* (Figure 7), an arrangement that also obtained reasonable support in the gene-content analysis (Supplementary File S2). *Neomegalonema* was originally proposed as *Meganema* (Thomsen et al., 2006) which was later on regarded as an illegitimate name, and supposed to be related to the “*Methylobacterium/Xanthobacter* group” within *Alphaproteobacteria* based on a 16S rRNA gene analysis with a reduced taxon sampling and without calculating branch support. Given the phylogenetic evidence presented here and the lack of evidence to the contrary, the genus should be transferred from *Rhizobiales* (*Hyphomicrobiales*) to *Rhodobacterales*. Instead

of assigning the genus to the already highly divergent and mainly marine family *Rhodobacteraceae* we suggest to place *Neomegalonema* into a family of its own within *Rhodobacterales*. This proposal is in accordance with the major phenotypic features of the genus (Supplementary Table S1).

Outgroup Families and Genera

A revision of the phylum *Spirochaetes* is beyond the scope of the current study but some cautionary remarks on its taxonomic classification seem appropriate.

Spirochaetaceae (Swellengrebel, 1907; Abt et al., 2012; Gupta et al., 2013) were shown as rather heterogeneous assemblage not particularly well supported as monophyletic in the GBDP tree and in the CCT (Figure 2 and Supplementary File S2). While *Borreliaceae* (Gupta et al., 2013) were already separated from *Spirochaetaceae*, the overall genomic and phenotypic divergence of the group still calls for splitting *Spirochaetaceae*.

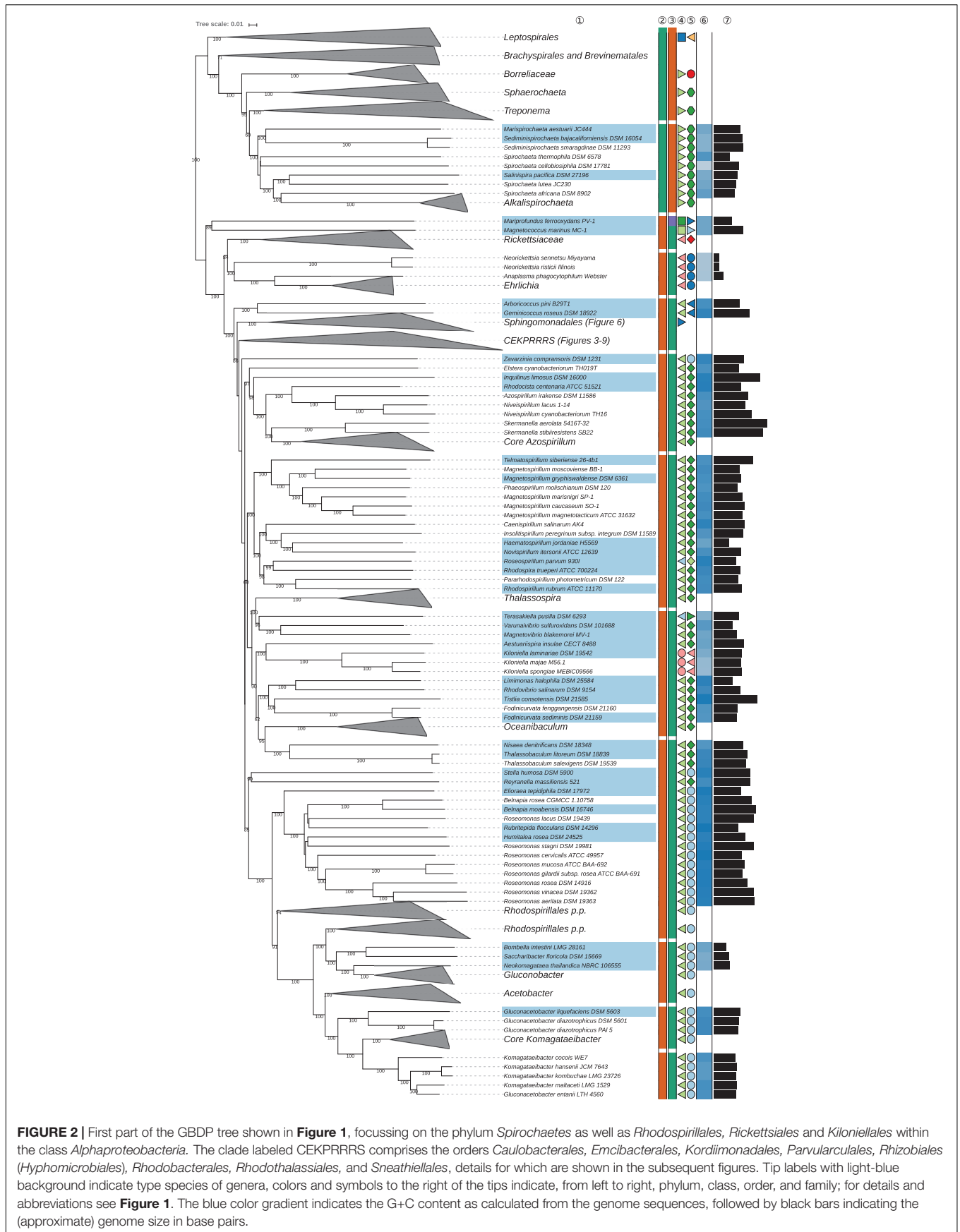


FIGURE 2 | First part of the GBDP tree shown in **Figure 1**, focussing on the phylum *Spirochaetes* as well as *Rhodospirillales*, *Rickettsiales* and *Kiloniellales* within the class *Alphaproteobacteria*. The clade labeled CEKPRRRS comprises the orders *Caulobacterales*, *Emcibacterales*, *Kordiimonadales*, *Parvularculales*, *Rhizobiales* (*Hyphomicrobiales*), *Rhodobacteriales*, *Rhodothalassiales*, and *Sneathiellales*, details for which are shown in the subsequent figures. Tip labels with light-blue background indicate type species of genera, colors and symbols to the right of the tips indicate, from left to right, phylum, class, order, and family; for details and abbreviations see **Figure 1**. The blue color gradient indicates the G+C content as calculated from the genome sequences, followed by black bars indicating the (approximate) genome size in base pairs.

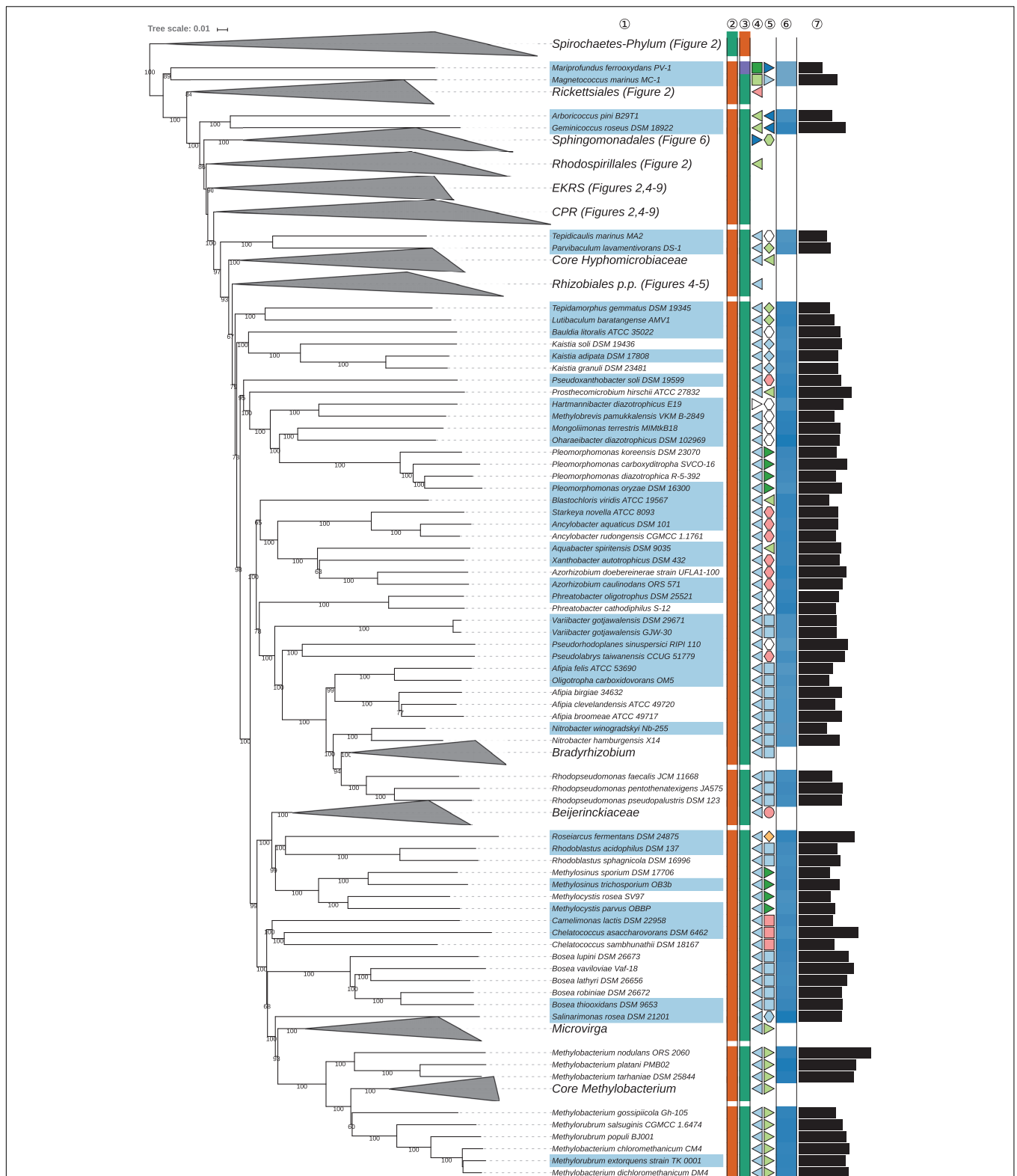


FIGURE 3 | Second part of the GBDP tree shown in **Figure 1**, focussing on parts of *Rhizobiales* (*Hyphomicrobiales*). The clade labeled EKRS comprises the orders *Emcibacterales*, *Kordiimonadales*, *Rhodothalassiales*, and *Sneathiellales*, whereas CPR denotes the clade including the orders *Caulobacterales*, *Parvularculales*, and *Rhodobacterales*, details for which are shown in the subsequent figures. Tip labels with light-blue background indicate type species of genera, colors and symbols to the right of the tips indicate, from left to right, phylum, class, order and family; for details and abbreviations see **Figure 1**. The blue color gradient indicates the G+C content as calculated from the genome sequences, followed by black bars indicating the (approximate) genome size in base pairs.

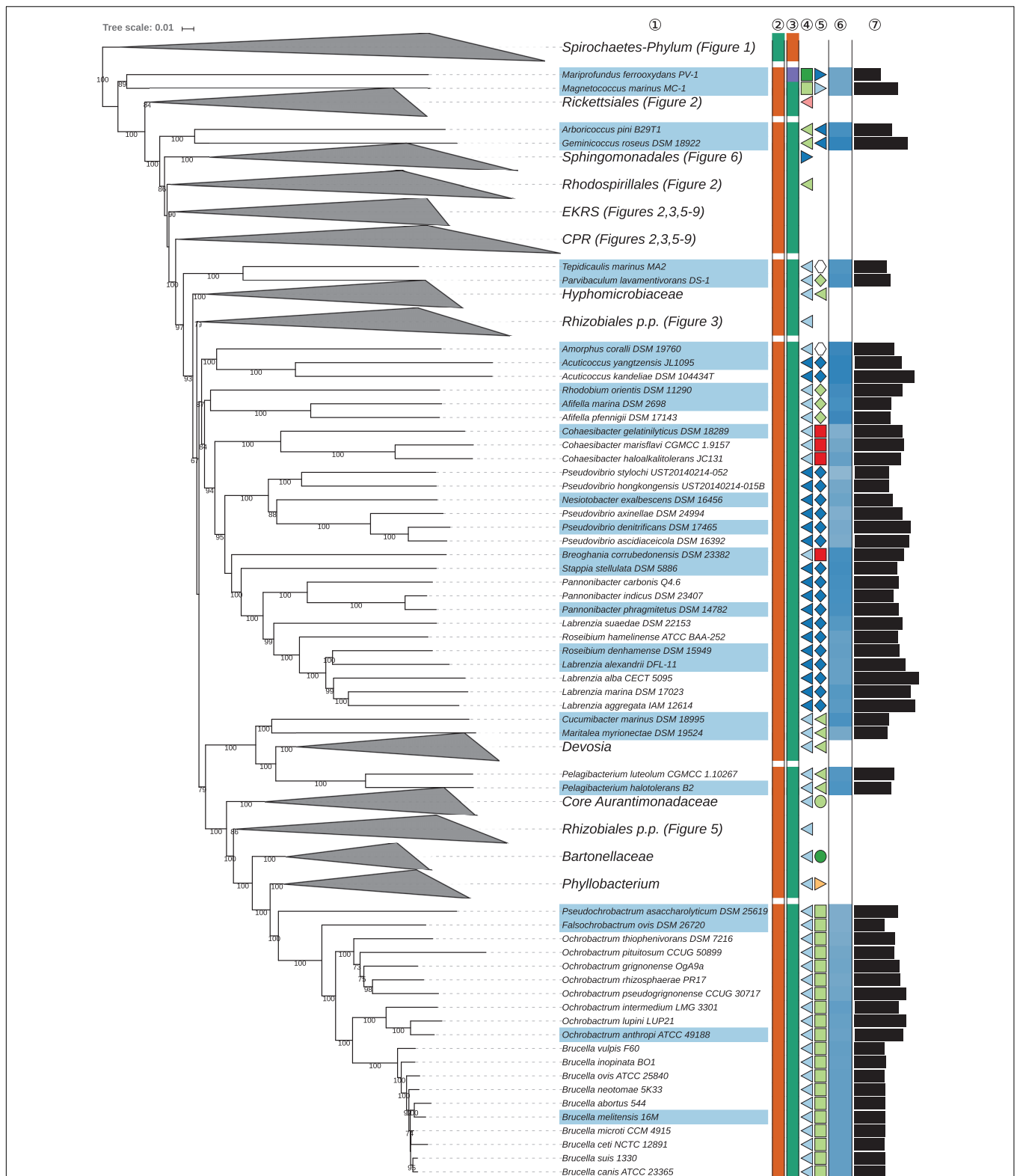


FIGURE 4 | Third part of the GBDP tree shown in **Figure 1**, focussing on parts of *Rhizobiales* (*Hyphomicrobiales*). The clade labeled EKRS comprises the orders *Emcibacterales*, *Kordiimonadales*, *Rhodothalassiales* and *Sneathiellales*, whereas CPR denotes the clade including the orders *Caulobacterales*, *Parvularculales*, and *Rhodobacterales*, details for which are shown in the subsequent figures. Tip labels with light-blue background indicate type species of genera, colors and symbols to the right of the tips indicate, from left to right, phylum, class, order and family; for details and abbreviations see **Figure 1**. The blue color gradient indicates the G+C content as calculated from the genome sequences, followed by black bars indicating the (approximate) genome size in base pairs.

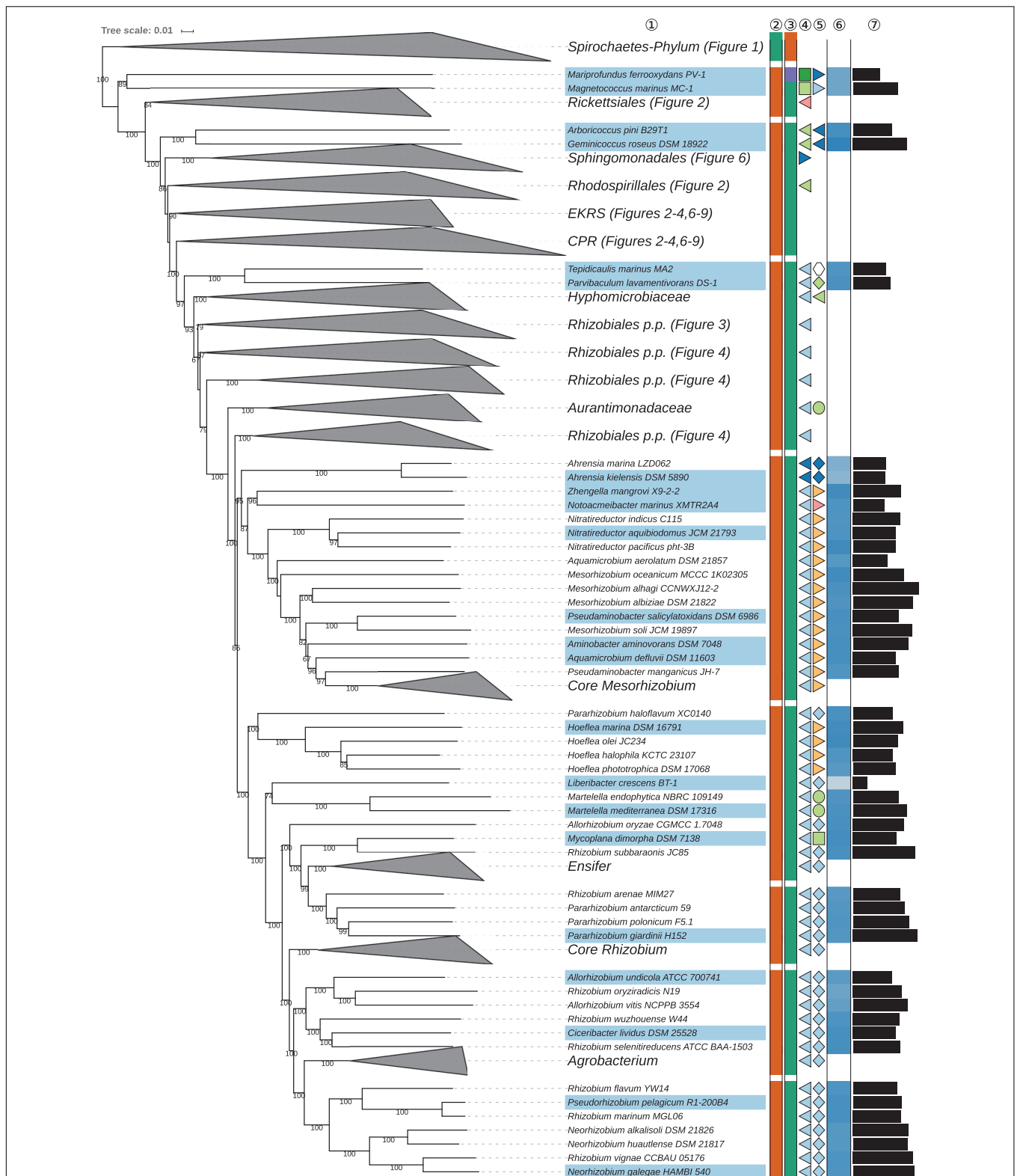
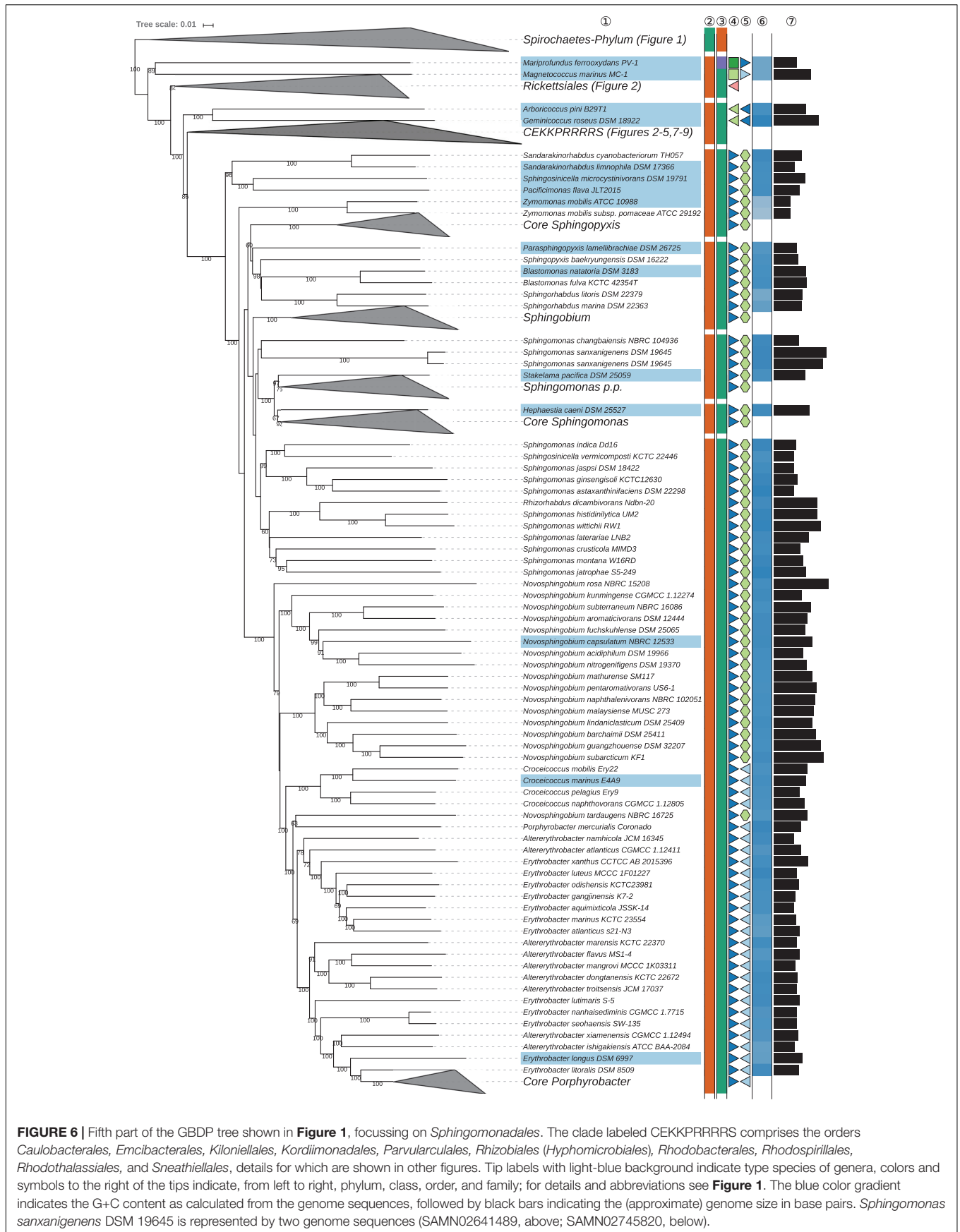


FIGURE 5 | Fourth part of the GBDP tree shown in **Figure 1**, focussing on parts of *Rhizobiales* (*Hyphomicrobiales*). The clade labeled EKRS comprises the orders *Emcibacterales*, *Kordiimonadales*, *Rhodothalassiales* and *Sneathiellales*, whereas CPR denotes the clade including the orders *Caulobacterales*, *Parvularculales*, and *Rhodobacterales*, details for which are shown in the subsequent figures. Tip labels with light-blue background indicate type species of genera, colors and symbols to the right of the tips indicate, from left to right, phylum, class, order, and family; for details and abbreviations see **Figure 1**. The blue color gradient indicates the G+C content as calculated from the genome sequences, followed by black bars indicating the (approximate) genome size in base pairs.



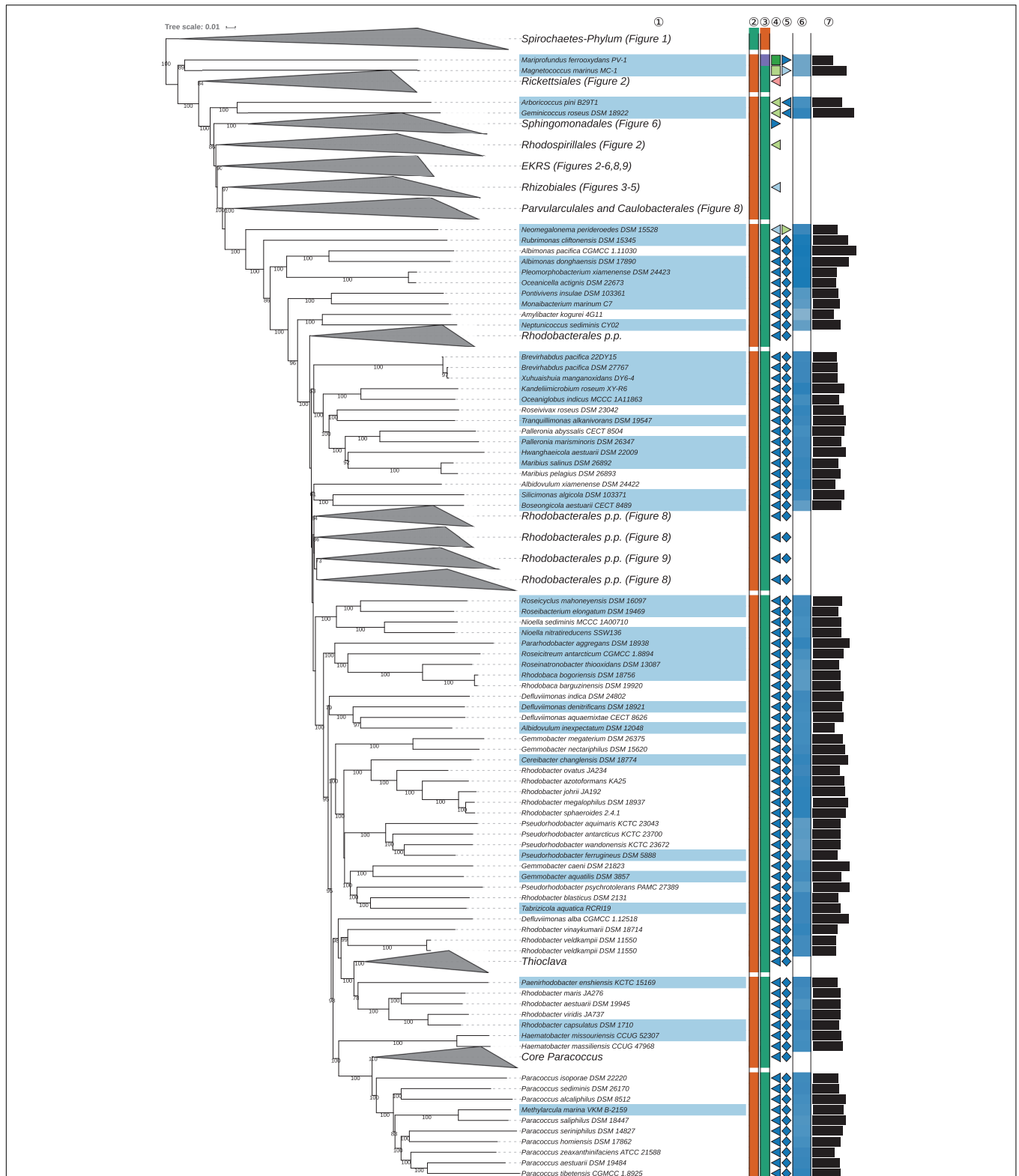


FIGURE 7 | Sixth part of the GBDP tree shown in **Figure 1**, focussing on parts of *Rhodobacterales*. The clade labeled EKRS comprises the orders *Emcibacterales*, *Kordiimonadales*, *Rhodothermalassiales*, and *Sneathiellales*, details for which are shown in other figures. Tip labels with light-blue background indicate type species of genera, colors and symbols to the right of the tips indicate, from left to right, phylum, class, order and family; for details and abbreviations see **Figure 1**. The blue color gradient indicates the G+C content as calculated from the genome sequences, followed by black bars indicating the (approximate) genome size in base pairs. *Rhodobacter veldekampii* DSM 11550 is represented by two genome sequences (SAMN10866319, above; SAMN08535030, below).

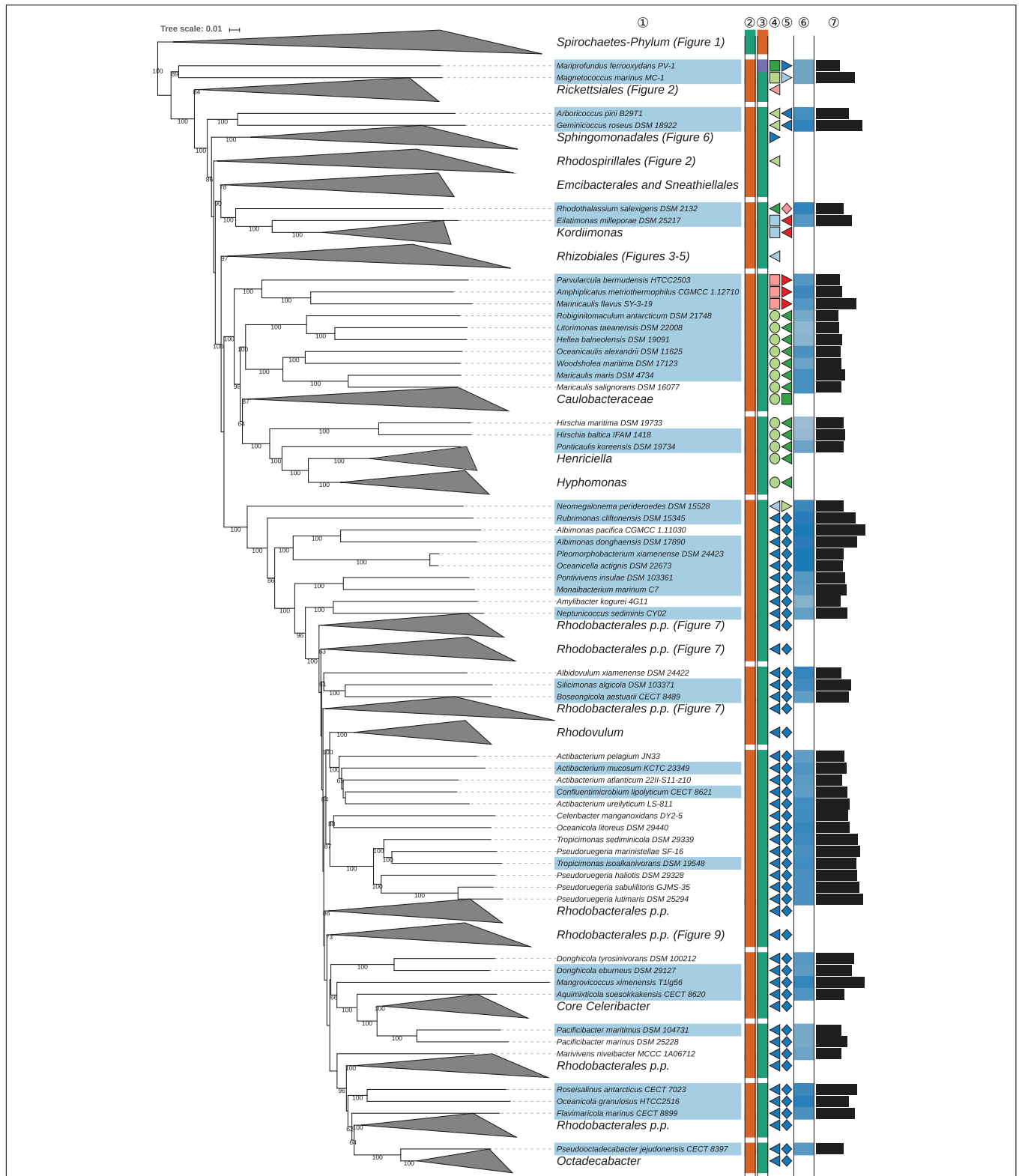


FIGURE 8 | Seventh part of the GBDP tree shown in **Figure 1**, focussing on *Caulobacterales*, *Parvularculales* and parts of *Rhodobacterales*. Tip labels with light-blue background indicate type species of genera, colors and symbols to the right of the tips indicate, from left to right, phylum, class, order, and family; for details and abbreviations see **Figure 1**. The blue color gradient indicates the G+C content as calculated from the genome sequences, followed by black bars indicating the (approximate) genome size in base pairs.

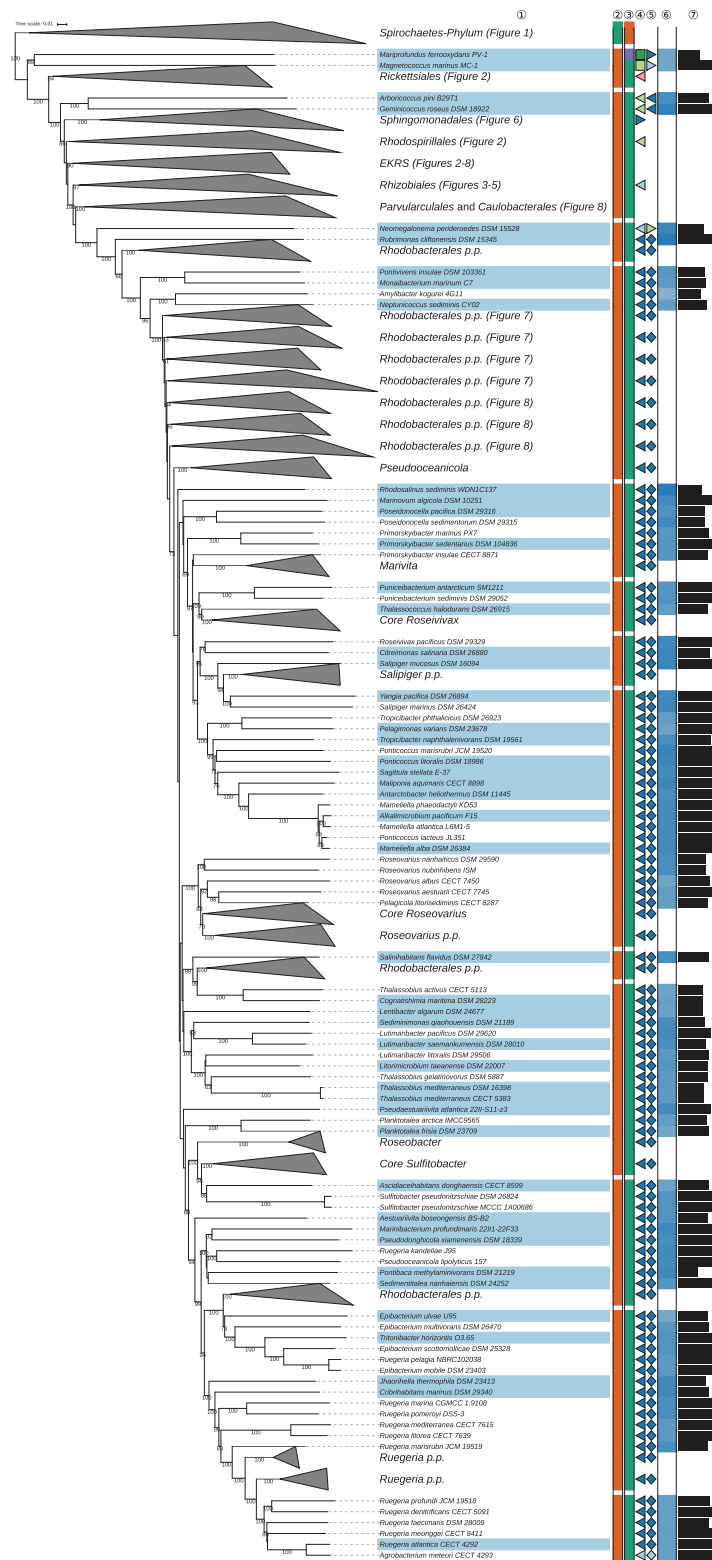


FIGURE 9 | Eighth part of the GBDP tree shown in **Figure 1**, focussing on parts of *Rhodobacterales*. The clade labeled EKRS comprises the orders *Emcibacteriales*, *Kordiimonadales*, *Rhodothalassiales*, and *Sneathiellales*, details for which are shown in other figures. Tip labels with light-blue background indicate type species of genera, colors and symbols to the right of the tips indicate, from left to right, phylum, class, order, and family; for details and abbreviations see **Figure 1**. The blue color gradient indicates the G+C content as calculated from the genome sequences, followed by black bars indicating the (approximate) genome size in base pairs.

TABLE 1 | Outcome of applying GGDC to calculate intergenomic dDDH values.

Strain 1	Strain 2	dDDH	Consequence
<i>Acetobacter pasteurianus</i> LMG 1262	<i>Acetobacter pasteurianus</i> subsp. <i>ascendens</i> LMG 1590	49	New species from subspecies
<i>Acetobacter pasteurianus</i> LMG 1262	<i>Acetobacter pasteurianus</i> subsp. <i>paradoxus</i> LMG 1591	49.8	New species from subspecies
<i>Acetobacter pasteurianus</i> subsp. <i>paradoxus</i> LMG 1591	<i>Acetobacter pasteurianus</i> subsp. <i>ascendens</i> LMG 1590	96.0	<i>A. pasteurianus</i> subsp. <i>paradoxus</i> is later heterotypic synonym
<i>Acetobacter peroxydans</i> ATCC 12874	<i>Acetobacter pasteurianus</i> LMG 1262	19	Not heterotypic synonyms (see discussion)
<i>Acetobacter peroxydans</i> ATCC 12874	<i>Acetobacter pasteurianus</i> subsp. <i>ascendens</i> LMG 1590	19	Not heterotypic synonyms (see discussion)
<i>Acetobacter peroxydans</i> ATCC 12874	<i>Acetobacter pasteurianus</i> subsp. <i>paradoxus</i> LMG 1591	19.3	Not heterotypic synonyms (see discussion)
<i>Acidiphilium angustum</i> ATCC 35903	<i>Acidiphilium rubrum</i> ATCC 35905	99.9	<i>A. angustum</i> is later heterotypic synonym
<i>Agrobacterium meteor</i> CECT 4293	<i>Ruegeria atlantica</i> CECT 4292	62.9	<i>A. meteor</i> is not later heterotypic synonym
<i>Alkalispirochaeta alkalica</i> DSM 8900	<i>Alkalispirochaeta sphaeroplastigenens</i> JC133	86.1	<i>A. sphaeroplastigenens</i> is later heterotypic synonym
<i>Borrelia bavariensis</i> PBi	<i>Borrelia garinii</i> CIP 103362	77.1	New subspecies of <i>B. garinii</i> from <i>B. bavariensis</i>
<i>Brucella melitensis</i> 16M	<i>Brucella ceti</i> NCTC 12891	97.8	<i>B. ceti</i> is later heterotypic synonym
<i>Brucella melitensis</i> 16M	<i>Brucella inopinata</i> BO1	81.2	<i>B. inopinata</i> is later heterotypic synonym
<i>Brucella melitensis</i> 16M	<i>Brucella microti</i> CCM 4915	98.1	<i>B. microti</i> is later heterotypic synonym
<i>Brucella melitensis</i> 16M	<i>Brucella vulpis</i> F60	80.5	<i>B. vulpis</i> is later heterotypic synonym
<i>Epibacterium mobile</i> DSM 23403	<i>Ruegeria pelagia</i> NBRC102038	76.9	New subspecies of <i>E. mobile</i> from <i>R. pelagia</i>
<i>Gluconobacter japonicus</i> LMG 1373	<i>Gluconobacter nephelii</i> LMG 26773	72.3	New subspecies of <i>G. japonicus</i> from species <i>G. nephelii</i>
<i>Hyphomonas neptunium</i> ATCC 15444	<i>Hyphomonas hirschiana</i> VP5	99.2	<i>H. hirschiana</i> is later heterotypic synonym
<i>Mameliella alba</i> DSM 26384	<i>Alkalimicrobium pacificum</i> F15	84.7	<i>A. pacificum</i> is later heterotypic synonym
<i>Mameliella alba</i> DSM 26384	<i>Mameliella atlantica</i> L6M1-5	84.2	<i>M. atlantica</i> is later heterotypic synonym
<i>Mameliella alba</i> DSM 26384	<i>Mameliella phaeodactyli</i> KD53	84.4	<i>M. phaeodactyli</i> is later heterotypic synonym
<i>Mameliella alba</i> DSM 26384	<i>Ponticoccus lacteus</i> JL351	100.0	<i>M. alba</i> is later heterotypic synonym
<i>Mameliella atlantica</i> L6M1-5	<i>Alkalimicrobium pacificum</i> F15	98.2	<i>M. atlantica</i> is later heterotypic synonym
<i>Mameliella phaeodactyli</i> KD53	<i>Alkalimicrobium pacificum</i> F15	83.9	<i>A. pacificum</i> is later heterotypic synonym
<i>Mameliella phaeodactyli</i> KD53	<i>Mameliella atlantica</i> L6M1-5	83.9	<i>M. atlantica</i> is later heterotypic synonym
<i>Mameliella phaeodactyli</i> KD53	<i>Ponticoccus lacteus</i> JL351	84.5	<i>M. phaeodactyli</i> is later heterotypic synonym
<i>Methylobacterium dichloromethanicum</i> DM4	<i>Methylobacterium chloromethanicum</i> CM4	73.6	New subspecies of <i>M. dichloromethanicum</i> from <i>M. chloromethanicum</i>
<i>Methylobacterium dichloromethanicum</i> DM4	<i>Methylorubrum extorquens</i> TK 0001	73.6	New subspecies of <i>M. dichloromethanicum</i> from <i>M. extorquens</i>

(Continued)

TABLE 1 | Continued

Strain 1	Strain 2	dDDH	Consequence
<i>Methylobacterium oryzae</i> CBMB20	<i>Methylobacterium phyllosphaerae</i> CBMB27	90.3	<i>M. phyllosphaerae</i> is later heterotypic synonym
<i>Methylobacterium radiotolerans</i> JCM 2831	<i>Methylobacterium organophilum</i> DSM 760	92.2	<i>M. organophilum</i> is later heterotypic synonym
<i>Oceanicella actignis</i> DSM 22673	<i>Pleomorphobacterium xiamenense</i> DSM 24423	88.4	<i>P. xiamenense</i> is later heterotypic synonym
<i>Ochrobactrum anthropi</i> ATCC 49188	<i>Ochrobactrum lupini</i> LUP21	83.9	<i>O. lupini</i> is later heterotypic synonym
<i>Paracoccus denitrificans</i> DSM 413	<i>Paracoccus pantotrophus</i> DSM 2944	42	Not heterotypic synonyms (see discussion)
<i>Paracoccus versutus</i> DSM 582	<i>Paracoccus bengalensis</i> DSM 17099	81.9	<i>P. bengalensis</i> is later heterotypic synonym
<i>Rhizobium marinum</i> MGL06	<i>Pseudorhizobium pelagicum</i> R1-200B4	76.3	New subspecies of <i>R. marinum</i> from <i>P. pelagicum</i>
<i>Rhizobium mongolense</i> USDA 1844	<i>Rhizobium loessense</i> CGMCC 1.3401	70.0	New subspecies of <i>R. mongolense</i> from species <i>R. loessense</i>
<i>Rhodobacter sphaeroides</i> 2.4.1	<i>Rhodobacter megalophilus</i> DSM 18937	81.6	<i>R. megalophilus</i> is later heterotypic synonym
<i>Rhodovulum viride</i> JA756	<i>Rhodovulum kholense</i> DSM 19783	84.1	<i>R. viride</i> is later heterotypic synonym
<i>Rickettsia conorii</i> Malish 7	<i>Rickettsia gravesii</i> ATCC VR-1664	73.0	New subspecies of <i>R. conorii</i> from species <i>R. gravesii</i>
<i>Rickettsia conorii</i> Malish 7	<i>Rickettsia heilongjiangensis</i> 054	76.7	New subspecies of <i>R. conorii</i> from species <i>R. heilongjiangensis</i> (also LHT of subsp. <i>Japonica</i> – see below)
<i>Rickettsia conorii</i> Malish 7	<i>Rickettsia honei</i> RB	85	<i>R. honei</i> is later heterotypic synonym
<i>Rickettsia conorii</i> Malish 7	<i>Rickettsia japonica</i> YH	77.1	New subspecies of <i>R. conorii</i> from species <i>R. japonica</i>
<i>Rickettsia conorii</i> Malish 7	<i>Rickettsia raoultii</i> Khabarovsk	74.7	New subspecies of <i>R. conorii</i> from species <i>R. raoultii</i>
<i>Rickettsia conorii</i> Malish 7	<i>Rickettsia sibirica</i> 246	90	<i>R. sibirica</i> is later heterotypic synonym
<i>Rickettsia conorii</i> Malish 7	<i>Rickettsia slovacica</i> 13-B	90.7	<i>R. slovacica</i> is later heterotypic synonym
<i>Rickettsia heilongjiangensis</i> 054	<i>Rickettsia japonica</i> YH	92.4	<i>R. heilongjiangensis</i> is later heterotypic synonym
<i>Rickettsia buchneri</i> ISO-7	<i>Rickettsia tamurae</i> AT-1	73	New subspecies of <i>R. tamurae</i> from species <i>R. buchneri</i>
<i>Roseivivax atlanticus</i> 22II-S10s	<i>Roseivivax marinus</i> DSM 27511	82.8	<i>R. atlanticus</i> is later heterotypic synonym
<i>Sphingobium indicum</i> MTCC 6364	<i>Sphingobium chinhatense</i> MTCC8598	82.9	<i>Sphingobium chinhatense</i> is later heterotypic synonym
<i>Sphingobium indicum</i> MTCC 6364	<i>Sphingobium lucknowense</i> CCM 7544	82.7	<i>Sphingobium lucknowense</i> is later heterotypic synonym
<i>Thalassobaculum salexigens</i> DSM 19539	<i>Thalassobaculum litoreum</i> DSM 18839	90.5	<i>T. salexigens</i> is later heterotypic synonym
<i>Xuhuaishuia manganoxidans</i> DY6-4	<i>Brevirhabdus pacifica</i> DSM 27767	99.5	<i>X. manganoxidans</i> is later heterotypic synonym

Only results that yield taxonomic consequences are shown.

TABLE 2 | *P*-values from the tip-permutation test of the GBDP tree shown in **Figures 1–9** and other results obtained for the selected genomic and phenotypic features.

Feature	Data type	Coverage	RI	<i>P</i> -value
Percent G+C content	Continuous	100%	0.736	1e-04
Approximate genome size in bp	Continuous	100%	0.627	1e-04
Cell length in μm	Continuous	74%	0.422	1e-04
Cell width in μm	Continuous	71%	0.303	1e-04
Motility by flagella	Discrete, binary	72%	0.584	1e-04
Relationship to oxygen	Discrete, ordered multi-state	99%	0.511	1e-04
Carotenoids	Discrete, binary	18%	0.513	1e-04
Bacteriochlorophyll	Discrete, binary	30%	0.454	1e-04
Average number of isoprene residues in major ubiquinones	Continuous	57%	0.476	1e-04

Genome size in base pairs is necessarily approximate in many cases because of unfinished genome sequences. The retention index (RI) can be used to compare the fit of distinct characters to a tree. The RI is bound between 0.0 and 1.0; the maximum of 1.0 indicates a perfect fit without any homoplasies.

The current taxonomic placement of *Sphaerochaeta* (Abt et al., 2012; Ritalahti et al., 2012; Miyazaki et al., 2014a; Arroua et al., 2017) which does not form spiral-shaped cells (**Supplementary Table S1**), makes *Spirochaetaceae* phenotypically heterogeneous. Spiral-shaped cells are apparently an apomorphy of the phylum and thus plesiomorphic within the phylum, hence this feature does not provide evidence for grouping *Treponema* within *Spirochaetaceae*.

An earlier taxonomic study already proposed the family *Treponemataceae* (Robinson, 1948) to accommodate the type genus *Treponema* (Schaudinn, 1905; Abt et al., 2013). Hence, we suggest to reuse the validly published name *Treponemataceae* and to place *Sphaerochaeta* in a phenotypically homogeneous family of its own. According to the CCT and UCT (**Supplementary File S2**), *Pleomorphochaeta* (Arroua et al., 2017) which like *Sphaerochaeta* displays spherical cells (**Supplementary File S1**), should be assigned to *Sphaerochaetaceae* fam. nov., too, whereas *Rectinema* (Koelschbach et al., 2017) should be placed in *Treponemataceae*. *Rectinema* produces non-motile rods but, according to its phylogenetic position (**Supplementary File S2**), the development of non-helical cells occurred independently of *Pleomorphochaeta* and *Sphaerochaeta*. In contrast to *Spirochaetaceae sensu stricto* as proposed here, *Sphaerochaetaceae* fam. nov. and *Treponemataceae* were strongly supported by the gene-content analysis (**Supplementary File S2**).

As for the outgroup genera, *Spirochaeta* (Pikuta et al., 2009; Miyazaki et al., 2014b; Shivani et al., 2015) of *Spirochaetaceae* was shown as paraphyletic in the GBDP tree and in the CCT (**Figure 2** and **Supplementary File S2**) because *Alkalispichoeta* (Sraavanthi et al., 2016) and *Salinispira* (Ben Hania et al., 2015) were nested within *Spirochaeta*. These problems were already visible in the original literature sources whose 16S rRNA gene analyses indicated that the proposal of these new genera would render *Spirochaeta* paraphyletic. A major obstacle in treating the genus with modern taxonomic methods is that the type species of *Spirochaeta*, *Spirochaeta plicatilis*, is not represented by a type strain (Skerman et al., 1980). One potential albeit radical solution is to place all other *Spirochaeta* species into genera of their own. Because of overall insufficient resolution in the 16S rRNA gene trees (**Supplementary File S2**), we refrain from a taxonomic revisions of the genus because genome sequences of relevance

are not yet available. The classification of *Spirochaetaceae sensu stricto* should be reconsidered once more genome sequences become available.

Rickettsiales Families

Rickettsiales is an order of *Alphaproteobacteria* that comprises pathogens with reduced genomes and a reduced G+C content (**Figure 2**). Our analysis did not call the monophyly of the order into question, but a nomenclatural issue became apparent in the course of this study.

We found that *Anaplasmataceae* (Philip, 1957; Dümmler et al., 2001) is illegitimate if one takes its last emendation into account as this family now includes *Ehrlichia* (Moshkovski, 1945) which is the type genus of *Ehrlichiae* (Moshkovski, 1945) which has priority. Our analyses do not argue for placing the two genera, which form a clade strongly supported even by the gene-content analysis, into distinct families (**Figure 1** and **Supplementary File S2**), hence we will propose below an emended description of *Ehrlichiae* as the correct name for the family of the genera currently included in *Anaplasmataceae*.

Rhodospirillales Families

A variety of families of *Rhodospirillales* appeared in need of a taxonomic revision in the light of our analyses (**Figure 2**). These discrepancies were not only caused by *Rhodospirillales* appearing to be intermixed with *Kiloniellales*.

Acetobacteraceae (Gillis and De Ley, 1980) were shown as non-monophyletic in the GBDP tree and in the CCT (**Figure 2** and **Supplementary File S2**) because of the relatively isolated position of *Stella* (Vasilyeva, 1985) and the even more distinct position of *Zavarzinia* (Meyer et al., 1993). In the original description of *Zavarzinia*, a phylogenetic analysis could not yet be conducted, and the genus was not assigned to any family. Later the genus was assigned to *Acetobacteraceae* (Boone et al., 2001b) but the reasoning behind this remained unclear. Here *Zavarzinia* was shown as branching first within *Rhodospirillales*. While the backbone support within the order was low, strong support indicates that *Zavarzinia* does not belong to core *Acetobacteraceae*. Given its isolated position in the GBDP and 16S rRNA gene trees, the genus is best assigned to a family of its own. This taxonomic consequence

did not appear in conflict with the major phenotypic features of *Zavarzinia* (**Supplementary Table S1**).

Stella appeared as sister group of the equally deviating genus of *Rhodospirillaceae*, *Reyranella* (Pagnier et al., 2011) with moderate support, and separated from core *Acetobacteraceae* by long branches. The original description of *Stella* did not explicitly assign the genus to a family. *Stella* was placed in *Acetobacteraceae* in Bergey's manual (Boone et al., 2001a); whether this placement was based on a phylogenetic assessment is unclear. Phenotypically the genus is rather unique because of its star-like morphology (**Supplementary Table S1**). All results thus suggest placing *Stella* into a family of its own. The same holds for *Reyranella*, which is treated below; the gene-content analysis does not support the sister-group relationship of the two genera.

When *Constrictibacter* (Yamada et al., 2011) was proposed it was placed in *Rhodospirillaceae* in a 16S rRNA gene tree with low support values. In the CCT (**Supplementary File S2**) with its much broader taxon sampling *Constrictibacter* formed a clade together with *Stella* albeit with low support. We thus tentatively include *Constrictibacter* in the family newly proposed to accommodate *Stella* (see above). Although phenotypic differences in morphology and respiration might suggest to alternatively place *Constrictibacter* into a family of its own this solution should be postponed until a *Constrictibacter* genome sequence is available.

Rhodospirillaceae (Pfennig and Trüper, 1971) appeared as paraphyletic in GBDP tree and in the CCT (**Figure 2** and **Supplementary File S2**) for a variety of reasons. For instance, *Roseospirillum* (Glaeser and Overmann, 1999) of *Rhodobiaceae* was nested within *Rhodospirillaceae*. *Roseospirillum* was placed as sister group of *Rhodospira* (Pfennig et al., 1997) with high support (**Figure 2**), a clade that in turn formed, with high support, the sister group of a clade containing the type species of the type genus of the family, *Rhodospirillum rubrum* (Molisch, 1907) these arrangements are even supported by the gene-content analysis (**Supplementary File S2**). For these reasons, we propose to include *Roseospirillum* into *Rhodospirillaceae*, which is also supported by the high phenotypic agreement between them (**Supplementary Table S1**). When *Roseospirillum* was proposed, bootstrapping was not conducted, and only few species could be included in the phylogenetic analysis at that time.

Furthermore, *Ferrovibrio* (Sorokina et al., 2012) *Taonella* (Xi et al., 2013) and *Marinibaculum* (Yu et al., 2016) formed an isolated but strongly supported clade with *Sneathiellaceae* (Kurahashi et al., 2008) in the CCT (**Supplementary File S2**). When *Ferrovibrio* was proposed, it was already placed in the order *Sneathiellales* but not explicitly in *Sneathiellaceae*. When *Taonella* and *Marinibaculum* were proposed both publications lacked strong support for the positioning of the respective taxa and both publications did not sample *Sneathiella* (Jordan et al., 2007). Therefore, we propose to tentatively assign *Ferrovibrio*, *Taonella*, and *Marinibaculum* to *Sneathiellaceae*. These taxonomic consequences are not precluded by the phenotypic features of the involved genera (**Supplementary Table S1**).

Similarly, *Terasakiella* (Satomi et al., 2002; Han et al., 2016) of *Methylocystaceae* and *Kiloniella* (Wiese et al., 2009;

Yang S.-H. et al., 2015) of *Kiloniellaceae* were nested within *Rhodospirillaceae* (**Figure 2**). However, even if these genera were included in *Rhodospirillaceae*, the family would lack any support. For this reason, to address the remaining causes of the non-monophyly of *Rhodospirillaceae* other measures are advisable. *Rhodospirillaceae* would not appear monophyletic even if these three genera were included. *Rhodospirillaceae* showed high genomic divergence (**Figure 2**) and unsupported by the gene-content analysis (**Supplementary File S2**). The family is phenotypically heterogeneous, as, e.g., most of its representatives are phototrophic whereas some genera are chemoorganoheterotrophs (**Supplementary Table S1**). Splitting *Rhodospirillaceae* into several families corresponding to well-supported clades can also solve this issue.

Azospirillaceae fam. nov. is thus proposed in agreement with the GBDP tree (**Figure 2** and **Supplementary File S2**) to accommodate *Niveispirillum* (Lin et al., 2014) *Azospirillum* (Tarrand et al., 1978; Falk et al., 1985) *Rhodocista* (Kawasaki et al., 1993) and *Skermanella* (Sly and Stackebrandt, 1999; Luo et al., 2012; Weon et al., 2007) *Nitrospirillum* (Lin et al., 2014) and *Desertibacter* (Liu et al., 2011) are also assigned to this family based on the 16S rRNA gene analyses (**Supplementary File S2**). Even though the gene-content analysis does not support the clade but only its two major subclades, this conclusion fits well to the major phenotypic features of these genera (**Supplementary Table S1**), most of which also show larger genomes than the other genera currently included in *Rhodospirillaceae*. *Azospirillum* and *Rhodocista* were placed in *Rhodospirillaceae* in Bergey's manual (Boone et al., 2001a) but it remained unclear to us whether this was based on a phylogenetic assessment. The proposals of these genera directly assigned them to *Rhodospirillaceae* but phylogenetic support for the monophyly of the family was not presented. The situation regarding genera such as *Elstera* (Rahalkar et al., 2012) and *Inquilinus* (Coenye et al., 2002) is less clear in the GBDP tree and particularly in the 16S rRNA gene trees, even the constrained ones. This holds also for *Lacibacterium* (Sheu et al., 2013) which lacks a published genome but was found to be the sister taxon of *Elstera* according to 16S rRNA gene analyses when it was proposed (Sheu et al., 2013) and in our findings (**Supplementary File S2**). These genera are tentatively assigned to the new family *Azospirillaceae*, too. Further reclassifications should be attempted once more genome sequences become available.

When *Terasakiella* was originally described, it was not assigned to any family. *Terasakiella* was placed in *Methylocystaceae* later on (Garrity et al., 2003b) but this proposal did not appear to be based on a phylogenetic analysis. The last emendation of the genus (Yoon and Kang, 2018) still assigned *Terasakiella* to *Methylocystaceae* but did not include the type species of the family in the phylogenetic analysis. We conclude that the taxonomic literature contains no phylogenetic evidence for an affiliation of the genus to the family. Similarly, *Magnetovibrio* (Williams et al., 2012) *Thalassospira* (López-López et al., 2002), and *Varunaivibrio* (Patwardhan and Vetriani, 2016) were placed in *Rhodospirillaceae* based on largely unresolved 16S rRNA gene trees with a reduced taxon sampling. Given the phylogenetic evidence presented here (**Figure 2** and

Supplementary File S2), we propose *Thalassospiraceae* fam. nov. to accommodate *Magnetovibrio* (Bazylnski et al., 2013b) *Terasakiella*, *Thalassospira* (López-López et al., 2002; Liu et al., 2007; Tsubouchi et al., 2014) and *Varunaivibrio*. *Magnetospira* (Williams et al., 2012) is also tentatively assigned to this family based on to the 16S rRNA gene analyses (**Supplementary File S2**). These taxonomic consequences are not precluded by the phenotypic features of the involved genera (**Supplementary Table S1**). The gene-content analysis does not support the newly proposed family but genome size and G+C content are rather homogeneous (**Figure 2** and **Supplementary File S2**).

When *Kiloniella*, *Kiloniellaceae* and *Kiloniellales* were proposed (Wiese et al., 2009) the phylogenetic analysis was characterized by low support at the backbone, and the monophyly of the resulting orders and families was not immediately evident. The most conservative solution for the observed discrepancy (**Figure 2**) is to retain *Kiloniellaceae* but to place it in *Rhodospirillales*. *Aestuariuspira* (Park et al., 2014e) should according to our phylogenetic results also be placed in the family. *Aestuariuspira* was placed in *Rhodospirillaceae* when the genus was originally proposed but this was based on a partially rather unresolved 16S rRNA gene tree that lacked a representative sampling of *Alphaproteobacteria*. Among the known major phenotypic features, it differs from *Kiloniella* only regarding motility (**Supplementary Table S1**). The clade comprising *Kiloniella* and *Aestuariuspira* also receives strong support in the gene-content analysis (**Supplementary File S2**).

Marivibrio (Chen S. et al., 2017b) was originally placed in *Rhodospirillaceae* based on a 16S rRNA gene analysis with low taxon sampling in which *Marivibrio* was grouped together with *Pelagibius* of *Rhodospirillaceae*. In the CCT *Marivibrio* was isolated from *Rhodospirillaceae* but formed a clade together with *Kiloniella* of *Kiloniellaceae* and *Aestuariuspira* as its sister taxon. Because of low support in the CCT we propose to tentatively include *Marivibrio* into *Kiloniellaceae*. Although phenotypic differences might suggest the alternative of assigning *Marivibrio* to its own family we here refrain from this solution due to a lack of genomic data.

When *Thalassocola* (Lin et al., 2015) was proposed it was placed in *Phyllobacteriaceae* in a 16S rRNA gene tree with low support. In the CCT (**Supplementary File S2**) *Kiloniella* of *Kiloniellaceae* appeared as the sister taxon of *Thalassocola* albeit with low support. We thus propose to tentatively include *Thalassocola* into *Kiloniellaceae* which is taxonomically more favorable to its current inclusion in *Phyllobacteriaceae*. Although phenotypic differences might suggest the alternative of assigning *Thalassocola* to its own family we refrain from this solution because of the low resolution and because it would be taxonomically less conservative.

Given that the non-monophyly of *Rhodospirillaceae* should be solved by splitting rather than by merging, the trees inferred from genome-scale data (**Figure 2** and **Supplementary File S2**) also call for the proposal of *Rhodovibrionaceae* fam. nov. to accommodate *Fodinicurvata* (Wang Y. et al., 2009) *Limimonas* (Amoozegar et al., 2013) *Rhodovibrio* (Imhoff et al., 1998) and *Tistlia* (Díaz-Cárdenas et al., 2010) *Limibacillus* (Kim et al., 2015)

and *Pelagibius* (Choi et al., 2009) are also tentatively assigned to this family based on the 16S rRNA gene analyses (**Supplementary File S2**). The creation of this family is neither contradicted by the gene-content analysis (even though it does not provide support) nor by major phenotypic features of the involved genera (**Supplementary Table S1**). For instance, while the resulting family is heterogeneous regarding the occurrence of phototrophy and related pigments, these character states appear relatively scattered across the phylogeny (**Figure 2** and **Supplementary File S2**). *Rhodovibrio* was placed in *Rhodospirillaceae* in Bergey's manual (Boone et al., 2001a) but it remained unclear to us whether this was based on a phylogenetic assessment. As in the case of the deviating genera of *Rhodospirillaceae* treated above, the original proposals of *Fodinicurvata*, *Limibacillus*, *Limimonas*, and *Tistlia* assigned these genera to the family, each time based on 16S rRNA gene trees that were either largely unresolved or lacked a representative taxon sampling, i.e., strong phylogenetic evidence for the monophyly of *Rhodospirillaceae* including these genera was not presented. In contrast, at least moderate bootstrap support was obtained in the taxonomic literature (Amoozegar et al., 2013) for a clade comprising *Fodinicurvata*, *Limibacillus*, *Limimonas*, *Rhodovibrio*, and *Tistlia*, in accordance with our results.

Based on the phylogenetic results (**Figure 2** and **Supplementary File S2**), *Thalassobaculaceae* fam. nov. is proposed to contain *Nisaea* (Urios et al., 2008) *Oceanibaculum* (Lai et al., 2009; Dong et al., 2010) and *Thalassobaculum* (Zhang G.I. et al., 2008; Urios et al., 2010). These genera were placed in *Rhodospirillaceae* when they were originally proposed, each time based on 16S rRNA gene trees that were either largely unresolved or lacked a representative taxon sampling, i.e., there was no strong phylogenetic evidence for the monophyly of *Rhodospirillaceae* including these genera in the taxonomic literature. We did not find any significant phenotypic differences between these genera (**Supplementary Table S1**). The monophyly of this family obtained no support in the gene-content analysis but moderate support in the 16S rRNA gene analyses (**Supplementary File S2**).

While taxonomically assigned to *Rhodospirillaceae*, *Reyranella massiliensis* (Pagnier et al., 2011) displayed an isolated position in the phylogenomic tree (**Figure 2**), distant to the type genus of the family. When *Reyranella* was proposed, it appeared as sister group of *Magnetospirillum magnetotacticum* (Schleifer et al., 1991) of *Rhodospirillaceae* but with low support only. More importantly, the low taxon sampling in that study did not allow for safely assigning *Reyranella* to a family; the same holds for the subsequent emendations of the genus (Kim et al., 2013; Lee H. et al., 2017) *Reyranella* is best assigned to a family of its own, which is not contradicted by the phenotype (**Supplementary Table S1**).

For several genera of *Rhodospirillaceae*, namely *Aliidongia* (Chen et al., 2017a), *Dongia* (Liu Y. et al., 2010), *Constrictibacter* (Yamada et al., 2011), *Defluviicoccus* (Maszenan et al., 2005), *Marivibrio* (Chen S. et al., 2017b), *Tagaea* (Jean et al., 2016), and *Tistrella* (Shi et al., 2002) our CCT results (**Supplementary File S2**) questioned their assignment to *Rhodospirillaceae*. *Aliidongia* was placed in *Rhodospirillaceae* when the genus was originally

proposed but this was based on a 16S rRNA gene analysis with low taxon sampling in which *Aliidongia* was grouped together with *Inquilinus* and *Dongia* of *Rhodospirillaceae* with low support. When *Dongia* was originally proposed, it grouped together in a 16S rRNA gene tree with *Rhodospirillaceae* genera including *Azospirillum*, *Rhodocista* and *Skermanella*, but with overall low taxon sampling. When *Tagaea* was originally proposed it was placed in a 16S rRNA gene tree in a well supported clade together with *Oceanibaculum*, *Nisaea*, and *Thalassobaculum* of *Rhodospirillaceae*. Yet the placement of the clade itself showed low support and overall taxon sampling lacked the type genus of *Rhodospirillaceae*. None of these genera could safely be placed in a family in the CCT (**Supplementary File S2**) hence we recommend to regard *Aliidongia*, *Dongia*, and *Tagaea* as genera *incertae sedis* until their phylogenetic position can be clarified once more genome sequences become available.

Defluviicoccus (Maszenan et al., 2005) was placed in *Rhodospirillaceae* (Garrity et al., 2007) after its original description but based on the original 16S rRNA gene analysis wherein *Defluviicoccus* was placed together with *Rhodospirillaceae* genera such as *Rhodospirillum*, *Azospirillum*, and *Magnetospirillum* yet with low taxon sampling. *Tistrella* was originally not placed in any family but was placed in *Rhodospirillaceae* later on in Bergey's Manual (Garrity et al., 2003b) which cited the original description of *Tistrella* even though it had cautioned against an assignment to a family because of low support in 16S rRNA gene analysis. *Defluviicoccus* and *Tistrella* were isolated from *Rhodospirillaceae* in the far better sampled CCT and formed a clade together with *Geminicoccus* and *Arboricoccus* of *Geminicoccaceae*. Support for this arrangement was also low, hence we suggest the tentative inclusion of *Defluviicoccus* and *Tistrella* in *Geminicoccaceae*. Although phenotypic differences might suggest to alternatively assign both genera to their own family we refrain from this solution due to a lack of genomic data.

Rhodospirillales Genera

Some genera of *Rhodospirillales* also appeared in need of a taxonomic revision in the light of our analyses (**Figure 2**) although to a lesser extent than the families of the order.

Within *Rhodospirillales*, *Azospirillum* (Tarrand et al., 1978; Falk et al., 1985) was shown as paraphyletic in the GBDP and in the 16S trees (**Figure 2** and **Supplementary File S2**) because *Azospirillum irakense* (Khammas et al., 1989) was placed as sister group of *Niveispirillum* (Cai et al., 2015, 2018b) with high support. While its genome sequence was lacking at the time of writing, the CCT showed that the type species of *Niveispirillum*, *N. fermenti* (Lin et al., 2014) was also placed in this clade, whereas the type species of *Azospirillum*, *A. lipoferum*, was placed in a clade together with the four other *Azospirillum* species represented in the GBDP tree. These arrangements also obtained support in the gene-content analysis (**Supplementary File S2**). It was already proposed to reclassify *A. irakense* as *N. irakense* (Lin et al., 2014) but this name was not validly published, and hence *Niveispirillum* remained non-monophyletic. While *A. irakense* differs from *Niveispirillum* by its microaerophilic lifestyle (**Supplementary**

Table S1), this alone is not a sufficient reason to separate two genera. We accordingly propose to place *A. irakense* in *Niveispirillum*.

Magnetospirillum (Schleifer et al., 1991) appeared as paraphyletic in the GBDP tree (**Figure 2**) because *Phaeospirillum molischianum* (Giesberger, 1947; Imhoff et al., 1998) was nested within *Magnetospirillum*. *Telmatospirillum siberiense* (Sizova et al., 2007) formed the sister group of this clade. In addition, in the CCT, *P. chandramohanii* (Anil Kumar et al., 2009), *P. fulvum* (van Niel, 1944; Imhoff et al., 1998), *P. oryzae* (Lakshmi et al., 2011), and *P. tilakii* (Raj et al., 2012) were also nested within *Magnetospirillum* (**Supplementary File S2**). When *Magnetospirillum* was proposed, the phylogenetic analysis was characterized by a low number of included taxa and by a lack of support values. When *Phaeospirillum* was proposed, a well resolved tree was presented that included only few species; in particular, *Magnetospirillum* was not considered (Imhoff et al., 1998). Hence, phylogenetic evidence for the separation of the two genera is lacking. *P. chandramohanii*, *P. fulvum*, *P. molischianum*, *P. oryzae*, and *P. tilakii* display a phenotype similar to the one of *Magnetospirillum* (**Supplementary Table S1**). Consequently, it is proposed that *P. chandramohanii*, *P. fulvum*, *P. molischianum*, *P. oryzae* and *P. tilakii* be classified in *Magnetospirillum*.

Roseomonas (Rihs et al., 1993; Sánchez-Porro et al., 2009; Venkata Ramana et al., 2010) was shown as polyphyletic in the GBDP tree (**Figure 2**) because *Roseomonas stagni* (Furuhata et al., 2008) and *Roseomonas lacus* (Jiang et al., 2006; Sánchez-Porro et al., 2009) were placed as sister group of *Humitalea rosea* (Margesin and Zhang, 2013) and *Rubritepida flocculans* (Alarico et al., 2002) respectively, albeit with low support. In the CCT, species from further genera, such as *Rhodovarius lipocyclicus* (Kämpfer et al., 2004) were nested within the main *Roseomonas* clade while *Roseomonas fauriae* (Rihs et al., 1993) was placed in a remote position as sister group of *Azospirillum formosense* (Lin et al., 2012) (**Supplementary File S2**). A previous study concluded that *R. fauriae* is a later heterotypic synonym of *A. formosense* (Helsel et al., 2006). While a genome sequence of the type strain of the type species of *Roseomonas*, *R. gilardii*, was lacking at the time of writing, it is represented by *R. gilardii* subsp. *rosea* in the GBDP tree and safely placed in the CCT. It would be premature, however, to propose new genera for *Roseomonas lacus* and *R. stagni* since the low resolution in even the constrained 16S rRNA gene trees currently hinders the assignment of those species not represented by a genome sequence to the resulting set of genera.

Gluconacetobacter (Yamada et al., 1997) appeared as polyphyletic in the GBDP tree (**Figure 2**) because *G. entanii* (Schüller et al., 2000) was nested within *Komagataeibacter* (Yamada et al., 2012) with high support both in the GBDP and the 16S rRNA gene trees (**Figure 2** and **Supplementary File S2**); even the gene-content analysis provided support. When *Komagataeibacter* was proposed to harbour species formerly placed in *Gluconacetobacter* (Yamada et al., 2012), *G. entanii* could not be transferred to the new genus because the type strain seemed unavailable from any culture collection. As long as this problem remains

unsolved a new combination for *G. entanii* cannot be proposed (Parker et al., 2019).

Rhizobiales (Hyphomicrobiales) Families

Many families of *Rhizobiales* (*Hyphomicrobiales*) appeared to be in need of a taxonomic revision according to our results (Figures 3–5), even more so than in *Rhodospirillales*. The discrepancies were on the one hand caused by *Rhizobiales* (*Hyphomicrobiales*) families which appeared intermixed and on the other hand caused by genera taxonomically assigned to *Rhodobacteraceae* within *Rhodobacterales* but phylogenetically placed within *Rhizobiales* (*Hyphomicrobiales*). Both kinds of cases are treated in this section.

Within *Rhizobiales* (*Hyphomicrobiales*), *Rhodobiaceae* (Garrity et al., 2005f) were shown as non-monophyletic in the GBDP tree and in the CCT (Figures 3–5 and Supplementary File S2) because representatives of this family were placed into phylogenetically quite distant clades. *Parvibaculum* (Schleheck et al., 2004) was placed together with *Tepidicaulis* (Takeuchi et al., 2015) in a clade that appeared as sister group (Figure 3) of the remaining *Rhizobiales* (*Hyphomicrobiales*). When *Parvibaculum* was proposed, a phylogenetic tree was not presented, and the genus was not assigned to any family. The original description of *Tepidicaulis* showed it as sister group of *Parvibaculum* with strong support. The gene-content analysis also strongly supported their sister-group relationship (Supplementary File S2). Thus placing this clade into a family separate from *Rhodobiaceae* appeared as most appropriate solution. This is not precluded by the phenotype of the involved genera (Supplementary Table S1). Additional genera may need to be added to the newly proposed family once genome sequences provide sufficient resolution.

Similarly, *Lutibaculum* (Anil Kumar et al., 2012) and *Tepidamorphus* (Albuquerque et al., 2010) formed a strongly supported clade of their own (Figure 3) within *Rhizobiales* (*Hyphomicrobiales*), without any obvious affiliation to an already proposed family. The phylogenies presented in the original descriptions of *Lutibaculum* and *Tepidamorphus* already suffered from low support at the backbone; our analyses of the 16S rRNA gene did not show any significant conflict with the phylogenomic tree either. Thus placing these two genera into a family separate from *Rhodobiaceae* appears as most appropriate solution. According to the 16S rRNA gene analyses (Supplementary File S2), *Butyratibacter* (Wang et al., 2017) and *Microbaculum* (Su et al., 2017) should also be placed in this family. This is not precluded by the phenotype of the involved genera (Supplementary Table S1). The gene-content analysis did not support the sister-group relationship of *Lutibaculum* and *Tepidamorphus* but they display quite similar G+C content values and genome sizes (Supplementary File S2).

The type genus of the family, *Rhodobium* (Hiraishi et al., 1995; Urdiain et al., 2008) was placed in an isolated position relative to the rest of the family (Figure 4), only showing a weakly supported sister-group relationship to *Afifella* (Urdiain et al., 2008). The original description of *Afifella* was characterized by the lack of branch support and low taxon sampling of the phylogenetic analysis; an assignment of the genus to a family was

not proposed. Later on (Su et al., 2017) *Afifella* was regarded as affiliated to *Rhodobiaceae*. A sister-group relationship of *Afifella* and *Rhodobium* is possible but only supported by the gene-content analysis, which is not the phylogenetic method of choice, while unsupported in the GBDP and 16S rRNA gene trees (Figure 4 and Supplementary File S2). Additional supermatrix analyses indicated that *Afifella* and *Rhodobium* do not form a clade (Supplementary File S2). For this reason, a new family is proposed to accommodate *Afifella*, which is not in disagreement with its phenotype (Supplementary Table S1).

The CCT called the assignment of *Andersenella* (Brettar et al., 2007) and *Rhodoligotrophos* (Fukuda et al., 2012) to *Rhodobiaceae* into question (Supplementary File S2). *Andersenella* was regarded as affiliated to *Rhodobiaceae* only after its original description (Su et al., 2017) *Rhodoligotrophos* was placed in *Rhodobiaceae* when it was originally proposed, which was based on a 16S rRNA gene tree that grouped *Rhodoligotrophos* together with *Parvibaculum* of *Rhodobiaceae*. Yet this tree showed a non-monophyletic *Rhodobiaceae*. In the CCT *Andersenella* and *Rhodoligotrophos* formed a clade together with *Parvibaculum* (Schleheck et al., 2004) and *Tepidicaulis* (Takeuchi et al., 2015) which we propose to transfer to the new family *Parvibaculaceae* (see above). *Andersenella* and *Rhodoligotrophos* may only tentatively be assigned to *Parvibaculaceae* because of low support in the CCT. As *Pyruvatibacter* (Wang G. et al., 2016) has not been assigned to a family yet and is located in the same clade we would also tentatively assign *Pyruvatibacter* to *Parvibaculaceae*.

Rhizobiaceae (Conn, 1938) were also shown as non-monophyletic in the GBDP tree and in the CCT (Figure 3 and Supplementary File S2) for several reasons. The genus *Kaistia* (Im et al., 2004) formed a well-supported subtree distinct from core *Rhizobiaceae* and close to *Bauldia* (Yee et al., 2010) which was not yet assigned to a family. The phylogenetic analysis of the 16S rRNA gene used for the proposal of *Bauldia* was characterized by low support at the backbone of the tree. In its original description *Kaistia* was not assigned to a family (Im et al., 2004); the genus was placed in *Rhizobiaceae* only later on (Garrity et al., 2007) but the rationale behind this decision remained obscure. The phenotype of the two genera is largely in agreement (Supplementary Table S1) and there is a certain amount of support for the clade in the gene-content analysis (Supplementary File S2). We accordingly propose a new family *Kaistiaceae*, fam. nov., to accommodate *Kaistia* and *Bauldia*.

As for *Hyphomicrobiaceae*, it should be mentioned that although *Gemmiger* (Gossling and Moore, 1975) was listed in Bergey's Manual (Boone et al., 2001a) as a genus of *Hyphomicrobiaceae* it was not considered in our analysis because a later study (Yarza et al., 2013) showed that *Gemmiger* does phylogenetically not even belong to the phylum *Proteobacteria*. Its taxonomic classification is beyond the scope of the current study.

Even apart from that genus, *Hyphomicrobiaceae* (Babudieri, 1950) appeared as non-monophyletic in the GBDP and in 16S gene rRNA trees (Figure 3 and Supplementary File S2) in other respects because *Aquabacter* (Irgens et al., 1991), *Blastochloris* (Hiraishi, 1997) and *Prosthecomicrobium* (Staley, 1984) as well as

a clade comprising the genera *Cucumibacter* (Hwang and Cho, 2008b), *Devosia* (Nakagawa and Yokotat, 1996; Rivas et al., 2003), *Maritalea* (Hwang et al., 2009b) and *Pelagibacterium* (Xu et al., 2011) were placed apart from the core *Hyphomicrobiaceae* clade that comprised the type genus of *Hyphomicrobiaceae*. Although the genome sequence of the type strain of the type species of the type genus of the family, *Hyphomicrobium vulgare* (Stutzer and Hartleb, 1899), was not available at the time of writing, the CCT and UCT placed the species with strong support within the clade comprising *H. nitrativorans* and *H. zavarzini* (**Supplementary File S2**). *Hyphomicrobiaceae* also appeared as the taxonomic home for *Methyloceanibacter* (Vekeman et al., 2016), which was originally not assigned to a family but was here located within core *Hyphomicrobiaceae* in **Figure 3**.

When *Aquabacter* was proposed (Irgens et al., 1991), a phylogenetic tree was not presented, and the publication did not assign the genus to a family. *Aquabacter* was placed in *Hyphomicrobiaceae* in Bergey's manual (Boone et al., 2001a) but the reason for doing so was not obvious to us. Including *Aquabacter* into *Xanthobacteraceae* appears to be the most conservative solution, which is not precluded by the phenotype (**Supplementary Table S1**). The *Aquabacter*-*Azorhizobium*-*Xanthobacter* clade obtained high support in the gene-content analysis while the 16S rRNA gene analyses even indicated that *Aquabacter*, *Xanthobacter* and *Azorhizobium* are difficult to discern as currently circumscribed (**Supplementary File S2**). This problem should be addressed once more type-strain genome sequences from the group become available.

The original description of *Prosthecomicrobium* and its type species, *P. hirschii*, did not include a 16S rRNA gene analysis (Staley, 1968, 1984). The current assignment of this genus to *Hyphomicrobiaceae* was called into question in the literature (Lee et al., 2005) and could not be confirmed by our study either. *Prosthecomicrobium* was first placed in *Hyphomicrobiaceae* in Bergey's manual (Boone et al., 2001b) but this assignment may not be based on a phylogenetic analysis. In the CCT (**Supplementary File S2**) *Prosthecomicrobium* forms a strongly supported clade with the genera *Ancalomicrobium* and *Pinisolibacter* (Staley, 1968; Dahal et al., 2018). Therefore we propose to place *Prosthecomicrobium* in *Ancalomicrobiaceae* (Dahal et al., 2018) which is not precluded by the phenotypic characteristics of these genera (**Supplementary Table S1**).

Phreatobacter (Tóth et al., 2014; Lee S.D. et al., 2017) was as yet not assigned to a family, whereas *Blastochloris* (Hiraishi, 1997) was assigned by some authors to *Hyphomicrobiaceae* (Garrity et al., 2003b), although other studies concluded that this genus cannot safely be assigned to a family based on 16S rRNA gene data (Lee et al., 2005). The GBDP tree showed both genera located within a highly supported clade also comprising *Bradyrhizobiaceae* and *Xanthobacteraceae* but the interrelationships between these four subclades remained unresolved (**Figure 3**). Similarly, the 16S rRNA gene analyses did not resolve the placement of these two isolated genera and did not indicate the affiliation to any existing family (**Supplementary File S2**). For this reason, we propose to assign each of the two genera to a family of its own. This solution is not precluded by the phenotype of the two genera (**Supplementary Table S1**).

The CCT (**Supplementary File S2**) called the assignment of *Rhodoplanes* (Hiraishi and Ueda, 1994b) to *Hyphomicrobiaceae* into question. *Rhodoplanes* was placed in *Hyphomicrobiaceae* by Bergey's Manual (Boone et al., 2001b) but the reason behind this decision remained unclear. In the CCT *Rhodoplanes* formed a clade together with genera of *Bradyrhizobiaceae* (Garrity et al., 2005e) such as *Variibacter* (Kim et al., 2014), *Afipia* (Brenner et al., 1991) and *Nitrobacter* (Winogradsky, 1892) *Pseudolabrys* (Kämpfer et al., 2006) and *Pseudorhodoplanes* (Tirandaz et al., 2015) appeared as closest relatives in the CCT. Because of low clade support we propose to tentatively assign *Rhodoplanes* to the same family as these genera; the nomenclature of *Bradyrhizobiaceae* is treated in detail below.

In the CCT (**Supplementary File S2**) *Angulomicrobium* (Vasil'eva et al., 1980) and *Methylorhabdus* (Doronina et al., 1995) of *Hyphomicrobiaceae* formed a strongly supported clade within *Xanthobacteraceae*. When *Angulomicrobium* was proposed it was not assigned to a family but later on Bergey's manual (Boone et al., 2001a) listed *Angulomicrobium* as a genus of *Hyphomicrobiaceae*. This was confirmed by 16S rRNA gene and lipid-composition analysis (Fritz et al., 2004) but branch support in the presented 16S rRNA gene tree was not shown and the analysis did not consider *Xanthobacter* (Wiegel et al., 1978), which is now the type genus of *Xanthobacteraceae*. When *Methylorhabdus* was proposed it was not assigned to a family but later on Bergey's manual (Boone et al., 2001a) listed *Methylorhabdus* as a genus of *Hyphomicrobiaceae*. A more recent edition of Bergey's manual (Brenner et al., 2005) mentioned that the highest similarity in DNA:DNA hybridization of *Methylorhabdus* was observed with *Xanthobacter* and only 10% with *Hyphomicrobium*. Due to their position in the CCT we propose to assign *Angulomicrobium* and *Methylorhabdus* to *Xanthobacteraceae*. This solution is not in conflict with their phenotype (**Supplementary Table S1**).

Xanthobacteraceae (Lee et al., 2005) appeared as both paraphyletic and polyphyletic in the GBDP tree and the CCT (**Figure 3** and **Supplementary File S2**) because *Pseudoxanthobacter* (Arun et al., 2008) was placed apart from the remaining *Xanthobacteraceae* while genera of other families, such as *Aquabacter spiritensis* of *Hyphomicrobiaceae*, were placed within *Xanthobacteraceae*. The original description of *Pseudoxanthobacter* did not explicitly assign the genus to a family, and the shown phylogeny suffered from low support at the backbone. The assignment of *Pseudoxanthobacter* to *Xanthobacteraceae* occurred only later (Ueki et al., 2010) based on mere sequence similarity search. According to the relatively isolated and not maximally supported position of *Pseudoxanthobacter* in the phylogenomic trees (**Figure 3** and **Supplementary File S2**) and the lack of evidence supporting its inclusion in *Xanthobacteraceae* it is proposed to assign it to a family of its own. This solution is not in conflict with the phenotype (**Supplementary Table S1**) and not in conflict with the gene-content analysis (**Supplementary File S2**).

While *Pleomorphomonas* (Xie and Yokota, 2005) was taxonomically assigned to *Methylocystaceae*, it here appeared as only distantly related to the type genus of the family (**Figure 3**). In contrast, a highly supported clade included both *Pleomorphomonas* and a set of genera not yet assigned

to family, *Hartmannibacter* (Suarez et al., 2014), *Methylobrevia* (Poroshina et al., 2015), *Mongoliimonas* (Xi et al., 2017) and *Oharaeibacter* (Lv et al., 2017). The 16S rRNA gene analyses (**Supplementary File S2**) also provided support for this clade, additionally including *Chthonobacter* (Kim et al., 2017). In line with the taxonomic consequences proposed above, the phylogenetic results call for suggesting a new family for these genera. Although the gene-content analysis did not provide support for the group, the establishment of this new family did not appear to be in conflict with the phenotype of the involved genera (**Supplementary Table S1**).

Bradyrhizobiaceae (Garrity et al., 2005e) and *Xanthobacteraceae* (Lee et al., 2005) were shown as non-monophyletic in the GBDP tree (**Figure 3**) due to the position of *Pseudolabrys* (Kämpfer et al., 2006) of *Xanthobacteraceae*, which was placed within *Bradyrhizobiaceae* together with *Pseudorhodoplanes* (Tirandaz et al., 2015), a genus that was as yet not assigned to a family. *Bradyrhizobiaceae* is actually illegitimate as this family includes *Nitrobacter* (Buchanan, 1917), which is the type genus of *Nitrobacteraceae* (Buchanan, 1917), which has priority (Tindall, 2019a). Our analyses do not call for placing *Nitrobacter* and *Bradyrhizobium* in distinct families (**Figure 3** and **Supplementary File S2**), hence we will below propose an emended description of *Nitrobacteraceae* as the correct name for the family of the genera currently assigned to the illegitimate *Bradyrhizobiaceae*. The following description of the results will nevertheless use the name *Bradyrhizobiaceae* throughout because this is the name used in our input data but the name will be marked as in need of a replacement.

Bradyrhizobiaceae (*Nitrobacteraceae*) also appeared as non-monophyletic in the GBDP tree (**Figure 3**) because the genera *Rhodoblastus* (Imhoff, 2001) and *Bosea* (Das et al., 1996; La Scola et al., 2003) were placed apart from core *Bradyrhizobiaceae* (*Nitrobacteraceae*). *Rhodoblastus* formed the sister group of *Roseiarcus* (Kulichevskaya et al., 2014) which is currently taxonomically assigned to its own family. This clade in turn formed the sister group of core *Methylocystaceae* including its type genus *Methylocystis* (Bowman et al., 1993), whereas the subsequent sister taxon was *Beijerinckiaceae* (Garrity et al., 2005d). In the CCT, *Rhodoblastus* was shown as closely related to *Roseiarcus* with strong support whereas the relationship of this clade to *Alsobacter* (Bao et al., 2014) was only poorly supported. While *Roseiarcus* was taxonomically placed in *Roseiarcaceae* when it was originally proposed, in its original description *Rhodoblastus* was not assigned to a family, and a phylogenetic analysis was not performed. *Rhodoblastus* was placed in *Bradyrhizobiaceae* (*Nitrobacteraceae*) in a later study (Garrity et al., 2003b) but the rationale behind this decision remained obscure. When *Roseiarcaceae* was proposed, *Rhodoblastus* was considered but the backbone of the 16S rRNA gene tree was only partially resolved. *Roseiarcaceae* has priority over *Alsobacteraceae* (Sun et al., 2018), hence the possibility of a later unification of the family does not preclude the assignment of *Rhodoblastus* to *Roseiarcaceae*, which we propose below. This solution is not conflict with the phenotype either (**Supplementary File S2**).

Bradyrhizobiaceae (*Nitrobacteraceae*) also appeared in the CCT as the taxonomic home for *Pseudorhodoplanes* (Tirandaz

et al., 2015), which was originally not assigned to a family, as well as for *Pseudolabrys* (Kämpfer et al., 2006) of *Xanthobacteraceae*. When the latter was proposed the 16S rRNA tree presented showed poor support for the specific placement and the genus was only assigned to the class *Alphaproteobacteria* in general. *Pseudolabrys* was later on placed in *Xanthobacteraceae* (Lin et al., 2015) based on a 16S rRNA gene analysis with low support. The CCT (**Supplementary File S2**) indicated that *Pseudolabrys* forms a clade with *Bradyrhizobiaceae* (*Nitrobacteraceae*) genera (Garrity et al., 2005e) namely *Variibacter* (Kim et al., 2014), *Afipia* (Brenner et al., 1991) and *Nitrobacter* (Winogradsky, 1892) *Pseudorhodoplanes* (Tirandaz et al., 2015) appeared as the sister genus of *Pseudolabrys* with strong support, even in the gene-content analysis. We thus propose to include *Pseudolabrys* in *Bradyrhizobiaceae* (*Nitrobacteraceae*), which is not precluded by its phenotype (**Supplementary Table S1**).

Bosea as well as *Salinarimonas* (Liu J.-H. et al., 2010) which was originally (Cai et al., 2011b) also assigned to *Bradyrhizobiaceae* (*Nitrobacteraceae*) but later on to a family of its own (Cole et al., 2018), were placed within a strongly supported clade (**Figure 3** and **Supplementary File S2**) containing *Methylobacteriaceae*, *Camelimonas* (Kämpfer et al., 2010b) *Chelatococcus asaccharovorans* (Auling et al., 1993), and *Chelatococcus sambhunathii* (Panday and Das, 2010). A similar arrangement was observed in the CCT with high support (**Supplementary File S2**). In the original description of *Bosea*, bootstrapping was not conducted, and only few species could be considered at that time. Neither its original description nor its emendation explicitly assigned *Bosea* to a family. The genus was placed in *Bradyrhizobiaceae* (*Nitrobacteraceae*) in Bergey's manual (Boone et al., 2001a) but the rationale was unclear. Other studies emphasized the uncertain placement of *Bosea* in 16S rRNA gene trees, much like the placement of *Chelatococcus* (Lee et al., 2005). When *Chelatococcus* was proposed and emended (Auling et al., 1993; Yoon et al., 2008) it already appeared as closely related to *Methylobacteriaceae* with moderate support. *Chelatococcus* was placed in *Beijerinckiaceae* in Bergey's manual but the reason for this decision remained unclear. *Camelimonas* was regarded as belonging to *Beijerinckiaceae* when *Thalassocola* was proposed (Lin et al., 2015) but the included 16S rRNA gene tree did not show a monophyletic *Beijerinckiaceae*. In contrast, the recent proposal to place *Chelatococcus* and *Camelimonas* in a separate family *Chelatococcaceae* (Dedysh et al., 2016) is in agreement with our results. Since the phylogenetic placement of *Bosea* does not allow for an inclusion of the genus into any of the families within the clade, the taxonomically most conservative solution is to create a new family, *Boseaceae* fam. nov.

When *Enterovirga* (Chen et al., 2017d) was proposed it was acknowledged that this genus shows high 16S rRNA similarities with several *Methylobacteriaceae* genera but also with *Chelatococcus* and *Pseudochelatococcus* of *Beijerinckiaceae* and *Bosea* of *Bradyrhizobiaceae* (*Nitrobacteraceae*). However, the presented 16S rRNA gene tree had insufficient support for assigning *Enterovirga* to a family. In the CCT (**Supplementary File S2**) *Enterovirga* was nested within *Methylobacteriaceae* (Garrity et al., 2005c) in a moderately supported clade. Given its phylogenetic position, it is thus proposed to tentatively include

Enterovirga in *Methylobacteriaceae*, which is not precluded by its phenotype (**Supplementary Table S1**).

The original descriptions of *Cucumibacter*, *Maritalea* and *Pelagibacterium* (**Figure 4**) provided strong support for a clade comprising these genera and *Devosia*. In these studies, the overall taxon sampling was insufficient to safely assign these genera to a family, even though the affiliation to *Hyphomicrobiaceae* was not called into question. When *Devosia* was originally proposed it was not assigned to a family, and even its later emendations (Rivas et al., 2003; Yoo et al., 2006; Yoon et al., 2007c; Zhang D.C. et al., 2012) hesitated to explicitly suggest an affiliation of the genus to a family. Previous studies already concluded that *Devosia* and *Prosthecomicrobium* cannot safely be assigned to a family based on 16S rRNA gene data (Lee et al., 2005). The CCT and UCT provided strong support for a clade comprising *Arsenicitalea* (Mu et al., 2016) *Cucumibacter*, *Devosia*, *Maritalea*, *Methyloterrigena* (Kim H.S. et al., 2016), *Paradevosia* (Geng et al., 2014), *Pelagibacterium* and *Youhaiella* (Wang Y.X. et al., 2015). It makes phylogenetic sense to taxonomically remove these genera from *Hyphomicrobiaceae* and assign them to a new family, which is not precluded by their phenotype (**Supplementary Table S1**).

Rhodobacteraceae (Garrity et al., 2005b) of *Rhodobacterales* were shown as non-monophyletic in the GBDP tree because the genera *Acuticoccus* (Hou et al., 2015), *Ahrensia* (Uchino et al., 1998; Liu J. et al., 2016), *Labrenzia* (Biebl et al., 2007; Bibi et al., 2014), *Nesiotobacter* (Donachie et al., 2006; Garrity et al., 2007), *Pannonibacter* (Borsodi et al., 2003; Biebl et al., 2007), *Pseudovibrio* (Shieh et al., 2004), *Roseibium* (Suzuki et al., 2000) and *Stappia* (Uchino et al., 1998; Biebl et al., 2007) were placed apart from the remaining *Rhodobacteraceae* and within *Rhizobiales* (*Hyphomicrobiales*) instead where they also caused the non-monophyly of some families (**Figure 4**). It should be noted that *Rhodobacteraceae* as originally proposed is illegitimate because the family included *Hyphomonas* (Moore et al., 1984), the type genus of *Hyphomonadaceae* (Lee et al., 2005), which has priority.

Acuticoccus showed a relatively isolated position (**Figure 4**) but also strong support for its sister-group relationship to *Amorphus* (Zeevi Ben Yosef et al., 2008), which was as yet not assigned to a family. It is questionable whether the restricted taxon sampling in the phylogenetic analysis that accompanied the original description of *Acuticoccus* really allowed for an assignment to a family but the genus was taxonomically placed in *Rhodobacteraceae* (Hou et al., 2015). Phenotypically, the features of *Acuticoccus* may be rather rare in *Alphaproteobacteria* as gliding motility was reported for the genus, whereas *Amorphus* was described as not-motile (**Supplementary Table S1**). For reasons of taxonomic conservatism, the two genera are best assigned to the same family, which is supported by the gene-content analysis (**Supplementary File S2**).

The original description of *Stappia* did not assign it to a family; this was done in an edition of Bergey's manual (Boone et al., 2001a) but it is not obvious whether this was based on a phylogenetic analysis. The same holds for the assignment of *Labrenzia* (Cai et al., 2011a), *Pannonibacter* (Garrity et al., 2003b), and *Pseudovibrio* (Garrity et al., 2007) to *Rhodobacteraceae*. Later studies, such as the proposal of

Nesiotobacter (Donachie et al., 2006), also failed to conduct a comparison with the type genus of *Rhodobacteraceae*. Rather, these studies assigned newly proposed genera to *Rhodobacteraceae* based on the closeness of these genera to genera that now appeared to phylogenetically not belong to the family. *Labrenzia*, *Nesiotobacter*, *Pannonibacter*, and *Roseibium* formed a moderately to well supported clade even in the unconstrained 16S rRNA gene analyses (**Supplementary File S2**). The GBDP topology (**Figure 4**) differs regarding the positioning of *Breoghania* (Gallego et al., 2010) but this discrepancy was not well supported. When *Breoghania* was proposed and assigned to *Cohaesibacteraceae*, none of the genera with which *Cohaesibacteraceae* now appeared intermixed were included in the taxon sampling. Additional supermatrix analyses (**Supplementary File S2**) indicated that *Breoghania* forms the sister group of a clade comprising the six genera, whereas *Cohaesibacter* (Hwang and Cho, 2008a) branches first. Given the results from the analysis of the 16S rRNA gene and genome-scale data it seems advisable to propose a new family to accommodate *Breoghania* as well as another new family to harbour *Labrenzia*, *Pannonibacter*, *Pseudovibrio* (including *Nesiotobacter* as proposed below), *Roseibium* and *Stappia*. These solutions are not in conflict with the phenotype of the involved genera (**Supplementary Table S1**).

Among the misplaced *Rhodobacteraceae*, *Ahrensia* formed an independent lineage with relatively uncertain affiliations to other families (**Figure 5**). The original description of *Ahrensia* did not assign it to a family, whereas its last emendation assigned it to *Phyllobacteriaceae* (Liu J. et al., 2016) Bergey's manual placed *Ahrensia* in *Rhodobacteraceae* (Boone et al., 2001a) but whether this was based on a phylogenetic assessment remained unclear to us. Similarly, the assignment of *Nesiotobacter* to *Rhodobacteraceae* (Garrity et al., 2007) may not have been based on phylogenetic argumentation. Given the phylogenomic results presented here, *Ahrensia* is best assigned to a separate family, which is not precluded by its phenotype (**Supplementary Table S1**). According to the 16S rRNA gene analyses, *Pseudahrensia* (Jung et al., 2012c) should also be assigned to this family (**Supplementary File S2**).

Phyllobacteriaceae (Mergaert and Swings, 2005) appeared as paraphyletic in the GBDP tree (**Figure 5**) because the genera *Aminobacter* (Urakami et al., 1992; Kämpfer et al., 2002a), *Nitratireductor* (Labbé et al., 2004; Jang et al., 2011), *Pseudaminobacter* (Kämpfer et al., 1999), *Aquamicrobium* (Bambauer et al., 1998; Lipski and Kämpfer, 2012; Wu Z.-G. et al., 2014), *Mesorhizobium* (Jarvis et al., 1997), *Hoeflea* (Peix et al., 2005; Rahul et al., 2015) and *Zhengella* (Liao et al., 2018) were placed apart from the clade containing the type genus of the family, *Phyllobacterium*. *Zhengella* formed the sister group of *Notoacmeibacter* (Huang et al., 2017) of *Notoacmeibacteraceae* with reasonable support, even in the gene-content analysis (**Supplementary File S2**). The taxonomically most conservative solution is to also assign *Zhengella* to this family, which is not precluded by the major phenotypic features found in the genus (**Supplementary Table S1**).

The original descriptions of *Mesorhizobium* and *Pseudaminobacter* (**Figure 5**) did not explicitly assign these

genera to a family. The recent emendations of *Aquamicrobium* (Figure 5) were accompanied by phylogenetic trees with low support at the backbone and a taxon sampling which we tend to regard as insufficient for safely assigning a genus to a family. The three genera were placed in *Phyllobacteriaceae* in an edition of Bergey's manual (Boone et al., 2001a) but it remained unclear to us whether this was based on a phylogenetic assessment. *Nitratireductor* (Figure 5) was assigned to *Phyllobacteriaceae* when it was originally proposed (Labbé et al., 2004) but this was based on a poorly resolved 16S rRNA gene tree with reduced taxon sampling. When *Aquamicrobium* (Bambauer et al., 1998) was proposed, bootstrapping was not conducted, and at that time only few species could be considered in the phylogenetic analysis. Insufficient taxon sampling was also present in the original description of *Nitratireductor*, in addition to poor branch support; the most recent emendation of the genus did not include the type species of the type genus of the family either. In the CCT, *Nitratireductor*, *Pseudaminobacter*, *Aminobacter*, *Aquamicrobium*, and *Mesorhizobium* formed a clade together with further genera such as *Chelativorans* (Doronina et al., 2010; Kämpfer et al., 2015a) and *Carbophilus* (Meyer et al., 1993) but branch support was extraordinarily low throughout (Supplementary File S2). For this reason, we refrain from taxonomic conclusions for these genera. The issue should be tackled once more type-strain genome sequences from the clade become available.

During our investigation we noticed that *Chelativorans intermedius* (Kämpfer et al., 2015a) (Supplementary File S2) was described as Gram-positive although the opposite is mentioned in the abstract of the same publication. Furthermore the description for *Chelativorans* (Doronina et al., 2010; Kämpfer et al., 2015a) defines the genus as Gram-negative. Gram-positivity would be unlikely for the whole family of *Phyllobacteriaceae* (Brenner et al., 2005) in general. We suspect this was an oversight of the authors and *Chelativorans intermedius* is most likely Gram-negative.

When *Hoeflea* was proposed, it was included in the family *Phyllobacteriaceae* even though this conclusion remained phylogenetically unsupported (Peix et al., 2005). Our phylogenomic analysis suggests the inclusion of *Hoeflea* in *Rhizobiaceae* (Figure 5 and Supplementary File S2). While the marine bacterium *Hoeflea* differs from *Rhizobiaceae* also regarding the presence of photosynthetic pigments, this character is highly homoplastic within the class *Alphaproteobacteria*. Assigning *Hoeflea* to *Rhizobiaceae* is not in conflict with its phenotype (Supplementary Table S1) and more conservative than generating a new family to accommodate the genus.

In the CCT (Supplementary File S2) *Lentilitoribacter* (Park et al., 2013b) of *Phyllobacteriaceae* (Mergaert and Swings, 2005) was nested within *Hoeflea* (Peix et al., 2005; Rahul et al., 2015) with reasonable support. When *Lentilitoribacter* was originally proposed it was placed in *Phyllobacteriaceae* in a 16S rRNA gene tree which lacked support and did not include *H. phototrophica*, which formed the sister group of *Lentilitoribacter* in the CCT. Although we refrain from resolving the paraphyly of *Hoeflea* until additional genomic

data become available we propose to include *Lentilitoribacter* in *Rhizobiaceae*, which is not precluded by its phenotype (Supplementary File S1).

Aurantimonadaceae (Garrity et al., 2003a) were shown as polyphyletic in the GBDP tree (Figures 4, 5) because *Martellella endophytica* (Bibi et al., 2013) and *Martellella mediterranea* (Rivas et al., 2005) were placed apart from core *Aurantimonadaceae* (Figure 4) and within a strongly supported clade (Figure 5) that included *Rhizobiaceae* and *Mycoplana* of *Brucellaceae*. When *Martellella* and its type species, *M. mediterranea*, were proposed, they were not assigned to any family and phylogenetically not placed within *Aurantimonadaceae* but rather within *Rhizobiaceae*. *Martellella* was placed in *Aurantimonadaceae* later on (Garrity et al., 2007) but the rationale behind this decision remained obscure. The CCT did not indicate the monophyly of *Aurantimonadaceae* either (Supplementary File S2). Consequently, it is proposed to include *Martellella* into *Rhizobiaceae*. This is not contradicted by the phenotypic characteristics (Supplementary Table S1). *Aurantimonadaceae* was originally proposed without a formal description and is not a validly published name. Therefore we newly propose *Aurantimonadaceae*, fam. nov., with a revised (reduced) set of genera to belong to this family.

The position of *Mycoplana dimorpha* (Urakami et al., 1990) which appeared nested within *Rhizobiaceae* (Conn, 1938) in Figure 5, also rendered *Brucellaceae* (Breed et al., 1957) polyphyletic in the GBDP tree; core *Brucellaceae* is shown in Figure 4. In the CCT, in addition to *Mycoplana dimorpha*, *Mycoplana ramosa* (Urakami et al., 1990) was also placed within the clade containing *Rhizobiaceae* (Supplementary File S2). *Mycoplana* (Gray and Thornton, 1928; Urakami et al., 1990) was originally proposed on basis of phenotypic characteristics without taking into account the 16S rRNA gene sequence as phylogenetic marker; it was even supposed to belong to *Mycobacteriaceae* (*Actinobacteria*). Later on *Mycoplana* was placed in *Brucellaceae* (Boone et al., 2001a) but the rationale behind this assignment remained unclear. *Mycoplana* displays phenotypic characteristics similar to those of *Rhizobiaceae* (Supplementary Table S1). Given its phylogenetic positioning, it is thus proposed to include *Mycoplana* in *Rhizobiaceae*.

Notoacmeibacter (Huang et al., 2017) not only formed a strongly supported clade together with *Mabikibacter* of *Mabikibacteraceae* (Choi et al., 2017) in the CCT but the distance between the two 16S rRNA gene sequences was exceptionally low (Supplementary File S2). The monotypic family *Mabikibacteraceae* was proposed briefly after *Notoacmeibacteraceae* hence neither publication was able to account for the respective other taxon. The high similarity of 99.9% in the 16S rRNA gene sequences (Meier-Kolthoff et al., 2013b) and the highly similar phenotypic characteristics (Supplementary File S1) could even indicate identity at the species level but solving this issue required genome sequencing of the type strain of *Mabikibacter*. We thus here only propose to transfer *Mabikibacter* to *Notoacmeibacteraceae*, which has priority. This transfer would also avoid the non-monophyly of

Notoacmeibacteraceae that resulted if only *Zhengella* were to be added to this family (as treated above).

Rhizobiales (Hyphomicrobiales) Genera

In addition to some families of *Rhizobiales* (*Hyphomicrobiales*), a variety of genera assigned to the order were found in need of a taxonomic revision, while the majority of the genera was shown as monophyletic (Figures 3–5). This section also treats the *Rhodobacterales* genera that needed to be taxonomically assigned to *Rhizobiales* (*Hyphomicrobiales*) as explained above in case their genus boundaries also needed to be reconsidered.

Within *Rhizobiales* (*Hyphomicrobiales*), *Afipia* (Brenner et al., 1991; La Scola et al., 2002) was shown as paraphyletic in the GBDP tree (Figure 3) because *Oligotropha carboxidovorans* (Meyer et al., 1993) formed the sister group of the type species of *Afipia*, *Afipia felis* (Brenner et al., 1991). *O. carboxidovorans* was originally proposed as a new species in a new genus on the basis of morphological, physiological and biochemical characteristics, as well as 16S rRNA signature oligonucleotides. However, in the original publication no phylogenetic tree was inferred and it was not clarified which of the character states represent apomorphies. The known phenotypic differences between the two genera are not pronounced (Supplementary Table S1). To include *O. carboxidovorans* in *Afipia*, which has priority, seems to be the taxonomically most conservative solution.

Methylobacterium (Patt et al., 1976) appeared non-monophyletic in the GBDP tree (Figure 3) because *Methylorubrum* (Green and Ardley, 2018) species such as *Methylorubrum salsuginis*, *M. populi* and *M. chloromethanicum* were nested within *Methylobacterium*. All species were only recently transferred from *Methylobacterium* to *Methylorubrum* (Green and Ardley, 2018). The purpose of splitting *Methylobacterium* was to obtain phenotypically more homogeneous genera. Yet if such an approach yields apparently non-monophyletic groups it is in conflict with the principles of phylogenetic systematics (Hennig, 1965; Klenk and Göker, 2010; Wiley and Lieberman, 2011). In particular, the cited study emphasized that only certain clades of *Methylobacterium sensu lato* should be assigned to either *Methylobacterium sensu stricto* or to *Methylorubrum* but new genera and new combinations for the remaining clades were not proposed. Since species names cannot lack a genus name, it would come as no surprise if this solution rendered *Methylobacterium* non-monophyletic. The utilization of methylamine as sole carbon source in *Methylorubrum* was suggested as the main feature for distinguishing it from *Methylobacterium sensu stricto* (Green and Ardley, 2018). But a single binary character cannot properly separate two taxa according to the principles of phylogenetic systematics because only one of the two character states is an apomorphy (Nouioui et al., 2018). Because of the low resolution in the 16S rRNA gene trees (Supplementary File S2) it seems more appropriate to treat the *Methylorubrum* species as species of *Methylobacterium* until more type-strain genome sequences from the group become available and the splitting of the genus can be completed.

Pseudovibrio (Shieh et al., 2004) was shown as paraphyletic in the GBDP tree (Figure 4) because *Nesiotobacter exalbescens*

(Donachie et al., 2006) was nested within *Pseudovibrio* with moderate support. When *Nesiotobacter* was proposed, the genus *Pseudovibrio* was not considered for the phylogenetic analysis of the 16S rRNA gene. While our 16S gene analyses (Supplementary File S2) showed *Nesiotobacter* as sister group of *Pseudovibrio*, *Nesiotobacter exalbescens* and *Pseudovibrio* display similar phenotypic characteristics (Supplementary Table S1). The gene-content analysis provided support for the entire clade but not for all of the subclades (Supplementary File S2). Therefore, we propose to include *N. exalbescens* into *Pseudovibrio* because the rationale of separating the two genera was not obvious.

Labrenzia (Biebl et al., 2007; Bibi et al., 2014) appeared as paraphyletic in the GBDP tree (Figure 4) because *Roseibium denhamense* (Suzuki et al., 2000; Biebl et al., 2007) and *R. hamelinense* (Suzuki et al., 2000; Biebl et al., 2007) were nested within *Labrenzia*, with *L. suaedae* (Bibi et al., 2014) branching first. *Pannonibacter* (Borsodi et al., 2003; Biebl et al., 2007) formed the sister group of the entire clade. In the CCT, *Roseibium aquae* (Zhong et al., 2014) and *R. sediminis* (Liu et al., 2017) were also placed within *Labrenzia* (Supplementary File S2). While the original proposals of *Roseibium* and *L. suaedae* showed phylogenetic trees with 83–93% support for the monophyly of *Roseibium*, the species now included in *Labrenzia* could not be considered when *Roseibium* was introduced. Support was already weak for the monophyly of *Labrenzia* when it was originally proposed. The paraphyly of *Labrenzia* was already evident in a more recent study (Camacho et al., 2016), which also showed an uncertain position of *L. suaedae* relative to the remaining genus. The *Roseibium* species display phenotypic characteristics similar to those of *Labrenzia* (Supplementary Table S1) while the gene-content analysis did not yield well-supported subgroups that could be proposed as genera (Supplementary File S2). For this reason, the best solution appears to be to merge the two genera, which is also the taxonomically most conservative approach.

Ochrobactrum (Holmes et al., 1988) was shown as paraphyletic in the GBDP tree (Figure 4) because the entire genus *Brucella* (Meyer and Shaw, 1920) was nested within *Ochrobactrum*. *O. thiophenivorans* (Kämpfer et al., 2008), *O. grignonense* (Lebuhn et al., 2000), *O. pituitosum* (Huber et al., 2010), *O. rhizosphaerae* (Kämpfer et al., 2008), *O. pseudogrignonense* (Kämpfer et al., 2007a) formed a clade that branched first, whereas the type species of *Ochrobactrum* appeared more closely related to *Brucella* than to this clade. In the CCT, *O. haematophilum* (Kämpfer et al., 2007a) and *O. pecoris* (Kämpfer et al., 2011) also belonged to the clade that branched first. The 16S rRNA gene data neither provided evidence for other *Ochrobactrum* species to form a clade with the type species to the exclusion of *Brucella*, including species such as *O. pseudintermedium* (Teyssier et al., 2007), *O. oryzae* (Tripathi et al., 2006), *O. gallinifacis* (Kämpfer et al., 2003) and *O. endophyticum* (Li L. et al., 2016) (Supplementary File S2). When *Ochrobactrum* was proposed, an analysis of the 16S rRNA gene could not yet be conducted. When *Brucella* was proposed, a phylogenetic analysis was not conducted; it was speculated that the genus may belong to *Enterobacteriaceae* but an assignment

to a family was not explicitly suggested. Among those taxonomic studies available to us that showed a phylogenetic analysis with a sufficient number of *Brucella* and *Ochrobactrum* species, a paraphyletic *Ochrobactrum* was always evident, particularly in the recent proposals of new species (Kämpfer et al., 2007a,b, 2008, 2009a, 2010a, 2013b, 2014; Lebuhn et al., 2000; Trujillo et al., 2005; Teyssier et al., 2007; Romanenko et al., 2008; Xu H.Y. et al., 2009; Huber et al., 2010; Imran et al., 2010; Woo et al., 2011; Li L. et al., 2016; Liu B.B. et al., 2016).

It is well known that in terms of DDH similarity, *Brucella* is only a single species (Verger et al., 1985); this is also reflected in the newly calculated dDDH values (Table 1). The overall genomic divergence of the *Brucella*-*Ochrobactrum* clade was lower than in many clades harboring a single genus only. *Brucella* differs from *Ochrobactrum* regarding its pathogenic lifestyle, which may be reflected in the lower genome size of *Brucella* (Figure 4). However, *Ochrobactrum* species are also known from clinical specimens, including its type species (Holmes et al., 1988), and a more pronounced genome-size reduction of pathogenic species nested within a partially non-pathogenic genus was observed elsewhere, as, e.g., in *Mycobacterium leprae* (Akinola, 2013). *Mycobacterium* can also serve as an example for a genus that harbours distinct risk groups (Bundesanstalt für Arbeitsschutz und Arbeitsmedizin, 2015), much like *Burkholderia* and *Yersinia*. Hence the difference between *Brucella* and *Ochrobactrum* regarding their risk-group assignment could hardly be used as an argument against their inclusion in the same genus. Known phenotypic differences, if any, appeared to be restricted to autapomorphies of *Brucella* that may well be linked to its evolutionary adaptation to pathogenesis (Supplementary Table S1). Despite the differences in genome size, the gene-content analysis provided more support for the combined *Brucella*-*Ochrobactrum* clade than for the subclades (Supplementary File S2). For these reasons, we propose to include *Ochrobactrum* in *Brucella*, which has priority. According to the available phenotypic information (Supplementary Table S1), the inclusion of the entire genus *Ochrobactrum* does not cause a need for the emendation of *Brucella* (Meyer and Shaw, 1920; Verger et al., 1985).

Mesorhizobium (Jarvis et al., 1997) appeared as non-monophyletic in the GBDP tree and in the CCT (Figure 5 and Supplementary File S2) since several *Mesorhizobium* species were intermixed with genera such as *Aquamicrobium* (Bambauer et al., 1998; Lipski and Kämpfer, 2012; Wu Z.-G. et al., 2014) *Nitratireductor* (Labbé et al., 2004) and *Pseudaminobacter* (Kämpfer et al., 1999) which were also shown as non-monophyletic. However, due to the low support of the branches, particularly in the comprehensive 16S rRNA gene trees, it is difficult to propose taxonomic conclusions for *Aquamicrobium*, *Mesorhizobium*, *Nitratireductor*, and *Pseudaminobacter*. These genera belong to a deviating branch of *Phyllobacteriaceae* that even proved to be difficult to classify at the family level, as explained above. We suppose that a more satisfying classification of these four genera can only be obtained once more genome sequences become available.

Allorhizobium (de Lajudie et al., 1998) and *Pararhizobium* (Mousavi et al., 2015) appeared as polyphyletic in GBDP and 16S

rRNA gene trees (Figure 5 and Supplementary File S2) because several species are mixed up with representatives of *Rhizobium* (Frank, 1889). When *Allorhizobium* was proposed, a tree with rather low support at backbone was presented which did not yield well-defined relationships between the genera. Later studies of the group presented much better resolved multi-gene analyses but restricted the taxon sampling to rhizobial and agrobacterial strains (Mousavi et al., 2015). The CCT included a well-supported clade including the type species of *Allorhizobium*, *A. undicola*, the other *Allorhizobium* species except for *A. oryzae*, as well as *Rhizobium oryzae* (Zhao et al., 2017), and *R. taibaishanense* (Yao et al., 2012). *Rhizobium* (Frank, 1889; Young et al., 2001) was shown as non-monophyletic for various reasons in the GBDP tree (Figure 5) and the CCT, including distantly placed species such as *R. arenae* (Zhang S. et al., 2017), *R. flavum* (Gu et al., 2014), *R. gei* (Shi et al., 2016), *R. marinum* (Liu Y. et al., 2015), *R. selenitireducens* (Hunter et al., 2007), *R. naphthalenivorans* (Kaiya et al., 2012), *R. subbaraonis* (Ramana C.V. et al., 2013) which were placed apart from the well-supported core *Rhizobium* clade that contained the type species of the genus.

The taxonomic literature disagreed on whether a broad concept of *Rhizobium*, i.e., including genera such as *Allorhizobium* and *Agrobacterium* (Conn, 1942), should be preferred (Young et al., 2001, 2003) or whether *Rhizobium* should be split into various genera (Farrand et al., 2003; Mousavi et al., 2015). Apparently distinct authors of new species names followed either one or the other of the two competing concepts (Willems, 2006), thus leading to the considerable mix-up of the species of *Rhizobium* (Figure 5). Given the overall genomic divergence of the group revealed here it appeared advisable to follow a narrow concept for *Rhizobium*. Further dissecting *Rhizobium* does not imply introducing many new genus names because names for the respective clades were already proposed in the literature. For instance, *R. oryzae* and *R. taibaishanense* can be assigned to the already existing genus *Allorhizobium* (Figure 5 and Supplementary File S2), which is not in disagreement with their phenotype (Supplementary Table S1) while the group is even supported in the gene-content analysis (Supplementary File S2). The new combination *Allorhizobium taibaishanense* was already proposed (Mousavi et al., 2015) but the name does not appear to be validly published.

On a similar vein, *R. subbaraonis* (Ramana C.V. et al., 2013) should be assigned to *Mycoplana* (Urakami et al., 1990; Gray and Thornton, 1928) whereas the phylogenetically relatively isolated *Pararhizobium haloflavum* (Shen et al., 2018) should be placed into a genus of its own (Figure 5, Supplementary File S2, and Supplementary Table S1). The inclusion of *Rhizobium subbaraonis* does not cause a need for the emendation of *Mycoplana* (Supplementary Table S1). The original description of *R. subbaraonis* did not include *Mycoplana*, whereas only a limited total number of species was considered when *P. haloflavum* was originally proposed.

The taxonomy of deviating species of *Allorhizobium* such as *A. borborensis*, *A. oryzae* and *A. pseudoryzae* as well as of the deviating *Pararhizobium* species *P. capsulatum* (Mousavi et al., 2015) cannot currently be improved because of low resolution in the comprehensive 16S rRNA gene trees (Supplementary File S2).

Similarly, while *Rhizobium* species such as *R. smilacinae* (Zhang et al., 2014b), *R. cellulosityticum* (García-Fraile et al., 2007), *R. zeae* (Celador-Iera et al., 2017), *R. wenxiniae* (Gao et al., 2017) and *R. yangtingense* (Chen W. et al., 2015) were nested within *Neorhizobium* (Mousavi et al., 2014), the clade containing both *Neorhizobium* and *Pseudorhizobium* (Kimes et al., 2015) was particularly poorly supported (**Supplementary File S2**). While *Rhizobium* species such as *R. naphthalenivorans* and *R. selenitireducens* could possibly be placed in *Ciceribacter* (Kathiravan et al., 2013) and others such as *R. arenae* and *R. gei* could potentially be included in *Pararhizobium*, these arrangements were also poorly resolved. Therefore it would currently be difficult to infer taxonomic conclusions. We suppose that a more satisfying classification of these genera can be obtained once more genome sequences become available. As an exception, *Rhizobium vignae* (Ren et al., 2011), which was placed as sister group of *N. galegae* (Mousavi et al., 2014) with strong support, can be assigned to *Neorhizobium*. While they are closely related, our dDDH results (41.4% similarity) values indicate that *R. vignae* and *N. galegae* are independent species. Therefore, we propose to include *R. vignae* in *Neorhizobium*. This proposal is not contradicted by phenotypic characteristics and the transfer of *R. vignae* does not cause a need for the emendation of *Neorhizobium* (**Supplementary Table S1**). The removal of *R. oryziradicis*, *R. taibaishanense*, *R. subbaraonis* and *R. vignae* does neither cause a need for the emendation of *Rhizobium* (Frank, 1889).

Rhodobacterales Genera

Rhodobacterales has so far been a monotypic order that only included *Rhodobacteraceae*. As mentioned above, this family as originally proposed is illegitimate because the family included *Hyphomonas* (Moore et al., 1984), the type genus of *Hyphomonadaceae* (Lee et al., 2005), which has priority. Except for the genera taxonomically assigned to *Rhodobacterales* but phylogenetically placed in *Rhizobiales* (*Hyphomicrobiales*), which were treated above, *Rhodobacteraceae* was monophyletic. However, whereas most of its genera were also shown as monophyletic in our analyses (**Figures 7–9**), some were shown to be in need of a taxonomic revision.

Roseivivax (Suzuki et al., 1999a; Park et al., 2010; Chen M.-H. et al., 2012) was shown as non-monophyletic in the GBDP tree and the CCT (**Figures 7, 9** and **Supplementary File S2**) because *R. roseus* (Zhang et al., 2014c) formed a clade (**Figure 7**) together with *Tranquillimonas alkanivorans* (Harwati et al., 2008) while *R. pacificus* (Wu et al., 2013) appeared (**Figure 9**) as sister group of *Citreimonas salinaria* (Choi and Cho, 2006). When *R. roseus* was originally proposed, it formed a group with *R. pacificus* which received only poor support in 16S rRNA gene trees, much like its relationship to core *Roseivivax*. Similarly, the phylogenetic position of *T. alkanivorans* and *C. salinaria* remained unresolved in these trees. The isolated position of the species in the 16S rRNA gene and genomic trees calls for the proposal of a new genus to accommodate *R. pacificus*. In addition, we propose to include *R. roseus* in *Tranquillimonas*. This is not contradicted by the phenotypic characteristics of

these taxa (**Supplementary Table S1**) even though the gene-content analysis does not lend support (while core *Roseivivax* is reasonably supported; **Supplementary File S2**). The removal of *R. roseus* and *R. pacificus* does not cause a need for the emendation of *Roseivivax* (**Supplementary Table S1**).

Defluviimonas (Foesel et al., 2011; Math et al., 2013) appeared as paraphyletic in the GBDP tree (**Figure 7**) because particularly *Defluviimonas alba* (Pan et al., 2015) but also *D. indica* (Jiang et al., 2014) were placed apart from the type species of *Defluviimonas*, *D. denitrificans*, which appeared more closely related to the type species of *Albidovulum*, *A. inexpectatum* (Albuquerque et al., 2002) whereas *Albidovulum xiamenense* (Yin et al., 2012) was in turn placed apart from its type species. In the original proposal of *A. xiamenense*, only weak support was obtained for the monophyly of *Albidovulum*. When *D. indica* was proposed, 90% support was obtained for the monophyly of *Defluviimonas* in a 16S rRNA gene analysis based on the neighbor-joining algorithm and a simplistic evolutionary model. We could not reproduce this finding here based on our ML analysis with a much larger taxon sampling (**Supplementary File S2**) which, even when unconstrained, placed *D. indica* as sister group of the clade comprising *A. inexpectatum* and core *Defluviimonas*. In the 16S rRNA gene trees (**Supplementary File S2**) *D. alba* was placed as sister group of *Frigidibacter albus* (Li and Zhou, 2015). When *D. alba* was proposed, no support for the monophyly of *Defluviimonas* was obtained, as the phylogenetic position of *D. alba* remained uncertain; *Albidovulum* was not considered. *D. alba* and *F. albus* show similar phenotypic characteristics (**Supplementary Table S1**). Therefore, one could propose to include *D. alba* in *Frigidibacter*. However, the 16S rRNA gene similarity between the two type strains is 99.79% when calculated using the recommended settings, which indicates that DNA:DNA hybridization should be carried out to rule out that the strains are conspecific (Meier-Kolthoff et al., 2013b). In contrast, we conclude that a new genus should be proposed to accommodate *D. indica*, which is also in accordance with the gene-content analysis (**Supplementary File S2**) as it yielded strong support for the remaining clade after removal of *D. indica*. Including, *D. aestuarii*, *D. aquaemixtae*, *D. denitrificans*, and *D. nitratreducens* in *Albidovulum* is a phylogenetically obvious solution but would render the remaining species of the genus, *D. alba* and *D. pyrenivorans*, illegitimate, whose phylogenetic position is still uncertain. In contrast, its isolated phylogenetic position indicates that *Albidovulum xiamenense* can safely be placed into a genus of its own, which is not precluded by its phenotype. The removal of *A. xiamenense* does not cause a need for the emendation of *Albidovulum* (**Supplementary Table S1**).

Gemmobacter (Rothe et al., 1987; Chen W.-M. et al., 2013) was shown as polyphyletic in the GBDP tree (**Figure 7**) because *G. nectariphilus* (Tanaka et al., 2004; Chen W.-M. et al., 2013) and *G. megaterium* (Liu J.-J. et al., 2014) were placed in a distant position relative to the type species, *G. aquatilis*. In addition, in the CCT *G. intermedius* (Kämpfer et al., 2015b) and *G. straminiformis* (Kang et al., 2017) formed an unsupported group together with *G. nectariphilus* and *G. megaterium* (**Supplementary File S2**). When these

Gemmobacter species were proposed the monophyly of the genus was already unsupported in 16S rRNA gene trees. We did not detect an obvious synapomorphy for the genus as currently circumscribed (**Supplementary Table S1**). Therefore, a new genus is proposed to accommodate *G. megaterium* and *G. nectariphilus*; *G. intermedius*, and *G. straminiformis* should also be assigned to this genus once their genome sequences confirm their position, which is currently uncertain in 16S rRNA gene trees. The removal of *G. megaterium* and *G. nectariphilus* does not cause a need for the emendation of *Gemmobacter* (**Supplementary Table S1**). The two resulting genera received high support in the gene-content analysis (**Supplementary File S2**).

Pseudorhodobacter (Uchino et al., 2002; Jung et al., 2012a; Chen C.-X. et al., 2013; Lee et al., 2013, 2016) appeared as paraphyletic in the GBDP tree (**Figure 7**) because *P. psychrotolerans* (Lee et al., 2016) was placed as sister group of *Rhodobacter blasticus* and *Tabrizicola*. In the CCT and UCT, *P. aquaticus* (Li A.-H. et al., 2016), *P. collinsensis* (Zhang et al., 2016), *P. psychrotolerans* (Lee et al., 2016) and *P. sinensis* (Li A.-H. et al., 2016) formed a reasonably well supported clade separate from core *Pseudorhodobacter* (**Supplementary File S2**) and showed similar phenotypic characteristics (**Supplementary Table S1**). The descriptions of these species were accompanied by poorly resolved 16S rRNA gene trees which did not clearly indicate the monophyly of *Pseudorhodobacter*. Given the results presented here, it is proposed to place these deviating *Pseudorhodobacter* species in a separate genus.

Rhodobacter (Imhoff et al., 1984; Srinivas et al., 2007b; Wang et al., 2014) was shown to be non-monophyletic in the GBDP tree with strong support (**Figure 7**) because a clade containing *R. veldkampii* (Hansen and Imhoff, 1985) and *R. vinaykumarii* (Srinivas et al., 2007b) was placed apart from the clade containing the type species of the genus. In addition, *R. azotoformans* (Hiraishi et al., 1996), *R. johrii* (Giriya et al., 2010), *R. megalophilus* (Arunasri et al., 2008), *R. ovatus* (Srinivas et al., 2008) and *R. sphaeroides* (van Niel, 1944; Imhoff et al., 1984) were placed apart from each of these two clades and formed the sister group of *Cereibacter* (Suresh et al., 2015) instead. Finally, *R. blasticus* (Kawasaki et al., 1993) appeared as sister group of *Tabrizicola aquatica* (Tarhriz et al., 2013). *Rhodobacter* already appeared non-monophyletic in the 16S rRNA gene trees presented in recent taxonomic studies such as the one that proposed *Tabrizicola* although phylogenetic resolution remained limited. The five *Rhodobacter* species placed adjacent to *Cereibacter* are phenotypically in agreement with this genus (**Supplementary Table S1**), which was also supported by the gene-content analysis (**Supplementary File S2**). Assigning these deviating *Rhodobacter* species to *Cereibacter* is more conservative than establishing a separate genus. Based on dDDH values, *R. megalophilus* is a later heterotypic synonym of *R. sphaeroides* (**Table 1**). Consequently, we propose to place *R. azotoformans*, *R. johrii*, *R. ovatus*, and *R. sphaeroides* in *Cereibacter*. Given their relatively isolated phylogenetic position a separate genus is proposed to accommodate *R. vinaykumarii* and *R. veldkampii*, which is not in conflict with their phenotype (**Supplementary Table S1**) even though the group is not supported by the gene-content analysis.

Similarly, *R. blasticus* can be placed in *Tabrizicola*; *Xinfangfangia* (Hu et al., 2018) was also shown to be closely related to this group in the 16S rRNA gene trees (**Supplementary File S2**) but *Tabrizicola* has priority. The removal of *R. azotoformans*, *R. johrii*, *R. ovatus*, *R. sphaeroides*, *R. vinaykumarii*, *R. veldkampii* and *R. blasticus* does not cause a need for the emendation of *Rhodobacter* (**Supplementary Table S1**).

Paracoccus (Davis et al., 1969; Ludwig et al., 1993; Liu et al., 2008) appeared as paraphyletic in the GBDP tree (**Figure 7**) because *Methylarcula marina* (Doronina et al., 2000) was placed as sister group of *Paracoccus saliphilus* (Wang Y.-X. et al., 2009). In the CCT, *Methylarcula terricola* (Doronina et al., 2000) was also nested within the genus *Paracoccus*. When *M. marina* and *M. terricola* were proposed, a 16S rRNA gene phylogenetic analysis showed strong support for a clade comprising *Methylarcula* and *Paracoccus* but only weak support for the monophyly of *Paracoccus* to the exclusion of *Methylarcula*. The known phenotypic features of the two genera also fit excellently to each other (**Supplementary Table S1**). Thus, we conclude that *Methylarcula* should be included in *Paracoccus*, which has priority. However, since the types strains of both *Methylarcula* species appear to have been deposited in a single culture collection only, alternative species names cannot currently be proposed (Parker et al., 2019).

Actibacterium (Lucena et al., 2012; Guo et al., 2017) appeared as paraphyletic in the GBDP tree (**Figure 8**) because *Confluentimicrobium lipolyticum* (Park et al., 2014d) was placed as sister group of *Actibacterium ureilyticum* (Lin et al., 2016). In the CCT, in addition to *C. lipolyticum*, *C. naphthalenivorans* (Jeong et al., 2015) also was placed within *Actibacterium* (**Supplementary File S2**). When *C. lipolyticum* was proposed, its phylogenetic position could not fully be resolved by 16S rRNA gene analysis, as it appeared external to *Actibacterium* but with low support. *C. lipolyticum* and *C. naphthalenivorans* show phenotypic characteristics similar to those of *Actibacterium* (**Supplementary Table S1**). Therefore, it is proposed to assign *C. lipolyticum* and *C. naphthalenivorans* to *Actibacterium*, which has priority.

Celeribacter (Ivanova et al., 2010; Lee et al., 2012) was shown as paraphyletic in the GBDP tree (**Figure 8**) because *C. manganoxidans* (Wang L. et al., 2015) was placed in a position relatively distant to a clade harboring *Pacificibacter marinus* (Park et al., 2014c) together with core *Celeribacter* including the type species, *C. marinus* (Baek et al., 2014). In the CCT and UCT, *C. manganoxidans* was also placed apart from the other *Celeribacter* species without any obvious phylogenetic affiliation to another genus (**Supplementary File S2**). When *C. manganoxidans* was proposed, its phylogenetic placement was already only poorly supported. Although *C. manganoxidans* and *Celeribacter* do not display consistent phenotypic differences from each other (**Supplementary Table S1**), the phylogenomic results coupled with the lack of phylogenetic evidence to the contrary indicate that a new genus should be proposed to accommodate *C. manganoxidans*.

Celeribacter also appeared as paraphyletic in the CCT because *Vadicella arenosi* (Romanenko et al., 2011c) was placed within this genus with high support. When *Vadicella* was proposed the

only phylogenetic evidence was a 16S rRNA gene tree with low backbone support. In addition at that time only *Celeribacter neptunius* (Ivanova et al., 2010) was considered for comparison in the 16S rRNA gene tree. Taking all other *Celeribacter* species and the phenotype of these species (**Supplementary File S1**) into account, the preferred solution is to include *Vadicella* in *Celeribacter*.

Tropicimonas (Harwati et al., 2009a; Oh et al., 2012) was shown as paraphyletic in GBDP tree (**Figure 8**) because *Pseudoruegeria marinistellae* (Zhang Y. et al., 2017) was placed as sister group of type species of *Tropicimonas*, *T. isoalkanivorans* (Harwati et al., 2009a). In addition, in CCT *Pseudoruegeria aestuarii* was also nested within the *Tropicimonas* clade (**Supplementary File S2**). When *P. marinistellae* was proposed, *T. isoalkanivorans* was not included in the phylogenetic analysis. Furthermore, species such as *P. aestuarii* (Cha et al., 2016), *P. haliotis* (Hyun et al., 2013b), *P. lutimaris* (Jung et al., 2010), and *P. sabulilitoris* (Park et al., 2014a) were also apart from the clade harboring the type species of the genus. However, the lack of a genome sequence for the type species of *Pseudoruegeria*, *P. aquimaris*, currently precludes reclassifications of *Pseudoruegeria* species, particularly because *Pseudoruegeria* has priority over *Tropicimonas*. In the CCT, *Tropicimonas arenosa* (Oh et al., 2016) was placed as sister group of *Oceanicola litoreus* (Park et al., 2013c) but supported with a low bootstrap value (**Supplementary File S2**). Due to the lack the genome sequences of *T. arenosa*, we refrain from taxonomic consequences for this species.

Oceanicola (Cho and Giovannoni, 2004) appeared as polyphyletic in the GBDP tree and CCT (**Figure 8** and **Supplementary File S2**) because *Oceanicola granulosis* (Cho and Giovannoni, 2004) was placed as sister group of *Roseisalinus antarcticus* (Labrenz et al., 2005) with strong support (even in the gene-content analysis) whereas *Oceanicola litoreus* (Park et al., 2013c) was placed in a distinct clade as sister group of *Celeribacter manganoxidans*. While this clade had only moderate support in the GBDP tree, the tree clearly indicated that *O. litoreus* does not form a clade together with *O. granulosis*, which is the type species of the genus. Similarly, *O. litoreus* was placed distantly to *O. granulosis* in the CCT, in that case close to *Tropicimonas arenosa* with low support (**Supplementary File S2**). When *O. litoreus* was proposed, it was placed as sister group of the other *Oceanicola* species with low support in a 16S rRNA gene tree. When *Roseisalinus antarcticus* was originally proposed, the presented tree displayed low support at the backbone, and the sampling did not include *Oceanicola*. The DSMZ nomenclature database indicates that a total of nine *Oceanicola* species had been proposed in the literature all except two were assigned to other genera in later studies. As revealed here it makes sense to taxonomically assign *O. litoreus* to a genus of its own, which is not precluded by its phenotype (**Supplementary Table S1**).

Primorskyibacter (Romanenko et al., 2011b) was shown as non-monophyletic in the GBDP tree (**Figure 9**) because *P. insulae* (Park et al., 2015a) occupied a relatively isolated position, distant from core *Primorskyibacter* including the type species, *P. sedentarius* (Romanenko et al., 2011b); this arrangement was also shown in the CCT (**Supplementary File S1**). When *P. insulae*

was originally proposed (Park et al., 2015a), the analysis of the 16S rRNA gene yielded only low branch support for the monophyly of *Primorskyibacter*. As the sister-group relationship between *P. insulae* and *Marivita* (Hwang et al., 2009a) is not supported in the phylogenomic tree, *P. insulae* should rather be placed in a genus of its own, which is not contradicted by the phenotype (**Supplementary Table 1**).

Salipiger (Martínez-Cánovas et al., 2004) appeared as paraphyletic in GBDP tree (**Figure 9**) because *Yangia pacifica* (Dai et al., 2006) was placed as sister group of *S. marinus* (Wirth and Whitman, 2018) with strong support. The taxonomic history of the genera is characterized by a decrease of support in 16S rRNA gene trees with an increasing number of species. When *Yangia* was proposed, 96% support for a clade comprising *Salipiger* and *Roseivivax* to the exclusion of *Yangia* was obtained. However, when *Citricella marina* was proposed (Lai et al., 2011a), which was later on included in *Salipiger*, 98% support for a sister-group relationship with *C. thiooxidans* was obtained while *Yangia* was shown as sister group of this clade with low support. Because the type species of *Salipiger*, *S. mucosus*, was branching first within the *Salipiger*-*Yangia* clade in the GBDP tree, generating separate genera would imply reclassifying all *Salipiger* species except for the type species. For this reason, it is taxonomically more conservative to include *Yangia* in *Salipiger*, which is supported by the lack of significant phenotypic differences between the two genera (**Supplementary Table S1**), while the gene-content analysis is inconclusive (**Supplementary File S2**). *Paraphaebacter pallidus* (Cai et al., 2017) may also have to be placed in *Salipiger* according to the 16S rRNA gene analyses. But due to low support and since the genome sequence of *P. pallidus* is not yet available, we refrain from taxonomic consequences for this species.

Tropicibacter (Harwati et al., 2009b) formed a paraphyletic group in the GBDP tree and the CCT (**Figure 9** and **Supplementary File S2**) because *T. phthalicus* (Iwaki et al., 2012) formed the sister group of *Pelagimonas* with strong support. When *T. phthalicus* was proposed, the 16S rRNA gene tree showed only poor support for a sister-group relationship between *T. phthalicus* and the type species, *T. naphthalenivorans*. While the gene-content analysis is inconclusive in this respect, assigning *T. phthalicus* to *Pelagimonas* is certainly the taxonomically most conservative solution to solve the discrepancy. This is not precluded by the known major phenotypic features of these taxa, as the only known difference is motility in *T. phthalicus* (**Supplementary Table 1**). The removal of *T. phthalicus* does not cause a need for the emendation of *Tropicibacter* (**Supplementary Table S1**).

Roseovarius (Labrenz et al., 1999) was shown as paraphyletic in the GBDP tree and in the CCT (**Figure 9** and **Supplementary File S2**) because *Pelagicola litorisediminis* (Park et al., 2013a) was nested within *Roseovarius* with a high bootstrap value. When *P. litorisediminis* was proposed, a phylogenetic analysis was presented that was unresolved at the backbone; in particular, the monophyly of *Roseovarius* was not supported at all. *P. litorisediminis* and *Roseovarius* show similar phenotypic characteristics (**Supplementary Table S1**). Consequently, we propose to include *P. litorisediminis* in *Roseovarius*,

which is the taxonomically most conservative solution. The clade obtains some support even in the gene-content analysis (**Supplementary File S2**), and the inclusion of *P. litorisediminis* does not cause a need for the emendation of *Roseovarius* (**Supplementary Table S1**).

Lutimaribacter (Yoon et al., 2009) appeared as non-monophyletic in the GBDP tree (**Figure 9**) because *Lutimaribacter litoralis* (Iwaki et al., 2013) was placed within a strongly supported clade containing *Litorimicrobium taeanense* (Jin et al., 2011) and core *Thalassobius* (Arahal et al., 2005) to the exclusion of the type species of *Lutimaribacter*. The original proposal of *Lutimaribacter litoralis* was accompanied by a 16S rRNA gene analysis with 90% support for a clade comprising *Lutimaribacter* together with *Oceanicola pacificus*. When *Litorimicrobium* was proposed (Jin et al., 2011), the presented tree displayed low support at backbone and the relationships between the genera remained ambiguous. This problem was already evident in the study that proposed *Thalassobius*. Given the phylogenomic results and the lack of evidence to the contrary in the 16S rRNA gene data, it is proposed to include *Lutimaribacter litoralis* and *Litorimicrobium taeanense* in *Thalassobius*, which has priority. Even though the clade obtains no support in the gene-content analysis, this solution is not precluded by the known phenotypic features (**Supplementary Table S1**). The removal of *Lutimaribacter litoralis* does not cause a need for the emendation of *Lutimaribacter* (**Supplementary Table S1**).

Thalassobius (Arahal et al., 2005) was shown as non-monophyletic in the GBDP and 16S rRNA gene trees (**Figure 9** and **Supplementary File S2**) because *T. activus* appeared more closely related to *Cognatishimia* (Wirth and Whitman, 2018) than to the type species, *T. mediterraneus*. When *T. activus* was proposed (Pujalte et al., 2018), it already did not form a clade together with the type species of the genus in a phylogenetic analysis of the 16S rRNA gene. Given their close phylogenetic relationship, which is strongly supported in the GBDP tree albeit unresolved in the gene-content analysis, it is proposed to include *T. activus* in *Cognatishimia*, which is not precluded by the known phenotypic features (**Supplementary Table S1**); among the major phenotypic features, the sole difference appears to be the lack of flagella in *T. activus*. *Thalassobius activus* was placed in *Cognatishimia* (Arahal et al., 2019) while the current study was under revision, hence no further taxonomic proposal needs to be made although it appears advisable to provide an emended description of *Cognatishimia*.

Sulfitobacter (Sorokin, 1995) was shown as a paraphyletic group in the GBDP tree and the CCT (**Figure 9** and **Supplementary File S2**) because *S. pseudonitzschiae* (Hong et al., 2015) was shown to be more closely related to *Ascidiaceihabitans* (Kim et al., 2016b) than to the type species of *Sulfitobacter*, albeit with low support. The original description of *S. pseudonitzschiae* showed a 16S rRNA gene in which *Sulfitobacter* did not appear monophyletic. Two *Roseobacter* species were even shown as more closely related as *S. pseudonitzschiae* to the type species of *Sulfitobacter*, *S. pontiacus*, with strong support, whereas *Ascidiaceihabitans* could not be considered. The original description of *Ascidiaceihabitans* in turn did not consider *S. pseudonitzschiae*. The CCT indicated *Pseudoseohaecicola* (Park

et al., 2015b) as sister group of *S. pseudonitzschiae* to the exclusion of *Ascidiaceihabitans* but since the support was only moderate we here refrain from taxonomic proposals for *Pseudoseohaecicola*. The issue should be revisited once the genome of the type strain of *Pseudoseohaecicola caenipelagi* becomes available. Similarly, as *Ascidiaceihabitans* has priority over *Pseudoseohaecicola*, it would be safe to place *S. pseudonitzschiae* in *Ascidiaceihabitans*, but resolution is low even in the GBDP tree.

Pseudoceanicola (Lai et al., 2015) formed a polyphyletic group in the GBDP tree (**Figure 9**) as *P. lipolyticus* (Huang et al., 2018) appeared as the sister taxon of *Ruegeria kandeliae* (Zhang L. et al., 2018) with strong support. *R. kandeliae* was in turn phylogenetically located apart from core *Ruegeria*. The CCT showed the same relationships while the UCT was unresolved (**Supplementary File S2**). Given their relatively isolated position in the genome-based phylogeny, we would propose to transfer *P. lipolyticus* and *R. kandeliae* to a single new genus, which is not contradicted by their phenotype (**Supplementary Table S1**). While not supported by the gene-content analysis (**Supplementary File S2**), this solution is certainly more conservative than assigning them to two distinct genera. The removal of *R. kandeliae* does not cause a need for the emendation of *Ruegeria* (Uchino et al., 1998; Martens et al., 2006; Yi et al., 2007). In the case of *P. lipolyticus*, however, we observed a significant discrepancy between the 16S rRNA gene tree and the GBDP tree (**Supplementary File S2**). While the remainder of the used GenBank genome sequence did not show signs of contamination, the rRNA genes, which covered almost the complete contig NZ_PGTB01000197, yielded a distinct phylogenetic location. For this reason, we cannot rule out that the protein-coding genes of the genome sequence do not, in contrast to the 16S rRNA gene, originate from *P. lipolyticus*. Hence, we only propose a new genus for *Ruegeria kandeliae*.

Epibacterium (Penesyan et al., 2013) was shown as a paraphyletic group in the GBDP tree and the CCT (**Figure 9** and **Supplementary File S2**) because all *Epibacterium* species except for the type species, *E. ulvae*, formed a strongly supported clade together with *Tritonibacter* (Klotz et al., 2018) and *Ruegeria pelagia* (Lee et al., 2007c). *R. pelagia* in turn appeared only distantly related to the type species of *Ruegeria*, *R. atlantica*. The taxonomically most conservative solution to this discrepancy between phylogeny and classification is to assign all deviating *Epibacterium* species – including *E. scottomollicae* (Vandecandelaere et al., 2008a; Wirth and Whitman, 2018) – to *Tritonibacter*, which is not precluded by their major phenotypic features (**Supplementary Table S1**) even though the gene-content analysis is inconclusive (**Supplementary File S2**). The inclusion of *E. scottomollicae* does not cause a need for the emendation of *Tritonibacter* (**Supplementary Table S1**).

Agrobacterium (Conn, 1942; Sawada et al., 1993) appeared as polyphyletic in the GBDP and 16S rRNA gene trees (**Figure 9** and **Supplementary File S2**) because *Agrobacterium meteori* (Rüger and Höfle, 1992) was placed as a sister group of *Ruegeria atlantica* (Rüger and Höfle, 1992; Uchino et al., 1998; Muramatsu et al., 2007; Yi et al., 2007; Vandecandelaere et al., 2008a) with high support. *A. meteori* was originally proposed on basis of phenotypic characteristics without taking into account the 16S

rRNA gene sequence as phylogenetic marker. The phenotype of *A. meteori* is quite similar to the one of *Ruegeria atlantica* (Supplementary Table S1), and according to an earlier study (Uchino et al., 1998) *A. meteori* is a later heterotypic synonym of *R. atlantica* (= *Agrobacterium atlanticum*). However, the dDDH value between their genome sequences was lower than the species boundary of 70% (Table 1). Accordingly, it is proposed to include *A. meteori* in *Ruegeria* as *R. meteori*. The removal of *A. meteori* does not cause a need for the emendation of *Agrobacterium* (Supplementary Table S1) and the inclusion of *A. meteori* does not cause a need for the emendation of *Ruegeria* (Uchino et al., 1998; Martens et al., 2006; Yi et al., 2007).

Aminobacter (Urakami et al., 1992; Kämpfer et al., 2002a) appeared as paraphyletic in the CCT (Supplementary File S2) because the monotypic genus *Carbophilus* (Meyer et al., 1993) was nested within *Aminobacter* with strong support. When *Carbophilus* was originally proposed *Aminobacter* was not taken into account. As the two share most phenotypic characteristics and mostly differ regarding their minor fatty acids (Supplementary Table S1) we propose to transfer *Carbophilus* to *Aminobacter*, which has priority; this is also the taxonomically most conservative solution.

Sphingomonadales Families

Sphingomonadales appeared to be a monophyletic order of *Alphaproteobacteria* in our analyses (Figure 6), which is in agreement with the presence of sphingolipids (Supplementary Table S1 and Supplementary File S2), a likely apomorphy of the group. The arrangement of the order into families seemed to be in need of a revision, however.

Within *Sphingomonadales*, *Sphingomonadaceae* (Kosako et al., 2000) appeared paraphyletic in the GBDP tree (Figure 6) because the clade comprising *Sandarakinorhabdus cyanobacteriorum* (Cai et al., 2018a), *S. limnophila* (Gich and Overmann, 2006; Kim M.C. et al., 2016), *Sphingosinicella microcystinivorans* (Maruyama et al., 2006; Geueke et al., 2007) and *Pacificimonas flava* (Liu K. et al., 2014), which appeared as sister group of the remaining taxa. These genera should better be placed in a separate family, which is supported by high overall genomic divergence within *Sphingomonadales* (Figure 6 and Supplementary File S2). The gene-content analysis did not resolve the backbone of the *Sphingomonadales* tree but did not yield significant conflict either. In published 16S rRNA gene trees *Sphingosinicella* was placed with only low support in *Sphingomonadaceae* (Maruyama et al., 2006). The original descriptions of *Sandarakinorhabdus* (Gich and Overmann, 2006) and *Pacificimonas* (Liu K. et al., 2014) were also accompanied by 16S rRNA gene trees with low support. In the CCT the additional genera *Polymorphobacter* (Fukuda et al., 2014), *Sandaracinobacter* (Yurkov et al., 2017) and *Sphingoaurantiacus* (Kim M.C. et al., 2016) appeared intermixed with the genera represented by genome sequences in the same clade and thus should tentatively also be assigned to the new family. The establishment of a new family for these genera is not in conflict with their phenotype (Supplementary Table S1).

The second conflict within *Sphingomonadales* was due to the fact that *Erythrobacteraceae* (Lee et al., 2005; Xu X.-W. et al., 2009) was nested within *Sphingomonadaceae* with high support

in the GBDP tree (Figure 6 and Supplementary File S2). In particular, *Novosphingobium* (Takeuchi et al., 2001) appeared intermixed with *Erythrobacteraceae*. *Sphingomonadaceae* originally encompassed the genera currently placed in *Erythrobacteraceae* such as *Erythrobacter* and *Porphyrobacter* (Kosako et al., 2000) before *Erythrobacteraceae* were proposed (Lee et al., 2005) on the basis of the analysis of 16S rRNA gene and chemotaxonomic data. The high branch support obtained in that study for the monophyly of both *Erythrobacteraceae* and *Sphingomonadaceae sensu stricto* could not be confirmed by our analyses, which are based on a much larger taxon sampling (Supplementary File S2). The presence of pigments (including bacteriochlorophyll α) in *Erythrobacteraceae* which are absent in genera such as *Sphingomonas* was also used as argument for the separation of the two families (Lee et al., 2005). However, a single character with two character states cannot properly be used to separate two taxa because this character would yield an apomorphy for at most one of the two taxa (Nouioui et al., 2018). The sizeable overall genomic divergence within *Sphingomonadales* (Figure 6 and Supplementary File S2) argues against placing all of its genera into a single family. For this reason, we propose to include *Novosphingobium* in *Erythrobacteraceae*. Considering that only apomorphies can be used to justify a taxon (Hennig, 1965; Wiley and Lieberman, 2011), this proposal did not appear to be in conflict with the phenotype of the involved taxa (Supplementary Table S1).

Additionally the positioning of a clade comprised of *Zymomonas mobilis* (Kluyver and van Niel, 1936) including *Zymomonas mobilis* subsp. *pomaceae* (De Ley and Swings, 1976; Coton et al., 2006) caused conflict regarding *Sphingomonadaceae* in the GBDP tree (Figure 6). *Zymomonas* (Kluyver and van Niel, 1936) also formed a branch isolated from the remaining *Sphingomonadaceae* in the CCT (Supplementary File S2). While the resolution of the backbone within *Sphingomonadales* was partially low in the GBDP tree, an additional supermatrix analysis (Supplementary File S2) confirmed the placement of *Zymomonas* apart from the type species of the family, *Sphingomonas*. In contrast to most *Sphingomonadaceae*, *Zymomonas* was described as facultatively anaerobic (Supplementary File S2). While this deviation, much like the lower G+C content and genome size, is probably an autapomorphy of *Zymomonas*, there is no obvious phenotypic argument for placing the genus within *Sphingomonadaceae* as previously suggested (Kosako et al., 2000). Therefore we propose to transfer *Zymomonas* to a family of its own.

Sphingomonadales Genera

Within *Sphingomonadales*, *Novosphingobium* (Takeuchi et al., 2001) appeared as non-monophyletic in the GBDP tree (Figure 6) as well as in the CCT (Supplementary File S2) because *N. tardaugens* (Fujii et al., 2003) was placed in a relatively isolated position with respect to core *Novosphingobium*, more closely related to *Altererythrobacter*, *Erythrobacter*, and *Porphyrobacter*. When *N. tardaugens* was proposed the reduced taxon sampling in the presented 16S rRNA gene tree did not allow for an assessment of the monophyly of the genus. Given the overall genomic divergence of *Erythrobacteraceae* (Lee

et al., 2005; Xu X.-W. et al., 2009), into which we propose to assign *Novosphingobium* as explained above, solving the non-monophyly of the major genera of the family by merging these genera does not seem taxonomically advisable. For this reason, we suggest a new genus to accommodate *N. tardaugens*, which is not contradicted by its phenotype (**Supplementary Table S1**). *N. tardaugens* also displayed a genome size more in accordance with the one found in other genera of *Erythrobacteraceae* than with the larger genomes of core *Novosphingobium*.

Erythrobacter (Shiba and Smidu, 1982; Subhash et al., 2013) was shown as non-monophyletic in the GBDP tree (**Figure 6**) because species such as *E. gangjinensis* (Lee et al., 2010), *E. luteus* (Lei et al., 2015), *E. atlanticus* (Zhuang et al., 2015), *E. marinus* (Jung et al., 2012b), *E. seohaensis* (Yoon et al., 2005b) and *E. nanhaisediminis* (Xu et al., 2010) were placed apart from the type species of *Erythrobacter*, *E. longus* (Shiba and Smidu, 1982) causing *Altererythrobacter* (Kwon et al., 2007; Xue et al., 2012, 2016) to appear intermixed with *Erythrobacter*. Moreover, *E. longus* was placed more closely to *Porphyrobacter* (Fuerst et al., 1993; Coil et al., 2015) than to the majority of the *Erythrobacter* species. *Porphyrobacter* appeared as polyphyletic in the GBDP tree (**Figure 6**) because *P. mercurialis* (Coil et al., 2015) was placed apart from the remaining *Porphyrobacter* species. Additionally, the single representative of *Qipengyuania*, *Q. sediminis* (Feng et al., 2015), was nested in the CCT within *Altererythrobacter* but with low support as in the original publication. *Blastomonas marina* (Meng et al., 2017) also was nested in the CCT within *Altererythrobacter*. These taxonomic problems were already observed by other authors as *Erythrobacter*, *Altererythrobacter*, and *Porphyrobacter* appeared intermixed in 16S rRNA gene phylogenies (Coil et al., 2015). Thus, we are well aware of the fact that after this modification *Altererythrobacter*, *Erythrobacter* and *Porphyrobacter* would still be intermixed (**Figure 6**) but given the low support in the 16S rRNA gene analyses (**Supplementary File S2**) the taxonomy of the family should be revisited once more type-strain genome sequences are available. For instance, the genome sequence of the type strain of the type species of *Altererythrobacter*, *A. epoxidivorans* (Kwon et al., 2007), was not yet available at the time of writing. We thus refrain from proposing taxonomic changes for these three genera.

Sphingosinicella (Maruyama et al., 2006; Geueke et al., 2007; Yasir et al., 2010) was shown as polyphyletic in the GBDP tree and in the CCT (**Figure 6** and **Supplementary File S2**) because *S. vermicomposti* (Yasir et al., 2010) was placed as sister group of *Sphingomonas indica* (Niharika et al., 2012) supported by a high bootstrap value. When *S. vermicomposti* was proposed, 98% support was obtained for the monophyly of *Sphingosinicella* in a 16S rRNA gene analysis based on the neighbor-joining algorithm and a simplistic evolutionary model. We could not reproduce this finding here based on our ML and MP analyses with a much larger taxon sampling (**Supplementary File S2**), as even the unconstrained analyses placed *S. vermicomposti* in a position quite distinct from core *Sphingosinicella*. The proposal of *Sphingomonas indica* was accompanied by a 16S rRNA gene tree that did not

resolved the monophyly of *Sphingomonas* (Yabuuchi et al., 1990, 1999, 2001; Takeuchi et al., 1993, 2001; Busse et al., 2003; Chen et al., 2012). Given the overall genomic divergence of *Sphingomonadaceae*, solving the non-monophyly of the major genera of the family by merging these genera does not seem taxonomically advisable. Our phylogenetic analyses thus suggested that *S. vermicomposti* and *Sphingomonas indica* are best assigned to an independent genus. The two species also display similar phenotypic characteristics (**Supplementary Table S1**) even though the gene-content analysis did not provide support (**Supplementary File S2**). The removal of *Sphingomonas indica* does not cause a need for the emendation of *Sphingomonas* (**Supplementary Table S1**).

Sphingopyxis (Takeuchi et al., 2001; Baik et al., 2013) appeared as paraphyletic in the GBDP tree and in and in the CCT (**Figure 6** and **Supplementary File S2**) because *Sphingopyxis baekryungensis* (Yoon et al., 2005a) was placed not within core *Sphingopyxis* but in a clade together with *Blastomonas* (Sly and Cahill, 1997) and two species of *Sphingorhabdus* (Jogler et al., 2013; Yang et al., 2017) with high support. Since these two *Sphingorhabdus* species were placed apart from the type species of the genus in the 16S rRNA gene analyses and because of the unclear assignment of *S. baekryungensis* to either *Blastomonas* or *Sphingorhabdus* we propose to place *S. baekryungensis* into a genus of its own, which is not precluded by its phenotype (**Supplementary Table S1**). When *S. baekryungensis* was originally proposed (Yoon et al., 2005a) a phylogenetic analysis with low taxon sampling was presented which lacked any support for the monophyly of *Sphingopyxis*; other evidence for the monophyly of the genus was not detected either. Taxonomic consequences for *Sphingorhabdus* cannot currently be drawn because of the lack of a genome sequence for the type strain of its type species, *S. planktonica*, and the lack of resolution in even the constrained 16S rRNA gene analyses.

We are aware of the fact that after this modification *Sphingomonas* still remained non-monophyletic because genera such as *Hephaestia* (Felföldi et al., 2014), *Rhizorhabdus* (Francis et al., 2014), and *Stakelama* (Chen C. et al., 2010) were nested within its range (**Figure 6**). Given the overall genomic divergence of the group, solving the non-monophyly by including these genera in *Sphingomonas* does not seem taxonomically advisable. When *Rhizorhabdus* was proposed, a couple of *Sphingomonas* species already appeared more closely related to it than to the type species of *Sphingomonas*, *S. paucimobilis* (Yabuuchi et al., 1990), but they were not included in the new genus. The type species of *Rhizorhabdus*, *R. argentea*, formed in the CCT and UCT a well-supported clade together with *R. dicambivorans* (Yao et al., 2016), *S. histidinilytica* (Nigam et al., 2010), *S. starnbergensis* (Chen H. et al., 2013) and *S. wittichii* (Yabuuchi et al., 2001; Kim M.C. et al., 2016). It thus makes sense to include these *Sphingomonas* species in *Rhizorhabdus*, which is not precluded by their phenotype (**Supplementary Table S1**). Given the otherwise low support in the 16S rRNA gene analyses (**Supplementary File S2**) we cannot propose analogous taxonomic consequences for *Hephaestia* and *Stakelama*. The taxonomy of *Sphingomonas* should be revisited once more type-strain genome sequences are available. The removal of *S. histidinilytica*, *S. starnbergensis*

and *S. wittichii* does not cause a need for the emendation of *Sphingomonas* (Supplementary Table S1).

Kordiimonadales and Caulobacterales Families

Only few discrepancies between taxonomic classification and phylogeny were observed in these relative small orders.

When *Kordiimonas* and with it the order *Kordiimonadales* was proposed (Kwon et al., 2005) no family to accommodate *Kordiimonas* was given. *Kordiimonadaceae* was later proposed (Xu et al., 2014) but has not been validly published yet. *Kordiimonas* formed a strongly supported clade together with *Eilatimonas* (Paramasivam et al., 2013) in the GBDP tree (Figure 8) and in the CCT (Supplementary File S2). When *Eilatimonas* was proposed, the genus already was shown in a 16S rRNA gene analysis as the sister group of *Kordiimonas* with strong support. Furthermore, *Temperatibacter* (Teramoto and Nishijima, 2014) of *Temperatibacteraceae* appeared as nested within *Kordiimonadaceae* in the CCT (Supplementary File S2), wherein the three genera formed a clade with strong support. The taxonomically most conservative solution is to include all these genera in an emended family *Temperatibacteraceae*, which is not precluded by their respective phenotypes (Supplementary Table S1).

Within *Caulobacterales*, *Hyphomonadaceae* (Lee et al., 2007d) appeared as paraphyletic in the GBDP tree because a clade comprising *Robiginitomaculum* to *Maricaulis* branched first, rendering core *Hyphomonadaceae* the sister group of *Caulobacteraceae* (Figure 8 and Supplementary File S2). However, support against the monophyly of *Hyphomonadaceae* was low. In the CCT an according clade was apparent that was composed of the genera *Algimonas* (Fukui et al., 2013), *Fretibacter* (Cho et al., 2013), *Glycocaulis* (Abraham et al., 2013; Lv et al., 2014), *Hellea* (Alain et al., 2008), *Hyphobacterium* (Sun et al., 2017), *Litorimonas* (Jung et al., 2011), *Maricaulis* (Abraham et al., 1999), *Marinicauda* (Zhang et al., 2013), *Oceanicaulis* (Strömpl et al., 2003), *Robiginitomaculum* (Lee et al., 2007d), and *Woodsholea* (Abraham et al., 2004), but this clade formed the sister group of core *Hyphomonadaceae* with moderate support. For this reason, we refrain from re-classifying these eleven genera into a separate family, which is not precluded by their phenotype (Supplementary Table S1).

Species and Subspecies

Values of dDDH similarity (Meier-Kolthoff et al., 2013a; Meier-Kolthoff and Göker, 2019) found to be higher or lower than expected given the current species and subspecies thresholds of 70% (Wayne et al., 1987) and 79%, respectively (Meier-Kolthoff et al., 2014b), as well as known and confirmed heterotypic synonyms, are shown in Table 1 for pairs of closely related strains. Multiple species and subspecies displayed a value above the 79% threshold, hence it is proposed that the according taxa be recognised as heterotypic synonyms at the subspecies level (see Table 1 for proposed synonyms). Conversely, some subspecies were shown to merit species status (Tindall, 2019b), specifically *Acetobacter pasteurianus*

subsp. *ascendens* (De Ley and Frateur, 1974) and *Acetobacter pasteurianus* subsp. *paradoxus* (De Ley and Frateur, 1974). The name *Acetobacter ascendens* was already proposed (Kim et al., 2018) but the name does not appear to be validly published.

Brevirhabdus pacifica (Wu et al., 2015) was shown as paraphyletic in the phylogenomic analysis (Figure 7) because *Xuhuaishuia manganoxidans* (Wang L. et al., 2016) was nested within the two genome-sequenced type-strain deposits of the species. The dDDH analysis confirmed this result, as *X. manganoxidans* appeared as a later heterotypic synonym of *B. pacifica*. As the genus *Brevirhabdus* was not considered in the study where *X. manganoxidans* was proposed, the phylogenetic relationship of those taxa could not be elucidated back then.

Mameliella (Zheng et al., 2010; Chen Z. et al., 2015) appeared as paraphyletic in the GBDP and in the 16S trees (Figure 9 and Supplementary File S2) because *Alkalimicrobium pacificum* (Zhang D.-C. et al., 2015) and *Ponticoccus lacteus* (Yang Y. et al., 2015) were nested within *Mameliella*. When *A. pacificum* was proposed, it appeared as sister group of *Mameliella alba* (Zheng et al., 2010). When *P. lacteus* was proposed, the genus *Mameliella* was not considered in the study, and hence their phylogenetic relationship could not be elucidated. According to a recent study (Liu et al., 2018), *A. pacificum* and *P. lacteus* are later heterotypic synonyms of *Mameliella alba*, as is *Mameliella atlantica* (Xu et al., 2015). This was confirmed by the here calculated dDDH values (Table 1).

Some dDDH values between pairs of species were found to be higher than 70%, the currently accepted threshold to differentiate among species (Wayne et al., 1987) and lower than 79%, the threshold defined to differentiate among subspecies (Meier-Kolthoff et al., 2014b). Based on the dDDH values we here concluded that *Rickettsia japonica* (Uchida et al., 1992) is best assigned to a subspecies of *Rickettsia conorii* (Brumpt, 1932). However, the type strain of *Rickettsia japonica* is only deposited in a single culture collection, which prevents us from proposing an according new combination. In addition, we propose that *Borrelia bavariensis* (Margos et al., 2013), *Gluconobacter nephelii* (Kommanee et al., 2011), *Methylobacterium chloromethanicum* (McDonald et al., 2001), *Methylorubrum extorquens* (Urakami and Komagata, 1984; Green and Ardley, 2018), *Pseudorhizobium pelagicum* (Kimes et al., 2015), *Rhizobium loessense* (Wei et al., 2003), *Rickettsia gravesii*, *Rickettsia heilongjiangensis*, *Rickettsia raoultii* (Mediannikov et al., 2008) *Rickettsia buchneri* (Kurtti et al., 2015), and *Ruegeria pelagia* (Lee et al., 2007c) be classified as *Borrelia garinii* subsp. *bavariensis*, subsp. nov., *Gluconobacter japonicus* subsp. *nephelii*, subsp. nov., *Methylobacterium dichloromethanicum* subsp. *chloromethanicum*, subsp. nov., *Methylobacterium dichloromethanicum* subsp. *extorquens*, subsp. nov., *Rhizobium marinum* subsp. *pelagicum*, subsp. nov., *Rhizobium mongolense* subsp. *loessense*, subsp. nov., *Rickettsia conorii* subsp. *gravesii*, subsp. nov., *Rickettsia conorii* subsp. *heilongjiangensis*, subsp. nov., *Rickettsia conorii* subsp. *raoultii*, subsp. nov., *Rickettsia tamurae* subsp. *buchneri*, subsp. nov., and *Tritonibacter mobilis* subsp. *pelagijs*, subsp. nov., respectively (Table 1).

Finally, in the present study, all of the pairs of strains considered to represent distinct deposits of the same type strain

were found to have dDDH similarities of 99.0% or above with the exception of *Celeribacter indicus* (Lai et al., 2014) strain MCCC 1A01112 and DSM 27257 (87.8%), *Celeribacter marinus* (Baek et al., 2014) strain IMCC12053 and DSM 100036 (94.8%), *Gluconacetobacter diazotrophicus* (Yamada et al., 1997) strain PAI 5 and DSM 5601 (92.1%), *Thalassobius mediterraneus* (Arahal et al., 2005) strain CECT 5383 and DSM 16398 (98.3%), *Thalassospira xiamenensis* (Liu et al., 2007) strain M-5 and DSM 17429 (94.7%), results which may account for the separation of each pair of these strains.

Phylogenetic Conservation of Genomic and Phenotypic Markers of Interest

Table 2 shows the *p*-values obtained by the tip-permutation test and the retention values of selected phenotypic and genomic features. All investigated characters showed a significant phylogenetic conservation ($\alpha = 0.001$) but the fit of each character to the tree varied considerably, as indicated by the retention index. A relatively high correspondence between G+C content and phylogeny and genome size and phylogeny was observed. Genome size varied between 0.85 Mbp in *Neorickettsia sennetsu* and 9.79 Mbp in *Bradyrhizobium arachidis* while G+C content varied between 26.86% in *Brachyspira alvinipulli* and 73.38% in *Rubritepida flocculans*. Morphology showed a significant but relatively low conservation but motility by flagella appeared certainly more conserved than cell length and particularly cell width.

Presence or absence of flagella also showed a better fit to the tree than the relationship to oxygen and the investigated chemotaxonomic features. Among these, presence or absence of carotenoids showed the highest conservation, followed by average number of isoprene residues in major ubiquinones and, finally, presence or absence of bacteriochlorophyll α . Particularly the chemotaxonomic features showed a low coverage in the taxon descriptions from the literature. The screening of the literature indicated that this may at least partially be due to the reluctance of researchers to report negative results. It is reasonable to assume that a perceived absence of bacteriochlorophyll α , carotenoids, or sphingolipids is not necessarily reported as such but simply omitted. In the case of sphingolipids the lack of reports for them outside *Sphingomonadales* even prevented the calculation of the metrics presented in **Table 2**. The less cautious coding that treated all missing values as indicating absence (**Supplementary Table S1**) yielded a high retention index for sphingolipids (0.739) whereas the retention indices of the other binary characters dropped compared to the values depicted in **Table 2**.

The gene-content analysis, specific aspects of which have already been discussed above, was largely in agreement with the GBDP tree even though certain parts of the trees were, predictably, in conflict (**Supplementary File S2**). For instance, using a branch-support threshold of 95% to indicate strong support or conflict, among the branches strongly supported by the GBDP analysis 40.6% were also strongly supported by the gene-content analysis, 6.7% were strongly contradicted and 52.7% of the cases the gene-content analysis remained neutral (**Supplementary Table S1**). Compared to the average

branch support of the GBDP analysis of 92.1%, the gene-content analysis yielded 68.0% average support by itself and on average 45.2% support for the branches in the GBDP tree (**Supplementary File S2**).

DISCUSSION

Causes of Conflict Between Phylogenomic Analyses and Taxonomic Classification

Most of the *Alphaproteobacteria* taxa already appeared monophyletic in this study eliminating need for a taxonomic revision. This partially reflects the work previously done by other authors where they proposed taxonomic changes within *Alphaproteobacteria* based on at least multi-gene if not phylogenomic datasets as, e.g., in the case of revisions of genera of *Rhodobacteraceae* (Breider et al., 2014; Wirth and Whitman, 2018). Much of the remaining discrepancies can be traced back to the way the 16S rRNA gene was interpreted in the taxonomic literature, which is discussed here while the interpretation of phenotypic features is treated in the next section.

In the case of some *Alphaproteobacteria* taxa such as *Mycoplana* (Urakami et al., 1990) and *Agrobacterium meteori* (Rüger and Höfle, 1992) the discrepancies between their classification and the modern methods was caused by the fact that they were described prior to the availability of 16S rRNA gene sequencing. In these low number of cases, the taxonomic conclusions that could be drawn with the 16S rRNA gene and those indicated by phylogenomic trees were essentially the same.

While in few cases, such as the original descriptions of *Angulomicrobium* and *Meganema*, branch support was not even calculated, most of the taxonomic discrepancies observed within the *Alphaproteobacteria* appeared to be caused by low resolution of the 16S rRNA genes used to propose the respective taxa. This held for genera such as *Alkalispirochaeta*, *Allorhizobium*, *Altererythrobacter*, *Celeribacter*, *Citricella*, *Erythrobacter*, *Lutimaribacter*, *Mesorhizobium*, *Neorhizobium*, *Novosphingobium*, *Ochrobactrum*, *Porphyrbacter*, *Rhizobium*, *Roseomonas*, *Sphingomonas*, *Sphingopyxis*, *Thalassobius*, and *Tropicimonas*, as well as the families *Hyphomicrobiaceae*, *Phyllobacteriaceae*, *Rhodobiaceae*, *Rhodospirillaceae*, and *Sphingomonadaceae*. Appropriately calculating branch support is a necessary but not a sufficient prerequisite for safely generating monophyletic taxa. When drawing taxonomic conclusions from some phylogenetic tree, taxa must also be chosen so as to correspond to highly supported clades (Vences et al., 2013). Such clades are not always present in 16S rRNA genes although all species must be assigned to a genus in the Linnaean system.

The second most important cause of non-monophyly in the class *Alphaproteobacteria* detected in the current study was incomplete taxon sampling. Actually non-monophyletic taxa may easily appear monophyletic when species or strains of relevance, in particular type strains of type species of genera or even type genera of families or orders, are omitted from phylogenetic analysis. Incomplete

taxon sampling affected the taxonomic assignment to families in the case of *Acuticoccus*, *Aquamicrobium*, *Breoghania*, *Cucumibacter*, *Devosia*, *Magnetovibrio*, *Maritalea*, *Marivibrio*, *Pelagibacterium*, *Reyranella*, *Tagaea*, *Terasakiella*, *Thalassospira*, and *Varunaivibrio*. Insufficient sampling also affected the assignment of species to genera at least in the case of *Novosphingobium tardaugens* and *Sphingopyxis baekryungensis*.

We found no evidence for a real conflict between the 16S rRNA gene and entire genomes in this study. In previous analyses (Hahnke et al., 2016; Nouioui et al., 2018) such conflicts already appeared to be rare compared to the overall number of taxa investigated and compared to the more common causes of taxonomic conflicts, which were the same as the ones listed above. Analyzing comprehensive sets of 16S rRNA gene sequences appears to be necessary unless a genome sequence is available for all type strains, particularly because taxonomic problems caused by insufficient taxon sampling seem to be quite common. The use of a backbone constraint can integrate information from analyses of more genes from few organisms into comprehensible sampled single-gene data (Liu X.-Z. et al., 2015; Hahnke et al., 2016; Nouioui et al., 2018). For example, the CCT was necessary to safely place type species that still lack a genome sequence and to detect instances where taxonomic conclusions would have been premature.

In previous studies (Hahnke et al., 2016; Nouioui et al., 2018) the taxonomic conclusions drawn from the GBDP tree were confirmed by corresponding supermatrix analyses in all of the cases investigated. In the present study it was also assessed whether conflict was evident between trees inferred from distinct data sets and, if so, to conduct analyses with alternative methods. We could not detect such conflict in *Alphaproteobacteria*, however, and accordingly restricted supermatrix analyses to cases in which the GBDP tree was insufficiently resolved for clarifying specific taxonomic questions. In these situations, conflict between the GBDP tree and the supermatrix analyses was not detected either. Our approach thus appeared to be as robust for *Alphaproteobacteria* as in previous studies on other phyla (Hahnke et al., 2016; Nouioui et al., 2018). Whole-genome methods, such as GBDP, yield truly genome-based phylogenies instead of approaches that use only a limited number of genes, which also rely on assumptions about the relative suitability of the selected genes compared to other genes (Lienau and DeSalle, 2009; Klenk and Göker, 2010). Distance methods for tree reconstruction still represent the most promising approach for accurately building phylogenies with a huge number of tips (Desper and Gascuel, 2004, 2006; Lefort et al., 2015). In an approach using GBDP in conjunction with FastME the time-consuming step is the calculation of the intergenomic distances, which can be done incrementally since the pairwise distances can be calculated independently of each other.

While the use of genome-scale data often yields more strongly resolved trees, it may also increase incongruities between distinct analyses (Jeffroy et al., 2006; Klenk and Göker, 2010). In this context overestimating phylogenetic confidence from genome-scale data must be avoided (Taylor and Piel, 2004). A reduction of the supposed incongruities between phylogenies and thereby more realistic support values for phylogenomic analyses can

be obtained by bootstrapping entire genes instead of single alignment positions (Falush et al., 2006; Siddall, 2010; Hahnke et al., 2016; Simon et al., 2017). GBDP pseudo-bootstrapping in conjunction with the greedy-with-trimming algorithm (Meier-Kolthoff et al., 2014a; Meier-Kolthoff and Göker, 2019) is akin to such a “partition bootstrap.” The concept of hierarchical classification itself has been called into question based on topological incongruities between analyses of single genes that were attributed to horizontal gene transfer (Bapteste and Boucher, 2009; Klenk and Göker, 2010). However, the addition of more genes (Breider et al., 2014), up to virtually all available ones, as in the present study, yields strong support even when based on a careful approach to statistical resampling. This observation indicates a strong hierarchical signal and thus no reason to abandon the hierarchical system of taxonomic classification.

Agreement and Conflict of Taxonomic Markers With Genome-Scale Phylogeny

Phylogenetic conservation of investigated phenotypic markers was detectable but varied and was on average not particularly pronounced (Table 2). This outcome is in overall agreement with an earlier study (Barberán et al., 2017) which compared a 16S rRNA gene tree to selected phenotypic features collected from recent taxonomic descriptions published in the *International Journal of Systematic and Evolutionary Microbiology* across phyla. While it comes as no surprise that cell shape is less conserved than presence or absence of flagella (Barberán et al., 2017), the relative performance of certain character deserves further discussion. Two distinct kinds of causes for the discrepancies between the phylogenomic trees and the traditional classification, which was at least partially based on phenotypic characters, are possible. The taxonomic interpretation of these characters could be insufficient (Montero-Calasanz et al., 2017; Nouioui et al., 2018), and the characters themselves could conflict with the phylogenomic trees. For distinguishing between these two options, the characters need to be examined as they were used in the taxonomic literature. For a historical assessment such as ours it makes no sense to analyze new, modified characters derived from the earlier ones. While it may be of interest in other respects to take the genetic background into account to form new characters, these new characters were not used for establishing the traditional classification in the first place.

Characters such as flagellum production or capability for photosynthesis are based on multiple genes usually arranged in gene clusters (Frank et al., 2015; Brinkmann et al., 2018) and thus can be assumed to be rather complex characters. According to Dollo's law, complex features arise only once but can be lost several times in evolution (Le Quesne, 1974; Farris, 1977). Accordingly, a group of organisms which display a complex feature are expected to be monophyletic or paraphyletic in a tree, but not polyphyletic (Nouioui et al., 2018). The failure to properly distinguish between plesiomorphic (ancestral) character states, which indicate paraphyletic groups, and apomorphic (derived) character states, which indicate monophyletic groups (Hennig, 1965; Wiley and Lieberman, 2011), may account for some of the discrepancies between the current taxonomic

classification and genome-scale trees (Montero-Calasanz et al., 2017; Nouioui et al., 2018). Homoplasy in the investigated characters most likely plays a role in other cases, and evolution according to Dollo's law alone could cause homoplasy in a complex character. In the case of the photosynthesis in *Alphaproteobacteria*, however, it was shown that horizontal transfer of single genes as well as of entire photosynthesis operons occurred in addition to frequent losses of the capability for photosynthesis (Brinkmann et al., 2018). Such vertical transfer of complex characters may not only be facilitated by the arrangement of the according genes in gene clusters but also by the location of these gene clusters on extrachromosomal elements. This holds not only for the photosynthesis operon (Brinkmann et al., 2018) but also for the flagellum gene cluster (Frank et al., 2015). Losses and horizontal transfer can both contribute to the low phylogenetic conservation of phenotypic features, which in turn can contribute to discrepancies between the taxonomic classification and the phylogeny. It should not be overlooked, however, that certain phenotypic features can have an excellent fit to the phylogeny, as most likely in the case of the production of sphingolipids in *Alphaproteobacteria* (**Supplementary File S2**).

As for genomic features, bacterial G+C content and bacterial genome size appeared to be strongly phylogenetically conserved in *Alphaproteobacteria* (**Supplementary File S2** and **Table 2**). For this reason, genome sizes have been added to the description of the reclassified and emended species as shown below. A significant correlation between genome size and G+C content was found in previous studies (Almpanis et al., 2018; Nouioui et al., 2018), which is not unexpected because symbiotic bacteria tend to have smaller genomes and to be richer in A+T content (Rocha and Danchin, 2002; Mann and Chen, 2010), an effect that may even impact the amino-acid content (Cole et al., 1998). Conversely, positive selection (Hildebrand et al., 2010) and G+C-biased gene conversion (Lassalle et al., 2015) can increase the G+C content. Although exceptions from the rule that reduced genomes have a low G+C content are known (McCutcheon et al., 2009), the rule was confirmed in the present study, particularly regarding genome size and G+C content reduction in pathogens such as *Bartonella*, *Borrelia* and *Rickettsiales* (**Supplementary File S2**). Because of this correlation caused by adaptive processes, genome size could thus be regarded as non-independent of G+C content, which would cast some doubt on its use as a taxonomic marker. Yet as shown previously (Nouioui et al., 2018) the overall correlation between G+C content and genome size is considerably reduced in strength after accounting for the impact of the phylogeny. This correlation may even only be due to G+C reduction effects in symbiotic bacteria with dramatically reduced genome sizes. The apparently non-random distribution with respect to the phylogeny of such reductions in *Alphaproteobacteria* (**Supplementary File S2**) also underlines the value of both G+C content and genome size as taxonomic markers in the class.

Now that it has been shown that within-species deviation in G+C content is at most 1% (Meier-Kolthoff et al., 2014c), many *Alphaproteobacteria* species descriptions were found to be

inaccurate or too imprecise. The same observation was made in our earlier studies (Hahnke et al., 2016; Nouioui et al., 2018) on other groups of bacteria. As such values not only assist in detecting strains that do not belong to the same species but also show significant correlation to phylogenetic trees it is good practise to strengthen species descriptions in this way. In contrast, in most cases it is premature to redefine genera and higher taxa of *Alphaproteobacteria* in this way since additional type-strain genome sequences would be needed before this issue could be addressed. Only few genera were comprehensively sampled genomically in this study, which allows for providing respective emendations below.

Single characters may or may not be optimal as taxonomic markers, as they are often chosen for historical reasons. The application of gene-content phylogenies is more attractive for taxonomic purposes as they can be based on a huge number of characters now that genome sequences are available for many species. Using distance methods for inferring gene-content phylogenies is not a new idea; in particular, distance formulas were favoured which disregard double absence of genes to account for independent genome reduction (Wolf et al., 2002; Huson and Steel, 2004; Yang et al., 2005). GBDP formula d_3 follows the same approach (Henz et al., 2005). While more sophisticated approaches have been proposed (Gu and Zhang, 2004; Huson and Steel, 2004), we here used GBDP to infer gene-content phylogenies because the method is established. GBDP also allows for a direct comparison with methods based on sequence identity as only a single factor, the distance formula (d_3 vs. d_5), needs to be considered.

It must be taken into account that gene-content phylogenies may fail to recover the "true" tree for a variety of reasons, including horizontal gene transfer and gene loss; depending on the perspective, this may lead to big-genome attraction or small-genome attraction (Wolf et al., 2001; Lake and Rivera, 2004). Last but not least, many published genome sequences are not closed, which does not necessarily add a bias but most likely some noise to gene-content data. For these reasons we do not recommend gene-content approaches for inferring phylogenies although for some data sets they can certainly yield the same topology as approaches based on sequence alignment (Breider et al., 2014). Rather, we regard gene content as of interest for selecting branches from a phylogenetic tree, which was inferred by using a standard genome-scale approach, to obtain a taxonomic classification. Using the gene content directly for the purpose of classification irrespective of whether or not monophyletic taxa are generated (Zhu et al., 2015) is not in agreement with the principles of phylogenetic classification (Wiley and Lieberman, 2011). However, taking gene-content data into account is of interest because gene content conveys metabolic and other phenotypic capabilities (Zhu et al., 2015).

Our results indicate that gene content can be used in this manner to improve the taxonomic classification. In this respect it may even be advantageous if certain parts of the gene-content tree conflicted with the standard genome-scale analysis because this would narrow down the number of branches of the tree to be selected to form taxa. The results of the present study also indicated that gene-content analysis can provide useful insights

into the evolution of *Alphaproteobacteria* and most likely also other groups of bacteria. For instance, the basal branches within *Rhodobacterales* are well supported in the gene-content analysis, reaching 100% for *Rhodobacteraceae*. This may be indicative of specific changes in gene content that occurred early on within the radiation of the order. As a variety of representatives of the family are dominant in marine habitats (Brinkhoff et al., 2008), these changes may be of considerably ecological interest. The genomic basis of the switches of *Rhodobacteraceae* between marine and non-marine habitats has recently been elucidated (Simon et al., 2017). A logical next step in future studies is to reconstruct the changes in gene content which took place at the basis of the *Rhodobacterales* part of the tree and led to the organisms that later on split into the numerous species of *Rhodobacteraceae*. For reasons of taxonomic conservatism, we here refrained from reclassifying monophyletic taxa solely based on their lack of support by the gene-content analysis. However, in this study the gene content appeared valuable for delineating new taxa in a variety of cases in which the existing taxa needed to be revised because they were evidently non-monophyletic. Considering gene content can apparently reduce arbitrariness in taxonomic decisions and increase the information content of the taxonomic system. It thus deserves attention in future studies on genome-based taxonomic classification of *Alphaproteobacteria* and other groups of organisms.

CONCLUSION AND OUTLOOK

The results of this study provide a further improved framework for the classification of the class *Alphaproteobacteria*. The newly proposed taxonomic classification provides a sound basis for future studies on these bacteria, not least on those of ecological interest such as *Rhodobacteraceae*, which are major players in many marine habitats. Discrepancies of the results from the comparative phylogenomic approach with aspects of the previous taxonomic classification based on the 16S rRNA gene were mainly caused by insufficient taxon sampling and disregarded or overestimated branch support. Exceptions in which the 16S rRNA gene is in real conflict with genome-scale phylogenies were not observed. While they are, expectedly, not in full agreement, the relatively high correspondence between gene-content phylogeny and standard genome-scale analyses yields “grist to the taxonomic mill.” Also encouraging is the strong agreement between G+C content, genome size and selected phenotypic features on the one hand and truly genome-scale phylogenies of *Alphaproteobacteria* on the other hand. Future phylogenomic studies should try to link such key features, their genomic basis and their evolutionary relationships, and make an attempt to clarify evolutionary relationships that could as yet not be resolved. This affects particularly those groups that were thoroughly sampled but are not yet well covered by genome sequencing. Success in *Alphaproteobacteria* may help to revitalize prokaryotic systematics as a fundamental scientific discipline in other parts of the bacterial tree of life, particularly if it manages to integrate the distinct types of rich data that are nowadays available.

Taxonomic Consequences: New Orders

Description of *Mariprofundales* ord. nov.

Ma.ri.pro.fun.da'les (N.L. masc. n. *Mariprofundus*, the type genus of the order; *-ales*, ending to denote an order; N.L. fem. pl. n. *Mariprofundales*, the order of *Mariprofundus*).

The description is the same as for the family *Mariprofundaceae* fam. nov. (Emerson et al., 2007), the sole family in the order, which was proposed earlier on but has not been validly published yet. The type genus of the order is *Mariprofundus*. Phylogenetic analyses of genome and 16S rRNA gene sequences indicate that the genus is best placed into an order of its own.

Taxonomic Consequences: New Families

Description of *Afifellaceae* fam. nov.

A.fi.fel.la'ce.ae (N.L. fem. dim. n. *Afifella*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Afifellaceae*, the *Afifella* family).

The description is as given for *Afifella* (Urdiain et al., 2008), which is the type and currently the sole genus of the family. This family has been separated from other families based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Ahrensiaceae* fam. nov.

Ah.rens.i.a'ce.ae (N.L. fem. n. *Ahrensia*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Ahrensiaceae*, the *Ahrensia* family).

Cells are Gram-negative, ovoid to rod-shaped, non-motile or motile by means of polar or peritrichous flagella. Aerobic, oxidase and catalase positive. The major ubiquinone is Q-10. The major named polar lipids are phosphatidylcholin, phosphatidylethanolamine, phosphatidylglycerol and diphosphatidylglycerol. The major fatty acid is C_{18:1} ω7c. The G+C content as calculated from genome sequences is around 48.1–50.1% while the range provided in the literature is 48.1–60.1 mol%. The family currently comprises the genera *Ahrensia* (the type genus) and *Pseudahrensia*.

Description of *Amorphaceae* fam. nov.

A.mor.pha'ce.ae (N.L. masc. n. *Amorphus*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Amorphaceae*, the *Amorphus* family).

Cells are Gram-negative, aerobic, with variable morphology and non-flagellated. The major ubiquinone is Q-10. The major fatty acids are C_{18:1} ω7c and C_{19:0} cyclo ω8c. The family currently comprises the genera *Acuticoccus* and *Amorphus* (the type genus). This family has been separated from other families based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Aurantimonadaceae* fam. nov.

Au.ran.ti.mo.na.da'ce.ae (N.L. fem. n. *Aurantimonas*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Aurantimonadaceae*, the *Aurantimonas* family).

Cells are Gram-negative, rod-shaped, aerobic to facultatively aerobic and either non-motile or motile by means of flagella. The major ubiquinone is Q-10. Usually catalase- and oxidase positive. Growth occurs under mesophilic conditions. Carotenoids can be present. NaCl requirement is variable. The major named

polar lipids are diphosphatidylglycerol, phosphatidylglycerol, phosphatidylcholin, phosphatidylethanolamine, phosphatidylmonomethylethanolamine and aminolipids. The major named fatty acids are usually C_{18:1} ω7c and C_{19:0} cyclo ω8c. The family currently comprises the genera *Mangrovicella*, *Jiella*, *Aurantimonas* (the type genus), *Aureimonas*, *Fulvimarina* and *Consotaella*.

Description of *Azospirillaceae* fam. nov.

A.zo.spi.ril.la'ce.ae (N.L. neut. dim. n. *Azospirillum*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Azospirillaceae*, the *Azospirillum* family).

Cells are Gram-negative, mostly rod-shaped, in general aerobic, usually motile by flagella, usually heterotrophic. The major ubiquinone is predominantly Q-10. The major named polar lipids are phosphatidylcholin, phosphatidylethanolamine, phosphatidylglycerol and diphosphatidylglycerol. The major fatty acids are usually C_{18:1} ω7c, C_{18:1} ω6c, C_{16:0} and C_{16:1} ω6c. The family currently comprises the genera *Niveispirillum*, *Azospirillum* (including *Conglomeromonas*), *Skermanella*, *Nitrospirillum*, *Rhodocista*, and *Desertibacter*. The genera *Elstera*, *Inquilinus* and *Lacibacterium* are tentatively assigned to this family. The type genus is *Azospirillum*.

Description of *Blastochloridaceae* fam. nov.

Blas.to.chlo.ri.da'ce.ae (N.L. fem. n. *Blastochloris*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Blastochloridaceae*, the *Blastochloris* family).

The description is as given for *Blastochloris* (Hiraishi, 1997), which is the type and currently the sole genus of the family. This family has been separated from *Hyphomicrobiaceae* based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Boseaceae* fam. nov.

Bo.se.a'ce.ae (N.L. fem. n. *Bosea*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Boseaceae*, the *Bosea* family).

The description is as given for *Bosea* (Das et al., 1996; La Scola et al., 2003), which is the type genus and currently the sole genus of the family. This family has been separated from *Nitrobacteraceae* (whose illegitimate synonym is *Bradyrhizobiaceae*) based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Breoghaniaceae* fam. nov.

Bre.o.gha.ni.a'ce.ae (N.L. fem. n. *Breoghania*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Breoghaniaceae*, the *Breoghania* family).

The description is as given for *Breoghania* (Gallego et al., 2010), which is the type and currently the sole genus of the family. This family has been separated from other families based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Devosiaceae* fam. nov.

De.vo.si.a'ce.ae (N.L. fem. n. *Devosia*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Devosiaceae*, the *Devosia* family).

Cells are Gram-negative, predominantly rod-shaped, aerobic, usually motile by flagella, and heterotrophic. The major ubiquinone is predominantly Q-10 whereas Q-9 and Q-11 present as minor ubiquinone in some species. The major polar lipids are phosphatidylglycerol, diphosphatidylglycerol and glycolipid. The major fatty acids are usually C_{18:1} ω7c, 11-methyl C_{18:1} ω7c, C_{18:1} ω6c, C_{18:0}, C_{16:0} ω6c and C_{19:0} cyclo ω8c. The family currently comprises the genera *Arsenicitalea*, *Cucumibacter*, *Devosia* (the type genus), *Maritalea* (including *Zhangella*), *Methyloterrigena*, *Paradevosia*, *Pelagibacterium*, and *Youhaiella*. This family has been separated from *Hyphomicrobiaceae* based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Kaistiaceae* fam. nov.

Kais.ti.a'ce.ae (N.L. fem. n. *Kaistia*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Kaistiaceae*, the *Kaistia* family).

Cells are Gram-negative, cocci or rod-shaped, non-motile, aerobic and chemoorganotrophic. The G+C content as calculated from genome sequences is around 64.5–67.1% while the range provided in the literature is 61.6–69.0 mol%. The family currently comprises the genera *Kaistia* (the type genus) and *Bauldia*.

Description of *Mariprofundaceae* fam. nov.

Ma.ri.pro.fun.da'ce.ae (N.L. masc. n. *Mariprofundus*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Mariprofundaceae*, the *Mariprofundus* family).

The description is that for *Mariprofundus* (Emerson et al., 2007), which is the type and currently sole genus of the family. The family was proposed earlier on but has not been validly published yet. It has been separated from other families based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Neomegalonemataceae* fam. nov.

Ne.o.me.ga.lo.ne.ma.ta'ce.ae (N.L. neut. n. *Neomegalonema*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Neomegalonemataceae*, the *Neomegalonema* family).

The description is as given for *Neomegalonema* (Oren, 2017b), which is the type and currently the sole genus of the family. This family has been separated from *Hyphomicrobiales* (known under the illegitimate synonym *Rhizobiales*) and from *Rhodobacteraceae* based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Parvibaculaceae* fam. nov.

Par.vi.ba.cu.la'ce.ae (N.L. neut. n. *Parvibaculum*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Parvibaculaceae*, the *Parvibaculum* family).

Cells are Gram-negative, usually rod-shaped, generally aerobic, motile by flagella or non-motile and heterotrophic. The major ubiquinone is Q-10 or Q-11. The major polar lipids are diphosphatidylglycerol, phosphatidylethanolamine and phosphatidylglycerol. The major fatty acid is usually C_{18:1} ω7c and in some cases C_{16:0} and C_{19:0} cyclo. The family currently comprises the genera *Parvibaculum* (the type genus) and

Tepidicaulis, *Anderseniella*, *Rhodoligotrophos* and *Pyruvatibacter* are tentatively assigned to this family as well.

Description of *Phreatobacteraceae* fam. nov.

Phre.a.to.bac.te.ra'ce.ae (N.L. masc. n. *Phreatobacter*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Phreatobacteraceae*, the *Phreatobacter* family).

The description is as given for *Phreatobacter* (Tóth et al., 2014; Lee S.D. et al., 2017), which is the type and currently the sole genus of the family. This family is proposed based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Pleomorphomonadaceae* fam. nov.

Ple.o.mor.pho.mo.na.da'ce.ae (N.L. fem. n. *Pleomorphomonas*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Pleomorphomonadaceae*, the *Pleomorphomonas* family).

Cells are Gram-negative, usually rod-shaped or spherical, generally aerobic and mostly diazotrophic. The major ubiquinone is predominantly Q-10. The major polar lipids are phosphatidylglycerol, phosphatidylcholin, phosphatidylethanolamine and sometimes phospholipid. The major fatty are usually C_{18:1} ω7c and C_{18:0}. The family currently comprises the genera *Chthonobacter*, *Hartmannibacter*, *Methylobreviis*, *Mongoliimonas*, *Oharaeibacter*, and *Pleomorphomonas* (the type genus). This family has been separated from other families based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Pseudoxanthobacteraceae* fam. nov.

Pseu.do.xan.tho.bac.te.ra'ce.ae (N.L. masc. n. *Pseudoxanthobacter*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Pseudoxanthobacteraceae*, the *Pseudoxanthobacter* family).

The description is as given for *Pseudoxanthobacter* (Arun et al., 2008), which is the type and currently sole genus of the family. This family has been separated from other families based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Reyranellaceae* fam. nov.

Rey.ra.nel.la'ce.ae (N.L. fem. dim. n. *Reyranella*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Reyranellaceae*, the *Reyranella* family).

The description is as given for *Reyranella* (Pagnier et al., 2011) which is the type and currently sole genus of the family. This family has been separated from other families based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Rhodovibrionaceae* fam. nov.

Rho.do.vi.bri.o.na'ce.ae (N.L. masc. n. *Rhodovibrio*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Rhodovibrionaceae*, the *Rhodovibrio* family).

Gram-negative, vibrioid, spiral or rod-shaped, non-motile or motile by means of polar flagella. Aerobic, facultatively anaerobic or anaerobic, with chemoorganotrophic or photoorganoheterotrophic metabolism. The major ubiquinone is Q-10; MK-10 was reported for *Rhodovibrio*. The major fatty

acids are C_{19:0} cyclo ω8c, C_{18:1} ω7c and C_{18:0}. The G+C content provided in the literature is 61.5–69.0 mol%. The family currently comprises the genera *Fodinicurvata*, *Limimonas*, *Rhodovibrio* (the type genus) and *Tistlia*. *Limibacillus* and *Pelagibius* are tentatively assigned to this family.

Description of *Sphaerochaetaceae* fam. nov.

Sphae.ro.chae.ta'ce.ae (N.L. fem. n. *Sphaerochaeta*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Sphaerochaetaceae*, the *Sphaerochaeta* family).

Cells are Gram-negative, mostly non-motile, pleomorphic, anaerobic and heterotrophic. The family currently comprises the genera *Pleomorphochaeta* and *Sphaerochaeta* (the type genus). This family has been separated from other families based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Sphingosinellaceae* fam. nov.

Sphin.go.si.ni.cel.la'ce.ae (N.L. fem. n. *Sphingosinella*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Sphingosinellaceae*, the *Sphingosinella* family).

Cells are Gram-negative, aerobic, rod-shaped, mostly motile heterotrophs. The major ubiquinone is Q-10. The major named polar lipids are phosphatidylethanolamine, phosphatidylglycerol and in some species diphosphatidylglycerol. The major fatty acids are usually C_{18:1} ω7c, C_{16:0} and C_{16:1} ω7c. The family currently comprises the genera *Pacificimonas*, *Sphingosinella* (the type genus), *Sandaracinobacter* and *Sandarakinorhabdus*. *Polymorphobacter* and *Sphingoaurantiacus* are tentatively assigned to this family. This family has been separated from other families based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Stappiaceae* fam. nov.

Stap.pi.a'ce.ae (N.L. fem. n. *Stappia*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Stappiaceae*, the *Stappia* family).

Cells are Gram-negative, usually rod-shaped, motile, mostly aerobic or facultatively anaerobic and heterotroph. The major ubiquinone is usually Q-10. The major fatty acids are predominantly C_{18:1} ω7c and C_{16:1} ω7c. The family currently comprises the genera *Pannonibacter*, *Pseudovibrio*, *Roseibium* (including *Labrenzia*) and *Stappia* (the type genus). This family has been separated from other families based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Stellaceae* fam. nov.

Stel.la'ce.ae (L. fem. n. *Stella*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Stellaceae*, the *Stella* family).

The description is as given for *Stella* (Vasilyeva, 1985), which is the type genus of the family, with the following modification. Cells are six-pronged stars, rods or ovoids. The family houses *Stella* and tentatively also *Constrictibacter*. This family has been separated from *Acetobacteraceae* based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Tepidamorphaceae* fam. nov.

Te.pid.a.mor.phá'ce.ae (N.L. masc. n. *Tepidamorphus*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Tepidamorphaceae*, the *Tepidamorphus* family).

Cells are Gram-negative, either ovoid or rod-shaped, predominantly aerobic, mostly motile via flagella and generally chemoorganotrophs. The major ubiquinone is Q-10. The major named polar lipids are diphosphatidylglycerol, phosphatidylethanolamine, and phosphatidylglycerol. The major fatty acids are usually C_{19:0} cyclo ω8c, C_{18:1} ω7c, C_{18:0} and C_{16:0}. The family currently comprises the genera *Butyratibacter*, *Lutibaculum*, *Microbaculum*, and *Tepidamorphus* (the type genus).

Description of *Terasakiellaceae* fam. nov.

Te.ra.sa.ki.el.lá'ce.ae (N.L. fem. dim. n. *Terasakiella*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Terasakiellaceae*, the *Terasakiella* family).

The description is as given for *Terasakiella* (Satomi et al., 2002; Han et al., 2016), which is the type and currently sole genus of the family. This family has been separated from other families based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Thalassobaculaceae* fam. nov.

Tha.las.so.ba.cu.lá'ce.ae (N.L. neut. n. *Thalassobaculum*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Thalassobaculaceae*, the *Thalassobaculum* family).

Gram-negative, rod-shaped, motile by means of one polar flagellum. Aerobic or facultatively anaerobic respiration and chemoorganotrophic metabolism. The major ubiquinone is Q-10. The major fatty acids are C_{18:1} ω7c, C_{16:1} ω7c and C_{16:0}. The G+C content as calculated from genome sequences is around 60.5–67.4% while the range provided in the literature is 60–68 mol%. The family currently comprises the genera *Nisaea*, *Oceanibaculum* and *Thalassobaculum* (the type genus).

Description of *Thalassospiraceae* fam. nov.

Tha.las.so.spi.rá'ce.ae (N.L. fem. n. *Thalassospira*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Thalassospiraceae*, the *Thalassospira* family).

Cells are Gram-negative, usually motile by flagella, mostly aerobic or microaerophilic with a heterotrophic or autolithotrophic metabolism. The major ubiquinone is predominantly Q-10. The major polar lipids are phosphatidylethanolamine and phosphatidylglycerol. The major fatty acids are usually C_{18:1} ω7c, C_{16:1} ω7c and C_{16:0}. The family currently comprises the genera *Magnetovibrio*, *Terasakiella*, *Thalassospira* (the type genus), *Varunaivibrio*. *Magnetospira* is tentatively assigned to this family. This family has been separated from other families based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Zavarziniaceae* fam. nov.

Za.var.zi.ni.á'ce.ae (N.L. fem. n. *Zavarzinia*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Zavarziniaceae*, the *Zavarzinia* family).

The description is as given for *Zavarzinia* (Meyer et al., 1993), which is the type and currently sole genus of the family. This family has been separated from *Acetobacteraceae* based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Zymomonadaceae* fam. nov.

Zy.mo.mo.na.da'ce.ae (N.L. fem. n. *Zymomonas*, type genus of the family; *-aceae*, ending to denote a family; N.L. fem. pl. n. *Zymomonadaceae*, the *Zymomonas* family).

The description is as given for *Zymomonas* (Kluyver and van Niel, 1936), which is the type and currently sole genus of the family. This family has been separated from other families based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Taxonomic Consequences: New Genera**Description of *Albibacillus* gen. nov.**

Al.bi.ba.cil'lus (L. masc. adj. *albus*, white; L. masc. n. *bacillus*, rod; N.L. masc. n. *Albibacillus*, white rod).

Gram-negative, rod-shaped, aerobic, oxidase and catalase positive. The major ubiquinone is Q-10. The major polar lipids are phosphatidylglycerol, phosphatidylethanolamine, phosphatidylmonomethyl ethanolamine and aminolipids. The major fatty acids are C_{18:1} ω7c and C_{19:0} cyclo ω8c. The G+C content is around 64–66%. The type species is *Albibacillus kandeliae*, *comb. nov.*

Description of *Allgaiera* gen. nov.

All.gai'er.a (N.L. fem. n. *Allgaiera*, named after the German microbiologist Martin Allgaier for his work on marine *Rhodobacteraceae*).

The description is as given for *Allgaiera indica*, *comb. nov.*, which is the type species. The genus has been separated from *Defluviimonas* based on physiology and phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Allosediminivita* gen. nov.

Al.lo.se.di.mi.ni.vi'ta (Gr. masc. adj. *allos*, another, other, different; N.L. fem. n. *Sediminivita*, a bacterial genus; N.L. fem. n. *Allosediminivita*, a genus different from *Sediminivita*).

The description is as given for *Allosediminivita pacifica*, *comb. nov.*, which is the type species. The genus has been separated from *Roseivivax* based on physiology and phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Allosphingosinicella* gen. nov.

Al.lo.sphin.go.si.ni.cel'la (Gr. masc. adj. *allos*, another, other, different; N.L. fem. n. *Sphingosinicella*, a bacterial genus; N.L. fem. n. *Allosphingosinicella*, a genus different from *Sphingosinicella*).

Cells are Gram-negative, non-motile, non-spore-forming and rod-shaped. Strictly aerobic. The major ubiquinone is Q-10. The major polar lipids are diphosphatidylglycerol, phosphatidylglycerol and phosphatidylethanolamine. The major fatty acids are C_{18:1} ω7c, C_{16:1} ω7c, C_{14:0} 2-OH and C_{16:0}. The G+C content as calculated from genome sequences is around 62.4–67.0% while the range provided in the literature

is 59.4–65.8 mol%. The type species is *Alloshingosinicella vermicomposti* comb. nov.

Description of *Bieblia* gen. nov.

Bieblia (N.L. fem. n. *Bieblia*, named after the German microbiologist Hanno Biebl for his work on marine *Rhodobacteraceae*).

Facultatively aerobic or anaerobic, Gram-negative, non-motile, rods or ovoids, mostly autotrophs. bacteriochlorophyll and carotenoids present. The G+C content is 64–69%. The type species is *Bieblia veldkampii*, comb. nov. The genus has been separated from *Rhodobacter* based on physiology and phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Caenibius* gen. nov.

Caenibius (L. neut. n. *caenum*, mud, referring to the isolation of the type strain from activated sludge; N.L. masc. n. *bius*, life (from Gr. n. *bios*); N.L. masc. n. *Caenibius*, sludge life).

The description is as given for *Caenibius tardaogens*, comb. nov., which is the type species. The genus has been separated from *Novosphingobium* based on physiology and phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Cypionkella* gen. nov.

Cypionkella (N.L. fem. dim. n. *Cypionkella*, named after the German microbiologist Heribert Cypionka for his work on marine *Rhodobacteraceae*).

Cells are Gram-negative, rod-shaped or oval, non-motile, mostly aerobic, heterotrophic. Catalase and oxidase positive. The predominant ubiquinone is Q-10. The major polar lipids are phosphatidylglycerol and phosphatidylcholin. The major fatty acid is C_{18:1} ω7c. The G+C content is 60–62%. The type species is *Cypionkella psychrotolerans*, comb. nov. The genus has been separated from *Pseudorhodobacter* based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Elkelangia* gen. nov.

Elkelangia (N.L. fem. n. *Elkelangia*, named after Elke Lang, a German microbiologist known for her work as long term curator of Gram negative bacteria at DSMZ).

The description is as given for *Elkelangia baekryungensis*, comb. nov., which is the type species. The genus has been separated from *Sphingopyxis* based on physiology and phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Meinhardsimonia* gen. nov.

Meinhardsimonia (N.L. fem. n. *Meinhardsimonia*, named after the German microbiologist Meinhard Simon for his work on marine *Rhodobacteraceae*).

The description is as given for *Meinhardsimonia xiamenensis*, comb. nov., which is the type species. The genus has been separated from *Albidovulum* based on physiology and phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Neoparahizobium* gen. nov.

Neoparahizobium (Gr. pref. *neo*, new; N.L. neut. n. *Pararahizobium*, the genus *Pararahizobium*; N.L. neut. n. *Neoparahizobium*, new *Pararahizobium*).

The type species is *Neoparahizobium haloflavum*, comb. nov. The genus has been separated from *Pararahizobium* based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Pacificitalea* gen. nov.

Pacificitalea (L. masc. adj. *pacificus*, peaceful, referring to the Pacific Ocean; L. fem. n. *talea*, a rod; N.L. fem. n. *Pacificitalea*, a rod isolated from the Pacific Ocean).

The description is as given for *Pacificitalea manganoxidans*, comb. nov., which is the type species. The genus has been separated from *Celeribacter* based on physiology and phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Pseudoprimorskyibacter* gen. nov.

Pseudoprimorskyibacter (Gr. masc. adj. *pseudês*, false; N.L. n. *primorskyi*-yos, primorsky kray, a far-Eastern region of the Russian federation where the first strains were isolated; N.L. masc. n. *bacter*, a rod; N.L. masc. n. *Pseudoprimorskyibacter*, like *Primorskyibacter*, referring to the close relationship to the genus *Primorskyibacter*).

The description is as given for *Pseudoprimorskyibacter insulae* comb. nov., which is the sole and type species. The genus has been separated from *Primorskyibacter* based on physiology and phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Vannielia* gen. nov.

Vannielia (N.L. fem. n. *Vannielia*, named to honor Cornelis Bernardus van Niel, and his many contributions to microbiology).

The description is as given for *Vannielia litorea*, comb. nov., which is the type species. The genus has been separated from *Oceanicola* based on physiology and phylogenetic analyses of genome and 16S rRNA gene sequences.

Description of *Wagnerdoeblera* gen. nov.

Wagnerdoeblera (N.L. fem. n. *Wagnerdoeblera*, named after the German microbiologist Irene Wagner-Döbler for her work on marine *Rhodobacteraceae*).

Gram-negative, non-motile, non-spore-forming bacteria. Cells are irregular rod-shaped. Aerobic. Oxidase and catalase positive. The major ubiquinone is Q-10. The major polar lipids are phosphatidylethanolamine, phosphatidylglycerol and phosphatidylcholine. The major fatty acid is C_{18:1} ω7c. The G+C content as calculated from genome sequences is around 64.9–66.2% while the range provided in the literature is 61.4–64.5 mol%. The type species is *Wagnerdoeblera nectariphila*, comb. nov.

Taxonomic Consequences: New (Combinations for) Species

Description of *Acetobacter ascendens* comb. nov., Change of Rank

A. ascendens (L. part. adj. *ascendens*, ascending, climbing).

Basonym: *Acetobacter pasteurianus* subsp. *ascendens* De Ley and Frateur, 1974 (Approved Lists 1980)

The description is as given for *Acetobacter pasteurianus* subsp. *ascendens* (De Ley and Frateur, 1974). The type strain is CCM 3612 = LMG 1590 = NCCB 51001.

Description of *Acetobacter paradoxus* comb. nov., Change of Rank

A. pa.ra.do'xus (L. masc. adj. *paradoxus*, strange, contrary to all expectation, paradoxical).

Basonym: *Acetobacter pasteurianus* subsp. *ascendens* De Ley and Frateur, 1974 (Approved Lists 1980)

The description is as given for *Acetobacter pasteurianus* subsp. *paradoxus* (De Ley and Frateur, 1974). The type strain is LMG 1591 = NCCB 53006.

Description of *Actibacterium lipolyticum* comb. nov.

A. li.po.ly'ti.cum (Gr. neut. n. *lipos*, fat; Gr. masc. adj. *lytikos*, able to loosen, dissolving; N.L. neut. adj. *lipolyticum*, dissolving fat or lipid).

Basonym: *Confluentimicrobium lipolyticum* Parker et al., 2019

The description is as given for *Confluentimicrobium lipolyticum* (Park et al., 2014d). The type strain is SSK1-4 = CECT 8621 = KCTC 42136.

Description of *Actibacterium naphthalenivorans* comb. nov.

A. naph.tha.le.ni.vo'rans (N.L. neut. n. *naphthalenum*, naphthalene; L. part. adj. *vorans*, devouring; N.L. part. adj. *naphthalenivorans*, naphthalene-consuming).

Basonym: *Confluentimicrobium naphthalenivorans* Jeong et al., 2015

The description is as given for *Confluentimicrobium naphthalenivorans* (Jeong et al., 2015). The type strain is NS6 = DSM 105040 = JCM 30828.

Description of *Afipia carboxidovorans* comb. nov.

A. car.bo.xi.do'vo.rans (L. masc. n. *carbo*, charcoal, carbon; Gr. masc. adj. *oxys*, sour, acid; L. v. *voro*, devour; N.L. part. adj. *carboxidovorans*, carbon-acid devouring).

Basonym: *Oligotropha carboxidovorans* (ex Meyer and Schlegel 1978) Meyer et al. 1994.

The description is as given for *Oligotropha carboxidovorans* (Meyer et al., 1993). The type strain is OM5 = DSM 1227 = ATCC 49405.

Description of *Albibacillus kandeliae* comb. nov.

A. kan.de'li.ae (N.L. gen. n. *kandeliae*, of *Kandelia*, referring to a genus of mangrove plant).

Basonym: *Ruegeria kandeliae* Zhang L. et al., 2018

The description is as given for *Ruegeria kandeliae* (Zhang L. et al., 2018). The type strain is DSM 104293 = MCCC 1K03284.

Description of *Allgaiera indica* comb. nov.

A. in'di.ca (L. fem. adj. *indica*, referring to the Indian Ocean, where the type strain was first isolated).

Basonym: *Defluviimonas indica* Jiang et al., 2014

The description is as given for *Defluviimonas indica* (Jiang et al., 2014). The type strain is 20V17 = DSM 24802 = JCM 17871.

Description of *Allorhizobium oryziradicis* comb. nov.

A. o.ry.zi.ra'di.cis (L. fem. n. *oryza*, rice; L. fem. n. *radix/-icis*, root; N.L. gen. n. *oryziradicis*, of the rice root).

Basonym: *Rhizobium oryziradicis* Zhao et al., 2017

The description is as given for *Rhizobium oryziradicis* (Zhao et al., 2017). The genomic G+C content of the type strain is 55.1%. Its approximate genome size is 5.16 Mbp. The type strain is KCTC 52413.

Description of *Allorhizobium taibaishanense* comb. nov.

A. tai.bai.shan.en'se (N.L. neut. adj. *taibaishanense*, of or belonging to the Taibaishan Mountains in the Shaanxi province of China, where the bacterium was isolated).

Basonym: *Rhizobium taibaishanense* Yao et al., 2012

The description is as given for *Rhizobium taibaishanense* (Yao et al., 2012). The type strain is DSM 100021 = HAMBI 3214.

Description of *Allosediminivita pacifica* comb. nov.

A. pa.ci'fi.ca (L. fem. adj. *pacifica*, peaceful, pertaining to the Pacific Ocean).

Basonym: *Roseivivax pacificus* Wu et al., 2013

The description is as given for *Roseivivax pacificus* (Wu et al., 2013) with the following modification. The G+C content of the type-strain genome is 66.2%, its approximate size 4.84 Mbp. The type strain is 22DY03 = DSM 29329 = JCM 18866.

Description of *Alloshingosinicella indica* comb. nov.

A. in'di.ca (L. fem. adj. *indica*, of India, the origin of the type strain).

Basonym: *Sphingomonas indica* Niharika et al., 2012

The description is as given for *Sphingomonas indica* (Niharika et al., 2012). The genomic G+C content of the type strain is 67.0%. Its approximate genome size is 2.81 Mbp. The type strain is Dd16 = CCM 7882 = DSM 25434.

Description of *Alloshingosinicella vermicomposti* comb. nov.

A. ver.mi.com.pos'ti (L. neut. n. *vermis*, worm; N.L. neut. n. *compostum*, compost; N.L. gen. n. *vermicomposti*, of vermicompost, referring to the isolation of the type strain from vermicompost).

Basonym: *Sphingosinicella vermicomposti* Yasir et al., 2010

The description is as given for *Sphingosinicella vermicomposti* (Yasir et al., 2010) with the following modification. The G+C content of the type-strain genome is 62.4%, its approximate size 2.51 Mbp. The type strain is YC7378 = DSM 21593 = KCTC 22446.

Description of *Aminobacter carboxidus* comb. nov.

A. car.bo'xi.dus (L. masc. adj. *carboxidus*, intended to mean connected with carbon oxides).

Basonym: *Carbophilus carboxidus* (ex Nozhevnikova and Zavarzin 1974) Meyer et al. 1994.

The description is as given for *Carbophilus carboxidus* (Meyer et al., 1993). The type strain is ATCC 51424 = CIP 105722 = DSM 1086.

Description of *Bieblia veldkampii* comb. nov.

B. veldkampii (N.L. gen. n. *veldkampii*, of Veldkamp, named after Hans Veldkamp, a Dutch microbiologist).

Basonym: *Rhodobacter veldkampii* Hansen and Imhoff, 1985

The description is as given for *Rhodobacter veldkampii* (Hansen and Imhoff, 1985) with the following restriction. The G+C content of the type-strain genome is 65.1%, its approximate size 3.26 Mbp. The type strain is BN 714 = DSM 11550 = ATCC 35703 = CIP 103912 = IFO 16458 = NBRC 16458.

Description of *Bieblia vinaykumarii* comb. nov.

B. vinaykumarii (N.L. gen. n. *vinaykumarii*, of Vinaykumar, named after the late Dr. M. Vinaykumar, an Indian microbiologist and research supervisor of Ch. V. Ramana. and Ch. Sasikala, who initiated work on anoxygenic phototrophic bacteria in India).

Basonym: *Rhodobacter vinaykumarii* Srinivas et al., 2007a

The description is as given for *Rhodobacter vinaykumarii* (Srinivas et al., 2007b). The type strain is CCUG 54311 = DSM 18714 = JCM 14544.

Description of *Brucella anthropi* comb. nov.

B. anthropi (Gr. masc. n. *anthropos*, a human being; N.L. gen. n. *anthropi*, of a human being).

Basonym: *Ochrobactrum anthropi* Holmes et al., 1988

The description is as given for *Ochrobactrum anthropi* (Holmes et al., 1988). The type strain is ATCC 49188 = CCUG 24695 = CIP 82.115 = DSMZ 6882 = IFO 15819 = JCM 21032 = LMG 3331 = NBRC 15819 = NCTC 12168.

Description of *Brucella ciceri* comb. nov.

B. ciceri (L. gen. n. *ciceri*, of chickpea (*Cicer arietinum*), referring to the habitat from which the type strain was isolated).

Basonym: *Ochrobactrum ciceri* Imran et al., 2010

The description is as given for *Ochrobactrum ciceri* (Imran et al., 2010). The type strain is CCUG 57879 = DSM 22292.

Description of *Brucella cytisi* comb. nov.

B. cytisi (N.L. masc. n. *Cytisus*, botanical genus name of the legume *Cytisus scoparius*; N.L. gen. n. *cytisi*, of *Cytisus*, referring to the isolation source of the first strains, nodules of *Cytisus scoparius*).

Basonym: *Ochrobactrum cytisi* Zurdo-Piñeiro et al., 2007

The description is as given for *Ochrobactrum cytisi* (Zurdo-Piñeiro et al., 2007). The type strain is CECT 7172 = DSM 19778 = LMG 22713.

Description of *Brucella daejeonensis* comb. nov.

B. daejeonensis (N.L. fem. adj. *daejeonensis*, of or pertaining to Daejeon, a city in South Korea, from where the type strain was isolated).

Basonym: *Ochrobactrum daejeonense* Woo et al., 2011

The description is as given for *Ochrobactrum daejeonense* (Woo et al., 2011). The type strain is DSM 26944 = JCM 16234 = KCTC 22458.

Description of *Brucella endophytica* comb. nov.

B. endophytica (Gr. pref. *endo*, within; Gr. neut. n. *phyton*, plant; L. neut. suff. *-icum*, adjectival suffix used with the sense of belonging to; N.L. fem. adj. *endophytica*, within plant, endophytic, because the type strain was isolated from the interior of a plant nodule).

Basonym: *Ochrobactrum endophyticum* Li L. et al., 2016

The description is as given for *Ochrobactrum endophyticum* (Li L. et al., 2016). The type strain is CGMCC 1.15082 = DSM 29930 = KCTC 42485.

Description of *Brucella gallinifaecis* comb. nov.

B. gallinifaecis (L. fem. n. *gallina*, hen; L. fem. n. *faex*, *faecis*, faeces; N.L. gen. n. *gallinifaecis*, of the faeces of a hen).

Basonym: *Ochrobactrum gallinifaecis* Kämpfer et al., 2003

The description is as given for *Ochrobactrum gallinifaecis* (Kämpfer et al., 2003). The type strain is CCUG 48291 = CIP 107753 = DSM 15295.

Description of *Brucella grignonensis* comb. nov.

B. grignonensis (N.L. fem. adj. *grignonensis*, pertaining to Grignon, region from which the strains were isolated).

Basonym: *Ochrobactrum grignonense* Lebuhn et al., 2000

The description is as given for *Ochrobactrum grignonense* (Lebuhn et al., 2000). The genomic G+C content of the type strain is 54.1%. Its approximate genome size is 4.84 Mbp. The type strain is CCUG 46362 = DSM 13338 = LMG 18954 = NBRC 102586.

Description of *Brucella haematophila* comb. nov.

B. haematophila (Gr. neut. n. *haima/-atos*, Latin transliteration *haema/-atos*, blood; N.L. adj. *philus/-a/-um*, from Greek adj. *philos/-ê/-on*, friend, loving; N.L. fem. adj. *haematophila*, blood-loving).

Basonym: *Ochrobactrum haematophilum* Kämpfer et al., 2007a

The description is as given for *Ochrobactrum haematophilum* (Kämpfer et al., 2007a). The type strain is CCUG 38531 = CIP 109452 = DSM 22355.

Description of *Brucella intermedia* comb. nov.

B. intermedia (L. fem. adj. *intermedia*, that is between, intermediate).

Basonym: *Ochrobactrum intermedium* Velasco et al., 1998

The description is as given for *Ochrobactrum intermedium* (Velasco et al., 1998). The type strain is CCUG 24694 = CIP 105838 = DSM 17986 = IFO 15820 = LMG 3301 = NBRC 15820 = NCTC 12171.

Description of *Brucella lupini* comb. nov.

B. lupini (L. gen. n. *lupini*, of a lupine, referring to the isolation source of this microorganism, nodules of *Lupinus albus*).

Basonym: *Ochrobactrum lupini* Trujillo et al. 2006.

The description is as given for *Ochrobactrum lupini* (Trujillo et al., 2005). The type strain is DSM 16930 = LMG 22726 = NBRC 102587.

Description of *Brucella oryzae* comb. nov.

B. o.ry'zæ (L. gen. n. *oryzae*, of rice, pertaining to the habitat from which the first strains were isolated).

Basonym: *Ochrobactrum oryzae* Tripathi et al., 2006

The description is as given for *Ochrobactrum oryzae* (Tripathi et al., 2006). The type strain is DSM 17471 = MTCC 4195 = NBRC 102588.

Description of *Brucella pecoris* comb. nov.

B. pe.co'ris (L. gen. n. *pecoris*, of livestock).

Basonym: *Ochrobactrum pecoris* Kämpfer et al., 2011

The description is as given for *Ochrobactrum pecoris* (Kämpfer et al., 2011). The type strain is CCM 7822 = CCUG 60088 = DSM 23868.

Description of *Brucella pituitosa* comb. nov.

B. pi.tu.i.to'sa (L. fem. adj. *pituitosa*, full of phlegm, *pituitous*, intended to mean slimy, referring to the consistency of the colonies after extended incubation).

Basonym: *Ochrobactrum pituitosum* Huber et al., 2010

The description is as given for *Ochrobactrum pituitosum* (Huber et al., 2010) with the following addition. The G+C content of the type-strain genome is 53.7%, its approximate size 4.28 Mbp. The type strain is CCUG 50899 = DSM 22207.

Description of *Brucella pseudintermedia* comb. nov.

B. pseud.in.ter.me'di.a (Gr. neut. adj. *pseudês*, false; L. fem. adj. *intermedia*, intermediate, and a specific epithet of the genus *Brucella*; N.L. fem. adj. *pseudintermedia*, a false *Brucella intermedia*).

Basonym: *Ochrobactrum pseudintermedium* Teyssier et al., 2007

The description is as given for *Ochrobactrum pseudintermedium* (Teyssier et al., 2007). The genomic G+C content of the type strain is 54.0%. Its approximate genome size is 5.53 Mbp. The type strain is CIP 109116 = DSM 17490.

Description of *Brucella pseudogrignonensis* comb. nov.

B. pseu.do.gri.gnon.en'sis (Gr. neut. adj. *pseudês*, false; N.L. fem. adj. *grignonensis*, a bacterial species epithet; N.L. fem. adj. *pseudogrignonensis*, a false *Brucella grignonensis*).

Basonym: *Ochrobactrum pseudogrignonense* Kämpfer et al., 2007a

The description is as given for *Ochrobactrum pseudogrignonense* (Kämpfer et al., 2007a) with the following addition. The G+C content of the type-strain genome is 54.0%, its approximate size 5.53 Mbp. The type strain is CCUG 30717 = CIP 109451 = DSM 22354.

Description of *Brucella rhizosphaerae* comb. nov.

B. rhi.zo.sphae'rae (Gr. fem. n. *rhiza*, root; L. fem. n. *sphaera*, a ball, sphere; N.L. n. *rhizosphaera*, rhizosphere; N.L. gen. n. *rhizosphaerae*, of the rhizosphere).

Basonym: *Ochrobactrum rhizosphaerae* Kämpfer et al., 2008

The description is as given for *Ochrobactrum rhizosphaerae* (Kämpfer et al., 2008). The genomic G+C content of the type

strain is 53.0%. Its approximate genome size is 4.90 Mbp. The type strain is CCM 7493 = CCUG 55411 = DSM 19824.

Description of *Brucella thiophenivorans* comb. nov.

B. thi.o.phe.ni.vo'rans (N.L. neut. n. *thiophenum*, thiophene; L. pres. part. *vorans*, devouring; N.L. part. adj. *thiophenivorans*, thiophene-devouring, referring to the ability to utilize thiophene 2-carboxylate as a sole source of carbon and sulfur).

Basonym: *Ochrobactrum thiophenivorans* Kämpfer et al., 2008

The description is as given for *Ochrobactrum thiophenivorans* (Kämpfer et al., 2008). The genomic G+C content of the type strain is 51.6%. Its approximate genome size is 4.36 Mbp. The type strain is CCM 7492 = CCUG 55412 = DSM 7216.

Description of *Brucella tritici* comb. nov.

B. tri.ti'ci (L. neut. n. *tritium*, wheat, and also the generic name for wheat, *Triticum*; L. gen. n. *tritici*, of wheat, of *Triticum*, from which the strains were isolated).

Basonym: *Ochrobactrum tritici* Lebuhn et al., 2000

The description is as given for *Ochrobactrum tritici* (Lebuhn et al., 2000). The type strain is CCUG 47104 = DSM 13340 = LMG 18957 = NBRC 102585.

Description of *Caenibius tardaugs* comb. nov.

C. tard.au'gens (L. masc. adj. *tardus*, slow; L. pres. part. *augens*, growing; N.L. part. adj. *tardaugs*, slowly growing).

Basonym: *Novosphingobium tardaugs* Fujii et al., 2003

The description is as given for *Novosphingobium tardaugs* (Fujii et al., 2003). The type strain is ARI-1 = DSM 16702 = JCM 11434.

Description of *Celeribacter arenosi* comb. nov.

C. a.re.no'si (L. gen. n. *arenosi*, of a sandy place, dwelling in marine sand).

Basonym: *Vadicella arenosi* Romanenko et al., 2011c

The description is as given for *Vadicella arenosi* (Romanenko et al., 2011c). The type strain is JCM 17190 = KMM 9024 = NRIC 0787.

Description of *Cereibacter azotoformans* comb. nov.

C. a.zo.to.for'mans (N.L. neut. n. *azotum*, (from Fr. n. *azote*), nitrogen; L. pres. part. *formans*, forming; N.L. part. adj. *azotoformans*, nitrogen forming).

Basonym: *Rhodobacter azotoformans* Hiraishi et al. 1997.

The description is as given for *Rhodobacter azotoformans* (Hiraishi et al., 1996) with the following modification. The G+C content of the type-strain genome is 68.4%, its approximate size 4.41 Mbp. The type strain is KA25 = JCM 9340 = NBRC 16436.

Description of *Cereibacter johrii* comb. nov.

C. joh'ri.i (N.L. gen. n. *johrii*, of B. N. Johri, an eminent and well-known Indian microbiologist).

Basonym: *Rhodobacter johrii* Girija et al., 2010

The description is as given for *Rhodobacter johrii* (Girija et al., 2010). The genomic G+C content of the type strain is 69.1%. Its approximate genome size is 4.51 Mbp. The type strain is JA192 = DSM 18678 = JCM 14543.

Description of *Cereibacter ovatus* comb. nov.

C. o.va'tus (L. masc. adj. *ovatus*, egg-shaped, ovate).

Basonym: *Rhodobacter ovatus* Srinivas et al., 2008

The description is as given for *Rhodobacter ovatus* (Srinivas et al., 2008) with the following modification. The G+C content of the type-strain genome is 66.5%, its approximate size 3.81 Mbp. The type strain is JA234 = CCUG 55049 = JCM 14779.

Description of *Cereibacter sphaeroides* comb. nov.

C. sphae.ro.i'des (L. fem. n. *sphaera*, sphere, globe; L. suff. *-oides*, from Greek suffix *eides*, from Greek noun *eidos*, that which is seen, form, shape, figure, resembling, similar; N.L. masc. adj. *sphaeroides*, spherical).

Basonym: *Rhodopseudomonas sphaeroides* van Niel, 1944 (Approved Lists 1980)

The description is as given for *Rhodobacter sphaeroides* (Imhoff et al., 1984). The genomic G+C content of the type strain is 68.8%. Its approximate genome size is 4.60 Mbp. The type strain is CECT 300 = DSM 158 = JCM 6121.

Description of *Cypionkella aquatica* comb. nov.

C. a.qua'ti.ca (L. fem. adj. *aquatica*, growing or found in water).

Basonym: *Pseudorhodobacter aquaticus* Li L. et al., 2016

The description is as given for *Pseudorhodobacter aquaticus* (Li A.-H. et al., 2016). The type strain is DC2N1-10 = CGMCC 1.14433 = KCTC 52040.

Description of *Cypionkella collinsensis* comb. nov.

C. col.lins.en'sis (N.L. fem. adj. *collinsensis*, pertaining to Collins, an icecap of Antarctic, from where the type strain was isolated).

Basonym: *Pseudorhodobacter collinsensis* Zhang et al., 2016

The description is as given for *Pseudorhodobacter collinsensis* (Zhang et al., 2016). The type strain is 4-T-34 = CCTCC AB 2014005 = LMG 28256.

Description of *Cypionkella psychrotolerans* comb. nov.

C. psy.chro.to'le.rans (Gr. masc. adj. *psychros*, cold; L. pres. part. *tolerans*, tolerating; N.L. part. adj. *psychrotolerans*, cold-tolerating).

Basonym: *Pseudorhodobacter psychrotolerans* Lee et al., 2016

The description is as given for *Pseudorhodobacter psychrotolerans* (Lee et al., 2016). The type strain is JCM 30764 = KCTC 42640.

Description of *Cypionkella sinensis* comb. nov.

C. sin.en'sis (N.L. fem. adj. *sinensis*, pertaining to China, referring to the geographical origin of the type strain).

Basonym: *Pseudorhodobacter sinensis* Li L. et al., 2016

The description is as given for *Pseudorhodobacter sinensis* (Li A.-H. et al., 2016). The type strain is Y1R2-4 = CGMCC 1.14435 = KCTC 52039.

Description of *Elkelangia baekryungensis* comb. nov.

L. baek.ryung.en'sis (N.L. fem. adj. *baekryungensis*, of Baekryung Island, an island of the Yellow Sea in Korea where the type strain was isolated).

Basonym: *Sphingopyxis baekryungensis* Yoon et al., 2005a

The description is as given for *Sphingopyxis baekryungensis* (Yoon et al., 2005a). The type strain is DSM 16222 = KCTC 12231.

Description of *Magnetospirillum chandramohanii* comb. nov.

M. chan.dra.mo.han'i.i (N.L. gen. n. *chandramohanii*, of Chandramohan, named after Dr. D. Chandramohan, an Indian marine microbiologist, who has played a crucial role in transforming microbiological research at the National Institute of Oceanography, India, into technologically rewarding activities).

Basonym: *Phaeospirillum chandramohanii* Anil Kumar et al., 2009

The description is as given for *Phaeospirillum chandramohanii* (Anil Kumar et al., 2009). The type strain is JA145 = JCM 14933 = KCTC 5703.

Description of *Magnetospirillum fulvum* comb. nov.

M. ful'vum (L. neut. adj. *fulvum*, deep yellow, reddish yellow, tawny).

Basonym: *Rhodospirillum fulvum* van Niel, 1944 (Approved Lists 1980)

The description is as given for *Phaeospirillum fulvum* (Imhoff et al., 1998). The type strain is NCIMB 11762 = ATCC 15798 = DSM 113.

Description of *Magnetospirillum molischianum* comb. nov.

M. mo.lisch.i.a'num (N.L. neut. adj. *molischianum*, pertaining to Molisch, named for H. Molisch, an Austrian botanist).

Basonym: *Rhodospirillum molischianum* Giesberger, 1947 (Approved Lists 1980)

The description is as given for *Phaeospirillum molischianum* (Imhoff et al., 1998). The genomic G+C content of the type strain is 61.5%. Its approximate genome size is 3.81 Mbp. The type strain is ATCC 14031 = DSM 120 = LMG 4354.

Description of *Magnetospirillum oryzae* comb. nov.

M. o.ry'zae (L. gen. n. *oryzae*, of rice, pertaining to the isolation of the type strain from rice paddy soil).

Basonym: *Phaeospirillum oryzae* Lakshmi et al., 2011

The description is as given for *Phaeospirillum oryzae* (Lakshmi et al., 2011). The type strain is JA317 = KCTC 5704 = NBRC 104938.

Description of *Magnetospirillum tilakii* comb. nov.

M. ti.la'ki.i (N.L. gen. n. *tilakii*, of Tilak, named after Dr. K. V. B. R. Tilak, an eminent microbiologist in India).

Basonym: *Phaeospirillum tilakii* Raj et al., 2012

The description is as given for *Phaeospirillum tilakii* (Raj et al., 2012). The type strain is JA492 = KCTC 15012 = NBRC 107650.

Description of *Meinhardsimonia xiamenensis* comb. nov.

M. xia.men.en'sis (N.L. fem. adj. *xiamenensis*, of or pertaining to Xiamen, the city where the organism was first isolated).

Basonym: *Albidovulum xiamenense* Yin et al., 2012

The description is as given for *Albidovulum xiamenense* (Yin et al., 2012). The genomic G+C content of the type

strain is 68.2%. Its approximate genome size is 3.13 Mbp. The type strain is CGMCC 1.10789 = DSM 24422 = LMG 26247 = MCCC 1A06317.

Description of *Mycoplana subbaraonis* comb. nov.

M. sub.ba.ra.o'nis (N.L. gen. n. *subbaraonis*, of Subba Rao, named after Professor N. S. Subba Rao, an eminent microbiologist who significantly contributed to the knowledge of *Rhizobium* biofertilizers in India).

Basonym: *Rhizobium subbaraonis* Ramana V.V. et al., 2013

The description is as given for *Rhizobium subbaraonis* (Ramana C.V. et al., 2013) with the following modification. The G+C content of the type-strain genome is 63.1%, its approximate size 6.58 Mbp. The type strain is DSM 24765 = KCTC 23614.

Description of *Neopararhizobium haloflavum* comb. nov.

N. ha.lo fla'vum (Gr. masc. n. *hals/halos*, salt; L. masc. adj. *flavus*, yellow; N.L. neut. adj. *haloflavum*, salty and yellow).

Basonym: *Pararhizobium haloflavum* Shen et al., 2018

The description is as given for *Pararhizobium haloflavum* (Shen et al., 2018). The type strain is KCTC 52582 = MCCC 1K03228.

Description of *Neorhizobium vignae* comb. nov.

N. vi'gnae (N.L. gen. n. *vignae*, of *Vigna*, referring to the fact that the majority of strains were isolated from the mung bean, *Vigna radiata*).

Basonym: *Rhizobium vignae* Ren et al., 2011

The description is as given for *Rhizobium vignae* (Ren et al., 2011). The type strain is HAMBI 3039 = DSM 25378 = LMG 25447.

Description of *Niveispirillum irakense* comb. nov.

N. i.rak.en'se (N.L. neut. adj. *irakense*, pertaining to the country of Iraq).

Basonym: *Azospirillum irakense* Khammas et al. 1991.

The description is as given for *Azospirillum irakense* (Khammas et al., 1989). The genomic G+C content of the type strain is 63.0%. Its approximate genome size is 5.45 Mbp. The type strain is KBC1 = ATCC 51182 = DSM 11586.

Description of *Pacificitalea manganoxidans* comb. nov.

P. man.gan.o'xi.dans (N.L. neut. n. *manganum*, manganese; N.L. pres. part. *oxidans*, oxidizing; N.L. part. adj. *manganoxidans*, manganese-oxidizing).

Basonym: *Celeribacter manganoxidans* Wang Y.X. et al., 2015

The description is as given for *Celeribacter manganoxidans* (Wang L. et al., 2015). The type strain is DY2-5 = DSM 27541 = JCM 19384.

Description of *Pelagimonas phthalicica* comb. nov.

P. phtha.li'ci.ca (N.L. neut. n. *acidum phthalicum*, phthalic acid; L. fem. suff. *-ica*, suffix used with the sense of belonging to; N.L. fem. adj. *phthalicica*, belonging to phthalic acid, referring to the substrate *phthalic* acid that can be utilized by the species).

Basonym: *Tropicibacter phthalicus* Iwaki et al., 2012

The description is as given for *Tropicibacter phthalicus* (Iwaki et al., 2012). The type strain is DSM 26923 = JCM 17793 = KCTC 23703.

Description of *Pseudoprimorskyibacter insulae* comb. nov.

P. in'su.lae (L. gen. n. *insulae*, of an island, referring to the source of isolation of the type strain).

Basonym: *Primorskyibacter insulae* Parker et al., 2019

The description is as given for *Primorskyibacter insulae* (Park et al., 2015a). The type strain is CECT 8871 = KCTC 42602.

Description of *Pseudovibrio exalbescens* comb. nov.

P. ex.al.bes'cens (L. part. adj. *exalbescens*, (from L. v. *exalbesco*) becoming white, growing white, referring to the fading color of maturing colonies).

Basonym: *Nesiotobacter exalbescens* Donachie et al., 2006

The description is as given for *Nesiotobacter exalbescens* (Donachie et al., 2006) with the following modification. The G+C content of the type-strain genome is 55.1%, its approximate size 4.15 Mbp. The type strain is LA33B = DSM 16456 = ATCC BAA-994.

Description of *Rhizorhabdus histidinilytica* comb. nov.

R. his.ti.di.ni.ly'ti.ca (N.L. neut. n. *histidinum*, histidine; N.L. fem. adj. *lytica*, from Greek fem. adj. *lytikê*, able to loose, able to dissolve; N.L. fem. adj. *histidinilytica*, histidine-dissolving).

Basonym: *Sphingomonas histidinilytica* Nigam et al., 2010

The description is as given for *Sphingomonas histidinilytica* (Nigam et al., 2010). The type strain is CCM 7545 = DSM 24951 = MTCC 9473.

Description of *Rhizorhabdus starnbergensis* comb. nov.

R. starn.berg.en'sis (N.L. fem. adj. *starnbergensis*, of or pertaining to Lake Starnberg, Bavaria, Germany, from where the organism was isolated).

Basonym: *Sphingomonas starnbergensis*

Chen W.-M. et al., 2013

The description is as given for *Sphingomonas starnbergensis* (Chen H. et al., 2013). The type strain is DSM 25077 = LMG 26763.

Description of *Rhizorhabdus wittichii* comb. nov.

R. wit.tich.i'i (N.L. gen. n. *wittichii*, of Wittich, referring to Rolf-Michael Wittich, the German bacteriologist who first isolated this potent metabolizer of dibenzo-p-dioxin from the water of the river Elbe and described the metabolism of the compound by this organism).

Basonym: *Sphingomonas wittichii* Yabuuchi et al., 2001

The description is as given for *Sphingomonas wittichii* (Kim M.C. et al., 2016). The type strain is CCUG 31198 = DSM 6014 = JCM 10273.

Description of *Roseibium aggregatum* comb. nov.

R. ag.gre.ga'tum (L. neut. adj. *aggregatum*, joined together).

Basonym: *Stappia aggregata* (ex Ahrens 1968) Uchino et al. 1999.

The description is as given for *Labrenzia aggregata* (Biebl et al., 2007). The type strain is ATCC 25650 = DSM 13394 = IFO 16684 = JCM 20685 = LMG 122 = NBRC 16684 = NCIMB 2208.

Description of *Roseibium album* comb. nov.

R. album (L. neut. adj. *album*, white).

Basonym: *Stappia alba* Pujalte et al. 2006.

The description is as given for *Labrenzia alba* (Biebl et al., 2007) with the following addition. The genomic G+C content of the type strain is 56.4%. Its approximate genome size is 6.90 Mbp. The type strain is CECT 5095 = CIP 108402 = DSM 18320 = DSM 18380.

Description of *Roseibium alexandrii* comb. nov.

R. alexandrii (N.L. gen. n. *alexandrii*, of *Alexandrium*, the genus name of the dinoflagellate *Alexandrium lusitanicum*, the source of isolation of the type strain).

Basonym: *Labrenzia alexandrii* Biebl et al., 2007

The description is as given for *Labrenzia alexandrii* (Biebl et al., 2007). The type strain is DSM 17067 = NCIMB 14079.

Description of *Roseibium marinum* comb. nov.

R. marinum (L. neut. adj. *marinum*, of the sea, marine).

Basonym: *Stappia marina* Kim et al. 2006.

The description is as given for *Labrenzia marina* (Biebl et al., 2007). The type strain is DSM 17023 = KCTC 12288.

Description of *Roseibium salinum* comb. nov.

R. salinum (N.L. neut. adj. *salinum*, salted, referring to the saline habitat of the micro-organism).

Basonym: *Labrenzia salina* Camacho et al., 2016

The description is as given for *Labrenzia salina* (Camacho et al., 2016). The type strain is CECT 8816 = DSM 29163.

Description of *Roseibium suaedae* comb. nov.

R. suaedae (N.L. gen. n. *suaedae*, of the plant *Suaeda corniculata*, referring to the isolation of the type strain from the roots of *Suaeda corniculata*).

Basonym: *Labrenzia suaedae* Bibi et al., 2014

The description is as given for *Labrenzia suaedae* (Bibi et al., 2014) with the following modification. The G+C content of the type-strain genome is 60.2%, its approximate size 5.14 Mbp. The type strain is DSM 22153 = KACC 13772.

Description of *Roseovarius litorisediminis* comb. nov.

R. litorisediminis (L. neut. n. *litus/-oris*, the seashore, coast; L. n. *sedimen/-inis*, sediment; N.L. gen. n. *litorisediminis*, of a coastal sediment, tidal flat sediment).

Basonym: *Pelagicola litorisediminis* Park et al. 2013.

The description is as given for *Pelagicola litorisediminis* (Park et al., 2013a). The type strain is D1-W8 = CECT 8287 = KCTC 32327.

Description of *Ruegeria meteori* comb. nov.

R. meteori (N.L. gen. n. *meteori*, of meteor, after the German research vessel Meteor).

Basonym: *Agrobacterium meteori* Rüger and Höfle, 1992

Agrobacterium meteori (Rüger and Höfle, 1992) with the following modification. The G+C content of the type-strain genome is 56.5%, its approximate size 4.83 Mbp. The type strain is ATCC 700001 = CECT 4293 = DSM 5824.

Description of *Salipiger pacificus* comb. nov.

S. pacificus (L. masc. adj. *pacificus*, peacemaking, pacific, and by extension pertaining to the Pacific Ocean, the origin of the type strain).

Basonym: *Yangia pacifica* Dai et al., 2006

The description is as given for *Yangia pacifica* (Dai et al., 2006). The genomic G+C content of the type strain is 66.3%. Its approximate genome size is 6.14 Mbp. The type strain is CGMCC 1.3455 = DSM 26894 = JCM 12573.

Description of *Tabrizicola blastica* comb. nov.

T. blastica (Gr. adj. *blastikos/-ê/-on*, budding, sprouting; N.L. fem. adj. *blastica*, budding, apt to bud).

Basonym: *Rhodopseudomonas blastica* Eckersley and Dow 1981.

The description is as given for *Rhodobacter blasticus* (Kawasaki et al., 1993). The type strain is ATCC 33485 = CIP 104374 = DSM 2131 = DSM 26431 = IFO 16437 = LMG 4305 = NBRC 16437 = NCIMB 11576.

Description of *Thalassobius litoralis* comb. nov.

T. litoralis (L. masc. adj. *litoralis*, of or belonging to the seashore, referring to the supralittoral habitat from which the type strain was isolated).

Basonym: *Lutimaribacter litoralis* Iwaki et al., 2013

The description is as given for *Lutimaribacter litoralis* (Iwaki et al., 2013). The type strain is DSM 29506 = JCM 17792 = KCTC 23660.

Description of *Thalassobius taeanensis* comb. nov.

T. taeanensis (N.L. masc. adj. *taeanensis*, of or belonging to Taean, from where the organism was isolated).

Basonym: *Litorimicrobium taeanense* Jin et al., 2011

The description is as given for *Litorimicrobium taeanense* (Jin et al., 2011). The genomic G+C content of the type strain is 60.5%. Its approximate genome size is 4.02 Mbp. The type strain is DSM 22007 = KACC 13706.

Description of *Tranquillimonas rosea* comb. nov.

T. rosea (L. fem. adj. *rosea*, rose-colored, pink).

Basonym: *Roseivivax roseus* Zhang et al., 2014a.

The description is as given for *Roseivivax roseus* (Zhang et al., 2014c) with the following modification. The G+C content of the type-strain genome is 67.8%, its approximate size 4.23 Mbp. The type strain is BH87090 = DSM 23042 = KCTC 22650.

Description of *Tritonibacter mobilis* comb. nov.

T. mobilis (L. masc. adj. *mobilis*, movable, motile).

Basonym: *Ruegeria mobilis* Muramatsu et al., 2007

The description is as given for *Epibacterium mobile* (Wirth and Whitman, 2018). The type strain is CIP 109181 = DSM 23403 = NBRC 101030.

Description of *Tritonibacter multivorans* comb. nov.

T. multivorans (L. masc. adj. *multus*, many, numerous; L. v. *vorare*, to devour, swallow; N.L. part. adj. *multivorans*, devouring many, referring to the utilization of numerous different substrates for growth).

Basonym: *Tropicibacter multivorans* Lucena et al., 2012

The description is as given for *Epibacterium multivorans* (Wirth and Whitman, 2018). The genomic G+C content of the type strain is 59.7%. Its approximate genome size is 4.15 Mbp. The type strain is CECT 7557 = DSM 26470 = KCTC 23350.

Description of *Tritonibacter scottomollicae* comb. nov.

T. scottomollicae (N.L. gen. n. *scottomollicae*, of Scotto-Mollica, in honor of Dr. Victoria Scotto-Mollica and Dr. Alfonso Mollica, both of whom were pioneers in the field of microbe-induced corrosion of steels and the generation of electroactive seawater biofilms).

Basonym: *Ruegeria scottomollicae* Vandecandelaere et al. 2008

The description is as given for *Epibacterium scottomollicae* (Wirth and Whitman, 2018). The type strain is CCUG 55858 = DSM 25328 = LMG 24367.

Description of *Tritonibacter ulvae* comb. nov.

T. ulvae (N.L. gen. n. *ulvae*, of *Ulva*, the name of a genus of green algae, as the type strain was isolated from a frond surface of *Ulva pertusa* Kjellman).

Basonym: *Epibacterium ulvae* Penesyan et al., 2013

The description is as given for *Epibacterium ulvae* (Penesyan et al., 2013). The type strain is DSM 24752 = LMG 26464.

Description of *Vanniella litorea* comb. nov.

V. litorea (L. fem. adj. *litorea*, living near the sea, of or belonging to the seashore).

Basonym: *Oceanicola litoreus* Park et al., 2013a

The description is as given for *Oceanicola litoreus* (Park et al., 2013c). The type strain is CCUG 62794 = DSM 29440 = KCTC 32083.

Description of *Wagnerdoeblera megaterium* comb. nov.

W. megaterium (Gr. masc. adj. *megas*, large; Gr. neut. n. *teras/-atos*, monster, beast; N.L. neut. n. *megaterium*, big beast).

Basonym: *Gemmobacter megaterium* Liu K. et al., 2014

The description is as given for *Gemmobacter megaterium* (Liu J.-J. et al., 2014) with the following modification. The G+C content of the type-strain genome is 64.9%, its approximate size 4.17 Mbp. The type strain is CF17 = DSM 26375 = JCM 18498.

Description of *Wagnerdoeblera nectariphila* comb. nov.

W. nectariphila (L. n. *nectar*, nectar; N.L. fem. adj. *phila*, friend, loving (from Gr. masc. adj. *philos*); N.L. fem. adj. *nectariphila*, loving nectar, referring to the stimulation of growth by excretions of other bacteria).

Basonym: *Gemmobacter nectariphilus* (Tanaka et al., 2004) Chen W.-M. et al., 2013

The description is as given for *Gemmobacter nectariphilus* (Chen W.-M. et al., 2013) with the following modification. The G+C content of the type-strain genome is 66.2%, its approximate size 4.52 Mbp. The type strain is AST4 = DSM 15620 = JCM 11959.

Taxonomic Consequences: New Subspecies**Description of *Borrelia garinii* subsp. *bavariensis* subsp. nov.**

B. garinii subsp. *bavariensis* (N.L. fem. adj. *bavariensis*, of or belonging to Bavaria, from where the type strain was isolated).

The description is as given for *Borrelia bavariensis* (Margos et al., 2013). The type strain is PBi = ATCC BAA-2496 = DSM 23469.

Description of *Gluconobacter japonicus* subsp. *nephelii* subsp. nov.

G. japonicus subsp. *nephelii* (N.L. neut. n. *Nepheleum*, the generic name of rambutan, *Nepheleum lappaceum*, a tropical fruit; N.L. gen. n. *nephelii*, of *Nepheleum*, from which the type strain was isolated).

The description is as given for *Gluconobacter nephelii* (Kommanee et al., 2011). The type strain is RBY-1 = BCC 36733 = NBRC 106061.

Description of *Methylobacterium dichloromethanicum* subsp. *chloromethanicum* subsp. nov.

M. dichloromethanicum subsp. *chloromethanicum* (N.L. neut. n. *chloromethanicum*, chloromethane-utilizing).

The description is as given for *Methylobacterium chloromethanicum* (McDonald et al., 2001). The type strain is CM4 = NCIMB 13688 = VKM B-2223.

Description of *Rhizobium marinum* subsp. *pelagicum* subsp. nov.

R. marinum subsp. *pelagicum* (L. neut. adj. *pelagicum*, of or belonging to the sea).

The description is as given for *Pseudorhizobium pelagicum* (Kimes et al., 2015). The type strain is R1-200B4 = CECT 8629 = LMG 28314.

Description of *Rhizobium mongolense* subsp. *loessense* subsp. nov.

R. mongolense subsp. *loessense* (N.L. neut. adj. *loessense*, referring to the Loess Plateau of China, where the bacterium was isolated).

The description is as given for *Rhizobium loessense* (Wei et al., 2003). The type strain is CGMCC 1.3401 = CIP 108030 = LMG 21975.

Description of *Rickettsia conorii* subsp. *gravesii* subsp. nov.

R. conorii subsp. *gravesii* (N.L. gen. n. *gravesii*, of Graves, named after Professor Stephen Graves, founder of the Australian

Rickettsial Reference Laboratory and a major contributor to rickettsial research in Australia).

The description is as given for *Rickettsia gravesii* (Abdad et al., 2017). The type strain is BWI-1 = ATCC VR-1664 = CSUR R172.

Description of *Rickettsia conorii* subsp. *heilongjiangensis* subsp. nov.

R. conorii subsp. *heilongjiangensis* (N.L. fem. adj. *heilongjiangensis*, from Heilongjiang, the Chinese province where the *D. silvarum* tick providing the first isolate was collected).

The description is as given for *Rickettsia heilongjiangensis* (Fournier et al., 2003). The genomic G+C content of the type strain is 32.3%. Its approximate genome size is 1.28 Mbp. The type strain is 054 = ATCC VR-1524 = CSUR 054.

Description of *Rickettsia conorii* subsp. *raoultii* subsp. nov.

R. conorii subsp. *raoultii* (N.L. gen. n. *raoultii*, of Raoult, named after Professor Didier Raoult, founder of the WHO-Collaborative Centre for Rickettsioses, Borrelioses and Tick-borne Infections in Marseilles, France, and a major contributor to the study of rickettsiae).

The description is as given for *Rickettsia raoultii* (Mediannikov et al., 2008). The type strain is Khabarovsk = ATCC VR-1596 = CSUR R3.

Description of *Rickettsia tamurae* subsp. *buchneri* subsp. nov.

R. tamurae subsp. *buchneri* (N.L. gen. n. *buchneri*, of Buchner, named in honor of Dr. Paul Buchner, a German biologist who made pioneering contributions to the identification of non-pathogenic tick endosymbionts that are transovarially transmitted).

The description is as given for *Rickettsia buchneri* (Kurtti et al., 2015). The type strain is ISO-7 = DSM 29016 = ATCC VR-1814.

Description of *Tritonibacter mobilis* subsp. *pelagius* subsp. nov.

T. mobilis subsp. *pelagius* (L. masc. adj. *pelagius*, of the sea).

The description is as given for *Ruegeria pelagia* (Lee et al., 2007c). The type strain is HTCC2662 = KCCM 42378 = NBRC 102038.

Taxonomic Consequences: Emendations of Orders

Emended Description of *Hyphomicrobiales* Douglas et al. 1957 (Approved Lists 1980)

The description is as given for *Rhizobiales* (Kuykendall, 2005), which is an illegitimate synonym, with the following additions. The order consists of the families *Ancalomicrobiaceae*, *Aurantimonadaceae*, *Bartonellaceae*, *Beijerinckiaceae*, *Nitrobacteraceae*, *Brucellaceae*, *Chelatococcaceae*, *Cohaesibacteraceae*, *Hyphomicrobiaceae*, *Methylobacteriaceae*, *Methylocystaceae*, *Notoacmeibacteraceae*, *Phyllobacteriaceae*, *Rhizobiaceae*, *Rhodobiaceae*, *Xanthobacteraceae*. In addition to the new families *Acuticoccaceae* fam. nov., *Affellaceae* fam. nov., *Ahrensiaceae* fam. nov., *Amorphaceae* fam. nov.,

Blastochloridaceae fam. nov., *Breoghaniaceae* fam. nov., *Devosiaceae* fam. nov., *Kaistiaceae* fam. nov., *Parvibaculaceae* fam. nov., *Phreatobacteraceae* fam. nov., *Pleomorphomonadaceae* fam. nov., *Pseudoxanthobacteraceae* fam. nov., *Stappiaceae* fam. nov. and *Tepidamorphaceae* fam. nov. The type genus is *Hyphomicrobium*.

Emended Description of *Kordiimonadales* Kwon et al. 2005

The description is as given before (Kwon et al., 2005) with the following modifications. Cells are Gram-negative, rod-shaped, motile, aerobic heterotrophs. This order houses *Kordiimonadaceae* fam. nov., which is currently the sole family of the order. The type genus is *Kordiimonas*.

Emended Description of *Rhodobacterales* Garrity et al. 2006

The description is as given before (Garrity et al., 2005d) with the following modifications. This order houses *Neomegalonemataceae* fam. nov. in addition to the previously included families. The type genus is *Rhodobacter*.

Emended Description of *Rhodospirillales* Pfennig and Trüper 1971 (Approved Lists 1980)

The description is as given before (Pfennig and Trüper, 1971) with the following modification. The order contains the families *Acetobacteraceae* and *Kiloniellaceae*. In addition to the new families *Azospirillaceae*, fam. nov., *Reyraneliaceae* fam. nov., *Rhodospirillaceae*, *Rhodovibrionaceae*, fam. nov., *Stellaceae* fam. nov., *Terasakiellaceae* fam. nov., *Thalassobaculaceae* fam. nov., *Thalassospiraceae* fam. nov. and *Zavarziniaceae* fam. nov. The order contains heterotrophs as well as autotrophs. The type genus is *Rhodospirillum*.

Emended Description of *Sphingomonadales* Yabuuchi and Kosako 2006

The description is as given before (Garrity et al., 2005d) with the following modification. This order houses *Zymomonadaceae*, fam. nov. and *Sphingosinicellaceae*, fam. nov., in addition to the previously included families. The type genus is *Sphingomonas*.

Emended Description of *Spirochaetales* Buchanan 1917 (Approved Lists 1980) emend. Gupta et al., 2013

The description is as given before (Gupta et al., 2013) with the following modification. This order contains the families *Sphaerochaetaceae*, *Spirochaetaceae*, and *Treponemataceae*. The order comprises motile as well as non-motile bacteria. The type genus is *Spirochaeta*.

Taxonomic Consequences: Emendations of Families

Emended Description of *Acetobacteraceae* (ex *Henrici* 1939) Gillis and De Ley 1980

The description is as given before (Gillis and De Ley, 1980) with the following modification. This family houses *Acidicaldus*, *Gluconacetobacter*, *Neosaia*, *Roseococcus*, *Swaminathania*, *Rubritepida*, *Saccharibacter*, *Swingsia*, *Teichococcus*,

Dankookia, *Crenalkalicoccus*, *Acetobacter*, *Ameyamaea*, *Asaia*, *Gluconobacter*, *Granulibacter*, *Humitalea*, *Kozakia*, *Muricoccus*, *Paracraurococcus*, *Tanticharoenia*, *Acidiphilium*, *Acidisoma*, *Acidisphaera*, *Acidocella*, *Acidomonas*, *Belnapia*, *Bombella*, *Craurococcus*, *Endobacter*, *Komagataebacter*, *Neokomagataea*, *Nguyenibacter*, *Rhodopila*, *Rhodovarius*, *Roseomonas* (including *Muricoccus* and *Teichococcus*), *Caldovatus*, *Elioraea*, *Siccirubricoccus* and *Rhodovastum*. The type genus is *Acetobacter*.

Emended Description of *Beijerinckiaceae* Garrity et al. 2006 emend. Dedysh et al. 2016

The description is as given before (Garrity et al., 2005d; Dedysh et al., 2016), with the following modification. This family houses *Beijerinckia* (the type genus), *Methylocapsa*, *Methylocella*, *Methyloferula*, *Methylorosula*, and *Methylovirgula*.

Emended Description of *Cohaesibacteraceae* Hwang and Cho 2018 emend. Gallego et al. 2010

The description is as given before (Hwang and Cho, 2008a; Gallego et al., 2010) with the following modification. This family houses *Cohaesibacter*, which is the type and currently the sole genus of the family.

Emended Description of *Ehrlichia* Moshkovski 1945 (Approved Lists 1980)

The description is as given for *Anaplasmataceae* (Philip, 1957; Dumler et al., 2001) with the following additions. This family houses *Anaplasma*, *Ehrlichia* (the type genus), *Lyticum* and *Neorickettsia*. The genera *Aegyptianella*, *Cowdria* and *Wolbachia* (for which cultures and 16S rRNA gene sequences of type strains are missing) are also tentatively assigned to this family.

Emended Description of *Erythrobacteraceae* Lee et al. 2005 emend. Xu et al. 2009

The description is as given before (Lee et al., 2005; Xu X.-W. et al., 2009) with the following modification. Some genera of this family contain carotenoids and bacteriochlorophyll α . This family houses *Novosphingobium*, in addition to the previously included genera. The type genus is *Erythrobacter*.

Emended Description of *Geminicoccaceae* Proença et al. 2018

The description is as given before (Proença et al., 2018) with the following modification. Cells are cocci, diplococci or rods. This family houses *Arboricoccus* and *Geminicoccus* (the type genus). *Defluviicoccus* and *Tistrella* are tentatively assigned to this family as well.

Emended Description of *Hyphomicrobiaceae* Babudieri 1950 (Approved Lists 1980)

Cells are Gram negative, mostly rod-shaped or ovoid, usually non-motile, predominantly aerobic. The family contains heterotrophic as well as phototrophic genera. The major ubiquinone is Q-10. This family houses *Caenibius*, *Dichotomicrobium*, *Filomicrobium*, *Hyphomicrobium* (the type genus), *Methyloceanibacter*, *Methyloligella*, *Pedomicrobium*, *Rhodomicrobium*, and *Seliberia*.

Emended Description of *Kiloniellaceae* Wiese et al. 2009

The description is as given before (Wiese et al., 2009) with the following modification. Cells are rod-, spiral- or vibrio-shaped. The G+C content of the DNA is 50-61%. This family houses *Kiloniella* (the type genus) and *Aestuariuspira*. *Marivibrio* and *Thalassocola* are tentatively assigned to this family as well.

Emended Description of *Methylobacteriaceae* Garrity et al. 2006

The description is as before (Garrity et al., 2005c) with the following modification. Colonies are usually pink or cream colored. Cells are Gram-negative, are rod-shaped, non-motile or motile. Aerobic with Chemoorganoheterotrophic or chemolithoheterotrophic metabolism. The major cellular fatty acids are usually C_{18:1} ω 7c and C_{16:1} ω 7c. The major ubiquinone is Q-10. The G+C content is 60-70 mol%. The family currently comprises the genera *Microvirga*, *Methylobacterium* (the type genus), *Protomonas* and *Psychroglaciecola*. *Enterovirga* is tentatively assigned to this family.

Emended Description of *Methylocystaceae* Bowman 2006

The description is as given before (Bowman, 2005) with the following modification. This family houses *Methylocystis* (the type genus) and *Methylosinus*.

Emended Description of *Nitrobacteraceae* Buchanan 1917 (Approved Lists 1980)

The description is as given for *Bradyrhizobiaceae* (Garrity et al., 2005e), which is an illegitimate synonym of the family, with the following additions. This family houses *Afipia*, *Blastobacter*, *Bradyrhizobium* (including *Agromonas*), *Nitrobacter* (the type genus), *Pseudolabrys*, *Pseudorhodoplanes*, *Rhodopseudomonas*, *Tardiphaga* and *Variibacter*. *Rhodoplanes* is tentatively assigned to this family as well.

Emended Description of *Notoacmeibacteraceae* Huang et al. 2017

The description is as before (Huang et al., 2017), with the following modification. Gram-stain-negative, oxidase- and catalase-positive, aerobic or facultatively anaerobic heterotrophs. The predominant respiratory quinone is Q-10. The major fatty acids are usually C_{18:1} ω 7c and C_{18:1} ω 6c. The family contains *Mabikibacter*, *Notoacmeibacter* (the type genus), and *Zhengella*.

Emended Description of *Phyllobacteriaceae* Mergaert and Swings 2006

The description is as given for *Phyllobacteriaceae* (Mergaert and Swings, 2005) with the following additions. Cells are Gram-negative, rod, ovoid or coccoid shaped and usually motile by flagella. Predominantly aerobic heterotrophs. Generally catalyze and oxidase positive. The predominant respiratory quinone is Q-10. The major polar lipids are phosphatidylcholin, phosphatidylethanolamine and phosphatidylglycerol. The major fatty acids is usually C_{18:1} ω 7c. The G+C content of the DNA is 56-64%. This family

houses *Aminobacter*, *Aquamicrobium*, *Chelativorans* (including *Thermovum*), *Chelatobacter*, *Corticibacterium*, *Defluviobacter*, *Mesorhizobium*, *Nitratireductor*, *Oricola*, *Phyllobacterium* (the type genus), *Pseudaminobacter*, *Pseudohoeflea*, *Roseitalea*, and *Tianweitania*.

Emended Description of *Rhizobiaceae* Conn 1938 (Approved Lists 1980)

The description is as before (Conn, 1938) with the following modification updated in accordance to later findings (Peix et al., 2005; Rahul et al., 2015). Cells are Gram-negative, mostly rod-shaped, usually motile, aerobic and generally heterotrophic with some autotrophic genera. The major respiratory quinone is Q-10. The G+C content is 49–68%. The family contains *Hoeflea*, *Lentilitoribacter*, *Martellella*, *Mycoplana*, and *Neoparahizobium* along with the previously included genera except for *Kaistia*, which has been removed from the family. The type genus is *Rhizobium*.

Emended Description of *Rhodobacteraceae* Garrity et al. 2006

The description is as given before (Garrity et al., 2005b) with the following modification. *Rhodobacteraceae* houses multiple and diverse genera but not *Ahrensia*, *Gemmobacter*, *Hyphomonas*, *Maricaulis*, *Methylarcula*, *Pannonibacter*, *Roseibium*, and *Stappia* as stated in the initial description. Additionally the following new genera are included to this family: *Albibacillus*, *Allgaiera*, *Allosediminivita*, *Bieblia*, *Cypionkella*, *Meinhardsimonia*, *Pacificitalea*, *Pseudoprimorskyibacter*, *Vanniella*, and *Wagnerdoeblera*. The type genus is *Rhodobacter*.

Emended Description of *Rhodobiaceae* Garrity et al. 2006

The description is as given before (Garrity et al., 2005f) with the following modification. This family houses *Rhodobium* which is the type and currently the sole genus of the family.

Emended Description of *Rhodospirillaceae* Pfennig and Trueper 1971 (Approved Lists 1980)

The description is as given before (Pfennig and Trüper, 1971), with the following modification. This family houses *Caenispirillum*, *Conglomeromonas*, *Haematospirillum*, *Insolitispirillum*, *Magnetospirillum*, *Marispirillum*, *Novispirillum*, *Pararhodospirillum*, *Phaeospirillum*, *Phaeovibrio*, *Rhodospira*, *Rhodospirillum* (the type genus), *Roseospira*, *Roseospirillum*, and *Telmatospirillum*.

Emended Description of *Roseiarcaceae* Kulichevskaya et al. 2014

The description is as before (Kulichevskaya et al., 2014) with the following modification after inclusion of *Rhodoblastus*. The major cellular fatty acids are usually C_{16:0}, C_{16:1}, C_{18:1} ω7c and sometimes C_{19:0} ω8c. The family contains *Roseiarcus* (the type genus) and *Rhodoblastus*.

Emended Description of *Sneathiellaceae* Kurahashi et al. 2008

The description is as before (Kurahashi et al., 2008) with the following modification. This family houses *Oceanibacterium*

and *Sneathiella* (the type genus). *Ferrovibrio*, *Taonella* and *Marinibaculum* are tentatively assigned to this family.

Emended Description of *Sphingomonadaceae* Kosako et al. 2000

The description is as given before (Kosako et al., 2000) with the following modification. This family houses *Blastomonas* (including *Erythromonas*), *Hephaestia*, *Parablastomonas*, *Parasphingopyxis*, *Rhizorhabdus*, *Rhizorhapis* (including *Rhizomonas*), *Sphingobium*, *Sphingomicrobium*, *Sphingomonas* (the type genus), *Sphingopyxis*, *Sphingorhabdus* and *Stakelama*. Additionally the following new genera are included as well: *Allospingosinicella* and *Elkelangia*.

Emended Description of *Spirochaetaceae* Swellengrebel 1907 (Approved Lists 1980) emend. Abt et al. 2012 emend. Gupta et al. 2013

The description is as given before (Gupta et al., 2013), with the following modification. This family houses *Alkalispirochaeta*, *Marispirochaeta*, *Oceanispirochaeta*, *Salinispira*, *Sediminspirochaeta*, and *Spirochaeta* (the type genus). The genera *Clevelandina*, *Diplocalyx*, *Hollandina* and *Pillotina* which lack published 16S rRNA gene sequences are also tentatively assigned to this family.

Emended Description of *Temperatibacteraceae* Teramoto and Nishijima 2014

Cells are Gram-negative, rod-shaped, motile, aerobic heterotrophs. The major ubiquinone is predominantly Q-10. The major polar lipids are phosphatidylethanolamine and phosphatidylglycerol. The major fatty acids are usually iso-C_{19:1} ω9c, iso-C_{17:0}, C_{18:1} ω7c, C_{17:1} ω6c, and iso-C_{15:0}. The family currently comprises the genera *Eilatimonas*, *Kordiimonas* and *Temperatibacter* (the type genus). The family *Kordiimonadaceae* was proposed earlier on, too (Xu et al., 2014), but has not been validly published yet. The emended family is based on phylogenetic analyses of genome and 16S rRNA gene sequences.

Emended Description of *Treponemataceae* Robinson 1948 (Approved Lists 1980)

The description is as given before (Robinson, 1948) with the following modification. Cells are mostly motile and of typical spirochaete-like, helical shape or rarely (in *Rectinema*) rod-shaped to spherical. The family contains *Rectinema* and *Treponema* (the type genus).

Emended Description of *Xanthobacteraceae* Lee et al. 2005

The description is as given before (Lee et al., 2005) with the following modification. Cells are rod-shaped, coccoid or ellipsoidal, aerobic and generally heterotrophic with some autotrophic genera. This family houses *Ancylobacter* (including *Microcyclus*), *Angulomicrobium*, *Aquabacter*, *Azorhizobium*, *Labrys*, *Methylorhabdus*, *Starkeya* and *Xanthobacter* (the type genus).

Taxonomic Consequences: Emendations of Genera

Emended Description of *Actibacterium* Lucena et al. 2012 emend. Guo et al. 2017

The description is as given before (Lucena et al., 2012; Guo et al., 2017) with additions following the inclusion of *Confluentimicrobium lipolyticum* and *C. naphthalenivorans*. Cells can be motile. Additionally another major polar lipid is frequently sulphoquinovosyldiacylglyceride. The type species is *Actibacterium mucosum*.

Emended Description of *Allorhizobium* De Lajudie et al. 1998

The description is as given before (de Lajudie et al., 1998) with additions following the inclusion of *Rhizobium oryzae* and *Rhizobium taibaishanense*. The genomic G+C content is 55.1–62.8%. The type species is *Allorhizobium undicola*.

Emended Description of *Celeribacter* Ivanova et al. 2010 emend. Lee et al. 2012

The description is as given before (Ivanova et al., 2010; Lee et al., 2012) with additions that reflect developments in the composition of the genus, notably the removal of *Celeribacter manganoxidans* and addition of *Vadicella arenosi*. The genomic G+C content is 56.7–60.9%. The type species is *Celeribacter neptunius*.

Emended Description of *Cereibacter* Suresh et al. 2015

The description is as given before (Suresh et al., 2015) with additions following the inclusion of *Rhodobacter azotoformans*, *Rhodobacter johrii*, *Rhodobacter ovatus* and *Rhodobacter sphaeroides*. Consists of motile (via flagella) as well as non-motile species. The genomic G+C content is 66.5–69.1%. The type species is *Cereibacter changlensis*.

Emended Description of *Cognatishimia* Wirth and Whitman 2018

After the inclusion of *Thalassobius activus* (Arahal et al., 2019) the original description (Wirth and Whitman, 2018) needs to be modified as follows. Cells are Gram-negative, motile or non-motile, rod- or coccus-shaped, aerobic chemotrophs. Some species require sodium chloride for growth. The predominant ubiquinone is Q-10. The major polar lipids are phosphatidylcholine and phosphatidylglycerol. The major fatty acid is C_{18:1} ω7c and in some species also C_{18:1} ω6c as well as C_{10:0} 3OH. The G+C content is 54.4–56.3%. The type species is *Cognatishimia maritima*.

Emended Description of *Magnetospirillum* Schleifer et al. 1991

The description is as given before (Schleifer et al., 1991) with additions following the inclusion of *Phaeospirillum molischianum*, *Phaeospirillum chandramohanii*, *Phaeospirillum fulvum*, *Phaeospirillum oryzae*, and *Phaeospirillum tilakii*. Cells are vibrio-, spiral- or helix-shaped and motile by means of flagella. Includes photoorganoheterotrophic anaerobic and

microaerophilic chemoorganotrophic species. Some species are magnetotactic and contain enveloped magnetosomes which are arranged in a chain within the cytoplasm. Mobility and magnetic behavior can be diminished or lost after several subcultivations. The G+C content is 60–71%. The type species is *Magnetospirillum gryphiswaldense*.

Emended Description of *Pelagimonas* Hahnke et al. 2013

The description is as given before (Hahnke et al., 2013) with additions following the inclusion of *Tropicibacter phthalicus*. Oxidase and catalase variable. The G+C content is 55.2–57.9%. The type species is *Pelagimonas varians*.

Emended Description of *Pseudorhodobacter* Uchino et al. 2002 emend. Lee et al. 2013 emend. Lee et al. 2016

The description is as given before (Uchino et al., 2002; Lee et al., 2013, 2016) with additions that reflect developments in the composition of the genus, notably the removal of *Pseudorhodobacter aquaticus*, *P. collinsensis*, *P. psychrotolerans*, and *P. sinensis*. The G+C content is 58.0–63.1%. The type species is *Pseudorhodobacter ferrugineus*.

Emended Description of *Pseudovibrio* Shieh et al. 2004

The description is as given before (Shieh et al., 2004) with additions following the inclusion of *Nesiotobacter exalbescens*. Mesophilic, growing at 20–35°C, some species able to grow at 45°C. Halophilic, no growth in the absence of NaCl. The G+C content is 47.0–55.8%. The type species is *Pseudovibrio denitrificans*.

Emended Description of *Salipiger* Martínez-Cánovas et al. 2004 emend. Wirth and Whitman 2018

The description is as given before (Martínez-Cánovas et al., 2004; Wirth and Whitman, 2018) with additions following the inclusion of *Yangia pacifica*. Cells are rod-shaped and of variable sizes with widths up to 1 μm and lengths in the range of 1–2.5 μm. The G+C content is 64.3–67.3%. The type species is *Salipiger mucosus*.

Emended Description of *Sphingopyxis* Takeuchi et al. 2001 emend. Baik et al. 2013

The description is as given before (Takeuchi et al., 2001; Baik et al., 2013) with additions that reflect developments in the composition of the genus, notably the removal of *Sphingopyxis baekryungensis*. The G+C content is 63.3–66.4%. The type species is *Sphingopyxis macrogoltabida*.

Emended Description of *Tabrizicola* Tarhriz et al. 2013

The description is as given before (Tarhriz et al., 2013) with additions following the inclusion of *Rhodobacter blasticus*. Cells are ovoid to rod-shaped, aerobic or facultatively anaerobic. Includes chemoheterotrophic as well as photoorganotrophic species. The G+C content is 66.4–66.5%. The type species is *Tabrizicola aquatica*.

Emended Description of *Thalassobius Arahall et al. 2005*

The description is as given before (Arahall et al., 2005) with additions that reflect developments in the composition of the genus, notably the removal of *Thalassobius activus* and addition of *Litorimicrobium taeanense* as well as *Lutimaribacter litoralis*. Cells are coccoid, rod-shaped or ovoid. The G+C content is 58.5–66.5%. The type species is *Thalassobius mediterraneus*.

Emended Description of *Tranquillimonas Harwati et al. 2008*

The description is as given before (Harwati et al., 2008) with additions following the inclusion of *Roseivivax roseus*. Includes motile as well as non-motile species. Oxidase variable. Cells are rod-shaped and of variable sizes, 0.2–1.0 μm width and 1.1–2.8 μm in length. The G+C content is 67.3–67.8%. The type species is *Tranquillimonas alkanivorans*.

Taxonomic Consequences: Emendations of Species

Emended Description of *Acetobacter acetii* (Pasteur 1864) Beijerinck 1898 (Approved Lists 1980)

The description is as before (Beijerinck, 1898) with the following addition. The G+C content of the type-strain genome is 57.1%, its approximate size 3.63 Mbp.

Emended Description of *Acetobacter cerevisiae* Cleenwerck et al. 2002

The description is as before (Cleenwerck et al., 2002) with the following restriction. The genomic G+C content of the type strain is 58.0%. Its approximate genome size is 3.09 Mbp.

Emended Description of *Acetobacter nitrogenifigens* Dutta and Gachhui 2006

The description is as before (Dutta and Gachhui, 2006) with the following modification. The genomic G+C content of the type strain is 60.5%. Its approximate genome size is 4.27 Mbp.

Emended Description of *Acetobacter okinawensis* Iino et al. 2013

The description is as before (Iino et al., 2012) with the following modification. The genomic G+C content of the type strain is 57.6%. Its approximate genome size is 3.17 Mbp.

Emended Description of *Acetobacter orleanensis* (Henneberg 1906) Lisdiyanti et al. 2001

The description is as before (Lisdiyanti et al., 2000) with the following addition. The genomic G+C content of the type strain is 56.4%. Its approximate genome size is 3.01 Mbp.

Emended Description of *Acetobacter papayae* Iino et al. 2013

The description is as before (Iino et al., 2012) with the following modification. The genomic G+C content of the type strain is 59.3%. Its approximate genome size is 3.04 Mbp.

Emended Description of *Acetobacter pasteurianus* (Hansen 1879) Beijerinck and Folpmers 1916 (Approved Lists 1980)

The description is as before (Beijerinck and Folpmers, 1916) with the following addition. The genomic G+C content of the type strain is 53.1%. Its approximate genome size is 2.98 Mbp.

Emended Description of *Acetobacter peroxydans* Visser't Hooft 1925 (Approved Lists 1980)

The description is as before (Visser't Hooft, 1925) with the following addition. The genomic G+C content of the type strain is 60.5%. Its approximate genome size is 2.71 Mbp.

Emended Description of *Acetobacter persici* Iino et al. 2013

The description is as before (Iino et al., 2012) with the following modification. The genomic G+C content of the type strain is 57.2%. Its approximate genome size is 3.70 Mbp.

Emended Description of *Acetobacter syzygii* Lisdiyanti et al. 2002

The description is as before (Lisdiyanti et al., 2001) with the following restriction. The G+C content of the type-strain genome is 55.5%, its approximate size 2.67 Mbp.

Emended Description of *Acidiphilium angustum* Wichlacz et al. 1986

The description is as before (Wichlacz et al., 1986) with the following modification. The genomic G+C content of the type strain is 63.6%. Its approximate genome size is 4.18 Mbp.

Emended Description of *Acidiphilium multivorum* Wakao et al. 1995

The description is as before (Wakao et al., 1994) with the following restriction. The genomic G+C content of the type strain is 67.0%. Its approximate genome size is 4.21 Mbp.

Emended Description of *Acidocella facilis* (Wichlacz et al. 1986) Kishimoto et al. 1996

The description is as before (Kishimoto et al., 1995) with the following restriction. The genomic G+C content of the type strain is 64.5%. Its approximate genome size is 3.40 Mbp.

Emended Description of *Acidomonas methanolica* (Uhlig et al. 1986) Urakami et al. 1989 emend. Yamashita et al. 2004

The description is as before (Yamashita et al., 2004) with the following modification. The G+C content of the type-strain genome is 64.7%, its approximate size 3.68 Mbp.

Emended Description of *Actibacterium ureilyticum* Lin et al. 2016

The description is as before (Lin et al., 2016) with the following modification. The genomic G+C content of the type strain is 64.3%. Its approximate genome size is 4.15 Mbp.

**Emended Description of *Aceticoccus yangtzensis*
Hou et al. 2017**

The description is as before (Hou et al., 2015) with the following modification. The genomic G+C content of the type strain is 68.6%. Its approximate genome size is 5.04 Mbp.

**Emended Description of *Aestuariivita boseongensis*
Park et al. 2014**

The description is as before (Park et al., 2014f) with the following modification. The G+C content of the type-strain genome is 61.1%, its approximate size 3.94 Mbp.

**Emended Description of *Afifella marina* (Imhoff 1984)
Urdiain et al. 2009**

The description is as before (Urdiain et al., 2008) with the following restriction. The genomic G+C content of the type strain is 63.2%. Its approximate genome size is 3.96 Mbp.

**Emended Description of *Afipia birgiae* La Scola et al.
2002**

The description is as before (La Scola et al., 2002) with the following modification. The genomic G+C content of the type strain is 60.8%. Its approximate genome size is 5.30 Mbp.

**Emended Description of *Afipia clevelandensis*
Brenner et al. 1992**

The description is as before (Brenner et al., 1991) with the following modification. The genomic G+C content of the type strain is 61.7%. Its approximate genome size is 4.39 Mbp.

**Emended Description of *Afipia felis* Brenner et al.
1992**

The description is as before (Brenner et al., 1991) with the following modification. The genomic G+C content of the type strain is 60.7%. Its approximate genome size is 4.20 Mbp.

**Emended Description of *Agrobacterium larrymoorei*
Bouzar and Jones 2001**

The description is as before (Bouzar and Jones, 2001) with the following addition. The G+C content of the type-strain genome is 57.2%, its approximate size 5.16 Mbp.

**Emended Description of *Agrobacterium nepotum*
(Pulawska et al. 2012) Mousavi et al. 2016**

The description is as before (Mousavi et al., 2015) with the following modification. The genomic G+C content of the type strain is 59.1%. Its approximate genome size is 5.33 Mbp.

**Emended Description of *Agrobacterium radiobacter*
(Beijerinck and van Delden 1902) Conn 1942
(Approved Lists 1980) emend. Zhang et al. 2014**

The description is as before (Zhang et al., 2014a) with the following restriction. The genomic G+C content of the type strain is 59.4%. Its approximate genome size is 5.50 Mbp.

**Emended Description of *Agrobacterium tumefaciens*
(Smith and Townsend 1907) Conn 1942**

The description is as before (Conn, 1942) with the following addition. The genomic G+C content of the type strain is 59.3%. Its approximate genome size is 5.66 Mbp.

**Emended Description of *Albidovulum inexpectatum*
Albuquerque et al. 2003**

The description is as before (Albuquerque et al., 2002) with the following modification. The genomic G+C content of the type strain is 64.8%. Its approximate genome size is 3.00 Mbp.

**Emended Description of *Albimonas pacifica* Li et al.
2013**

The description is as before (Li G.-W. et al., 2013) with the following modification. The genomic G+C content of the type strain is 72.9%. Its approximate genome size is 6.03 Mbp.

**Emended Description of *Aliiroseovarius halocynthiae*
(Kim et al. 2012) Park et al. 2015**

The description is as before (Park et al., 2015c) with the following modification. The G+C content of the type-strain genome is 57.1%, its approximate size 3.40 Mbp.

**Emended Description of *Aliiroseovarius*
sediminilitoris (Park and Yoon 2013) Park et al. 201**

The description is as before (Park et al., 2015c) with the following modification. The G+C content of the type-strain genome is 58.7%, its approximate size 3.41 Mbp.

**Emended Description of *Alkalimicrobium pacificum*
Zhang et al. 2015**

The description is as before (Zhang G. et al., 2015) with the following modification. The genomic G+C content of the type strain is 65.0%. Its approximate genome size is 5.79 Mbp.

**Emended Description of *Alkalispirochaeta alkalica*
(Zhilina et al. 1996) Sravanthi et al. 2016**

The description is as before (Sravanthi et al., 2016) with the following modification. The genomic G+C content of the type strain is 60.5%. Its approximate genome size is 3.34 Mbp.

**Emended Description of *Alkalispirochaeta americana*
(Hoover et al. 2003) Sravanthi et al. 2016**

The description is as before (Sravanthi et al., 2016) with the following modification. The genomic G+C content of the type strain is 57.5%. Its approximate genome size is 3.31 Mbp.

**Emended Description of *Alkalispirochaeta*
sphaeroplastigenens (Vishnuvardhan Reddy et al.
2013) Sravanthi et al. 2016**

The description is as before (Sravanthi et al., 2016) with the following addition. The G+C content of the type-strain genome is 60.5%, its approximate size 3.35 Mbp.

Emended Description of *Allorhizobium oryzae* (Peng et al. 2008) Mousavi et al. 2016

The description is as before (Mousavi et al., 2015) with the following modification. The genomic G+C content of the type strain is 62.8%. Its approximate genome size is 5.39 Mbp.

Emended Description of *Allorhizobium vitis* (Ophel and Kerr 1990) Mousavi et al. 2016

The description is as before (Mousavi et al., 2015) with the following modification. The genomic G+C content of the type strain is 57.6%. Its approximate genome size is 5.74 Mbp.

Emended Description of *Altererythrobacter atlanticus* Wu et al. 2014

The description is as before (Wu Y.-H. et al., 2014) with the following modification. The genomic G+C content of the type strain is 61.9%. Its approximate genome size is 3.48 Mbp.

Emended Description of *Altererythrobacter ishigakiensis* Matsumoto et al. 2011

The description is as before (Matsumoto et al., 2011) with the following modification. The genomic G+C content of the type strain is 56.9%. Its approximate genome size is 2.67 Mbp.

Emended Description of *Altererythrobacter marensis* Seo and Lee 2010

The description is as before (Seo and Lee, 2010) with the following modification. The genomic G+C content of the type strain is 64.7%. Its approximate genome size is 2.89 Mbp.

Emended Description of *Altererythrobacter namhicola* Park et al. 2011

The description is as before (Park S.C. et al., 2011) with the following modification. The genomic G+C content of the type strain is 65.0%. Its approximate genome size is 2.59 Mbp.

Emended Description of *Amylibacter kogurei* Wong et al. 2018

The description is as before (Wong et al., 2018) with the following modification. The G+C content of the type-strain genome is 48.8%, its approximate size 2.98 Mbp.

Emended Description of *Ancylobacter aquaticus* (Ørskov 1928) Raj 1983

The description is as before (Raj, 1983) with the following addition. The G+C content of the type-strain genome is 67.0%, its approximate size 4.83 Mbp.

Emended Description of *Aquamicrobium aerolatum* Kämpfer et al. 2009

The description is as before (Kämpfer et al., 2009b) with the following addition. The genomic G+C content of the type strain is 60.1%. Its approximate genome size is 3.64 Mbp.

Emended Description of *Aquamicrobium defluvii* Bambauer et al. 1998

The description is as before (Bambauer et al., 1998) with the following modification. The G+C content of the type-strain genome is 63.2%, its approximate size 4.52 Mbp.

Emended Description of *Arboricoccus pini* Proença et al. 2018

The description is as before (Proença et al., 2018) with the following modification. The G+C content of the type-strain genome is 63.2%.

Emended Description of *Asaia prunellae* Suzuki et al. 2012

The description is as before (Suzuki et al., 2010) with the following modification. The genomic G+C content of the type strain is 55.8%. Its approximate genome size is 3.18 Mbp.

Emended Description of *Asticcacaulis benevestitus* Vasilyeva et al. 2006

The description is as before (Vasilyeva et al., 2006) with the following modification. The genomic G+C content of the type strain is 58.4%. Its approximate genome size is 4.99 Mbp.

Emended Description of *Asticcacaulis excentricus* Poindexter 1964 (Approved Lists 1980)

The description is as before (Poindexter, 1964) with the following addition. The genomic G+C content of the type strain is 59.5%. Its approximate genome size is 4.31 Mbp.

Emended Description of *Aurantimonas coralicida* Denner et al. 2003 emend. Rathsack et al. 2011

The description is as before (Rathsack et al., 2011) with the following addition. The genomic G+C content of the type strain is 66.7%. Its approximate genome size is 4.62 Mbp.

Emended Description of *Aureimonas altamirensis* (Jurado et al. 2006) Rathsack et al. 2011

The description is as before (Rathsack et al., 2011) with the following modification. The genomic G+C content of the type strain is 64.8%. Its approximate genome size is 4.19 Mbp.

Emended Description of *Aureimonas frigidaquae* (Kim et al. 2008) Rathsack et al. 2011

The description is as before (Rathsack et al., 2011) with the following modification. The G+C content of the type-strain genome is 66.1%, its approximate size 4.10 Mbp.

Emended Description of *Azorhizobium caulinodans* Dreyfus et al. 1988

The description is as before (Dreyfus et al., 1988) with the following modification. The genomic G+C content of the type strain is 67.3%. Its approximate genome size is 5.37 Mbp.

Emended Description of *Azorhizobium doebereineriae* Moreira et al. 2006

The description is as before (Moreira et al., 2006) with the following addition. The genomic G+C content of the type strain is 68.9%. Its approximate genome size is 5.82 Mbp.

Emended Description of *Azospirillum brasilense* Tarrand et al. 1979

The description is as before (Tarrand et al., 1978) with the following addition. The genomic G+C content of the type strain is 68.3%. Its approximate genome size is 7.14 Mbp.

**Emended Description of *Azospirillum thiophilum*
Lavrinenko et al. 2010**

The description is as before (Lavrinenko et al., 2010) with the following modification. The genomic G+C content of the type strain is 68.2%. Its approximate genome size is 7.61 Mbp.

**Emended Description of *Bartonella bacilliformis*
(Strong et al. 1913) Strong et al. 1915 (Approved Lists
1980)**

The description is as before (Strong et al., 1915) with the following addition. The genomic G+C content of the type strain is 38.2%. Its approximate genome size is 1.45 Mbp.

**Emended Description of *Bartonella clarridgeiae*
Lawson and Collins 1996**

The description is as before (Lawson and Collins, 1996) with the following addition. The genomic G+C content of the type strain is 35.7%. Its approximate genome size is 1.49 Mbp.

Emended Description of *Bartonella doshiae* Birtles et al. 1995

The description is as before (Birtles et al., 1995) with the following modification. The genomic G+C content of the type strain is 37.9%. Its approximate genome size is 1.77 Mbp.

Emended Description of *Bartonella elizabethae* (Daly et al. 1993) Brenner et al. 1993

The description is as before (Brenner et al., 1993) with the following modification. The genomic G+C content of the type strain is 38.3%. Its approximate genome size is 1.96 Mbp.

Emended Description of *Bartonella grahamii* Birtles et al. 1995

The description is as before (Birtles et al., 1995) with the following modification. The genomic G+C content of the type strain is 38.0%. Its approximate genome size is 2.19 Mbp.

**Emended Description of *Bartonella henselae*
(Regnery et al. 1992) Brenner et al. 1993**

The description is as before (Brenner et al., 1993) with the following modification. The genomic G+C content of the type strain is 38.2%. Its approximate genome size is 1.93 Mbp.

Emended Description of *Bartonella koehlerae* Droz et al. 2000

The description is as before (Droz et al., 1999) with the following addition. The genomic G+C content of the type strain is 37.6%. Its approximate genome size is 1.74 Mbp.

**Emended Description of *Bartonella rattaaustraliani*
Gundi et al. 2009**

The description is as before (Gundi et al., 2009) with the following addition. The genomic G+C content of the type strain is 38.8%. Its approximate genome size is 2.16 Mbp.

**Emended Description of *Bartonella rochalimae*
Eremeeva et al. 2012**

The description is as before (Eremeeva et al., 2007) with the following addition. The genomic G+C content of the type strain is 35.8%. Its approximate genome size is 1.54 Mbp.

**Emended Description of *Bartonella schoenbuchensis*
Dehio et al. 2001**

The description is as before (Dehio et al., 2001) with the following addition. The genomic G+C content of the type strain is 37.6%. Its approximate genome size is 1.74 Mbp.

Emended Description of *Bauldia litoralis* (Bauld et al. 1983) Yee et al. 2010

The description is as before (Yee et al., 2010) with the following modification. The genomic G+C content of the type strain is 65.8%. Its approximate genome size is 5.09 Mbp.

Emended Description of *Beijerinckia indica* (Starkey and De 1939) Derx 1950 (Approved Lists 1980)

The description is as before (Derx, 1950) with the following addition. The genomic G+C content of the type strain is 57.0%. Its approximate genome size is 4.42 Mbp.

Emended Description of *Beijerinckia mobilis* Derx 1950 (Approved Lists 1980)

The description is as before (Derx, 1950) with the following addition. The genomic G+C content of the type strain is 57.2%. Its approximate genome size is 4.32 Mbp.

Emended Description of *Belnapia moabensis* Reddy et al. 2006

The description is as before (Reddy et al., 2006) with the following modification. The genomic G+C content of the type strain is 68.9%. Its approximate genome size is 6.72 Mbp.

Emended Description of *Blastochloris viridis* (Drews and Giesbrecht 1966) Hiraishi 1997

The description is as before (Hiraishi, 1997) with the following addition. The genomic G+C content of the type strain is 67.9%. Its approximate genome size is 3.72 Mbp.

Emended Description of *Blastomonas natatoria* (Sly 1985) Sly and Cahill 1997 emend. Hiraishi et al. 2000

The description is as before (Hiraishi et al., 2000) with the following modification. The G+C content of the type-strain genome is 63.4%, its approximate size 4.05 Mbp.

Emended Description of *Borrelia bavariensis* Margos et al. 2013

The description is as before (Margos et al., 2013) with the following addition. The G+C content of the type-strain genome is 28.1%, its approximate size 0.99 Mbp.

Emended Description of *Borrelia bissettae* Margos et al. 2016

The description is as before (Margos et al., 2016) with the following modification. The genomic G+C content of the type strain is 28.3%. Its approximate genome size is 1.40 Mbp.

Emended Description of *Borrelia burgdorferi* Johnson et al. 1984 emend. Baranton et al. 1992

The description is as before (Baranton et al., 1992) with the following restriction. The genomic G+C content of the type strain is 28.2%. Its approximate genome size is 1.52 Mbp.

Emended Description of *Borrelia coriaceae* Johnson et al. 1987

The description is as before (Johnson et al., 1987) with the following modification. The genomic G+C content of the type strain is 29.3%. Its approximate genome size is 1.57 Mbp.

Emended Description of *Borrelia mayonii* Pritt et al. 2016

The description is as before (Pritt et al., 2016) with the following addition. The genomic G+C content of the type strain is 27.9%. Its approximate genome size is 1.31 Mbp.

Emended Description of *Borrelia valaisiana* Wang et al. 1997

The description is as before (Wang et al., 1997) with the following addition. The genomic G+C content of the type strain is 27.5%. Its approximate genome size is 1.26 Mbp.

Emended Description of *Bosea lathyri* De Meyer and Willems 2012

The description is as before (De Meyer and Willems, 2012) with the following modification. The genomic G+C content of the type strain is 64.8%. Its approximate genome size is 5.92 Mbp.

Emended Description of *Bosea robiniae* De Meyer and Willems 2012

The description is as before (De Meyer and Willems, 2012) with the following modification. The genomic G+C content of the type strain is 66.3%. Its approximate genome size is 5.28 Mbp.

Emended Description of *Brachyspira alvinipulli* Stanton et al. 1998

The description is as before (Stanton et al., 1998) with the following modification. The genomic G+C content of the type strain is 26.9%. Its approximate genome size is 3.41 Mbp.

Emended Description of *Brachyspira hyodysenteriae* (Harris et al. 1972) Ochiai et al. 1998

The description is as before (Ochiai et al., 1997) with the following modification. The genomic G+C content of the type strain is 27.0%. Its approximate genome size is 3.05 Mbp.

Emended Description of *Brachyspira innocens* (Kinyon and Harris 1979) Ochiai et al. 1998

The description is as before (Ochiai et al., 1997) with the following modification. The genomic G+C content of the type strain is 27.7%. Its approximate genome size is 3.28 Mbp.

Emended Description of *Brachyspira intermedia* (Stanton et al. 1997) Hampson and La 2006

The description is as before (Hampson and La, 2006) with the following modification. The genomic G+C content of the type strain is 27.2%. Its approximate genome size is 3.31 Mbp.

Emended Description of *Brachyspira pilosicoli* (Trott et al. 1996) Ochiai et al. 1998

The description is as before (Ochiai et al., 1997) with the following modification. The genomic G+C content of the type strain is 27.9%. Its approximate genome size is 2.56 Mbp.

Emended Description of *Bradyrhizobium arachidis* Wang et al. 2015

The description is as before (Wang et al., 2013) with the following modification. The genomic G+C content of the type strain is 63.6%. Its approximate genome size is 9.79 Mbp.

Emended Description of *Bradyrhizobium elkanii* Kuykendall et al. 1993

The description is as before (Kuykendall et al., 1992) with the following addition. The genomic G+C content of the type strain is 63.7%. Its approximate genome size is 9.48 Mbp.

Emended Description of *Bradyrhizobium embrapense* Delamuta et al. 2015

The description is as before (Delamuta et al., 2015) with the following modification. The genomic G+C content of the type strain is 64.0%. Its approximate genome size is 8.27 Mbp.

Emended Description of *Bradyrhizobium japonicum* (Kirchner 1896) Jordan 1982

The description is as before (Jordan, 1982) with the following restriction. The genomic G+C content of the type strain is 63.7%. Its approximate genome size is 9.21 Mbp.

Emended Description of *Bradyrhizobium jicamae* Ramírez-Bahena et al. 2009

The description is as before (Ramírez-Bahena et al., 2009) with the following modification. The genomic G+C content of the type strain is 62.4%. Its approximate genome size is 8.71 Mbp.

Emended Description of *Bradyrhizobium lablabi* Chang et al. 2011

The description is as before (Chang et al., 2011) with the following modification. The genomic G+C content of the type strain is 62.6%. Its approximate genome size is 8.80 Mbp.

Emended Description of *Bradyrhizobium ottawaense* Yu et al. 2014

The description is as before (Yu et al., 2014) with the following modification. The genomic G+C content of the type strain is 63.8%. Its approximate genome size is 8.68 Mbp.

Emended Description of *Brevinema andersonii* Defosse et al. 1995

The description is as before (Defosse et al., 1995) with the following modification. The genomic G+C content of the type strain is 35.2%. Its approximate genome size is 1.50 Mbp.

Emended Description of *Brevirhabdus pacifica* Wu et al. 2015

The description is as before (Wu et al., 2015) with the following modification. The genomic G+C content of the type strain is 66.2%. Its approximate genome size is 3.30 Mbp.

Emended Description of *Brevundimonas aveniformis* Ryu et al. 2007

The description is as before (Ryu et al., 2007) with the following modification. The genomic G+C content of the type strain is 65.1%. Its approximate genome size is 2.58 Mbp.

Emended Description of *Brevundimonas bacteroides* (Poindexter 1964) Abraham et al. 1999

The description is as before (Abraham et al., 1999) with the following addition. The genomic G+C content of the type strain is 68.2%. Its approximate genome size is 3.22 Mbp.

Emended Description of *Brevundimonas diminuta* (Leifson and Hugh 1954) Segers et al. 1994

The description is as before (Segers et al., 1994) with the following restriction. The genomic G+C content of the type strain is 67.1%. Its approximate genome size is 3.24 Mbp.

Emended Description of *Brevundimonas subvibrioides* (Poindexter 1964) Abraham et al. 1999

The description is as before (Abraham et al., 1999) with the following addition. The genomic G+C content of the type strain is 68.4%. Its approximate genome size is 3.45 Mbp.

Emended Description of *Brevundimonas vesicularis* (Büsing et al. 1953) Segers et al. 1994

The description is as before (Segers et al., 1994) with the following modification. The genomic G+C content of the type strain is 66.3%. Its approximate genome size is 3.36 Mbp.

Emended Description of *Brevundimonas viscosa* Wang et al. 2012

The description is as before (Wang et al., 2012) with the following modification. The genomic G+C content of the type strain is 70.4%. Its approximate genome size is 3.00 Mbp.

Emended Description of *Brucella abortus* (Schmidt 1901) Meyer and Shaw 1920 (Approved Lists 1980)

The description is as before (Meyer and Shaw, 1920) with the following addition. The genomic G+C content of the type strain is 57.2%. Its approximate genome size is 3.29 Mbp.

Emended Description of *Brucella canis* Carmichael and Bruner 1968 (Approved Lists 1980)

The description is as before (Carmichael and Bruner, 1968) with the following addition. The genomic G+C content of the type strain is 57.2%. Its approximate genome size is 3.31 Mbp.

Emended Description of *Brucella ceti* Foster et al. 2007

The description is as before (Foster et al., 2007) with the following addition. The genomic G+C content of the type strain is 57.3%. Its approximate genome size is 3.27 Mbp.

Emended Description of *Brucella inopinata* Scholz et al. 2010

The description is as before (Scholz et al., 2010) with the following addition. The genomic G+C content of the type strain is 57.1%. Its approximate genome size is 3.37 Mbp.

Emended Description of *Brucella melitensis* (Hughes 1893) Meyer and Shaw 1920 (Approved Lists 1980) emend. Verger et al. 1985

The description is as before (Verger et al., 1985) with the following addition. The genomic G+C content of the type strain is 57.2%. Its approximate genome size is 3.29 Mbp.

Emended Description of *Brucella microti* Scholz et al. 2008

The description is as before (Scholz et al., 2008) with the following addition. The genomic G+C content of the type strain is 57.3%. Its approximate genome size is 3.34 Mbp.

Emended Description of *Brucella neotomae* Stoenner and Lackman 1957 (Approved Lists 1980)

The description is as before (Stoenner and Lackman, 1957) with the following addition. The genomic G+C content of the type strain is 57.3%. Its approximate genome size is 3.30 Mbp.

Emended Description of *Brucella ovis* Buddle 1956 (Approved Lists 1980)

The description is as before (Buddle, 1956) with the following addition. The genomic G+C content of the type strain is 57.2%. Its approximate genome size is 3.28 Mbp.

Emended Description of *Brucella suis* Huddleson 1929 (Approved Lists 1980)

The description is as before (Huddleson, 1929) with the following addition. The genomic G+C content of the type strain is 57.3%. Its approximate genome size is 3.32 Mbp.

Emended Description of *Caenispirillum salinarum* Ritika et al. 2012

The description is as before (Ritika et al., 2012) with the following modification. The genomic G+C content of the type strain is 68.8%. Its approximate genome size is 4.95 Mbp.

Emended Description of *Camelimonas lactis* Kämpfer et al. 2010

The description is as before (Kämpfer et al., 2010b) with the following modification. The G+C content of the type-strain genome is 66.3%, its approximate size 4.17 Mbp.

Emended Description of *Caulobacter crescentus* Poindexter 1964 (Approved Lists 1980)

The description is as before (Poindexter, 1964) with the following addition. The G+C content of the type-strain genome is 67.2%, its approximate size 4.12 Mbp.

Emended Description of *Caulobacter henricii* Poindexter 1964 (Approved Lists 1980)

The description is as before (Poindexter, 1964) with the following modification. The genomic G+C content of the type strain is 65.8%. Its approximate genome size is 3.96 Mbp.

**Emended Description of *Caulobacter mirabilis*
Abraham et al. 2008**

The description is as before (Abraham et al., 2008) with the following modification. The G+C content of the type-strain genome is 69.3%, its approximate size 4.58 Mbp.

**Emended Description of *Caulobacter vibrioides*
Henrici and Johnson 1935 (Approved Lists 1980)**

The description is as before (Henrici and Johnson, 1935) with the following addition. The G+C content of the type-strain genome is 67.2%, its approximate size 3.97 Mbp.

**Emended Description of *Celeribacter baekdonensis*
Lee et al. 2012**

The description is as before (Lee et al., 2012) with the following modification. The genomic G+C content of the type strain is 58.1%. Its approximate genome size is 4.44 Mbp.

**Emended Description of *Celeribacter halophilus*
(Wang et al. 2012) Lai et al. 2014**

The description is as before (Lai et al., 2014) with the following modification. The genomic G+C content of the type strain is 58.1%. Its approximate genome size is 3.87 Mbp.

**Emended Description of *Celeribacter marinus* Baek
et al. 2014**

The description is as before (Baek et al., 2014) with the following modification. The genomic G+C content of the type strain is 56.2%. Its approximate genome size is 3.10 Mbp.

**Emended Description of *Celeribacter neptunius*
Ivanova et al. 2010**

The description is as before (Ivanova et al., 2010) with the following modification. The genomic G+C content of the type strain is 61.7%. Its approximate genome size is 4.40 Mbp.

**Emended Description of *Cereibacter changlensis*
(Anil Kumar et al. 2007) Suresh et al. 2015**

The description is as before (Suresh et al., 2015) with the following modification. The genomic G+C content of the type strain is 68.1%. Its approximate genome size is 4.92 Mbp.

**Emended Description of *Ciceribacter lividus*
Kathiravan et al. 2013**

The description is as before (Kathiravan et al., 2013) with the following modification. The G+C content of the type-strain genome is 63.2%, its approximate size 4.52 Mbp.

**Emended Description of *Citreicella aestuarii* Park et
al. 2011**

The description is as before (Park M.S. et al., 2011) with the following modification. The genomic G+C content of the type strain is 64.3%. Its approximate genome size is 4.66 Mbp.

**Emended Description of *Citreicella thiooxidans*
Sorokin et al. 2006**

The description is as before (Sorokin et al., 2005a) with the following restriction. The genomic G+C content of the type strain is 67.3%. Its approximate genome size is 5.87 Mbp.

**Emended Description of *Cognatiyoonia koreensis*
(Weon et al. 2006) Wirth and Whitman 2018**

The description is as before (Wirth and Whitman, 2018) with the following modification. The G+C content of the type-strain genome is 57.2%, its approximate size 3.65 Mbp.

**Emended Description of *Cognatiyoonia sediminum*
(Liang et al. 2015) Wirth and Whitman 2018**

The description is as before (Wirth and Whitman, 2018) with the following modification. The G+C content of the type-strain genome is 54.4%, its approximate size 3.26 Mbp.

**Emended Description of *Cohaesibacter gelatinilyticus*
Hwang and Cho 2008 emend. Gallego et al. 2010**

The description is as before (Gallego et al., 2010) with the following modification. The genomic G+C content of the type strain is 50.5%. Its approximate genome size is 5.20 Mbp.

**Emended Description of *Cohaesibacter*
haloalkalitolerans Sultanpuram et al. 2013**

The description is as before (Sultanpuram et al., 2013) with the following modification. The G+C content of the type-strain genome is 57.1%, its approximate size 5.01 Mbp.

**Emended Description of *Cohaesibacter marisflavi* Qu
et al. 2011**

The description is as before (Qu et al., 2011) with the following modification. The genomic G+C content of the type strain is 53.8%. Its approximate genome size is 5.34 Mbp.

**Emended Description of *Cribrihabitans marinus* Chen
et al. 2014**

The description is as before (Chen et al., 2014) with the following modification. The genomic G+C content of the type strain is 66.0%. Its approximate genome size is 4.18 Mbp.

**Emended Description of *Defluviimonas alba* Pan et
al. 2015**

The description is as before (Pan et al., 2015) with the following restriction. The genomic G+C content of the type strain is 66.5%. Its approximate genome size is 4.99 Mbp.

**Emended Description of *Defluviimonas aquaemixtae*
Jung et al. 2014**

The description is as before (Jung et al., 2014b) with the following modification. The G+C content of the type-strain genome is 64.4%, its approximate size 4.24 Mbp.

**Emended Description of *Devosia chinhatensis* Kumar
et al. 2008**

The description is as before (Kumar et al., 2008) with the following addition. The genomic G+C content of the type strain is 62.4%. Its approximate genome size is 3.50 Mbp.

**Emended Description of *Devosia crocina* Verma et al.
2009**

The description is as before (Verma et al., 2009) with the following addition. The genomic G+C content of the type strain is 61.3%. Its approximate genome size is 3.72 Mbp.

Emended Description of *Devosia elaeis* Mohd Nor et al. 2017

The description is as before (Mohd Nor et al., 2017) with the following modification. The G+C content of the type-strain genome is 64.1%, its approximate size 3.88 Mbp.

Emended Description of *Devosia epidermidihirudinis* Galatis et al. 2013

The description is as before (Galatis et al., 2013) with the following addition. The genomic G+C content of the type strain is 61.1%. Its approximate genome size is 3.86 Mbp.

Emended Description of *Devosia geojensis* Ryu et al. 2008

The description is as before (Ryu et al., 2008) with the following modification. The genomic G+C content of the type strain is 65.9%. Its approximate genome size is 4.47 Mbp.

Emended Description of *Devosia soli* Yoo et al. 2006

The description is as before (Yoo et al., 2006) with the following modification. The genomic G+C content of the type strain is 61.0%. Its approximate genome size is 4.14 Mbp.

Emended Description of *Devosia submarina* Romanenko et al. 2013

The description is as before (Romanenko et al., 2013) with the following addition. The G+C content of the type-strain genome is 60.4%, its approximate size 3.98 Mbp.

Emended Description of *Dichotomicrobium thermohalophilum* Hirsch and Hoffmann 1989

The description is as before (Hirsch and Hoffmann, 1989) with the following restriction. The genomic G+C content of the type strain is 64.3%. Its approximate genome size is 2.99 Mbp.

Emended Description of *Ehrlichia chaffeensis* Anderson et al. 1992 emend. Dumler et al. 2001

The description is as before (Dumler et al., 2001) with the following addition. The genomic G+C content of the type strain is 30.1%.

Emended Description of *Ehrlichia muris* Wen et al. 1995 emend. Dumler et al. 2001

The description is as before (Dumler et al., 2001) with the following addition. The genomic G+C content of the type strain is 29.7%. Its approximate genome size is 1.20 Mbp.

Emended Description of *Ehrlichia ruminantium* (Cowdry 1925) Dumler et al. 2001

The description is as before (Dumler et al., 2001) with the following addition. The genomic G+C content of the type strain is 27.5%. Its approximate genome size is 1.51 Mbp.

Emended Description of *Elioraea tepidiphila* Albuquerque et al. 2008

The description is as before (Albuquerque et al., 2008) with the following restriction. The genomic G+C content of the type strain is 71.3%. Its approximate genome size is 4.30 Mbp.

Emended Description of *Ensifer adhaerens* Casida 1982

The description is as before (Casida, 1982) with the following restriction. The genomic G+C content of the type strain is 62.3%. Its approximate genome size is 7.28 Mbp.

Emended Description of *Ensifer americanus* (Toledo et al. 2004) Wang et al. 2015

The description is as before (Wang Y.C. et al., 2013) with the following addition. The genomic G+C content of the type strain is 62.3%. Its approximate genome size is 6.65 Mbp.

Emended Description of *Ensifer arboris* (Nick et al. 1999) Young 2003

The description is as before (Young, 2003) with the following restriction. The genomic G+C content of the type strain is 62.0%. Its approximate genome size is 6.85 Mbp.

Emended Description of *Ensifer fredii* (Scholla and Elkan 1984) Young 2003

The description is as before (Young, 2003) with the following addition. The genomic G+C content of the type strain is 62.3%. Its approximate genome size is 6.58 Mbp.

Emended Description of *Ensifer saheli* (de Lajudie et al. 1994) Young 2003

The description is as before (Young, 2003) with the following modification. The genomic G+C content of the type strain is 63.6%. Its approximate genome size is 5.99 Mbp.

Emended Description of *Ensifer shofinae* Chen et al. 2017

The description is as before (Chen et al., 2017c) with the following modification. The G+C content of the type-strain genome is 61.6%.

Emended Description of *Ensifer sojae* Li et al. 2011

The description is as before (Li et al., 2011) with the following modification. The genomic G+C content of the type strain is 62.0%. Its approximate genome size is 5.96 Mbp.

Emended Description of *Epibacterium multivorans* (Lucena et al. 2012) Wirth and Whitman 2018

The description is as before (Wirth and Whitman, 2018) with the following modification. The G+C content of the type-strain genome is 59.7%, its approximate size 4.15 Mbp.

Emended Description of *Erythrobacter gangjinensis* Lee et al. 2010

The description is as before (Lee et al., 2010) with the following modification. The genomic G+C content of the type strain is 62.7%. Its approximate genome size is 2.72 Mbp.

Emended Description of *Erythrobacter litoralis* Yurkov et al. 1994

The description is as before (Yurkov et al., 1994) with the following modification. The genomic G+C content of the type strain is 65.2%. Its approximate genome size is 3.21 Mbp.

Emended Description of *Erythrobacter longus* Shiba and Simidu 1982

The description is as before (Shiba and Smidu, 1982) with the following modification. The genomic G+C content of the type strain is 57.4%. Its approximate genome size is 3.60 Mbp.

Emended Description of *Erythrobacter marinus* Jung et al. 2012

The description is as before (Jung et al., 2012b) with the following modification. The genomic G+C content of the type strain is 59.1%. Its approximate genome size is 2.84 Mbp.

Emended Description of *Erythrobacter nanhaisediminis* Xu et al. 2010

The description is as before (Xu et al., 2010) with the following modification. The genomic G+C content of the type strain is 62.0%. Its approximate genome size is 2.90 Mbp.

Emended Description of *Erythrobacter odishensis* Subhash et al. 2013

The description is as before (Subhash et al., 2013) with the following modification. The G+C content of the type-strain genome is 63.7%, its approximate size 3.19 Mbp.

Emended Description of *Falsochrobactrum ovis* Kämpfer et al. 2013

The description is as before (Kämpfer et al., 2013b) with the following modification. The G+C content of the type-strain genome is 50.7%, its approximate size 3.27 Mbp.

Emended Description of *Filomicrobium insigne* Wu et al. 2009

The description is as before (Wu et al., 2009) with the following modification. The genomic G+C content of the type strain is 57.4%. Its approximate genome size is 3.85 Mbp.

Emended Description of *Fodinicurvata fenggangensis* Wang et al. 2009

The description is as before (Wang Y. et al., 2009) with the following modification. The genomic G+C content of the type strain is 61.0%. Its approximate genome size is 3.77 Mbp.

Emended Description of *Fulvimarina manganoxydans* Ren et al. 2014

The description is as before (Ren et al., 2014) with the following modification. The genomic G+C content of the type strain is 62.9%. Its approximate genome size is 4.83 Mbp.

Emended Description of *Fulvimarina pelagi* Cho and Giovannoni 2003 emend. Rathsack et al. 2011

The description is as before (Rathsack et al., 2011) with the following modification. The genomic G+C content of the type strain is 61.2%. Its approximate genome size is 3.80 Mbp.

Emended Description of *Geminicoccus roseus* Foessel et al. 2008

The description is as before (Foessel et al., 2007) with the following modification. The genomic G+C content of the type strain is 68.5%. Its approximate genome size is 5.70 Mbp.

Emended Description of *Gemmobacter aquatilis* Rothe et al. 1988 emend. Chen et al. 2013

The description is as before (Chen W.-M. et al., 2013) with the following modification. The genomic G+C content of the type strain is 65.1%. Its approximate genome size is 3.96 Mbp.

Emended Description of *Gemmobacter caeni* (Zheng et al. 2011) Chen et al. 2013

The description is as before (Chen W.-M. et al., 2013) with the following modification. The genomic G+C content of the type strain is 64.7%. Its approximate genome size is 5.13 Mbp.

Emended Description of *Gluconacetobacter diazotrophicus* (Gillis et al. 1989) Yamada et al. 1998

The description is as before (Yamada et al., 1997) with the following restriction. The genomic G+C content of the type strain is 66.3%. Its approximate genome size is 3.91 Mbp.

Emended Description of *Gluconacetobacter entanii* Schüller et al. 2000

The description is as before (Schüller et al., 2000) with the following modification. The G+C content of the type-strain genome is 62.6%, its approximate size 3.59 Mbp.

Emended Description of *Gluconacetobacter liquefaciens* (Asai 1935) Yamada et al. 1998

The description is as before (Yamada et al., 1997) with the following restriction. The G+C content of the type-strain genome is 64.4%, its approximate size 4.18 Mbp.

Emended Description of *Gluconobacter cerinus* (ex Asai 1935) Yamada and Akita 1984 emend. Katsura et al. 2002

The description is as before (Katsura et al., 2002) with the following restriction. The G+C content of the type-strain genome is 55.6%, its approximate size 3.59 Mbp.

Emended Description of *Gluconobacter frateurii* Mason and Claus 1989

The description is as before (Mason and Claus, 1989) with the following restriction. The G+C content of the type-strain genome is 56.1%, its approximate size 3.31 Mbp.

Emended Description of *Gluconobacter kondonii* Malimas et al. 2008

The description is as before (Malimas et al., 2007) with the following modification. The G+C content of the type-strain genome is 58.3%, its approximate size 3.27 Mbp.

Emended Description of *Gluconobacter nephelii* Kommanee et al. 2011

The description is as before (Kommanee et al., 2011) with the following modification. The G+C content of the type-strain genome is 55.8%, its approximate size 3.16 Mbp.

Emended Description of *Gluconobacter oxydans* (Henneberg 1897) De Ley 1961 (Approved Lists 1980) emend. Mason and Claus 1989

The description is as before (Mason and Claus, 1989) with the following restriction. The G+C content of the type-strain genome is 60.8%, its approximate size 2.91 Mbp.

Emended Description of *Haematobacter massiliensis* (Greub and Raoult 2006) Hesel et al. 2007

The description is as before (Hesel et al., 2007) with the following addition. The genomic G+C content of the type strain is 64.6%. Its approximate genome size is 4.13 Mbp.

Emended Description of *Haematobacter missouriensis* Hesel et al. 2007

The description is as before (Hesel et al., 2007) with the following modification. The genomic G+C content of the type strain is 64.3%. Its approximate genome size is 3.96 Mbp.

Emended Description of *Haematospirillum jordaniae* Humrighouse et al. 2016

The description is as before (Humrighouse et al., 2016) with the following addition. The genomic G+C content of the type strain is 55.4%. Its approximate genome size is 2.47 Mbp.

Emended Description of *Hartmannibacter diazotrophicus* Suarez et al. 2014

The description is as before (Suarez et al., 2014) with the following restriction. The G+C content of the type-strain genome is 64.0%, its approximate size 5.45 Mbp.

Emended Description of *Hellea balneolensis* Alain et al. 2008

The description is as before (Alain et al., 2008) with the following modification. The genomic G+C content of the type strain is 48.4%. Its approximate genome size is 3.21 Mbp.

Emended Description of *Henriciella algicola* Abraham et al. 2017

The description is as before (Abraham et al., 2017) with the following modification. The G+C content of the type-strain genome is 60.4%, its approximate size 3.20 Mbp.

Emended Description of *Henriciella aquimarina* Lee et al. 2011

The description is as before (Lee et al., 2011) with the following modification. The genomic G+C content of the type strain is 62.2%. Its approximate genome size is 4.34 Mbp.

Emended Description of *Henriciella barbarendis* Abraham et al. 2017

The description is as before (Abraham et al., 2017) with the following modification. The G+C content of the type-strain genome is 59.2%, its approximate size 3.33 Mbp.

Emended Description of *Henriciella litoralis* Lee et al. 2011

The description is as before (Lee et al., 2011) with the following modification. The genomic G+C content of the type strain is 58.9%. Its approximate genome size is 3.78 Mbp.

Emended Description of *Henriciella marina* Quan et al. 2009

The description is as before (Quan et al., 2009) with the following modification. The genomic G+C content of the type strain is 59.9%. Its approximate genome size is 3.28 Mbp.

Emended Description of *Hoeflea halophila* Jung et al. 2013

The description is as before (Jung et al., 2013) with the following modification. The G+C content of the type-strain genome is 61.1%, its approximate size 4.19 Mbp.

Emended Description of *Hoeflea marina* Peix et al. 2005

The description is as before (Peix et al., 2005) with the following modification. The G+C content of the type-strain genome is 65.0%, its approximate size 5.26 Mbp.

Emended Description of *Hoeflea olei* Rahul et al. 2015

The description is as before (Rahul et al., 2015) with the following modification. The genomic G+C content of the type strain is 65.6%. Its approximate genome size is 4.72 Mbp.

Emended Description of *Humitalea rosea* Margesin and Zhang 2013

The description is as before (Margesin and Zhang, 2013) with the following modification. The genomic G+C content of the type strain is 69.6%. Its approximate genome size is 4.97 Mbp.

Emended Description of *Hwanghaeicola aestuarii* Kim et al. 2010

The description is as before (Kim J.M. et al., 2010) with the following modification. The genomic G+C content of the type strain is 66.0%. Its approximate genome size is 4.54 Mbp.

Emended Description of *Hyphomicrobium zavarzinii* Hirsch 1989

The description is as before (Hirsch, 1989) with the following modification. The genomic G+C content of the type strain is 63.7%. Its approximate genome size is 4.65 Mbp.

Emended Description of *Hyphomonas adhaerens* Weiner et al. 2000

The description is as before (Weiner et al., 2000) with the following modification. The genomic G+C content of the type strain is 61.3%. Its approximate genome size is 3.67 Mbp.

Emended Description of *Hyphomonas hirschiiana* Weiner et al. 1985

The description is as before (Weiner et al., 1985) with the following modification. The genomic G+C content of the type strain is 61.9%. Its approximate genome size is 3.69 Mbp.

Emended Description of *Hyphomonas jannaschiana* Weiner et al. 1985

The description is as before (Weiner et al., 1985) with the following modification. The genomic G+C content of the type strain is 61.4%. Its approximate genome size is 3.64 Mbp.

Emended Description of *Hyphomonas johnsonii* Weiner et al. 2000

The description is as before (Weiner et al., 2000) with the following modification. The genomic G+C content of the type strain is 62.5%. Its approximate genome size is 3.62 Mbp.

Emended Description of *Hyphomonas oceanitis* Weiner et al. 1985

The description is as before (Weiner et al., 1985) with the following modification. The genomic G+C content of the type strain is 60.2%. Its approximate genome size is 4.28 Mbp.

Emended Description of *Hyphomonas polymorpha* (ex Pongratz 1957) Moore et al. 1984

The description is as before (Moore et al., 1984) with the following modification. The genomic G+C content of the type strain is 62.3%. Its approximate genome size is 4.05 Mbp.

Emended Description of *Jannaschia faecimaris* Jung and Yoon 2014

The description is as before (Jung and Yoon, 2014) with the following modification. The genomic G+C content of the type strain is 62.0%. Its approximate genome size is 3.81 Mbp.

Emended Description of *Jannaschia pohangensis* Kim et al. 2008

The description is as before (Kim B.Y. et al., 2008) with the following modification. The genomic G+C content of the type strain is 65.5%. Its approximate genome size is 3.73 Mbp.

Emended Description of *Jannaschia rubra* Macián et al. 2005

The description is as before (Macián et al., 2005) with the following modification. The genomic G+C content of the type strain is 67.9%. Its approximate genome size is 3.55 Mbp.

Emended Description of *Jannaschia seosinensis* Choi et al. 2006

The description is as before (Choi et al., 2006) with the following modification. The genomic G+C content of the type strain is 65.3%. Its approximate genome size is 3.83 Mbp.

Emended Description of *Jhaorihella thermophila* Rekha et al. 2011

The description is as before (Rekha et al., 2011) with the following modification. The genomic G+C content of the type strain is 66.0%. Its approximate genome size is 3.77 Mbp.

Emended Description of *Kaistia granuli* Lee et al. 2007

The description is as before (Lee et al., 2007a) with the following modification. The genomic G+C content of the type strain is 65.9%. Its approximate genome size is 4.77 Mbp.

Emended Description of *Kaistia soli* Weon et al. 2008

The description is as before (Weon et al., 2008b) with the following modification. The genomic G+C content of the type strain is 64.5%. Its approximate genome size is 5.24 Mbp.

Emended Description of *Kiloniella majae* Gerpe et al. 2017

The description is as before (Gerpe et al., 2017) with the following addition. The G+C content of the type-strain genome is 45.5%, its approximate size 4.39 Mbp.

Emended Description of *Komagataeibacter europaeus* (Sievers et al. 1992) Yamada et al. 2013

The description is as before (Yamada et al., 2012) with the following restriction. The genomic G+C content of the type strain is 61.3%. Its approximate genome size is 4.23 Mbp.

Emended Description of *Komagataeibacter kombuchae* (Dutta and Gachhui 2007) Yamada et al. 2013

The description is as before (Yamada et al., 2012) with the following modification. The genomic G+C content of the type strain is 59.4%. Its approximate genome size is 3.59 Mbp.

Emended Description of *Komagataeibacter oboediens* (Sokollek et al. 1998) Yamada et al. 2013

The description is as before (Yamada et al., 2012) with the following modification. The G+C content of the type-strain genome is 61.4%, its approximate size 3.75 Mbp.

Emended Description of *Komagataeibacter xylinus* (Brown 1886) Yamada et al. 2013

The description is as before (Yamada et al., 2012) with the following restriction. The genomic G+C content of the type strain is 62.3%. Its approximate genome size is 3.63 Mbp.

Emended Description of *Kordiimonas gwangyangensis* Kwon et al. 2005 emend. Yang et al. 2013

The description is as before (Yang et al., 2013) with the following restriction. The genomic G+C content of the type strain is 57.5%. Its approximate genome size is 4.08 Mbp.

Emended Description of *Kordiimonas lacus* Xu et al. 2011 emend. Wu et al. 2016

The description is as before (Wu et al., 2016) with the following modification. The genomic G+C content of the type strain is 57.2%. Its approximate genome size is 4.02 Mbp.

Emended Description of *Leisingera methylohalidivorans* Schaefer et al. 2002 emend. Vandecandelaere et al. 2008

The description is as before (Vandecandelaere et al., 2008b) with the following modification. The genomic G+C content of the type strain is 62.3%. Its approximate genome size is 4.65 Mbp.

Emended Description of *Lentibacter algarum* Li et al. 2012

The description is as before (Li et al., 2012) with the following modification. The genomic G+C content of the type strain is 55.7%. Its approximate genome size is 3.29 Mbp.

Emended Description of *Leptonema illini* Hovind-Hougen 1983

The description is as before (Hovind-Hougen, 1979) with the following restriction. The genomic G+C content of the type strain is 54.3%. Its approximate genome size is 4.52 Mbp.

Emended Description of *Leptospira alexanderi* Brenner et al. 1999

The description is as before (Brenner et al., 1999) with the following modification. The genomic G+C content of the type strain is 40.2%. Its approximate genome size is 4.22 Mbp.

Emended Description of *Leptospira alstonii* Smythe et al. 2013

The description is as before (Smythe et al., 2013) with the following restriction. The genomic G+C content of the type strain is 42.5%. Its approximate genome size is 4.44 Mbp.

Emended Description of *Leptospira biflexa* (Wolbach and Binger 1914) Noguchi 1918 (Approved Lists 1980) emend. Faine and Stallman 1982

The description is as before (Faine and Stallman, 1982) with the following addition. The genomic G+C content of the type strain is 38.9%. Its approximate genome size is 3.95 Mbp.

Emended Description of *Leptospira fainei* Perolat et al. 1998

The description is as before (Perolat et al., 1998) with the following addition. The genomic G+C content of the type strain is 43.5%. Its approximate genome size is 4.29 Mbp.

Emended Description of *Leptospira inadai* Yasuda et al. 1987

The description is as before (Yasuda et al., 1987) with the following restriction. The genomic G+C content of the type strain is 44.6%. Its approximate genome size is 4.46 Mbp.

Emended Description of *Leptospira interrogans* (Stimson 1907) Wenyon 1926 (Approved Lists 1980) emend. Faine and Stallman 1982

The description is as before (Faine and Stallman, 1982) with the following addition. The genomic G+C content of the type strain is 35.0%. Its approximate genome size is 4.60 Mbp.

Emended Description of *Leptospira kirschneri* Ramadass et al. 1992

The description is as before (Ramadass et al., 1992) with the following addition. The genomic G+C content of the type strain is 35.9%. Its approximate genome size is 4.41 Mbp.

Emended Description of *Leptospira kmetyi* Slack et al. 2009

The description is as before (Slack et al., 2009) with the following modification. The genomic G+C content of the type strain is 44.8%. Its approximate genome size is 4.42 Mbp.

Emended Description of *Leptospira licerasiae* Matthias et al. 2009

The description is as before (Matthias et al., 2008) with the following modification. The genomic G+C content of the type strain is 41.1%. Its approximate genome size is 4.21 Mbp.

Emended Description of *Leptospira meyeri* Yasuda et al. 1987

The description is as before (Yasuda et al., 1987) with the following modification. The genomic G+C content of the type strain is 38.0%. Its approximate genome size is 4.24 Mbp.

Emended Description of *Leptospira noguchii* Yasuda et al. 1987

The description is as before (Yasuda et al., 1987) with the following restriction. The genomic G+C content of the type strain is 35.5%. Its approximate genome size is 4.71 Mbp.

Emended Description of *Leptospira santarosai* Yasuda et al. 1987

The description is as before (Yasuda et al., 1987) with the following restriction. The genomic G+C content of the type strain is 41.8%. Its approximate genome size is 3.98 Mbp.

Emended Description of *Leptospira terpstrae* Smythe et al. 2013

The description is as before (Smythe et al., 2013) with the following restriction. The genomic G+C content of the type strain is 38.2%. Its approximate genome size is 4.09 Mbp.

Emended Description of *Leptospira vanthielii* Smythe et al. 2013

The description is as before (Smythe et al., 2013) with the following restriction. The genomic G+C content of the type strain is 38.9%. Its approximate genome size is 4.23 Mbp.

Emended Description of *Leptospira wolbachii* Yasuda et al. 1987

The description is as before (Yasuda et al., 1987) with the following modification. The genomic G+C content of the type strain is 39.2%. Its approximate genome size is 4.08 Mbp.

Emended Description of *Leptospira wolffii* Slack et al. 2008

The description is as before (Slack et al., 2008) with the following modification. The genomic G+C content of the type strain is 45.6%. Its approximate genome size is 4.40 Mbp.

Emended Description of *Leptospira yanagawae* Smythe et al. 2013

The description is as before (Smythe et al., 2013) with the following restriction. The genomic G+C content of the type strain is 38.2%. Its approximate genome size is 4.06 Mbp.

Emended Description of *Limimanicola cinnabarinus* (Tsubuchi et al. 2013) Wirth and Whitman 2018

The description is as before (Wirth and Whitman, 2018) with the following modification. The G+C content of the type-strain genome is 66.7%, its approximate size 3.90 Mbp.

Emended Description of *Limimanicola hongkongensis* (Lau et al. 2004) Wirth and Whitman 2018

The description is as before (Wirth and Whitman, 2018) with the following modification. The G+C content of the type-strain genome is 68.3%, its approximate size 3.19 Mbp.

Emended Description of *Limimanicola pyoseonensis* (Moon et al. 2010) Wirth and Whitman 2018

The description is as before (Wirth and Whitman, 2018) with the following modification. The G+C content of the type-strain genome is 70.3%, its approximate size 3.91 Mbp.

Emended Description of *Limimonas halophila* Amoozegar et al. 2013

The description is as before (Amoozegar et al., 2013) with the following modification. The genomic G+C content of the type strain is 69.5%. Its approximate genome size is 3.04 Mbp.

Emended Description of *Litoreibacter albidus* Romanenko et al. 2011

The description is as before (Romanenko et al., 2011a) with the following modification. The genomic G+C content of the type strain is 59.2%. Its approximate genome size is 3.58 Mbp.

Emended Description of *Litoreibacter arenae* (Kim et al. 2009) Kim et al. 2012

The description is as before (Kim et al., 2012a) with the following modification. The genomic G+C content of the type strain is 60.2%. Its approximate genome size is 3.69 Mbp.

Emended Description of *Litoreibacter janthinus* Romanenko et al. 2011

The description is as before (Romanenko et al., 2011a) with the following modification. The genomic G+C content of the type strain is 57.5%. Its approximate genome size is 3.75 Mbp.

Emended Description of *Litorimonas taeanensis* Jung et al. 2011 emend. Nedashkovskaya et al. 2013

The description is as before (Nedashkovskaya et al., 2013) with the following modification. The G+C content of the type-strain genome is 46.9%, its approximate size 2.78 Mbp.

Emended Description of *Loktanella atrilutea* Hosoya and Yokota 2007

The description is as before (Hosoya and Yokota, 2007) with the following modification. The genomic G+C content of the type strain is 64.9%. Its approximate genome size is 4.21 Mbp.

Emended Description of *Loktanella cinnabarina* Tsubouchi et al. 2013

The description is as before (Tsubouchi et al., 2013) with the following modification. The genomic G+C content of the type strain is 66.7%. Its approximate genome size is 3.90 Mbp.

Emended Description of *Loktanella hongkongensis* Lau et al. 2004

The description is as before (Lau et al., 2004) with the following modification. The genomic G+C content of the type strain is 68.3%. Its approximate genome size is 3.19 Mbp.

Emended Description of *Loktanella koreensis* Weon et al. 2006

The description is as before (Weon et al., 2006) with the following modification. The genomic G+C content of the type strain is 57.2%. Its approximate genome size is 3.65 Mbp.

Emended Description of *Loktanella maritima* Tanaka et al. 2014

The description is as before (Tanaka et al., 2014) with the following addition. The genomic G+C content of the type strain is 53.4%. Its approximate genome size is 3.68 Mbp.

Emended Description of *Loktanella pyoseonensis* Moon et al. 2010

The description is as before (Moon et al., 2010) with the following modification. The genomic G+C content of the type strain is 70.3%. Its approximate genome size is 3.91 Mbp.

Emended Description of *Loktanella rosea* Ivanova et al. 2005

The description is as before (Ivanova et al., 2005) with the following restriction. The genomic G+C content of the type strain is 57.7%. Its approximate genome size is 3.51 Mbp.

Emended Description of *Loktanella sediminum* Liang et al. 2015

The description is as before (Liang et al., 2015) with the following modification. The genomic G+C content of the type strain is 54.4%. Its approximate genome size is 3.26 Mbp.

Emended Description of *Loktanella tamlensis* Lee 2012

The description is as before (Lee, 2012) with the following modification. The genomic G+C content of the type strain is 56.9%. Its approximate genome size is 3.19 Mbp.

Emended Description of *Loktanella vestfoldensis* Van Trappen et al. 2004

The description is as before (Van Trappen et al., 2004) with the following modification. The genomic G+C content of the type strain is 61.8%. Its approximate genome size is 3.72 Mbp.

Emended Description of *Lutibaculum baratangense* Anil Kumar et al. 2012

The description is as before (Anil Kumar et al., 2012) with the following modification. The genomic G+C content of the type strain is 68.6%. Its approximate genome size is 4.30 Mbp.

Emended Description of *Magnetospirillum gryphiswaldense* Schleifer et al. 1992

The description is as before (Schleifer et al., 1991) with the following modification. The genomic G+C content of the type strain is 63.3%. Its approximate genome size is 4.37 Mbp.

Emended Description of *Magnetospirillum marisnigri* Dziuba et al. 2016

The description is as before (Dziuba et al., 2016) with the following modification. The genomic G+C content of the type strain is 64.7%. Its approximate genome size is 4.62 Mbp.

Emended Description of *Magnetovibrio blakemorei* Bazyliński et al. 2013

The description is as before (Bazyliński et al., 2013b) with the following modification. The genomic G+C content of the type strain is 54.3%.

Emended Description of *Maliponia aquimaris* Jung et al. 2016

The description is as before (Jung et al., 2016) with the following modification. The G+C content of the type-strain genome is 67.2%, its approximate size 5.31 Mbp.

Emended Description of *Mameliella alba* Zheng et al. 2010

The description is as before (Zheng et al., 2010) with the following modification. The genomic G+C content of the type strain is 65.2%. Its approximate genome size is 5.26 Mbp.

Emended Description of *Mameliella atlantica* Xu et al. 2015

The description is as before (Xu et al., 2015) with the following modification. The genomic G+C content of the type strain is 65.0%. Its approximate genome size is 5.90 Mbp.

Emended Description of *Maribius salinus* Choi et al. 2007

The description is as before (Choi et al., 2007) with the following modification. The genomic G+C content of the type strain is 67.7%. Its approximate genome size is 3.57 Mbp.

Emended Description of *Marinovum algicola* (Lafay et al. 1995) Martens et al. 2006

The description is as before (Martens et al., 2006) with the following addition. The genomic G+C content of the type strain is 65.0%. Its approximate genome size is 5.39 Mbp.

Emended Description of *Maritimibacter alkaliphilus* Lee et al. 2007

The description is as before (Lee et al., 2007b) with the following modification. The genomic G+C content of the type strain is 64.1%. Its approximate genome size is 4.53 Mbp.

Emended Description of *Marivita hallyeonensis* Yoon et al. 2012

The description is as before (Yoon et al., 2012) with the following modification. The genomic G+C content of the type strain is 60.4%. Its approximate genome size is 4.19 Mbp.

Emended Description of *Martellella mediterranea* Rivas et al. 2005

The description is as before (Rivas et al., 2005) with the following modification. The genomic G+C content of the type strain is 62.4%. Its approximate genome size is 5.64 Mbp.

Emended Description of *Mesorhizobium albiziae* Wang et al. 2007

The description is as before (Wang et al., 2007) with the following modification. The genomic G+C content of the type strain is 62.1%. Its approximate genome size is 6.27 Mbp.

Emended Description of *Mesorhizobium alhagi* Chen et al. 2010

The description is as before (Chen W.-M. et al., 2010) with the following restriction. The genomic G+C content of the type strain is 62.7%. Its approximate genome size is 6.97 Mbp.

Emended Description of *Mesorhizobium erdmanii* Martínez-Hidalgo et al. 2015

The description is as before (Martínez-Hidalgo et al., 2015) with the following modification. The genomic G+C content of the type strain is 62.7%. Its approximate genome size is 7.02 Mbp.

Emended Description of *Mesorhizobium loti* (Jarvis et al. 1982) Jarvis et al. 1997 emend. Hameed et al. 2015

The description is as before (Hameed et al., 2015) with the following restriction. The G+C content of the type-strain genome is 62.4%, its approximate size 7.45 Mbp.

Emended Description of *Mesorhizobium mediterraneum* (Nour et al. 1995) Jarvis et al. 1997

The description is as before (Jarvis et al., 1997) with the following addition. The genomic G+C content of the type strain is 62.0%. Its approximate genome size is 7.20 Mbp.

Emended Description of *Mesorhizobium metallidurans* Vidal et al. 2009

The description is as before (Vidal et al., 2009) with the following addition. The genomic G+C content of the type strain is 62.5%. Its approximate genome size is 6.23 Mbp.

Emended Description of *Mesorhizobium muleiense* Zhang et al. 2012

The description is as before (Zhang J.J. et al., 2012) with the following modification. The genomic G+C content of the type strain is 62.3%. Its approximate genome size is 6.81 Mbp.

Emended Description of *Mesorhizobium qingshengii* Zheng et al. 2013

The description is as before (Zheng et al., 2013) with the following modification. The genomic G+C content of the type strain is 62.7%. Its approximate genome size is 7.06 Mbp.

Emended Description of *Mesorhizobium soli* Nguyen et al. 2015

The description is as before (Nguyen et al., 2015) with the following modification. The G+C content of the type-strain genome is 62.6%, its approximate size 6.27 Mbp.

Emended Description of *Mesorhizobium temperatum* Gao et al. 2004

The description is as before (Gao et al., 2004) with the following modification. The genomic G+C content of the type strain is 61.9%. Its approximate genome size is 7.17 Mbp.

Emended Description of *Methylococcus marina* Doronina et al. 2000

The description is as before (Doronina et al., 2000) with the following modification. The G+C content of the type-strain genome is 63.0%, its approximate size 4.23 Mbp.

Emended Description of *Methylobacterium chloromethanicum* McDonald et al. 2001

The description is as before (McDonald et al., 2001) with the following modification. The G+C content of the type-strain genome is 68.1%, its approximate size 6.18 Mbp.

Emended Description of *Methylobacterium gossypicola* Madhaiyan et al. 2012

The description is as before (Madhaiyan et al., 2012) with the following modification. The genomic G+C content of the type strain is 68.7%. Its approximate genome size is 4.52 Mbp.

Emended Description of *Methylobacterium komagatae* Kato et al. 2008

The description is as before (Kato et al., 2008) with the following modification. The genomic G+C content of the type strain is 67.5%. Its approximate genome size is 5.50 Mbp.

Emended Description of *Methylobacterium nodulans* Jourand et al. 2004

The description is as before (Jourand et al., 2004) with the following addition. The genomic G+C content of the type strain is 68.4%. Its approximate genome size is 8.84 Mbp.

Emended Description of *Methylobacterium organophilum* Patt et al. 1976 (Approved Lists 1980)

The description is as before (Patt et al., 1976) with the following modification. The G+C content of the type-strain genome is 71.4%, its approximate size 6.75 Mbp.

Emended Description of *Methylobacterium oryzae* Madhaiyan et al. 2007

The description is as before (Madhaiyan et al., 2007) with the following modification. The genomic G+C content of the type strain is 69.5%. Its approximate genome size is 6.52 Mbp.

Emended Description of *Methylobacterium phyllosphaerae* Madhaiyan et al. 2009

The description is as before (Madhaiyan et al., 2009) with the following modification. The genomic G+C content of the type strain is 69.6%. Its approximate genome size is 6.20 Mbp.

Emended Description of *Methylobacterium phyllostachyos* Madhaiyan and Poonguzhali 2014

The description is as before (Madhaiyan and Poonguzhali, 2014) with the following modification. The genomic G+C content of the type strain is 68.7%. Its approximate genome size is 6.01 Mbp.

Emended Description of *Methylobacterium platani* Kang et al. 2007

The description is as before (Kang et al., 2007) with the following modification. The genomic G+C content of the type strain is 71.2%. Its approximate genome size is 7.01 Mbp.

Emended Description of *Methylobacterium pseudosasicola* Madhaiyan and Poonguzhali 2014

The description is as before (Madhaiyan and Poonguzhali, 2014) with the following modification. The genomic G+C content of the type strain is 68.4%. Its approximate genome size is 6.85 Mbp.

Emended Description of *Methylobacterium radiotolerans* (Ito and Iizuka 1971) Green and Bousfield 1983

The description is as before (Green and Bousfield, 1983) with the following addition. The genomic G+C content of the type strain is 71.0%. Its approximate genome size is 6.90 Mbp.

Emended Description of *Methylobacterium tarhaniae* Veyisoglu et al. 2013

The description is as before (Veyisoglu et al., 2013) with the following modification. The genomic G+C content of the type strain is 70.4%. Its approximate genome size is 6.74 Mbp.

Emended Description of *Methylobrevia pamukkalensis* Poroshina et al. 2015

The description is as before (Poroshina et al., 2015) with the following modification. The genomic G+C content of the type strain is 68.9%. Its approximate genome size is 4.38 Mbp.

Emended Description of *Methylocapsa acidiphila* Dedysh et al. 2002

The description is as before (Dedysh et al., 2002) with the following modification. The genomic G+C content of the type strain is 61.8%. Its approximate genome size is 4.10 Mbp.

Emended Description of *Methyloceanibacter caenitepidi* Takeuchi et al. 2014

The description is as before (Takeuchi et al., 2014) with the following modification. The genomic G+C content of the type strain is 62.8%. Its approximate genome size is 3.42 Mbp.

Emended Description of *Methylocella silvestris* Dunfield et al. 2003

The description is as before (Dunfield et al., 2003) with the following modification. The genomic G+C content of the type strain is 63.1%. Its approximate genome size is 4.31 Mbp.

Emended Description of *Methylocystis parvus* (ex Whittenbury et al. 1970) Bowman et al. 1993

The description is as before (Bowman et al., 1993) with the following restriction. The genomic G+C content of the type strain is 63.4%. Its approximate genome size is 4.48 Mbp.

Emended Description of *Methyloferula stellata* Vorobev et al. 2011

The description is as before (Vorobev et al., 2011) with the following addition. The genomic G+C content of the type strain is 59.5%. Its approximate genome size is 4.24 Mbp.

Emended Description of *Methyloligella halotolerans* Doronina et al. 2014

The description is as before (Doronina et al., 2013) with the following modification. The genomic G+C content of the type strain is 63.6%. Its approximate genome size is 3.19 Mbp.

Emended Description of *Methylorubrum extorquens* (Urakami and Komagata 1984) Green and Ardley 2018

The description is as before (Green and Ardley, 2018) with the following restriction. The G+C content of the type-strain genome is 68.3%, its approximate size 5.72 Mbp.

Emended Description of *Methylorubrum populi* (Van Aken et al. 2004) Green and Ardley 2018

The description is as before (Green and Ardley, 2018) with the following modification. The genomic G+C content of the type strain is 69.4%. Its approximate genome size is 5.85 Mbp.

Emended Description of *Methylorubrum salsuginis* (Wang et al. 2007) Green and Ardley 2018

The description is as before (Green and Ardley, 2018) with the following addition. The genomic G+C content of the type strain is 69.6%. Its approximate genome size is 5.32 Mbp.

Emended Description of *Methylosinus sporium* (ex Whittenbury et al. 1970) Bowman et al. 1993

The description is as before (Bowman et al., 1993) with the following restriction. The G+C content of the type-strain genome is 65.2%, its approximate size 3.79 Mbp.

Emended Description of *Methylosinus trichosporium* (ex Whittenbury et al. 1970) Bowman et al. 1993

The description is as before (Bowman et al., 1993) with the following modification. The genomic G+C content of the type strain is 65.9%. Its approximate genome size is 4.96 Mbp.

Emended Description of *Microvirga guangxiensis* Zhang et al. 2009

The description is as before (Zhang et al., 2009) with the following modification. The genomic G+C content of the type strain is 61.4%. Its approximate genome size is 4.72 Mbp.

Emended Description of *Microvirga subterranea* Kanso and Patel 2003

The description is as before (Kanso and Patel, 2003) with the following modification. The G+C content of the type-strain genome is 65.1%, its approximate size 5.15 Mbp.

Emended Description of *Microvirga vignae* Radl et al. 2014

The description is as before (Radl et al., 2014) with the following modification. The genomic G+C content of the type strain is 61.1%. Its approximate genome size is 6.47 Mbp.

Emended Description of *Monaibacterium marinum* Chernikova et al. 2017

The description is as before (Chernikova et al., 2017) with the following modification. The G+C content of the type-strain genome is 58.9%, its approximate size 3.73 Mbp.

Emended Description of *Nautella italica* Vandecandelaere et al. 2009

The description is as before (Vandecandelaere et al., 2009) with the following restriction. The genomic G+C content of the type strain is 60.0%. Its approximate genome size is 4.06 Mbp.

Emended Description of *Neosaia chiangmaiensis* Yukphan et al. 2006

The description is as before (Yukphan et al., 2005) with the following addition. The genomic G+C content of the type strain is 61.5%. Its approximate genome size is 3.41 Mbp.

Emended Description of *Neokomagataea thailandica* Yukphan et al. 2011

The description is as before (Yukphan et al., 2011) with the following modification. The genomic G+C content of the type strain is 52.4%. Its approximate genome size is 2.49 Mbp.

Emended Description of *Neomegalonema perideroedes* (Thomsen et al. 2006) Oren 2017

The description is as before (Oren, 2017b) with the following modification. The G+C content of the type-strain genome is 67.2%, its approximate size 3.41 Mbp.

Emended Description of *Neorhizobium alkalisoli* (Lu et al. 2009) Mousavi et al. 2015

The description is as before (Mousavi et al., 2014) with the following modification. The G+C content of the type-strain genome is 60.3%, its approximate size 5.87 Mbp.

Emended Description of *Neorhizobium galegae* (Lindström 1989) Mousavi et al. 2015

The description is as before (Mousavi et al., 2014) with the following restriction. The genomic G+C content of the type strain is 61.2%. Its approximate genome size is 6.46 Mbp.

Emended Description of *Neorhizobium huautlense* (Wang et al. 1998) Mousavi et al. 2015

The description is as before (Mousavi et al., 2014) with the following restriction. The G+C content of the type-strain genome is 60.0%, its approximate size 5.73 Mbp.

Emended Description of *Neorickettsia risticii* (Holland et al. 1985) Dumler et al. 2001

The description is as before (Dumler et al., 2001) with the following addition. The genomic G+C content of the type strain is 41.3%.

Emended Description of *Neorickettsia sennetsu* (Misao and Kobayashi 1956) Dumler et al. 2001

The description is as before (Dumler et al., 2001) with the following addition. The genomic G+C content of the type strain is 41.1%.

Emended Description of *Neptunicoccus sediminis* Zhang et al. 2018

The description is as before (Zhang Y.-J. et al., 2018) with the following addition. The G+C content of the type-strain genome is 57.5%, its approximate size 3.86 Mbp.

Emended Description of *Nereida ignava* Pujalte et al. 2005

The description is as before (Pujalte et al., 2005) with the following modification. The genomic G+C content of the type strain is 54.1%. Its approximate genome size is 2.84 Mbp.

Emended Description of *Nitratireductor aquibiodomus* Labbé et al. 2004

The description is as before (Labbé et al., 2004) with the following modification. The genomic G+C content of the type strain is 61.3%. Its approximate genome size is 4.52 Mbp.

Emended Description of *Nitratireductor indicus* Lai et al. 2011

The description is as before (Lai et al., 2011c) with the following modification. The genomic G+C content of the type strain is 60.9%. Its approximate genome size is 4.99 Mbp.

Emended Description of *Nitratireductor pacificus* Lai et al. 2011

The description is as before (Lai et al., 2011b) with the following modification. The genomic G+C content of the type strain is 65.5%. Its approximate genome size is 4.47 Mbp.

Emended Description of *Nitrobacter winogradskyi* Winslow et al. 1917 (Approved Lists 1980)

The description is as before (Winslow et al., 1917) with the following addition. The genomic G+C content of the type strain is 62.0%. Its approximate genome size is 3.40 Mbp.

Emended Description of *Novosphingobium acidiphilum* Glaeser et al. 2009

The description is as before (Glaeser et al., 2009) with the following addition. The genomic G+C content of the type strain is 64.3%. Its approximate genome size is 3.71 Mbp.

Emended Description of *Novosphingobium aromaticivorans* (Balkwill et al. 1997) Takeuchi et al. 2001

The description is as before (Takeuchi et al., 2001) with the following restriction. The genomic G+C content of the type strain is 65.1%. Its approximate genome size is 4.23 Mbp.

Emended Description of *Novosphingobium barchaimii* Niharika et al. 2013

The description is as before (Niharika et al., 2013b) with the following modification. The genomic G+C content of the type strain is 64.0%. Its approximate genome size is 5.31 Mbp.

Emended Description of *Novosphingobium capsulatum* (Leifson 1962) Takeuchi et al. 2001

The description is as before (Takeuchi et al., 2001) with the following modification. The genomic G+C content of the type strain is 65.7%. Its approximate genome size is 4.84 Mbp.

Emended Description of *Novosphingobium fuchskuhlense* Glaeser et al. 2013

The description is as before (Glaeser et al., 2013) with the following addition. The genomic G+C content of the type strain is 65.4%. Its approximate genome size is 3.96 Mbp.

Emended Description of *Novosphingobium guangzhouense* Sha et al. 2017

The description is as before (Sha et al., 2017) with the following modification. The G+C content of the type-strain genome is 63.5%, its approximate size 5.97 Mbp.

Emended Description of *Novosphingobium lindaniclasticum* Saxena et al. 2013

The description is as before (Saxena et al., 2013) with the following modification. The genomic G+C content of the type strain is 64.6%. Its approximate genome size is 4.86 Mbp.

Emended Description of *Novosphingobium mathureense* Gupta et al. 2009

The description is as before (Gupta et al., 2009) with the following addition. The genomic G+C content of the type strain is 63.3%. Its approximate genome size is 4.84 Mbp.

Emended Description of *Novosphingobium nitrogenifigens* Addison et al. 2007

The description is as before (Addison et al., 2007) with the following addition. The genomic G+C content of the type strain is 64.0%. Its approximate genome size is 4.15 Mbp.

Emended Description of *Novosphingobium pentaromativorans* Sohn et al. 2004

The description is as before (Sohn et al., 2004) with the following modification. The genomic G+C content of the type strain is 63.0%. Its approximate genome size is 5.46 Mbp.

Emended Description of *Novosphingobium subarcticum* (Nohynek et al. 1996) Takeuchi et al. 2001

The description is as before (Takeuchi et al., 2001) with the following restriction. The genomic G+C content of the type strain is 65.1%. Its approximate genome size is 6.30 Mbp.

Emended Description of *Novosphingobium subterraneum* (Balkwill et al. 1997) Takeuchi et al. 2001

The description is as before (Takeuchi et al., 2001) with the following modification. The genomic G+C content of the type strain is 63.3%. Its approximate genome size is 4.70 Mbp.

Emended Description of *Oceanibacterium hippocampi* Balcázar et al. 2013

The description is as before (Balcázar et al., 2012) with the following modification. The genomic G+C content of the type strain is 66.7%. Its approximate genome size is 4.83 Mbp.

Emended Description of *Oceanibaculum pacificum* Dong et al. 2010

The description is as before (Dong et al., 2010) with the following modification. The genomic G+C content of the type strain is 65.7%. Its approximate genome size is 3.89 Mbp.

Emended Description of *Oceanicella actignis* Albuquerque et al. 2012

The description is as before (Albuquerque et al., 2012) with the following modification. The genomic G+C content of the type strain is 72.4%. Its approximate genome size is 3.28 Mbp.

Emended Description of *Oceanicola granulosus* Cho and Giovannoni 2004

The description is as before (Cho and Giovannoni, 2004) with the following modification. The genomic G+C content of the type strain is 70.4%. Its approximate genome size is 4.04 Mbp.

Emended Description of *Octadecabacter antarcticus* Gosink et al. 1998 emend. Billerbeck et al. 2015

The description is as before (Billerbeck et al., 2015) with the following modification. The genomic G+C content of the type strain is 54.6%. Its approximate genome size is 4.88 Mbp.

Emended Description of *Octadecabacter arcticus* Gosink et al. 1998 emend. Billerbeck et al. 2015

The description is as before (Billerbeck et al., 2015) with the following modification. The genomic G+C content of the type strain is 55.1%. Its approximate genome size is 5.48 Mbp.

Emended Description of *Octadecabacter ascidiaceicola* Kim et al. 2016

The description is as before (Kim et al., 2016a) with the following modification. The G+C content of the type-strain genome is 54.9%, its approximate size 3.23 Mbp.

Emended Description of *Oharaeibacter diazotrophicus* Lv et al. 2017

The description is as before (Lv et al., 2017) with the following modification. The G+C content of the type-strain genome is 71.6%, its approximate size 4.99 Mbp.

Emended Description of *Orientia tsutsugamushi* (Hayashi 1920) Tamura et al. 1995

The description is as before (Tamura et al., 1995) with the following restriction. The genomic G+C content of the type strain is 29.9%. Its approximate genome size is 1.45 Mbp.

Emended Description of *Pacificibacter marinus* (Jung et al. 2011) Park et al. 2015

The description is as before (Park et al., 2014c) with the following modification. The genomic G+C content of the type strain is 52.0%. Its approximate genome size is 3.87 Mbp.

Emended Description of *Palleronia marisminoris* Martínez-Checa et al. 2005 emend. Albuquerque et al. 2015

The description is as before (Albuquerque et al., 2015) with the following modification. The genomic G+C content of the type strain is 66.2%. Its approximate genome size is 3.94 Mbp.

Emended Description of *Pannonibacter phragmitetus* Borsodi et al. 2003

The description is as before (Borsodi et al., 2003) with the following modification. The genomic G+C content of the type strain is 63.1%. Its approximate genome size is 4.78 Mbp.

Emended Description of *Paracoccus aestuarii* Roh et al. 2009

The description is as before (Roh et al., 2009) with the following modification. The G+C content of the type-strain genome is 67.7%, its approximate size 3.74 Mbp.

Emended Description of *Paracoccus alcaliphilus* Urakami et al. 1989

The description is as before (Urakami et al., 1989) with the following restriction. The genomic G+C content of the type strain is 64.3%. Its approximate genome size is 4.61 Mbp.

Emended Description of *Paracoccus alkenifer* Lipski et al. 1998

The description is as before (Lipski et al., 1998) with the following addition. The genomic G+C content of the type strain is 67.3%. Its approximate genome size is 3.19 Mbp.

Emended Description of *Paracoccus bengalensis* Ghosh et al. 2006

The description is as before (Ghosh et al., 2006) with the following modification. The G+C content of the type-strain genome is 67.4%, its approximate size 4.99 Mbp.

Emended Description of *Paracoccus contaminans* Kämpfer et al. 2016

The description is as before (Kämpfer et al., 2016) with the following modification. The genomic G+C content of the type strain is 68.7%. Its approximate genome size is 3.03 Mbp.

Emended Description of *Paracoccus denitrificans* (Beijerinck and Minkman 1910) Davis 1969 (Approved Lists 1980) emend. Rainey et al., 1999

The description is as before (Rainey et al., 1999) with the following restriction. The genomic G+C content of the type strain is 66.8%. Its approximate genome size is 5.19 Mbp.

Emended Description of *Paracoccus halophilus* Liu et al. 2008

The description is as before (Liu et al., 2008) with the following modification. The genomic G+C content of the type strain is 65.2%. Its approximate genome size is 4.01 Mbp.

Emended Description of *Paracoccus isopora* Chen et al. 2011

The description is as before (Chen et al., 2011a) with the following modification. The genomic G+C content of the type strain is 65.8%. Its approximate genome size is 3.52 Mbp.

Emended Description of *Paracoccus pantotrophus* (Robertson and Kuenen 1984) Rainey et al. 1999

The description is as before (Rainey et al., 1999) with the following modification. The G+C content of the type-strain genome is 67.6%, its approximate size 4.41 Mbp.

Emended Description of *Paracoccus sediminis* Pan et al. 2014

The description is as before (Pan et al., 2014) with the following modification. The genomic G+C content of the type strain is 66.0%. Its approximate genome size is 3.65 Mbp.

Emended Description of *Paracoccus seriniphilus* Pukall et al. 2003

The description is as before (Pukall et al., 2003) with the following modification. The genomic G+C content of the type strain is 61.6%. Its approximate genome size is 4.20 Mbp.

Emended Description of *Paracoccus solventivorans* Siller et al. 1996 emend. Lipski et al. 1998

The description is as before (Lipski et al., 1998) with the following restriction. The genomic G+C content of the type strain is 68.7%. Its approximate genome size is 3.38 Mbp.

Emended Description of *Paracoccus sphaerophysae* Deng et al. 2011

The description is as before (Deng et al., 2011) with the following modification. The genomic G+C content of the type strain is 69.1%. Its approximate genome size is 3.36 Mbp.

Emended Description of *Paracoccus yeei* Daneshvar et al. 2003

The description is as before (Daneshvar et al., 2003) with the following modification. The genomic G+C content of the type strain is 67.5%. Its approximate genome size is 4.43 Mbp.

Emended Description of *Pararhizobium giardinii* (Amarger et al. 1997) Mousavi et al. 2016

The description is as before (Mousavi et al., 2015) with the following addition. The genomic G+C content of the type strain is 60.7%. Its approximate genome size is 6.81 Mbp.

Emended Description of *Pararhodospirillum photometricum* (Molisch 1907) Lakshmi et al. 2014

The description is as before (Lakshmi et al., 2014) with the following addition. The genomic G+C content of the type strain is 64.7%. Its approximate genome size is 3.88 Mbp.

Emended Description of *Parvibaculum lavamentivorans* Schleheck et al. 2004

The description is as before (Schleheck et al., 2004) with the following modification. The genomic G+C content of the type strain is 62.3%. Its approximate genome size is 3.91 Mbp.

Emended Description of *Pelagibaca bermudensis* Cho and Giovannoni 2006

The description is as before (Cho and Giovannoni, 2006) with the following modification. The genomic G+C content of the type strain is 66.4%. Its approximate genome size is 5.43 Mbp.

Emended Description of *Pelagibacterium halotolerans* Xu et al. 2011

The description is as before (Xu et al., 2011) with the following modification. The genomic G+C content of the type strain is 61.4%. Its approximate genome size is 3.95 Mbp.

Emended Description of *Pelagibacterium luteolum* Xu et al. 2011

The description is as before (Xu et al., 2011) with the following modification. The genomic G+C content of the type strain is 60.4%. Its approximate genome size is 4.30 Mbp.

Emended Description of *Pelagicola litoralis* Kim et al. 2008

The description is as before (Kim Y.-G. et al., 2008) with the following modification. The genomic G+C content of the type strain is 54.8%. Its approximate genome size is 3.64 Mbp.

Emended Description of *Phaeobacter gallaeciensis* (Ruiz-Ponte et al. 1998) Martens et al. 2006

The description is as before (Martens et al., 2006) with the following modification. The genomic G+C content of the type strain is 59.4%. Its approximate genome size is 4.54 Mbp.

Emended Description of *Phaeobacter italicus* (Vandecastelaere et al. 2009) Wirth and Whitman 2018

The description is as before (Wirth and Whitman, 2018) with the following restriction. The G+C content of the type-strain genome is 60.0%, its approximate size 4.06 Mbp.

Emended Description of *Phenylobacterium composti* Weon et al. 2008

The description is as before (Weon et al., 2008a) with the following modification. The genomic G+C content of the type strain is 70.0%. Its approximate genome size is 3.30 Mbp.

Emended Description of *Phenylobacterium deserti* Khan et al. 2017

The description is as before (Khan et al., 2017) with the following modification. The G+C content of the type-strain genome is 68.2%, its approximate size 3.87 Mbp.

Emended Description of *Phenylobacterium immobile* Lingens et al. 1985

The description is as before (Lingens et al., 1985) with the following modification. The genomic G+C content of the type strain is 66.7%. Its approximate genome size is 3.33 Mbp.

Emended Description of *Phenylobacterium kunshanense* Chu et al. 2015

The description is as before (Chu et al., 2015) with the following modification. The G+C content of the type-strain genome is 69.3%, its approximate size 4.18 Mbp.

Emended Description of *Phyllobacterium brassicacearum* Mantelin et al. 2006

The description is as before (Mantelin et al., 2006) with the following modification. The G+C content of the type-strain genome is 57.3%, its approximate size 5.79 Mbp.

Emended Description of *Phyllobacterium endophyticum* Flores-Félix et al. 2013

The description is as before (Flores-Félix et al., 2013) with the following modification. The G+C content of the type-strain genome is 57.0%, its approximate size 5.51 Mbp.

Emended Description of *Phyllobacterium leguminum* Mantelin et al. 2006

The description is as before (Mantelin et al., 2006) with the following modification. The G+C content of the type-strain genome is 59.8%, its approximate size 3.72 Mbp.

Emended Description of *Phyllobacterium rubiacearum* (ex von Faber 1912) Knösel 1984

The description is as before (Knösel, 1984) with the following modification. The G+C content of the type-strain genome is 59.2%, its approximate size 5.58 Mbp.

Emended Description of *Phyllobacterium salinisoli* León-Barrios et al. 2018

The description is as before (León-Barrios et al., 2018) with the following modification. The G+C content of the type-strain genome is 59.9%, its approximate size 5.04 Mbp.

Emended Description of *Phyllobacterium sophorae* Jiao et al. 2015

The description is as before (Jiao et al., 2015) with the following modification. The G+C content of the type-strain genome is 57.0%, its approximate size 6.36 Mbp.

Emended Description of *Pleomorphomonas diazotrophica* Madhaiyan et al. 2013

The description is as before (Madhaiyan et al., 2013) with the following modification. The G+C content of the type-strain genome is 65.1%, its approximate size 4.53 Mbp.

Emended Description of *Pleomorphomonas koreensis* Im et al. 2006

The description is as before (Im et al., 2006) with the following modification. The genomic G+C content of the type strain is 67.2%. Its approximate genome size is 4.62 Mbp.

Emended Description of *Pontibaca methylaminivorans* Kim et al. 2010

The description is as before (Kim K.K. et al., 2010) with the following modification. The genomic G+C content of the type strain is 66.5%. Its approximate genome size is 2.65 Mbp.

Emended Description of *Ponticaulis koreensis* Kang and Lee 2009

The description is as before (Kang and Lee, 2009) with the following modification. The genomic G+C content of the type strain is 54.8%. Its approximate genome size is 3.40 Mbp.

Emended Description of *Ponticoccus lacteus* Yang et al. 2015

The description is as before (Yang Y. et al., 2015) with the following modification. The genomic G+C content of the type strain is 65.1%. Its approximate genome size is 5.42 Mbp.

Emended Description of *Porphyrobacter cryptus* da Costa et al. 2003

The description is as before (Rainey et al., 2003) with the following modification. The genomic G+C content of the type strain is 67.9%. Its approximate genome size is 2.95 Mbp.

Emended Description of *Porphyrobacter neustonensis* Fuerst et al. 1993

The description is as before (Fuerst et al., 1993) with the following modification. The genomic G+C content of the type strain is 65.3%. Its approximate genome size is 3.09 Mbp.

Emended Description of *Primorskyibacter sedentarius* Romanenko et al. 2011

The description is as before (Romanenko et al., 2011b) with the following restriction. The G+C content of the type-strain genome is 60.8%, its approximate size 5.06 Mbp.

Emended Description of *Prosthecomicrobium hirschii* Staley 1984

The description is as before (Staley, 1984) with the following restriction. The genomic G+C content of the type strain is 68.9%. Its approximate genome size is 6.46 Mbp.

Emended Description of *Pseudaminobacter salicylatoxidans* Kämpfer et al. 1999

The description is as before (Kämpfer et al., 1999) with the following modification. The G+C content of the type-strain genome is 62.7%, its approximate size 4.84 Mbp.

Emended Description of *Pseudodonghicola xiamenensis* (Tan et al. 2009) Hameed et al. 2014

The description is as before (Hameed et al., 2014) with the following modification. The genomic G+C content of the type strain is 63.6%. Its approximate genome size is 4.73 Mbp.

Emended Description of *Pseudolabrys taiwanensis* Kämpfer et al. 2006

The description is as before (Kämpfer et al., 2006) with the following modification. The G+C content of the type-strain genome is 64.4%, its approximate size 5.59 Mbp.

Emended Description of *Pseudoceanicola antarcticus* (Huo et al. 2014) Lai et al. 2015

The description is as before (Lai et al., 2015) with the following modification. The G+C content of the type-strain genome is 66.3%, its approximate size 4.23 Mbp.

Emended Description of *Pseudoceanicola batsensis* (Cho and Giovannoni 2004) Lai et al. 2015

The description is as before (Lai et al., 2015) with the following modification. The genomic G+C content of the type strain is 66.1%. Its approximate genome size is 4.44 Mbp.

Emended Description of *Pseudoceanicola marinus* (Lin et al. 2007) Lai et al. 2015

The description is as before (Lai et al., 2015) with the following modification. The genomic G+C content of the type strain is 66.8%. Its approximate genome size is 4.53 Mbp.

Emended Description of *Pseudoceanicola nanhaiensis* (Gu et al. 2007) Lai et al. 2015

The description is as before (Lai et al., 2015) with the following modification. The genomic G+C content of the type strain is 67.9%. Its approximate genome size is 4.66 Mbp.

Emended Description of *Pseudoceanicola nitratreducens* (Zheng et al. 2010) Lai et al. 2015

The description is as before (Lai et al., 2015) with the following modification. The genomic G+C content of the type strain is 64.2%. Its approximate genome size is 4.07 Mbp.

Emended Description of *Pseudorhodobacter antarcticus* Chen et al. 2013

The description is as before (Chen C.-X. et al., 2013) with the following modification. The genomic G+C content of the type strain is 59.1%. Its approximate genome size is 3.88 Mbp.

Emended Description of *Pseudorhodobacter aquimaris* Jung et al. 2012

The description is as before (Jung et al., 2012a) with the following modification. The genomic G+C content of the type strain is 58.7%. Its approximate genome size is 3.82 Mbp.

Emended Description of *Pseudorhodobacter wandonensis* Lee et al. 2013

The description is as before (Lee et al., 2013) with the following modification. The genomic G+C content of the type strain is 57.8%. Its approximate genome size is 3.89 Mbp.

Emended Description of *Pseudoroseovarius halocynthiae* (Kim et al. 2012) Sun et al. 2015

The description is as before (Sun et al., 2015) with the following modification. The genomic G+C content of the type strain is 57.1%. Its approximate genome size is 3.40 Mbp.

Emended Description of *Pseudoroseovarius sediminilitoris* (Park and Yoon 2013) Sun et al. 2015

The description is as before (Sun et al., 2015) with the following modification. The genomic G+C content of the type strain is 58.7%. Its approximate genome size is 3.41 Mbp.

Emended Description of *Pseudoruegeria haliotis* Hyun et al. 2013

The description is as before (Hyun et al., 2013b) with the following modification. The genomic G+C content of the type strain is 63.0%. Its approximate genome size is 5.04 Mbp.

Emended Description of *Pseudoruegeria lutimaris* Jung et al. 2010

The description is as before (Jung et al., 2010) with the following modification. The genomic G+C content of the type strain is 62.3%. Its approximate genome size is 5.81 Mbp.

Emended Description of *Pseudoruegeria sabulilitoris* Park et al. 2014

The description is as before (Park et al., 2014a) with the following modification. The genomic G+C content of the type strain is 62.4%. Its approximate genome size is 5.32 Mbp.

Emended Description of *Puniceibacterium sediminis* Zhang et al. 2015

The description is as before (Zhang D.-C. et al., 2015) with the following modification. The genomic G+C content of the type strain is 60.8%. Its approximate genome size is 4.64 Mbp.

Emended Description of *Reyranella massiliensis* Pagnier et al. 2011

The description is as before (Pagnier et al., 2011) with the following addition. The genomic G+C content of the type strain is 64.9%. Its approximate genome size is 5.77 Mbp.

Emended Description of *Rhizobium altiplani* Baraúna et al. 2016

The description is as before (Baraúna et al., 2016) with the following modification. The G+C content of the type-strain genome is 59.5%, its approximate size 8.10 Mbp.

Emended Description of *Rhizobium esperanzae* Cordeiro et al. 2017

The description is as before (Cordeiro et al., 2017) with the following modification. The G+C content of the type-strain genome is 61.1%, its approximate size 6.29 Mbp.

Emended Description of *Rhizobium etli* Segovia et al. 1993

The description is as before (Segovia et al., 1993) with the following addition. The genomic G+C content of the type strain is 61.0%. Its approximate genome size is 6.53 Mbp.

Emended Description of *Rhizobium flavum* Gu et al. 2014

The description is as before (Gu et al., 2014) with the following modification. The genomic G+C content of the type strain is 61.6%. Its approximate genome size is 4.66 Mbp.

Emended Description of *Rhizobium hainanense* Chen et al. 1997

The description is as before (Chen et al., 1997) with the following modification. The genomic G+C content of the type strain is 59.6%. Its approximate genome size is 7.25 Mbp.

Emended Description of *Rhizobium jaguaris* Rincón-Rosales et al. 2013

The description is as before (Rincón-Rosales et al., 2013) with the following addition. The G+C content of the type-strain genome is 59.4%, its approximate size 8.03 Mbp.

Emended Description of *Rhizobium leguminosarum* (Frank 1879) Frank 1889 (Approved Lists 1980) emend. Ramírez-Bahena et al. 2008

The description is as before (Ramírez-Bahena et al., 2008) with the following modification. The genomic G+C content of the type strain is 60.6%. Its approximate genome size is 7.81 Mbp.

Emended Description of *Rhizobium leucaenae* Ribeiro et al. 2012

The description is as before (Ribeiro et al., 2012) with the following modification. The genomic G+C content of the type strain is 59.4%. Its approximate genome size is 6.68 Mbp.

Emended Description of *Rhizobium lusitanum* Valverde et al. 2006

The description is as before (Valverde et al., 2006) with the following modification. The genomic G+C content of the type strain is 59.6%. Its approximate genome size is 7.92 Mbp.

Emended Description of *Rhizobium miluonense* Gu et al. 2008

The description is as before (Gu et al., 2008) with the following modification. The genomic G+C content of the type strain is 59.7%. Its approximate genome size is 6.81 Mbp.

Emended Description of *Rhizobium mongolense* van Berkum et al. 1998

The description is as before (van Berkum et al., 1998) with the following addition. The genomic G+C content of the type strain is 59.5%. Its approximate genome size is 7.17 Mbp.

Emended Description of *Rhizobium multihospitium* Han et al. 2008

The description is as before (Han et al., 2008) with the following modification. The genomic G+C content of the type strain is 59.8%. Its approximate genome size is 7.32 Mbp.

Emended Description of *Rhizobium rhizogenes* (Riker et al. 1930) Young et al. 2001

The description is as before (Young et al., 2001) with the following restriction. The genomic G+C content of the type strain is 59.9%. Its approximate genome size is 7.04 Mbp.

Emended Description of *Rhizobium selenitireducens* Hunter et al. 2008

The description is as before (Hunter et al., 2007) with the following modification. The genomic G+C content of the type strain is 63.5%. Its approximate genome size is 4.97 Mbp.

Emended Description of *Rhizobium tropici* Martínez-Romero et al. 1991

The description is as before (Martínez-Romero et al., 1991) with the following addition. The genomic G+C content of the type strain is 59.5%. Its approximate genome size is 6.69 Mbp.

Emended Description of *Rhodobacter aestuarii* Venkata Ramana et al. 2009

The description is as before (Venkata Ramana et al., 2009) with the following modification. The genomic G+C content of the type strain is 61.1%. Its approximate genome size is 3.84 Mbp.

Emended Description of *Rhodobacter blasticus* (Eckersley and Dow 1981) Kawasaki et al. 1994

The description is as before (Kawasaki et al., 1993) with the following modification. The G+C content of the type-strain genome is 66.5%, its approximate size 3.59 Mbp.

Emended Description of *Rhodobacter capsulatus* (Molisch 1907) Imhoff et al. 1984

The description is as before (Imhoff et al., 1984) with the following addition. The genomic G+C content of the type strain is 66.5%. Its approximate genome size is 3.67 Mbp.

Emended Description of *Rhodobacter maris* Venkata Ramana et al. 2008

The description is as before (Venkata Ramana et al., 2008) with the following modification. The G+C content of the type-strain genome is 65.1%, its approximate size 3.83 Mbp.

Emended Description of *Rhodobacter megalophilus* Arunasri et al. 2008

The description is as before (Arunasri et al., 2008) with the following modification. The genomic G+C content of the type strain is 68.8%. Its approximate genome size is 4.86 Mbp.

Emended Description of *Rhodobacter viridis* Shalem Raj et al. 2013

The description is as before (Shalem Raj et al., 2013) with the following modification. The G+C content of the type-strain genome is 65.4%, its approximate size 3.86 Mbp.

Emended Description of *Rhodoblastus acidophilus* (Pfennig 1969) Imhoff 2001

The description is as before (Imhoff, 2001) with the following restriction. The genomic G+C content of the type strain is 65.2%. Its approximate genome size is 4.71 Mbp.

Emended Description of *Rhodoblastus sphagnicola* Kulichevskaya et al. 2006

The description is as before (Kulichevskaya et al., 2006) with the following modification. The G+C content of the type-strain genome is 63.9%, its approximate size 5.09 Mbp.

Emended Description of *Rhodomicrobium udaipurense* Ramana et al. 2013

The description is as before (Ramana V.V. et al., 2013) with the following modification. The genomic G+C content of the type strain is 62.5%. Its approximate genome size is 3.63 Mbp.

Emended Description of *Rhodomicrobium vannielii* Duchow and Douglas 1949 (Approved Lists 1980)

The description is as before (Duchow and Douglas, 1949) with the following addition. The genomic G+C content of the type strain is 62.2%. Its approximate genome size is 4.01 Mbp.

Emended Description of *Rhodopseudomonas pentothematexigens* Kumar et al. 2013

The description is as before (Kumar et al., 2013) with the following modification. The G+C content of the type-strain genome is 66.0%, its approximate size 5.38 Mbp.

Emended Description of *Rhodopseudomonas pseudopalustris* Venkata Ramana et al. 2012

The description is as before (Venkata Ramana et al., 2012) with the following modification. The genomic G+C content of the type strain is 64.6%. Its approximate genome size is 5.27 Mbp.

Emended Description of *Rhodospira trueperi* Pfennig et al. 1998

The description is as before (Pfennig et al., 1997) with the following modification. The genomic G+C content of the type strain is 67.0%. Its approximate genome size is 4.21 Mbp.

Emended Description of *Rhodospirillum rubrum* (Esmarch 1887) Molisch 1907 (Approved Lists 1980)

The description is as before (Molisch, 1907) with the following addition. The genomic G+C content of the type strain is 65.4%. Its approximate genome size is 4.41 Mbp.

Emended Description of *Rhodothalassium salexigens* (Drews 1982) Imhoff et al. 1998

The description is as before (Imhoff et al., 1998) with the following restriction. The G+C content of the type-strain genome is 68.6%, its approximate size 3.35 Mbp.

Emended Description of *Rhodovibrio salinarum* (Nissen and Dundas 1985) Imhoff et al. 1998

The description is as before (Imhoff et al., 1998) with the following modification. The genomic G+C content of the type strain is 66.0%. Its approximate genome size is 4.18 Mbp.

Emended Description of *Rhodovulum euryhalinum* (Kompantseva 1989) Hiraishi and Ueda 1994

The description is as before (Hiraishi and Ueda, 1994a) with the following modification. The G+C content of the type-strain genome is 67.9%, its approximate size 3.78 Mbp.

Emended Description of *Rhodovulum imhoffii* Srinivas et al. 2007

The description is as before (Srinivas et al., 2007a) with the following modification. The genomic G+C content of the type strain is 63.1%. Its approximate genome size is 2.91 Mbp.

Emended Description of *Rhodovulum kholense* Anil Kumar et al. 2008

The description is as before (Anil Kumar et al., 2008) with the following modification. The genomic G+C content of the type strain is 67.8%. Its approximate genome size is 4.46 Mbp.

Emended Description of *Rhodovulum marinum* Srinivas et al. 2006

The description is as before (Srinivas et al., 2006) with the following modification. The G+C content of the type-strain genome is 67.2%, its approximate size 3.94 Mbp.

Emended Description of *Rhodovulum viride* Srinivas et al. 2014

The description is as before (Srinivas et al., 2014) with the following modification. The G+C content of the type-strain genome is 67.7%, its approximate size 4.52 Mbp.

Emended Description of *Rickettsia australis* Philip 1950 (Approved Lists 1980)

The description is as before (Philip, 1950) with the following addition. The genomic G+C content of the type strain is 32.3%. Its approximate genome size is 1.32 Mbp.

Emended Description of *Rickettsia bellii* Philip et al. 1983

The description is as before (Philip et al., 1983) with the following modification. The genomic G+C content of the type strain is 31.6%. Its approximate genome size is 1.52 Mbp.

Emended Description of *Rickettsia conorii* Brumpt 1932 (Approved Lists 1980)

The description is as before (Brumpt, 1932) with the following addition. The genomic G+C content of the type strain is 32.4%. Its approximate genome size is 1.27 Mbp.

Emended Description of *Rickettsia heilongjiangensis* Fournier et al. 2006

The description is as before (Fournier et al., 2003) with the following addition. The G+C content of the type-strain genome is 32.3%, its approximate size 1.28 Mbp.

Emended Description of *Rickettsia honei* Stenos et al. 1998

The description is as before (Stenos et al., 1998) with the following addition. The genomic G+C content of the type strain is 32.4%. Its approximate genome size is 1.27 Mbp.

Emended Description of *Rickettsia hoogstraalii* Duh et al. 2010

The description is as before (Duh et al., 2010) with the following addition. The genomic G+C content of the type strain is 32.4%. Its approximate genome size is 1.48 Mbp.

Emended Description of *Rickettsia japonica* Uchida et al. 1992

The description is as before (Uchida et al., 1992) with the following restriction. The genomic G+C content of the type strain is 32.4%. Its approximate genome size is 1.28 Mbp.

Emended Description of *Rickettsia prowazekii* Rocha-Lima 1916 (Approved Lists 1980)

The description is as before (da Rocha-Lima, 1916) with the following addition. The genomic G+C content of the type strain is 29.0%. Its approximate genome size is 1.11 Mbp.

Emended Description of *Rickettsia raoultii* Mediannikov et al. 2008

The description is as before (Mediannikov et al., 2008) with the following modification. The G+C content of the type-strain genome is 32.6%, its approximate size 1.48 Mbp.

Emended Description of *Rickettsia sibirica* Zdrodovskii 1948 (Approved Lists 1980)

The description is as before (Zdrodovskii, 1948) with the following addition. The genomic G+C content of the type strain is 32.5%. Its approximate genome size is 1.25 Mbp.

Emended Description of *Rickettsia slovacica* Sekeyová et al. 1998

The description is as before (Sekeyová et al., 1998) with the following addition. The genomic G+C content of the type strain is 32.5%. Its approximate genome size is 1.28 Mbp.

Emended Description of *Rickettsia tamurae* Fournier et al. 2006

The description is as before (Fournier et al., 2006) with the following addition. The genomic G+C content of the type strain is 32.5%. Its approximate genome size is 1.45 Mbp.

Emended Description of *Rickettsia typhi* (Wolbach and Todd 1920) Philip 1943 (Approved Lists 1980)

The description is as before (Philip, 1943) with the following addition. The genomic G+C content of the type strain is 28.9%. Its approximate genome size is 1.11 Mbp.

Emended Description of *Robiginitomaculum antarcticum* Lee et al. 2007

The description is as before (Lee et al., 2007d) with the following modification. The genomic G+C content of the type strain is 52.5%. Its approximate genome size is 2.77 Mbp.

Emended Description of *Roseiarcus fermentans* Kulichevskaya et al. 2014

The description is as before (Kulichevskaya et al., 2014) with the following modification. The G+C content of the type-strain genome is 68.2%, its approximate size 6.79 Mbp.

Emended Description of *Roseibacterium elongatum* Suzuki et al. 2006

The description is as before (Suzuki et al., 2006) with the following modification. The genomic G+C content of the type strain is 65.7%. Its approximate genome size is 3.56 Mbp.

Emended Description of *Roseibium denhamense* Suzuki et al. 2000 emend. Biebl et al. 2007

The description is as before (Biebl et al., 2007) with the following restriction. The G+C content of the type-strain genome is 57.3%, its approximate size 4.85 Mbp.

Emended Description of *Roseibium hamelinense* Suzuki et al. 2000 emend. Biebl et al. 2007

The description is as before (Biebl et al., 2007) with the following restriction. The G+C content of the type-strain genome is 56.4%, its approximate size 4.72 Mbp.

Emended Description of *Roseinatronobacter thiooxidans* Sorokin et al. 2000

The description is as before (Sorokin et al., 2000) with the following modification. The genomic G+C content of the type strain is 60.1%. Its approximate genome size is 3.68 Mbp.

Emended Description of *Roseivivax halodurans* Suzuki et al. 1999

The description is as before (Suzuki et al., 1999a) with the following modification. The genomic G+C content of the type strain is 66.3%. Its approximate genome size is 4.49 Mbp.

Emended Description of *Roseivivax halotolerans* Suzuki et al. 1999

The description is as before (Suzuki et al., 1999a) with the following modification. The genomic G+C content of the type strain is 64.1%. Its approximate genome size is 3.77 Mbp.

Emended Description of *Roseivivax isopora* Chen et al. 2012

The description is as before (Chen M.-H. et al., 2012) with the following restriction. The genomic G+C content of the type strain is 69.8%. Its approximate genome size is 4.90 Mbp.

Emended Description of *Roseivivax jejudonensis* Jung et al. 2015

The description is as before (Jung et al., 2014a) with the following modification. The genomic G+C content of the type strain is 68.0%. Its approximate genome size is 4.31 Mbp.

Emended Description of *Roseivivax lentus* Park et al. 2010

The description is as before (Park et al., 2010) with the following modification. The genomic G+C content of the type strain is 66.1%. Its approximate genome size is 4.44 Mbp.

Emended Description of *Roseobacter denitrificans* Shiba 1991

The description is as before (Shiba, 1991) with the following modification. The genomic G+C content of the type strain is 58.9%. Its approximate genome size is 4.32 Mbp.

Emended Description of *Roseobacter litoralis* Shiba 1991

The description is as before (Shiba, 1991) with the following restriction. The genomic G+C content of the type strain is 57.2%. Its approximate genome size is 4.75 Mbp.

Emended Description of *Roseomonas aerilata* Yoo et al. 2008

The description is as before (Yoo et al., 2008) with the following modification. The genomic G+C content of the type strain is 69.7%. Its approximate genome size is 6.43 Mbp.

Emended Description of *Roseomonas cervicalis* Rihs et al. 1998 emend. Sánchez-Porro et al. 2009

The description is as before (Sánchez-Porro et al., 2009) with the following modification. The genomic G+C content of the type strain is 72.0%. Its approximate genome size is 4.44 Mbp.

Emended Description of *Roseomonas lacus* Jiang et al. 2006 emend. Sánchez-Porro et al. 2009

The description is as before (Sánchez-Porro et al., 2009) with the following modification. The genomic G+C content of the type strain is 68.7%. Its approximate genome size is 6.39 Mbp.

Emended Description of *Roseomonas mucosa* Han et al. 2003 emend. Sánchez-Porro et al. 2009

The description is as before (Sánchez-Porro et al., 2009) with the following addition. The genomic G+C content of the type strain is 70.4%. Its approximate genome size is 4.86 Mbp.

Emended Description of *Roseomonas rosea* (Kämpfer et al. 2003) Sánchez-Porro et al. 2009

The description is as before (Sánchez-Porro et al., 2009) with the following modification. The genomic G+C content of the type strain is 70.8%. Its approximate genome size is 5.34 Mbp.

Emended Description of *Roseomonas stagni* Furuhashi et al. 2008

The description is as before (Furuhashi et al., 2008) with the following modification. The genomic G+C content of the type strain is 70.7%. Its approximate genome size is 6.38 Mbp.

Emended Description of *Roseomonas vinacea* Zhang et al. 2008

The description is as before (Zhang Y.-Q. et al., 2008) with the following modification. The genomic G+C content of the type strain is 70.3%. Its approximate genome size is 6.35 Mbp.

Emended Description of *Roseospiillum parvum* Glaeser and Overmann 2001

The description is as before (Glaeser and Overmann, 1999) with the following modification. The genomic G+C content of the type strain is 69.9%. Its approximate genome size is 3.50 Mbp.

Emended Description of *Roseovarius azorensis* Rajasabapathy et al. 2014

The description is as before (Rajasabapathy et al., 2014) with the following modification. The genomic G+C content of the type strain is 63.1%. Its approximate genome size is 3.86 Mbp.

Emended Description of *Roseovarius confluentis* Jia et al. 2017

The description is as before (Jia et al., 2017) with the following modification. The G+C content of the type-strain genome is 63.2%, its approximate size 4.46 Mbp.

Emended Description of *Roseovarius halotolerans* Oh et al. 2009

The description is as before (Oh et al., 2009) with the following modification. The genomic G+C content of the type strain is 63.8%. Its approximate genome size is 3.73 Mbp.

Emended Description of *Roseovarius lutimaris* Choi et al. 2013

The description is as before (Choi et al., 2013) with the following modification. The genomic G+C content of the type strain is 59.9%. Its approximate genome size is 4.28 Mbp.

Emended Description of *Roseovarius marisflavi* Li et al. 2014

The description is as before (Li Z. et al., 2013) with the following modification. The genomic G+C content of the type strain is 60.3%. Its approximate genome size is 4.08 Mbp.

Emended Description of *Roseovarius nanhaiticus* Wang et al. 2010

The description is as before (Wang et al., 2010) with the following modification. The genomic G+C content of the type strain is 63.3%. Its approximate genome size is 3.70 Mbp.

Emended Description of *Roseovarius nubinhibens* González et al. 2003

The description is as before (González et al., 2003) with the following modification. The genomic G+C content of the type strain is 63.9%. Its approximate genome size is 3.67 Mbp.

Emended Description of *Roseovarius tolerans* Labrenz et al. 1999

The description is as before (Labrenz et al., 1999) with the following restriction. The genomic G+C content of the type strain is 63.1%. Its approximate genome size is 3.77 Mbp.

Emended Description of *Rubrimonas cliftonensis* Suzuki et al. 1999

The description is as before (Suzuki et al., 1999b) with the following modification. The genomic G+C content of the type strain is 71.6%. Its approximate genome size is 4.86 Mbp.

Emended Description of *Rubritepida flocculans* Alarico et al. 2002

The description is as before (Alarico et al., 2002) with the following modification. The genomic G+C content of the type strain is 73.4%. Its approximate genome size is 3.84 Mbp.

Emended Description of *Ruegeria atlantica* (Rüger and Höfle 1992) Uchino et al. 1999 emend. Vandecastelaere et al. 2008

The description is as before (Vandecastelaere et al., 2008a) with the following restriction. The genomic G+C content of the type strain is 56.4%. Its approximate genome size is 4.82 Mbp.

Emended Description of *Ruegeria faecimaris* Oh et al. 2011

The description is as before (Oh et al., 2011) with the following modification. The genomic G+C content of the type strain is 56.7%. Its approximate genome size is 4.12 Mbp.

Emended Description of *Ruegeria halocynthiae* Kim et al. 2012

The description is as before (Kim et al., 2012b) with the following modification. The genomic G+C content of the type strain is 56.5%. Its approximate genome size is 4.24 Mbp.

Emended Description of *Ruegeria intermedia* Kämpfer et al. 2013

The description is as before (Kämpfer et al., 2013a) with the following addition. The genomic G+C content of the type strain is 64.0%. Its approximate genome size is 3.86 Mbp.

Emended Description of *Ruegeria lacuscaerulensis* (Petursdottir and Kristjansson 1999) Yi et al. 2007 emend. Vandecandelaere et al. 2008

The description is as before (Vandecandelaere et al., 2008a) with the following modification. The genomic G+C content of the type strain is 63.0%. Its approximate genome size is 3.52 Mbp.

Emended Description of *Ruegeria pomeroyi* (González et al. 2003) Yi et al. 2007 emend. Vandecandelaere et al. 2008

The description is as before (Vandecandelaere et al., 2008a) with the following modification. The genomic G+C content of the type strain is 64.1%. Its approximate genome size is 4.60 Mbp.

Emended Description of *Saccharibacter floricola* Jojima et al. 2004

The description is as before (Jojima et al., 2004) with the following modification. The genomic G+C content of the type strain is 51.2%. Its approximate genome size is 2.38 Mbp.

Emended Description of *Salipiger aestuarii* (Park et al. 2011) Wirth and Whitman 2018

The description is as before (Wirth and Whitman, 2018) with the following modification. The G+C content of the type-strain genome is 64.3%, its approximate size 4.66 Mbp.

Emended Description of *Salipiger bermudensis* (Cho and Giovannoni 2006) Wirth and Whitman 2018

The description is as before (Wirth and Whitman, 2018) with the following modification. The G+C content of the type-strain genome is 66.4%, its approximate size 5.43 Mbp.

Emended Description of *Salipiger mucosus* Martínez-Cánovas et al. 2004

The description is as before (Martínez-Cánovas et al., 2004) with the following modification. The genomic G+C content of the type strain is 67.3%. Its approximate genome size is 5.67 Mbp.

Emended Description of *Salipiger nanhaiensis* Dai et al. 2015

The description is as before (Dai et al., 2015) with the following modification. The genomic G+C content of the type strain is 66.9%. Its approximate genome size is 5.16 Mbp.

Emended Description of *Salipiger thiooxidans* (Sorokin et al. 2006) Wirth and Whitman 2018

The description is as before (Wirth and Whitman, 2018) with the following restriction. The G+C content of the type-strain genome is 67.3%, its approximate size 5.87 Mbp.

Emended Description of *Sediminispirochaeta smaragdinae* (Magot et al. 1998) Shivani et al. 2016

The description is as before (Shivani et al., 2016) with the following modification. The genomic G+C content of the type strain is 49.0%. Its approximate genome size is 4.65 Mbp.

Emended Description of *Shimia abyssii* (Nogi et al. 2016) Wirth and Whitman 2018

The description is as before (Wirth and Whitman, 2018) with the following modification. The G+C content of the type-strain genome is 56.2%, its approximate size 4.73 Mbp.

Emended Description of *Shimia haliotis* Hyun et al. 2013

The description is as before (Hyun et al., 2013a) with the following modification. The genomic G+C content of the type strain is 58.0%. Its approximate genome size is 4.00 Mbp.

Emended Description of *Shimia isopora* Chen et al. 2011

The description is as before (Chen et al., 2011b) with the following modification. The genomic G+C content of the type strain is 56.7%. Its approximate genome size is 4.23 Mbp.

Emended Description of *Skermanella stibiensis* Luo et al. 2012

The description is as before (Luo et al., 2012) with the following modification. The genomic G+C content of the type strain is 65.9%. Its approximate genome size is 7.87 Mbp.

Emended Description of *Sneathiella glossodoripedis* Kurahashi et al. 2008

The description is as before (Kurahashi et al., 2008) with the following modification. The genomic G+C content of the type strain is 46.9%. Its approximate genome size is 3.63 Mbp.

Emended Description of *Sphaerochaeta coccoides* (Dröge et al. 2006) Abt et al. 2012

The description is as before (Abt et al., 2012) with the following modification. The genomic G+C content of the type strain is 50.6%. Its approximate genome size is 2.23 Mbp.

Emended Description of *Sphaerochaeta globosa* Ritalahti et al. 2012

The description is as before (Ritalahti et al., 2012) with the following modification. The genomic G+C content of the type strain is 48.9%. Its approximate genome size is 3.32 Mbp.

Emended Description of *Sphaerochaeta pleomorpha* Ritalahti et al. 2012

The description is as before (Ritalahti et al., 2012) with the following restriction. The genomic G+C content of the type strain is 46.2%. Its approximate genome size is 3.59 Mbp.

Emended Description of *Sphingobium abikonense* Kumari et al. 2009

The description is as before (Kumari et al., 2009) with the following addition. The genomic G+C content of the type strain is 63.5%. Its approximate genome size is 3.75 Mbp.

Emended Description of *Sphingobium amiense* Ushiba et al. 2003

The description is as before (Ushiba et al., 2003) with the following modification. The genomic G+C content of the type strain is 64.7%. Its approximate genome size is 4.54 Mbp.

Emended Description of *Sphingobium baderi* Kaur et al. 2013

The description is as before (Kaur et al., 2013) with the following modification. The genomic G+C content of the type strain is 63.6%. Its approximate genome size is 4.69 Mbp.

Emended Description of *Sphingobium chinhatense* Dadhwal et al. 2009

The description is as before (Dadhwal et al., 2009) with the following addition. The genomic G+C content of the type strain is 64.1%. Its approximate genome size is 5.85 Mbp.

Emended Description of *Sphingobium chlorophenolicum* (Nohynek et al. 1996) Takeuchi et al. 2001

The description is as before (Takeuchi et al., 2001) with the following restriction. The genomic G+C content of the type strain is 64.3%. Its approximate genome size is 4.80 Mbp.

Emended Description of *Sphingobium cloacae* (Fujii et al. 2001) Prakash and Lal 2006

The description is as before (Prakash and Lal, 2006) with the following modification. The genomic G+C content of the type strain is 64.6%. Its approximate genome size is 4.29 Mbp.

Emended Description of *Sphingobium czechense* Niharika et al. 2013

The description is as before (Niharika et al., 2013a) with the following modification. The genomic G+C content of the type strain is 63.6%. Its approximate genome size is 4.66 Mbp.

Emended Description of *Sphingobium faniae* Guo et al. 2010

The description is as before (Guo et al., 2010) with the following restriction. The genomic G+C content of the type strain is 63.3%. Its approximate genome size is 4.84 Mbp.

Emended Description of *Sphingobium herbicidovorans* (Zipper et al. 1997) Takeuchi et al. 2001

The description is as before (Takeuchi et al., 2001) with the following addition. The genomic G+C content of the type strain is 62.4%. Its approximate genome size is 4.03 Mbp.

Emended Description of *Sphingobium hydrophobicum* Chen et al. 2016

The description is as before (Chen et al., 2016) with the following modification. The genomic G+C content of the type strain is 63.2%. Its approximate genome size is 4.60 Mbp.

Emended Description of *Sphingobium indicum* Pal et al. 2005

The description is as before (Pal et al., 2005) with the following addition. The genomic G+C content of the type strain is 65.0%. Its approximate genome size is 4.08 Mbp.

Emended Description of *Sphingobium lactosutens* Kumari et al. 2009

The description is as before (Kumari et al., 2009) with the following addition. The genomic G+C content of the type strain is 63.0%. Its approximate genome size is 5.36 Mbp.

Emended Description of *Sphingobium lucknowense* Garg et al. 2012

The description is as before (Garg et al., 2012) with the following modification. The genomic G+C content of the type strain is 64.3%. Its approximate genome size is 4.44 Mbp.

Emended Description of *Sphingobium quisquiliarum* Bala et al. 2010

The description is as before (Bala et al., 2010) with the following modification. The genomic G+C content of the type strain is 64.0%. Its approximate genome size is 4.17 Mbp.

Emended Description of *Sphingobium ummariense* Singh and Lal 2009

The description is as before (Singh and Lal, 2009) with the following modification. The genomic G+C content of the type strain is 65.0%. Its approximate genome size is 4.75 Mbp.

Emended Description of *Sphingobium yanoikuyae* (Yabuuchi et al. 1990) Takeuchi et al. 2001

The description is as before (Takeuchi et al., 2001) with the following modification. The genomic G+C content of the type strain is 64.4%. Its approximate genome size is 5.50 Mbp.

Emended Description of *Sphingomonas aerolata* Busse et al. 2003

The description is as before (Busse et al., 2003) with the following modification. The G+C content of the type-strain genome is 66.5%, its approximate size 3.83 Mbp.

**Emended Description of *Sphingomonas aestuarii*
Roh et al. 2009**

The description is as before (Roh et al., 2009) with the following addition. The genomic G+C content of the type strain is 64.5%. Its approximate genome size is 2.99 Mbp.

**Emended Description of *Sphingomonas aurantiaca*
Busse et al. 2003**

The description is as before (Busse et al., 2003) with the following modification. The G+C content of the type-strain genome is 66.2%, its approximate size 4.41 Mbp.

**Emended Description of *Sphingomonas azotifigens*
Xie and Yokota 2006**

The description is as before (Xie and Yokota, 2006) with the following restriction. The genomic G+C content of the type strain is 67.3%. Its approximate genome size is 5.15 Mbp.

**Emended Description of *Sphingomonas echinoides*
(Heumann 1962) Denner et al. 1999**

The description is as before (Denner et al., 1999) with the following modification. The genomic G+C content of the type strain is 64.7%. Its approximate genome size is 4.18 Mbp.

**Emended Description of *Sphingomonas faeni* Busse
et al. 2003**

The description is as before (Busse et al., 2003) with the following modification. The G+C content of the type-strain genome is 64.8%, its approximate size 4.38 Mbp.

**Emended Description of *Sphingomonas
guangdongensis* Feng et al. 2014**

The description is as before (Feng et al., 2014) with the following restriction. The G+C content of the type-strain genome is 68.6%, its approximate size 3.54 Mbp.

**Emended Description of *Sphingomonas
hengshuiensis* Wei et al. 2015**

The description is as before (Wei et al., 2015) with the following modification. The genomic G+C content of the type strain is 66.7%. Its approximate genome size is 5.23 Mbp.

**Emended Description of *Sphingomonas jaspsi* Asker
et al. 2007**

The description is as before (Asker et al., 2007) with the following modification. The genomic G+C content of the type strain is 64.7%. Its approximate genome size is 2.55 Mbp.

**Emended Description of *Sphingomonas jatrophae*
Madhaiyan et al. 2017**

The description is as before (Madhaiyan et al., 2013) with the following modification. The G+C content of the type-strain genome is 68.5%, its approximate size 4.06 Mbp.

**Emended Description of *Sphingomonas laterariae*
Kaur et al. 2012**

The description is as before (Kaur et al., 2012) with the following modification. The genomic G+C content of the type strain is 65.5%. Its approximate genome size is 4.42 Mbp.

**Emended Description of *Sphingomonas mali*
Takeuchi et al. 1995**

The description is as before (Takeuchi et al., 1995) with the following modification. The genomic G+C content of the type strain is 64.9%. Its approximate genome size is 5.23 Mbp.

**Emended Description of *Sphingomonas melonis*
Buonaurio et al. 2002**

The description is as before (Buonaurio et al., 2002) with the following modification. The genomic G+C content of the type strain is 67.0%. Its approximate genome size is 4.10 Mbp.

**Emended Description of *Sphingomonas mucosissima*
Reddy and Garcia-Pichel 2007**

The description is as before (Reddy and Garcia-Pichel, 2007) with the following addition. The genomic G+C content of the type strain is 65.1%. Its approximate genome size is 3.58 Mbp.

**Emended Description of *Sphingomonas panacis*
Singh et al. 2017**

The description is as before (Singh et al., 2016) with the following modification. The genomic G+C content of the type strain is 65.5%. Its approximate genome size is 5.32 Mbp.

**Emended Description of *Sphingomonas
parapaucimobilis* Yabuuchi et al. 1990**

The description is as before (Yabuuchi et al., 1990) with the following modification. The genomic G+C content of the type strain is 66.4%. Its approximate genome size is 3.99 Mbp.

**Emended Description of *Sphingomonas paucimobilis*
(Holmes et al. 1977) Yabuuchi et al. 1990**

The description is as before (Yabuuchi et al., 1990) with the following restriction. The genomic G+C content of the type strain is 65.7%. Its approximate genome size is 4.33 Mbp.

**Emended Description of *Sphingomonas
phyllosphaerae* Rivas et al. 2004**

The description is as before (Rivas et al., 2004) with the following modification. The genomic G+C content of the type strain is 67.2%. Its approximate genome size is 3.92 Mbp.

**Emended Description of *Sphingomonas puititosa*
Denner et al. 2001**

The description is as before (Denner et al., 2001) with the following modification. The genomic G+C content of the type strain is 67.1%. Its approximate genome size is 4.74 Mbp.

**Emended Description of *Sphingomonas rubra* Huo et
al. 2011**

The description is as before (Huo et al., 2011) with the following modification. The genomic G+C content of the type strain is 68.8%. Its approximate genome size is 3.20 Mbp.

**Emended Description of *Sphingomonas sanguinis*
Takeuchi et al. 1993**

The description is as before (Takeuchi et al., 1993) with the following modification. The genomic G+C content of the type strain is 66.1%. Its approximate genome size is 4.05 Mbp.

Emended Description of *Sphingomonas soli* Yang et al. 2006

The description is as before (Yang et al., 2006) with the following modification. The genomic G+C content of the type strain is 65.1%. Its approximate genome size is 3.51 Mbp.

Emended Description of *Sphingopyxis bauzanensis* Zhang et al. 2010

The description is as before (Zhang et al., 2010) with the following modification. The genomic G+C content of the type strain is 63.3%. Its approximate genome size is 4.26 Mbp.

Emended Description of *Sphingopyxis granuli* Kim et al. 2011

The description is as before (Kim et al., 2005) with the following modification. The genomic G+C content of the type strain is 66.4%. Its approximate genome size is 4.26 Mbp.

Emended Description of *Sphingopyxis indica* Jindal et al. 2013

The description is as before (Jindal et al., 2013) with the following modification. The genomic G+C content of the type strain is 65.7%. Its approximate genome size is 4.15 Mbp.

Emended Description of *Sphingopyxis macrogoltabida* (Takeuchi et al. 1993) Takeuchi et al. 2001

The description is as before (Takeuchi et al., 2001) with the following restriction. The genomic G+C content of the type strain is 64.9%. Its approximate genome size is 5.75 Mbp.

Emended Description of *Sphingopyxis terrae* (Takeuchi et al. 1993) Takeuchi et al. 2001

The description is as before (Takeuchi et al., 2001) with the following restriction. The genomic G+C content of the type strain is 64.6%. Its approximate genome size is 3.98 Mbp.

Emended Description of *Sphingopyxis ummariensis* Sharma et al. 2010

The description is as before (Sharma et al., 2010) with the following modification. The genomic G+C content of the type strain is 65.2%. Its approximate genome size is 3.58 Mbp.

Emended Description of *Sphingopyxis witflariensis* Kämpfer et al. 2002

The description is as before (Kämpfer et al., 2002b) with the following addition. The genomic G+C content of the type strain is 63.3%. Its approximate genome size is 4.31 Mbp.

Emended Description of *Sphingorhabdus litoris* (Kim et al. 2008) Jogler et al. 2013

The description is as before (Jogler et al., 2013) with the following addition. The genomic G+C content of the type strain is 52.7%. Its approximate genome size is 3.61 Mbp.

Emended Description of *Sphingorhabdus marina* (Kim et al. 2008) Jogler et al. 2013

The description is as before (Jogler et al., 2013) with the following addition. The genomic G+C content of the type strain is 57.4%. Its approximate genome size is 3.55 Mbp.

Emended Description of *Spirochaeta africana* Zhilina et al. 1996

The description is as before (Zhilina et al., 1996) with the following modification. The genomic G+C content of the type strain is 57.8%. Its approximate genome size is 3.29 Mbp.

Emended Description of *Spirochaeta cellobiosiphila* Breznak and Warnecke 2008

The description is as before (Breznak and Warnecke, 2008) with the following modification. The genomic G+C content of the type strain is 37.0%. Its approximate genome size is 3.95 Mbp.

Emended Description of *Spirochaeta thermophila* Aksenova et al. 1992

The description is as before (Aksenova et al., 1992) with the following modification. The genomic G+C content of the type strain is 60.9%. Its approximate genome size is 2.56 Mbp.

Emended Description of *Stakelama pacifica* Chen et al. 2010

The description is as before (Chen C. et al., 2010) with the following modification. The G+C content of the type-strain genome is 62.9%, its approximate size 3.98 Mbp.

Emended Description of *Stappia stellulata* (Rüger and Höfle 1992) Uchino et al. 1999 emend. Biebl et al. 2007

The description is as before (Biebl et al., 2007) with the following modification. The genomic G+C content of the type strain is 64.7%. Its approximate genome size is 4.62 Mbp.

Emended Description of *Starkeya novella* (Starkey 1934) Kelly et al. 2000

The description is as before (Kelly et al., 2000) with the following restriction. The genomic G+C content of the type strain is 67.9%. Its approximate genome size is 4.77 Mbp.

Emended Description of *Stella humosa* Vasilyeva 1985

The description is as before (Vasilyeva, 1985) with the following restriction. The G+C content of the type-strain genome is 69.9%, its approximate size 5.82 Mbp.

Emended Description of *Sulfitobacter donghicola* Yoon et al. 2007

The description is as before (Yoon et al., 2007a) with the following modification. The genomic G+C content of the type strain is 55.2%. Its approximate genome size is 3.54 Mbp.

Emended Description of *Sulfitobacter dubius* Ivanova et al. 2004

The description is as before (Ivanova et al., 2004) with the following modification. The genomic G+C content of the type strain is 60.2%. Its approximate genome size is 3.67 Mbp.

Emended Description of *Sulfitobacter guttiformis* (Labrenz et al. 2000) Yoon et al. 2007

The description is as before (Yoon et al., 2007a) with the following restriction. The genomic G+C content of the type strain is 56.1%. Its approximate genome size is 3.98 Mbp.

Emended Description of *Sulfitobacter litoralis* Park et al. 2007

The description is as before (Park et al., 2007) with the following addition. The genomic G+C content of the type strain is 58.5%. Its approximate genome size is 3.68 Mbp.

Emended Description of *Sulfitobacter pontiacus* Sorokin 1996

The description is as before (Sorokin, 1995) with the following modification. The genomic G+C content of the type strain is 60.3%. Its approximate genome size is 3.76 Mbp.

Emended Description of *Tanticharoenia sakaeratensis* Yukphan et al. 2008

The description is as before (Yukphan et al., 2008) with the following modification. The G+C content of the type-strain genome is 64.2%, its approximate size 3.50 Mbp.

Emended Description of *Telmatospirillum siberiense* Sizova et al. 2007

The description is as before (Sizova et al., 2007) with the following modification. The G+C content of the type-strain genome is 62.3%, its approximate size 6.20 Mbp.

Emended Description of *Terasakiella pusilla* (Terasaki 1973) Satomi et al. 2002 emend. Han et al. 2016

The description is as before (Han et al., 2016) with the following modification. The genomic G+C content of the type strain is 50.0%. Its approximate genome size is 4.05 Mbp.

Emended Description of *Thalassobaculum salexigens* Urios et al. 2010

The description is as before (Urios et al., 2010) with the following modification. The genomic G+C content of the type strain is 67.4%. Its approximate genome size is 5.08 Mbp.

Emended Description of *Thalassobius abyssi* Nogi et al. 2016

The description is as before (Nogi et al., 2016) with the following modification. The genomic G+C content of the type strain is 56.2%. Its approximate genome size is 4.73 Mbp.

Emended Description of *Thalassobius mediterraneus* Arahall et al. 2005

The description is as before (Arahall et al., 2005) with the following modification. The genomic G+C content of the type strain is 58.7%. Its approximate genome size is 3.41 Mbp.

Emended Description of *Thalassospira alkalitolerans* Tsubouchi et al. 2014

The description is as before (Tsubouchi et al., 2014) with the following modification. The genomic G+C content of the type strain is 53.1%. Its approximate genome size is 4.79 Mbp.

Emended Description of *Thalassospira lucentensis* López-López et al. 2002

The description is as before (López-López et al., 2002) with the following modification. The genomic G+C content of the type strain is 53.4%. Its approximate genome size is 4.75 Mbp.

Emended Description of *Thalassospira povalilytica* Nogi et al. 2014

The description is as before (Nogi et al., 2014) with the following modification. The G+C content of the type-strain genome is 53.6%, its approximate size 4.72 Mbp.

Emended Description of *Thalassospira profundimaris* Liu et al. 2007

The description is as before (Liu et al., 2007) with the following modification. The genomic G+C content of the type strain is 55.2%. Its approximate genome size is 4.38 Mbp.

Emended Description of *Thalassospira xiamenensis* Liu et al. 2007

The description is as before (Liu et al., 2007) with the following modification. The genomic G+C content of the type strain is 54.7%. Its approximate genome size is 4.77 Mbp.

Emended Description of *Thioclava electrotropha* Chang et al. 2018

The description is as before (Chang et al., 2018) with the following addition. The G+C content of the type-strain genome is 63.8%, its approximate size 4.41 Mbp.

Emended Description of *Thioclava pacifica* Sorokin et al. 2005

The description is as before (Sorokin et al., 2005b) with the following modification. The genomic G+C content of the type strain is 63.9%. Its approximate genome size is 3.73 Mbp.

Emended Description of *Tistlia consotensis* Díaz-Cárdenas et al. 2010

The description is as before (Díaz-Cárdenas et al., 2010) with the following restriction. The genomic G+C content of the type strain is 71.5%. Its approximate genome size is 6.93 Mbp.

Emended Description of *Tranquillimonas alkanivorans* Harwati et al. 2008

The description is as before (Harwati et al., 2008) with the following modification. The genomic G+C content of the type strain is 67.3%. Its approximate genome size is 4.54 Mbp.

Emended Description of *Treponema berlinense* Nordhoff et al. 2005

The description is as before (Nordhoff et al., 2005) with the following addition. The genomic G+C content of the type strain is 39.4%. Its approximate genome size is 2.52 Mbp.

Emended Description of *Treponema brennaborensis* Schrank et al. 1999

The description is as before (Schrank et al., 1999) with the following addition. The genomic G+C content of the type strain is 51.5%. Its approximate genome size is 3.06 Mbp.

Emended Description of *Treponema denticola* (ex Flügge 1886) Chan et al. 1993

The description is as before (Chan et al., 1993) with the following restriction. The genomic G+C content of the type strain is 37.9%. Its approximate genome size is 2.84 Mbp.

Emended Description of *Treponema lecithinolyticum* Wyss et al. 1999

The description is as before (Wyss et al., 1999) with the following addition. The genomic G+C content of the type strain is 43.8%. Its approximate genome size is 2.33 Mbp.

Emended Description of *Treponema maltophilum* Wyss et al. 1996

The description is as before (Wyss et al., 1996) with the following addition. The genomic G+C content of the type strain is 47.9%. Its approximate genome size is 2.53 Mbp.

Emended Description of *Treponema medium* Umemoto et al. 1997

The description is as before (Umemoto et al., 1997) with the following modification. The genomic G+C content of the type strain is 44.3%. Its approximate genome size is 2.72 Mbp.

Emended Description of *Treponema porcinum* Nordhoff et al. 2005

The description is as before (Nordhoff et al., 2005) with the following addition. The genomic G+C content of the type strain is 42.5%. Its approximate genome size is 2.51 Mbp.

Emended Description of *Treponema putidum* Wyss et al. 2004

The description is as before (Wyss et al., 2004) with the following addition. The genomic G+C content of the type strain is 37.3%. Its approximate genome size is 2.77 Mbp.

Emended Description of *Treponema socranskii* Smibert et al. 1984

The description is as before (Smibert et al., 1984) with the following modification. The genomic G+C content of the type strain is 49.4%. Its approximate genome size is 2.80 Mbp.

Emended Description of *Treponema succinifaciens* Cwyk and Canale-Parola 1981

The description is as before (Cwyk and Canale-Parola, 1979) with the following modification. The genomic G+C content of the type strain is 39.2%. Its approximate genome size is 2.73 Mbp.

Emended Description of *Tropicibacter naphthalenivorans* Harwati et al. 2009

The description is as before (Harwati et al., 2009b) with the following modification. The genomic G+C content of the type strain is 63.2%. Its approximate genome size is 4.45 Mbp.

Emended Description of *Tropicimonas isoalkanivorans* Harwati et al. 2009

The description is as before (Harwati et al., 2009a) with the following modification. The genomic G+C content of the type strain is 64.6%. Its approximate genome size is 4.98 Mbp.

Emended Description of *Tropicimonas sediminicola* Shin et al. 2012

The description is as before (Shin et al., 2012) with the following modification. The genomic G+C content of the type strain is 66.4%. Its approximate genome size is 5.17 Mbp.

Emended Description of *Turneriella parva* (Hovind-Hougen et al. 1982) Levett et al. 2005

The description is as before (Levett et al., 2005) with the following modification. The genomic G+C content of the type strain is 53.6%. Its approximate genome size is 4.41 Mbp.

Emended Description of *Wenxinia marina* Ying et al. 2007

The description is as before (Ying et al., 2007) with the following modification. The genomic G+C content of the type strain is 70.5%. Its approximate genome size is 4.18 Mbp.

Emended Description of *Wenxinia saemankumensis* Park et al. 2014

The description is as before (Park et al., 2014b) with the following modification. The genomic G+C content of the type strain is 71.2%. Its approximate genome size is 3.58 Mbp.

Emended Description of *Woodsholea maritima* Abraham et al. 2004

The description is as before (Abraham et al., 2004) with the following modification. The genomic G+C content of the type strain is 55.7%. Its approximate genome size is 3.10 Mbp.

Emended Description of *Xanthobacter autotrophicus* (Baumgarten et al. 1974) Wiegel et al. 1978 (Approved Lists 1980)

The description is as before (Wiegel et al., 1978) with the following addition. The genomic G+C content of the type strain is 67.5%. Its approximate genome size is 5.03 Mbp.

Emended Description of *Yoonia maritima* (Tanaka et al. 2014) Wirth and Whitman 2018

The description is as before (Wirth and Whitman, 2018) with the following addition. The G+C content of the type-strain genome is 53.4%, its approximate size 3.68 Mbp.

Emended Description of *Yoonia rosea* (Ivanova et al. 2005) Wirth and Whitman 2018

The description is as before (Wirth and Whitman, 2018) with the following restriction. The G+C content of the type-strain genome is 57.7%, its approximate size 3.51 Mbp.

Emended Description of *Yoonia tamlensis* (Lee 2012) Wirth and Whitman 2018

The description is as before (Wirth and Whitman, 2018) with the following modification. The G+C content of the type-strain genome is 56.9%, its approximate size 3.19 Mbp.

Emended Description of *Yoonia vestfoldensis* (Van Trappen et al. 2004) Wirth and Whitman 2018

The description is as before (Wirth and Whitman, 2018) with the following modification. The G+C content of the type-strain genome is 61.8%, its approximate size 3.72 Mbp.

Emended Description of *Zavarzinia compransoris* (ex Nozhevnikova and Zavarzin 1974) Meyer et al. 1994

The description is as before (Meyer et al., 1993) with the following modification. The G+C content of the type-strain genome is 68.1%, its approximate size 4.75 Mbp.

Emended Description of *Zymomonas mobilis* (Lindner 1928) De Ley and Swings 1976 (Approved Lists 1980)

The description is as before (De Ley and Swings, 1976) with the following addition. The genomic G+C content of the type strain is 46.1%. Its approximate genome size is 2.14 Mbp.

Taxonomic Consequences: Emendations of Subspecies

Emended Description of *Acetobacter pasteurianus* subsp. *ascendens* (Henneberg 1898) De Ley and Frateur 1974 (Approved Lists 1980)

The description is as before (De Ley and Frateur, 1974) with the following addition. The G+C content of the type-strain genome is 53.2%, its approximate size 3.00 Mbp.

Emended Description of *Acetobacter pasteurianus* subsp. *paradoxus* (Frateur 1950) De Ley and Frateur 1974 (Approved Lists 1980)

The description is as before (De Ley and Frateur, 1974) with the following addition. The G+C content of the type-strain genome is 53.3%, its approximate size 3.22 Mbp.

Emended Description of *Bartonella vinsonii* subsp. *arupensis* Welch et al. 2000

The description is as before (Welch et al., 1999) with the following addition. The G+C content of the type-strain genome is 38.6%, its approximate size 1.75 Mbp.

Emended Description of *Bartonella vinsonii* subsp. *berkhoffii* Kordick et al. 1996

The description is as before (Kordick et al., 1996) with the following addition. The G+C content of the type-strain genome is 38.9%, its approximate size 1.79 Mbp.

Emended Description of *Insolitispirillum peregrinum* subsp. *integrum* (Terasaki 1973) Yoon et al. 2007

The description is as before (Yoon et al., 2007b) with the following modification. The G+C content of the type-strain genome is 61.9%, its approximate size 4.64 Mbp.

Emended Description of *Roseomonas gilardii* subsp. *rosea* Han et al. 2003 emend. Sánchez-Porro et al. 2009

The description is as before (Sánchez-Porro et al., 2009) with the following addition. The G+C content of the type-strain genome is 70.7%, its approximate size 4.61 Mbp.

Emended Description of *Treponema socranskii* subsp. *paredis* Smibert et al. 1984

The description is as before (Smibert et al., 1984) with the following addition. The G+C content of the type-strain genome is 48.3%, its approximate size 2.73 Mbp.

Emended Description of *Zymomonas mobilis* subsp. *pomaceae* (Millis 1956) De Ley and Swings 1976 (Approved Lists 1980) emend. Coton et al. 2006

The description is as before (Coton et al., 2006) with the following addition. The G+C content of the type-strain genome is 44.0%, its approximate size 2.06 Mbp.

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in the INSDC databases, in the IMG database and in the TYGS database.

AUTHOR CONTRIBUTIONS

BT, SG, and MG organized strain selection, cultivation, DNA preparation, and quality control at DSMZ. TW and NK organized genome sequencing, assembly, annotation, and quality control at JGI. JM-K and MG phylogenetically and statistically analyzed the data. AH and JM-K prepared the figures. L-MW, MS, ML, and AH collected the phenotypic information. AH, ML, MG, and MS interpreted the phenotypic information. AH, ML, MG, and JM-K wrote the manuscript. All authors read and approved the final manuscript.

FUNDING

This work was conducted by the Joint Genome Institute, a United States Department of Energy Office of Science User Facility, is supported under Contract No. DE-AC02-05CH11231. This work was conducted by German Collection of Microorganisms and Cell Cultures GmbH (DSMZ), a member of the Leibniz association, is supported as part of the SFB/Transregio 51 by the German Research Council.

ACKNOWLEDGMENTS

We are grateful to Beatrice Trümper, Meike Döppner, and Katrin von Nyssen (all DSMZ) for technical assistance in DNA preparation, to a variety of colleagues, particularly Regine Fähnrich, Susanne Schneider, Iljana Schroeder and Andrea Schütze, for cultivation of *Rhodobacteraceae* and outgroup

strains, and to Tugce Kaman (all DSMZ) for assistance in collecting phenotypic information from the literature. Holger Scholz (Institut für Mikrobiologie der Bundeswehr, Germany) provided valuable hints on the classification of *Brucella* and *Ochrobactrum*, which is gratefully acknowledged.

REFERENCES

- Abdad, M. Y., Abdallah, R. A., El Karkouri, K., Beye, M., Stenos, J., Owen, H., et al. (2017). *Rickettsia gravesii* sp. nov.: a novel spotted fever group rickettsia in Western Australian *Amblyomma triguttatum* triguttatum ticks. *Int. J. Syst. Evol. Microbiol.* 67, 3156–3161. doi: 10.1099/ijsem.0.001865
- Abraham, W. R., de Carvalho, M. P., da Costa Neves, T. S. P., Memoria, M. T., Tartuci, I. T., Vancanneyt, M., et al. (2017). Proposal of *Henriciella barborensis* sp. nov. and *Henriciella algicola* sp. nov., stalked species of the genus and emendation of the genus *Henriciella*. *Int. J. Syst. Evol. Microbiol.* 67, 2804–2810. doi: 10.1099/ijsem.0.002024
- Abraham, W.-R., Lünsdorf, H., Vancanneyt, M., and Smit, J. (2013). Cauliform bacteria lacking phospholipids from an abyssal hydrothermal vent: proposal of *Glycocaulis abyssi* gen. nov., sp. nov., belonging to the family Hyphomonadaceae. *Int. J. Syst. Evol. Microbiol.* 63, 2207–2215. doi: 10.1099/ijms.0.047894-0
- Abraham, W. R., Macedo, A. J., Lünsdorf, H., Fischer, R., Pawelczyk, S., Smit, J., et al. (2008). Phylogeny by a polyphasic approach of the order *Caulobacterales*, proposal of *Caulobacter mirabilis* sp. nov., *Phenylobacterium haematophilum* sp. nov. and *Phenylobacterium conjunctum* sp. nov., and emendation of the genus *Phenylobacterium*. *Int. J. Syst. Evol. Microbiol.* 58(Pt 8), 1939–1949. doi: 10.1099/ijms.0.65567-0
- Abraham, W.-R., Strömpl, C., Meyer, H., Lindholst, S., Moore, E. R. B., Christ, R., et al. (1999). Phylogeny and polyphasic taxonomy of *Caulobacter* species. Proposal of *Maricaulis* gen. nov. with *Maricaulis maris* (Poindexter) comb. nov. as the type species, and emended description of the genera *Brevundimonas* and *Caulobacter*. *Int. J. Syst. Bacteriol.* 49(Pt 3), 1053–1073. doi: 10.1099/00207713-49-3-1053
- Abraham, W.-R., Strömpl, C., Vancanneyt, M., Bannasar, A., Swings, J., Lünsdorf, H., et al. (2004). *Woodsholea maritima* gen. nov., sp. nov., a marine bacterium with a low diversity of polar lipids. *Int. J. Syst. Evol. Microbiol.* 54(Pt 4), 1227–1234. doi: 10.1099/ijms.0.02943-0
- Abt, B., Göker, M., Scheuner, C., Han, C., Lu, M., Misra, M., et al. (2013). Genome sequence of the thermophilic fresh-water bacterium *Spirochaeta caldaria* type strain (H1T), reclassification of *Spirochaeta caldaria*, *Spirochaeta stenostrepta*, and *Spirochaeta zuelzeriae* in the genus *Treponema* as *Treponema caldaria* comb. nov., *Treponema stenostrepta* comb. nov., and *Treponema zuelzeriae* comb. nov., and emendation of the genus *Treponema*. *Stand. Genomic Sci.* 8, 88–105. doi: 10.4056/sigs.3096473
- Abt, B., Han, C., Scheuner, C., Lu, M., Lapidus, A., Nolan, M., et al. (2012). Complete genome sequence of the termite hindgut bacterium *Sphaerochaeta coccoides* type strain (SPN1T), reclassification in the genus *Sphaerochaeta* as *Sphaerochaeta coccoides* comb. nov. and emendations of the family *Spirochaetaceae* and the genus *Sphaerochaeta*. *Stand. Genomic Sci.* 6, 194–209. doi: 10.4056/sigs.2796069
- Addison, S. L., Foote, S. M., Reid, N. M., and Lloyd-Jones, G. (2007). *Novosphingobium nitrogenifigens* sp. nov., a polyhydroxyalkanoate-accumulating diazotroph isolated from a New Zealand pulp and paper wastewater. *Int. J. Syst. Evol. Microbiol.* 57, 2467–2471. doi: 10.1099/ijms.0.64627-0
- Akinola, R. O. (2013). A systems level comparison of *Mycobacterium tuberculosis*, *Mycobacterium leprae* and *Mycobacterium smegmatis* based on functional interaction network analysis. *J. Bacteriol. Parasitol.* 4:173. doi: 10.4172/2155-9597.1000173
- Aksenova, H. Y., Rainey, F. A., Janssen, P. H., Zavarzin, G. A., and Morgan, H. W. (1992). *Spirochaeta thermophila* sp. nov., an obligately anaerobic, polysaccharolytic, extremely thermophilic bacterium. *Int. J. Syst. Evol. Microbiol.* 42, 175–177. doi: 10.1099/00207713-42-1-175
- Alain, K., Tindall, B. J., Intertaglia, L., Catala, P., and Lebaron, P. (2008). *Hellea balneolensis* gen. nov., sp. nov., a prothecate alphaproteobacterium from the Mediterranean Sea. *Int. J. Syst. Evol. Microbiol.* 58, 2511–2519. doi: 10.1099/ijms.0.65424-0
- Alarico, S., Rainey, F. A., Empadinhas, N., Schumann, P., Nobre, M. F., and da Costa, M. S. (2002). *Rubritepida flocculans* gen. nov., sp. nov., a new slightly thermophilic member of the α -1 subclass of the *Proteobacteria*. *Syst. Appl. Microbiol.* 25, 198–206. doi: 10.1078/0723-2020-00116
- Albuquerque, L., França, L., Tabor, M., La Cono, V., Yakimov, M., and da Costa, M. S. (2015). *Palleronia abyssalis* sp. nov., isolated from the deep Mediterranean Sea and the emended description of the genus *Palleronia* and of the species *Palleronia marisminoris*. *Antonie Van Leeuwenhoek* 107, 633–642. doi: 10.1007/s10482-014-0358-2
- Albuquerque, L., Rainey, F. A., Nobre, M. F., and da Costa, M. S. (2008). *Elioraea tepidiphila* gen. nov., sp. nov., a slightly thermophilic member of the Alphaproteobacteria. *Int. J. Syst. Evol. Microbiol.* 58, 773–778. doi: 10.1099/ijms.0.65294-0
- Albuquerque, L., Rainey, F. A., Nobre, M. F., and da Costa, M. S. (2012). *Oceanicella actignis* gen. nov., sp. nov., a halophilic slightly thermophilic member of the Alphaproteobacteria. *Syst. Appl. Microbiol.* 35, 385–389. doi: 10.1016/j.syapm.2012.07.001
- Albuquerque, L., Rainey, F. A., Pena, A., Tiago, I., Verissimo, A., Nobre, M. F., et al. (2010). *Tepidamorpha gemmatus* gen. nov., sp. nov., a slightly thermophilic member of the Alphaproteobacteria. *Syst. Appl. Microbiol.* 33, 60–66. doi: 10.1016/j.syapm.2010.01.002
- Albuquerque, L., Santos, J., Travassos, P., Nobre, M. F., Rainey, F. A., Wait, R., et al. (2002). *Albidovulum inexpectatum* gen. nov., sp. nov., a nonphotosynthetic and slightly thermophilic bacterium from a marine hot spring that is very closely related to members of the photosynthetic genus *Rhodovulum*. *Appl. Environ. Microbiol.* 68, 4266–4273. doi: 10.1128/AEM.68.9.4266
- Almpanis, A., Swain, M., Gatherer, D., and McEwan, N. (2018). Correlation between bacterial G+C content, genome size and the G+C content of associated plasmids and bacteriophages. *Microb. Genomics* 4:e000168. doi: 10.1099/mgen.0.000168
- Amoozegar, M. A., Makhdomi-kakhki, A., Ramezani, M., Nikou, M. M., Abolhassan, S., Fazeli, S., et al. (2013). *Limimonas halophila* gen. nov., sp. nov., an extremely halophilic bacterium in the family Rhodospirillaceae. *Int. J. Syst. Evol. Microbiol.* 63, 1562–1567. doi: 10.1099/ijms.0.041236-0
- Anil Kumar, P., Aparna, P., Srinivas, T. N. R., Sasikala, C., and Ramana, C. V. (2008). *Rhodovulum kholense* sp. nov. *Int. J. Syst. Evol. Microbiol.* 58(Pt 7), 1723–1726. doi: 10.1099/ijms.0.65620-0
- Anil Kumar, P., Srinivas, T. N. R., Manasa, P., Madhu, S., and Shivaji, S. (2012). *Lutibaculum baratangene* gen. nov., sp. nov., a proteobacterium isolated from a mud volcano. *Int. J. Syst. Evol. Microbiol.* 62, 2025–2031. doi: 10.1099/ijms.0.036350-0
- Anil Kumar, P., Srinivas, T. N. R., Takaichi, S., Maoka, T., Sasikala, C., and Ramana, C. V. (2009). *Phaeospirillum chandramohanii* sp. nov., a phototrophic alphaproteobacterium with carotenoid glycosides. *Int. J. Syst. Evol. Microbiol.* 59, 2089–2093. doi: 10.1099/ijms.0.009019-0
- Arahal, D. R., La Mura, A., Lucena, T., Rodrigo-Torres, L., Aznar, R., and Pujalte, M. J. (2019). *Shimia thalassica* sp. nov., and reclassification of *Pseudopelagicola gijangensis* as *Shimia gijangensis* comb. nov., and *Thalassobius activus* as *Cognatishimia activa* comb. nov. *Int. J. Syst. Evol. Microbiol.* 69, 3405–3413. doi: 10.1099/ijsem.0.003629
- Arahal, D. R., Macián, M. C., Garay, E., and Pujalte, M. J. (2005). *Thalassobius mediterraneus* gen. nov., sp. nov., and reclassification of *Ruegeria gelatinovorans* as *Thalassobius gelatinovorans* comb. nov. *Int. J. Syst. Evol. Microbiol.* 55, 2371–2376. doi: 10.1099/ijms.0.63842-0
- Arroua, B., Ranchou-Peyruse, A., Ranchou-Peyruse, M., Magot, M., Urios, L., and Grimaud, R. (2017). *Pleomorphochaeta caudata* gen. nov., sp. nov., an anaerobic bacterium isolated from an offshore oil well, reclassification of *Sphaerochaeta multiformis* MO-SPC2T as *Pleomorphochaeta multiformis* MO-SPC2T comb.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmicb.2020.00468/full#supplementary-material>

- nov. as the type strain of this novel genus and emended description of the genus *Sphaerochaeta*. *Int. J. Syst. Evol. Microbiol.* 67, 417–424. doi: 10.1099/ijsem.0.001641
- Arun, A. B., Schumann, P., Chu, H.-I., Tan, C.-C., Chen, W.-M., Lai, W.-A., et al. (2008). *Pseudoxanthobacter soli* gen. nov., sp. nov., a nitrogen-fixing alphaproteobacterium isolated from soil. *Int. J. Syst. Evol. Microbiol.* 58, 1571–1575. doi: 10.1099/ijms.0.65206-0
- Arunasri, K., Venkata Ramana, V., Spröer, C., Sasikala, C., and Ramana, C. V. (2008). *Rhodobacter megalophilus* sp. nov., a phototroph from the Indian Himalayas possessing a wide temperature range for growth. *Int. J. Syst. Evol. Microbiol.* 58, 1792–1796. doi: 10.1099/ijms.0.65642-0
- Asker, D., Beppu, T., and Ueda, K. (2007). *Sphingomonas jaspisi* sp. nov., a novel carotenoid-producing bacterium isolated from Misasa, Tottori, Japan. *Int. J. Syst. Evol. Microbiol.* 57, 1435–1441. doi: 10.1099/ijms.0.64828-0
- Auch, A. F., Henz, S. R., Holland, B. R., and Göker, M. (2006). Genome BLAST distance phylogenies inferred from whole plastid and whole mitochondrion genome sequences. *BMC Bioinformatics* 7:350. doi: 10.1186/1471-2105-7-350
- Auling, G., Hans-Jürgen, B., Egli, T., El-banna, T., and Stackebrandt, E. (1993). Description of the Gram-Negative, obligately aerobic, nitrilotriacetate (NTA)-utilizing bacteria as *Chelatobacter heintzii*, gen. nov., sp. nov., and *Chelatococcus asaccharovorans*, gen. nov., sp. nov. *Syst. Appl. Microbiol.* 16, 104–112. doi: 10.1016/S0723-2020(11)80254-7
- Babudieri, B. (1950). Natura delle cosidette “S-formen” delle leptospire. Loro identificazione con *Hyphomicrobium vulgare* Stutzer e Hartleb. Studio di quest. Ultimo germe. *R. C. I. St. Suppl. Sanita Roma* 13, 580–591.
- Baek, K., Choi, A., Kang, I., and Cho, J.-C. (2014). *Celeribacter marinus* sp. nov., isolated from coastal seawater. *Int. J. Syst. Evol. Microbiol.* 64, 1323–1327. doi: 10.1099/ijms.0.060673-0
- Baik, K. S., Choe, H. N., Park, S. C., Hwang, Y. M., Kim, E. M., Park, C., et al. (2013). *Sphingopyxis rigui* sp. nov. and *Sphingopyxis wooponensis* sp. nov., isolated from wetland freshwater, and emended description of the genus *Sphingopyxis*. *Int. J. Syst. Evol. Microbiol.* 63, 1297–1303. doi: 10.1099/ijms.0.044057-0
- Bala, K., Sharma, P., and Lal, R. (2010). *Sphingobium quisquiliarum* sp. nov., a hexachlorocyclohexane (HCH)-degrading bacterium isolated from an HCH-contaminated soil. *Int. J. Syst. Evol. Microbiol.* 60, 429–433. doi: 10.1099/ijms.0.010868-0
- Balcázar, J. L., Planas, M., and José, P. (2012). *Oceanibacterium hippocampi* gen. nov., sp. nov., isolated from cutaneous mucus of wild seahorses (*Hippocampus guttulatus*). *Antonie Van Leeuwenhoek* 102, 187–191. doi: 10.1007/s10482-012-9726-y
- Bambauer, A., Rainey, F. A., Stackebrandt, E., and Winter, J. (1998). Characterization of *Aquamicrobium defluvi* gen. nov. sp. nov., a thiophene-2-carboxylate-metabolizing bacterium from activated sludge. *Arch. Microbiol.* 169, 293–302. doi: 10.1007/s002030050575
- Bao, Z., Sato, Y., Fujimura, R., and Ohta, H. (2014). *Alsobacter metallidurans* gen. nov., sp. nov., a thallium-tolerant soil bacterium in the order Rhizobiales. *Int. J. Syst. Evol. Microbiol.* 64, 775–780. doi: 10.1099/ijms.0.054783-0
- Baptiste, E., and Boucher, Y. (2009). “Epistemological impacts of horizontal gene transfer on classification in microbiology,” in *Horizontal Gene Transfer. Methods in Molecular Biology*, eds M. B. Gogarten, J. P. Gogarten, and L. C. Olendzenski (Totowa, NJ: Humana Press), 55–72. doi: 10.1007/978-1-60327-853-9
- Baranton, G. U. Y., Postic, D., Girons, S., Boerlin, P., Piffaretti, J., Assous, M., et al. (1992). Delineation of *Borrelia burgdorferi* sensu stricto, *Borrelia garinii* sp. nov., and group VS461 associated with Lyme borreliosis. *Int. J. Syst. Bacteriol.* 42, 378–383. doi: 10.1099/00207713-42-3-378
- Baraúna, A. C., Rouws, L. F. M., Simoes-Araujo, J. L., dos Reis, F. B. Jr., Iannetta, P. P. M., Maluk, M., et al. (2016). *Rhizobium altiplanii* sp. nov., isolated from effective nodules on *Mimosa pudica* growing in untypically alkaline soil in central Brazil. *Int. J. Syst. Evol. Microbiol.* 66, 4118–4124. doi: 10.1099/ijsem.0.001322
- Barberán, A., Velazquez, H. C., Jones, S., and Fierer, N. (2017). Hiding in plain sight: mining bacterial species records for phenotypic trait information. *mSphere* 2:e00237-17. doi: 10.1128/mSphere.00237-17
- Bates, S. T., Cropsey, G. W. G., Caporaso, J. G., Knight, R., and Fierer, N. (2011). Bacterial communities associated with the lichen symbiosis. *Appl. Environ. Microbiol.* 77, 1309–1314. doi: 10.1128/AEM.02257-10
- Bazyliński, D. A., Williams, T. J., Lefèvre, C. T., Berg, R. J., Zhang, C. L., Bowser, S. S., et al. (2013a). *Magnetococcus marinus* gen. nov., sp. nov., a marine, magnetotactic bacterium that represents a novel lineage (Magnetococcales fam. nov., Magnetococcales ord. nov.) at the base of the Alphaproteobacteria. *Int. J. Syst. Evol. Microbiol.* 63, 801–808. doi: 10.1099/ijms.0.038927-0
- Bazyliński, D. A., Williams, T. J., Lefèvre, C. T., Trubitsyn, D., Fang, J., Beveridge, T. J., et al. (2013b). *Magnetovibrio blakemorei* gen. nov., sp. nov., a magnetotactic bacterium (Alphaproteobacteria: Rhodospirillaceae) isolated from a salt marsh. *Int. J. Syst. Evol. Microbiol.* 63, 1824–1833. doi: 10.1099/ijms.0.044453-0
- Beijerinck, M. W. (1898). Ueber die arten der essigbakterien. *Cent. für Bakteriol. Parasitenkd. und Infekt.* 4, 209–216.
- Beijerinck, M. W., and Folpmers, T. (1916). Verslagen van de gewone vergadering der wis- en natuurkundige afdeling. *K. Akad. van Wet. te Amsterdam* 18, 1198–1200.
- Belas, R., Horikawa, E., Aizawa, S.-I., and Suvanasuthi, R. (2009). Genetic determinants of *Silicibacter* sp. TM1040 motility. *J. Bacteriol.* 191, 4502–4512. doi: 10.1128/JB.00429-09
- Ben Hania, W., Joseph, M., Schumann, P., Bunk, B., Fiebig, A., Spröer, C., et al. (2015). Complete genome sequence and description of *Salinispira pacifica* gen. nov., sp. nov., a novel spirochaete isolated from a hypersaline microbial mat. *Stand. Genomic Sci.* 10, 1–14. doi: 10.1186/1944-3277-10-7
- Bibi, F., Chung, E. J., Khan, A., Jeon, C. O., and Chung, Y. R. (2013). *Marteella endophytica* sp. nov., an antifungal bacterium associated with a halophyte. *Int. J. Syst. Evol. Microbiol.* 63, 2914–2919. doi: 10.1099/ijms.0.048785-0
- Bibi, F., Jeong, J. H., Chung, E. J., Jeon, C. O., and Chung, Y. R. (2014). *Labrenzia suaedae* sp. nov., a marine bacterium isolated from a halophyte, and emended description of the genus *Labrenzia*. *Int. J. Syst. Evol. Microbiol.* 64, 1116–1122. doi: 10.1099/ijms.0.052860-0
- Biebl, H., Pukall, R., Lünsdorf, H., Schulz, S., Allgaier, M., Tindall, B. J., et al. (2007). Description of *Labrenzia alexandrii* gen. nov., sp. nov., a novel alphaproteobacterium containing bacteriochlorophyll α , and a proposal for reclassification of *Stappia aggregata* as *Labrenzia aggregata* comb. nov., of *Stappia marina* as *Labrenzia marina* comb. *Int. J. Syst. Evol. Microbiol.* 57, 1095–1107. doi: 10.1099/ijms.0.64821-0
- Billerbeck, S., Orchard, J., Tindall, B. J., Giebel, H.-A., Brinkhoff, T., and Simon, M. (2015). Description of *Octadecabacter temperatus* sp. nov., isolated from the southern North Sea, emended descriptions of the genus *Octadecabacter* and its species and reclassification of *Octadecabacter jejudonensis* Park and Yoon 2014 as *Pseudooctadecabacter jejudonensis* gen. nov., comb. nov. *Int. J. Syst. Evol. Microbiol.* 65(Pt 6), 1967–1974. doi: 10.1099/ijms.0.000205
- Birtles, R. J., Harrison, T. G., Saunders, N. A., and Molyneux, D. H. (1995). Proposals to unify the genera *Grahamella* and *Bartonella*, with descriptions of *Bartonella talpae* comb. nov., *Bartonella peromysci* comb. nov., and three new species, *Bartonella grahamii* sp. nov., *Bartonella taylorii* sp. nov., and *Bartonella doshiae* sp. nov. *Int. J. Syst. Bacteriol.* 45, 1–8. doi: 10.1099/00207713-45-1-1
- Boone, D. R., Castenholz, R. W., and Garrity, G. M. (2001a). *Bergey's Manual of Systematic Bacteriology: The Archaea and the Deeply Branching and Phototrophic Bacteria*, 2nd Edn, Vol. 1. New York, NY: Springer, doi: 10.1007/978-0-387-68489-5
- Boone, D. R., Castenholz, R. W., and Garrity, G. M. (2001b). “Taxonomic outline of the Archaea and Bacteria,” in *Bergey's Manual of Systematic Bacteriology: The Archaea and the Deeply Branching and Phototrophic Bacteria*, Vol. 1 ed. W. B. Whitman (New York, NY: Springer), 155–166.
- Borsodi, A. K., Micsinai, A., Kovács, G., Tóth, E., Schumann, P., Kovács, A. L., et al. (2003). *Pannonibacter phragmitetus* gen. nov., sp. nov., a novel alkalitolerant bacterium isolated from decomposing reed rhizomes in a Hungarian soda lake. *Int. J. Syst. Evol. Microbiol.* 53, 555–561. doi: 10.1099/ijms.0.02356-0
- Bouzar, H., and Jones, J. B. (2001). *Agrobacterium larrymoorei* sp. nov., a pathogen isolated from aerial tumours of *Ficus benjamina*. *Int. J. Syst. Evol. Microbiol.* 51, 1023–1026. doi: 10.1099/00207713-51-3-1023
- Bowman, J. P. (2005). “Family V. Methylocystaceae fam. nov.” in *Bergey's Manual of Systematic Bacteriology: The Proteobacteria, Part C, the Alpha-, Beta-, Delta-, and Epsilonbacteria*, Vol. 2, eds D. J. Brenner, N. R. Krieg, J. T. Staley, and G. M. Garrity (New York, NY: Springer), 411–422.
- Bowman, J. P., Sly, L. I., Nichols, P. D., and Hayward, A. C. (1993). Revised taxonomy of the methanotrophs: description of *Methylobacter* gen. nov., emendation of *Methylococcus*, validation of *Methylosinus* and *Methylocystis*

- species, and a proposal that the family Methylococcaceae includes only the group I methanotrophs. *Int. J. Syst. Evol. Microbiol.* 43, 735–753. doi: 10.1099/00207713-43-4-735
- Breed, R. S., Murray, E. G. D., and Smith, N. (eds) (1957). *Bergey's Manual of Determinative Bacteriology*, 7th Edn. Baltimore, MD: The Williams & Wilkins Co.
- Breider, S., Scheuner, C., Schumann, P., Fiebig, A., Petersen, J., Pradella, S., et al. (2014). Genome-scale data suggest reclassifications in the *Leisingera-Phaeobacter* cluster including proposals for *Sedimentitalea* gen. nov. and *Pseudophaeobacter* gen. nov. *Front. Microbiol.* 5:416. doi: 10.3389/fmicb.2014.00416
- Brenner, D. J., Hollis, D. G., Moss, C. W., English, C. K., Hall, G. S., Vincent, J., et al. (1991). Proposal of *Afipia* gen. nov., with *Afipia felis* sp. nov. (formerly the cat scratch disease bacillus), *Afipia clevelandensis* sp. nov. (formerly the Cleveland clinic foundation strain), *Afipia broomeae* sp. nov., and three unnamed genospecies. *J. Clin. Microbiol.* 29, 2450–2460. doi: 10.1128/jcm.29.11.2450-2460.1991
- Brenner, D. J., Kaufmann, A. F., Sulzer, K. R., Steigerwalt, A. G., Rogers, F. C., and Weyant, R. (1999). Further determination of DNA relatedness between serogroups and serovars in the family Leptospiraceae with a proposal for *Leptospira alexanderi* sp. nov. and four new *Leptospira* genospecies. *Int. J. Syst. Bacteriol.* 49, 839–858. doi: 10.1099/00207713-49-2-839
- Brenner, D. J., Krieg, N. R., Staley, J. T., and Garrity, G. M. (eds) (2005). *Bergey's Manual of Systematic Bacteriology: The Proteobacteria; Part C, the Alpha-, Beta-, Delta-, and Epsilonproteobacteria*, 2nd Edn, Vol. 2. Bosten, MA: Springer.
- Brenner, D. J., O'Connor, S. P., Winkler, H. H., and Steigerwalt, A. G. (1993). Proposals to unify the genera *Bartonella* and *Rochalimaea*, with descriptions of *Bartonella quintana* comb. nov., *Bartonella vinsonii* comb. nov., *Bartonella henselae* comb. nov. and *Bartonella elizabethae* comb. nov. and to remove the family Bartonellaceae from the order Rickettsiales. *Int. J. Syst. Bacteriol.* 43, 777–786. doi: 10.1099/00207713-43-4-777
- Brettar, I., Christen, R., Bötzel, J., Lünsdorf, H., and Höfle, M. G. (2007). *Andersenella baltica* gen. nov., sp. nov., a novel marine bacterium of the Alphaproteobacteria isolated from sediment in the central Baltic Sea. *Int. J. Syst. Evol. Microbiol.* 57, 2399–2405. doi: 10.1099/ijs.0.65007-0
- Breznak, J. A., and Warnecke, F. (2008). *Spirochaeta cellobiosiphila* sp. nov., a facultatively anaerobic, marine spirochaete. *Int. J. Syst. Evol. Microbiol.* 58, 2762–2768. doi: 10.1099/ijs.0.2008/001263-0
- Brinkhoff, T., Giebel, H.-A., and Simon, M. (2008). Diversity, ecology, and genomics of the *Roseobacter* clade: a short overview. *Arch. Microbiol.* 189, 531–539. doi: 10.1007/s00203-008-0353-y
- Brinkmann, H., Göker, M., Koblížek, M., Wagner-Döbler, I., and Petersen, J. (2018). Horizontal operon transfer, plasmids, and the evolution of photosynthesis in Rhodobacteraceae. *ISME J.* 12, 1994–2010. doi: 10.1038/s41396-018-0150-9
- Brumpt, E. (1932). Longévitité du virus de la fièvre boutonneuse (*Rickettsia conori*, n. sp.) chez la Tique, *Rhipicephalus sanguineus*. *C. R. Soc. Biol. Fil.* 110, 1199–1202.
- Buchanan, R. E. (1917). Studies on the nomenclature and classification of the bacteria: III. the families of the Eubacteriales. *J. Bacteriol.* 2, 347–350. doi: 10.1128/jb.2.4.347-350.1917
- Buddle, M. B. (1956). Studies on *Brucella ovis* (n. sp.), a cause of genital disease of sheep in New Zealand and Australia. *J. Hyg. (Lond)* 54, 351–364. doi: 10.1017/s0022172400044612
- Bundesanstalt für Arbeitsschutz und Arbeitsmedizin (2015). Technische regel für biologische arbeitsstoffe TRBA 466, einstuftung von Prokaryonten (Bacteria und Archaea) in Risikogruppen. *Einstufung von Prokaryonten (Bacteria und Archaea) Risikogruppen* 25, 1–382.
- Buonaurio, R., Stravato, V. M., Kosako, Y., Fujiwara, N., Naka, T., Kobayashi, K., et al. (2002). *Sphingomonas melonis* sp. nov., a novel pathogen that causes brown spots on yellow Spanish melon fruits. *Int. J. Syst. Evol. Microbiol.* 52, 2081–2087. doi: 10.1099/ijs.0.02063-0
- Busse, H. J., Denner, E. B. M., Buczolits, S., Salkinoja-Salonen, M., Bennisar, A., and Kämpfer, P. (2003). *Sphingomonas aurantiaca* sp. nov., *Sphingomonas aerolata* sp. nov. and *Sphingomonas faeni* sp. nov., air- and dustborne and Antarctic, orange-pigmented, psychrotolerant bacteria, and emended description of the genus *Sphingomonas*. *Int. J. Syst. Evol. Microbiol.* 53, 1253–1260. doi: 10.1099/ijs.0.02461-0
- Cai, H., Cui, H., Zeng, Y., An, M., and Jiang, H. (2018a). *Sandarakinorhabdus cyanobacteriorum* sp. nov., a novel bacterium isolated from cyanobacterial aggregates in a eutrophic lake. *Int. J. Syst. Evol. Microbiol.* 68, 730–735. doi: 10.1099/ijsem.0.002571
- Cai, H., Cui, H., Zeng, Y., Wang, Y., and Jiang, H. (2018b). *Niveispirillum lacus* sp. nov., isolated from cyanobacterial aggregates in a eutrophic lake. *Int. J. Syst. Evol. Microbiol.* 68, 507–512. doi: 10.1099/ijsem.0.002526
- Cai, H., Wang, Y., Xu, H., Yan, Z., Jia, B., Maszenan, A. M., et al. (2015). *Niveispirillum cyanobacteriorum* sp. nov., a nitrogen-fixing bacterium isolated from cyanobacterial aggregates in a eutrophic lake. *Int. J. Syst. Evol. Microbiol.* 65, 2537–2541. doi: 10.1099/ijs.0.000299
- Cai, M., Wang, L., Cai, H., Li, Y., Tang, Y. Q., and Wu, X. L. (2011a). *Rubrimonas shengliensis* sp. nov. and *Polymorphum gilvum* gen. nov., sp. nov., novel members of Alphaproteobacteria from crude oil contaminated saline soil. *Syst. Appl. Microbiol.* 34, 321–327. doi: 10.1016/j.syapm.2011.03.004
- Cai, M., Wang, L., Cai, H., Li, Y., Wang, Y.-N., Tang, Y.-Q., et al. (2011b). *Salinarimonas ramus* sp. nov. and *Tessaracoccus oleagri* sp. nov., isolated from a crude oil-contaminated saline soil. *Int. J. Syst. Evol. Microbiol.* 61, 1767–1775. doi: 10.1099/ijs.0.025932-0
- Cai, X., Wang, Y., Yang, X., Liu, J., Wu, Y., and Zhang, X.-H. (2017). *Paraphaeobacter pallidus* gen. nov., sp. nov., isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 67, 2520–2526. doi: 10.1099/ijsem.0.001935
- Camacho, C., Coulouris, G., Avagyan, V., Ma, N., Papadopoulos, J., Bealer, K., et al. (2009). BLAST+: architecture and applications. *BMC Bioinformatics* 10:421. doi: 10.1186/1471-2105-10-421
- Camacho, M., Redondo-Gómez, S., Rodríguez-Llorente, I., Rohde, M., Spröer, C., Schumann, P., et al. (2016). *Labrenzia salina* sp. nov., isolated from the rhizosphere of the halophyte *Arthrocnemum macrostachyum*. *Int. J. Syst. Evol. Microbiol.* 66, 5173–5180. doi: 10.1099/ijsem.0.001492
- Carmichael, L. E., and Bruner, D. W. (1968). Characteristics of a newly-recognized species of *Brucella* responsible for infectious canine abortions. *Cornell Vet.* 48, 579–592.
- Carro, L., Nouioui, I., Sangal, V., Meier-Kolthoff, J. P., Trujillo, M. E., Montero-Calasan, M., et al. (2018). Genome-based classification of micromonosporae with a focus on their biotechnological and ecological potential. *Sci. Rep.* 8:525. doi: 10.1038/s41598-017-17392-0
- Casida, L. E. (1982). *Ensifer adhaerens* gen. nov., sp. nov.: a bacterial predator of bacteria in soil? *Int. J. Syst. Bacteriol.* 32, 339–345. doi: 10.1099/00207713-32-3-339
- Celador-lera, L., Menéndez, E., Peix, A., Igual, J. M., Velázquez, E., and Rivas, R. (2017). *Rhizobium zeae* sp. nov., isolated from maize (*Zea mays* L.) roots. *Int. J. Syst. Evol. Microbiol.* 67, 2306–2311. doi: 10.1099/ijsem.0.001944
- Cha, I.-T., Park, I., Lee, H.-W., Lee, H., Park, J.-M., Roh, S. W., et al. (2016). *Pseudoruegeria aestuarii* sp. nov., of the family Rhodobacteraceae, isolated from a tidal flat. *Int. J. Syst. Evol. Microbiol.* 66, 3125–3131. doi: 10.1099/ijsem.0.001156
- Chan, E. C. S., Siboo, R., Keng, T., Psarra, N., Hurley, R., Cheng, S.-L., et al. (1993). *Treponema denticola* (ex Brumpt 1925) sp. nov., nom. rev., and identification of new Spirochete isolates from periodontal pockets. *Int. J. Syst. Bacteriol.* 43, 196–203. doi: 10.1099/00207713-43-2-196
- Chang, R., Bird, L., Barr, C., Osburn, M., Wilbanks, E., Neelson, K., et al. (2018). *Thioclava electrotropha* sp. nov., a versatile electrode and sulfur-oxidizing bacterium from marine sediments. *Int. J. Syst. Evol. Microbiol.* 68, 1652–1658. doi: 10.1099/ijsem.0.002723
- Chang, Y. L., Wang, J. Y., Wang, E. T., Liu, H. C., Sui, X. H., and Chen, W. X. (2011). *Bradyrhizobium lablabi* sp. nov., isolated from effective nodules of *Lablab purpureus* and *Arachis hypogaea*. *Int. J. Syst. Evol. Microbiol.* 61, 2496–2502. doi: 10.1099/ijs.0.027110-0
- Chen, C., Zheng, Q., Wang, Y. N., Yan, X. J., Hao, L. K., Du, X., et al. (2010). *Stakelama pacifica* gen. nov., sp. nov., a new member of the family Sphingomonadaceae isolated from the Pacific Ocean. *Int. J. Syst. Evol. Microbiol.* 60, 2857–2861. doi: 10.1099/ijs.0.018945-0
- Chen, C.-X., Zhang, X.-Y., Liu, C., Yu, Y., Liu, A., Li, G.-W., et al. (2013). *Pseudorhodobacter antarcticus* sp. nov., isolated from Antarctic intertidal sandy sediment, and emended description of the genus *Pseudorhodobacter* Uchino et al., 2002 emend. Jung et al. 2012. *Int. J. Syst. Evol. Microbiol.* 63(Pt 3), 849–854. doi: 10.1099/ijs.0.042184-0

- Chen, H., Jogler, M., Rohde, M., Klenk, H. P., Busse, H. J., Tindall, B. J., et al. (2012). Reclassification and emended description of *Caulobacter leidyi* as *Sphingomonas leidyi* comb. nov., and emendation of the genus *Sphingomonas*. *Int. J. Syst. Evol. Microbiol.* 62, 2835–2843. doi: 10.1099/ijs.0.039636-0
- Chen, H., Jogler, M., Tindall, B. J., Klenk, H. P., Rohde, M., Busse, H. J., et al. (2013). *Sphingomonas starnbergensis* sp. nov., isolated from a prealpine freshwater lake. *Int. J. Syst. Evol. Microbiol.* 63, 1017–1023. doi: 10.1099/ijs.0.042887-0
- Chen, I. M. A., Chu, K., Palaniappan, K., Pillay, M., Ratner, A., Huang, J., et al. (2019). IMG/M v.5.0: an integrated data management and comparative analysis system for microbial genomes and microbiomes. *Nucleic Acids Res.* 47, D666–D677. doi: 10.1093/nar/gky901
- Chen, M.-H., Sheu, S.-Y., Chen, C. A., Wang, J.-T., and Chen, W.-M. (2011a). *Paracoccus isoporae* sp. nov., isolated from the reef-building coral *Isopora palifera*. *Int. J. Syst. Evol. Microbiol.* 61, 1138–1143. doi: 10.1099/ijs.0.023333-0
- Chen, M.-H., Sheu, S.-Y., Chen, C. A., Wang, J.-T., and Chen, W.-M. (2011b). *Shimia isoporae* sp. nov., isolated from the reef-building coral *Isopora palifera*. *Int. J. Syst. Evol. Microbiol.* 61, 823–827. doi: 10.1099/ijs.0.022848-0
- Chen, M.-H., Sheu, S.-Y., Chen, C. A., Wang, J.-T., and Chen, W.-M. (2012). *Roseivivax isoporae* sp. nov., isolated from a reef-building coral, and emended description of the genus *Roseivivax*. *Int. J. Syst. Evol. Microbiol.* 62, 1259–1264. doi: 10.1099/ijs.0.032961-0
- Chen, M. H., Zhou, X. Y., Ou, F. H., Xia, F., Lv, Y. Y., and Qiu, L. H. (2017a). *Aliidongia dinghuisensis* gen. nov., sp. nov., a poly- β -hydroxybutyrate-producing bacterium isolated from pinus massoniana forest soil. *Int. J. Syst. Evol. Microbiol.* 67, 212–217. doi: 10.1099/ijs.0.001588
- Chen, S., Xu, Y., Zheng, C., and Ke, L. X. (2017b). *Marivibrio halodurans* gen. nov., sp. nov., a marine bacterium in the family Rhodospirillaceae isolated from underground rock salt. *Int. J. Syst. Evol. Microbiol.* 67, 4266–4271. doi: 10.1099/ijs.0.002309
- Chen, W., Sheng, X.-F., He, L.-Y., and Huang, Z. (2015). *Rhizobium yangtingense* sp. nov., a mineral-weathering bacterium. *Int. J. Syst. Evol. Microbiol.* 65, 412–417. doi: 10.1099/ijs.0.064428-0
- Chen, W. H., Yang, S. H., Li, Z. H., Zhang, X. X., Sui, X. H., Wang, E. T., et al. (2017c). *Ensifer shofinae* sp. nov., a novel rhizobial species isolated from root nodules of soybean (*Glycine max*). *Syst. Appl. Microbiol.* 40, 144–149. doi: 10.1016/j.syapm.2017.01.002
- Chen, W.-M., Cho, N.-T., Huang, W.-C., Young, C.-C., and Sheu, S.-Y. (2013). Description of *Gemmobacter fontiphilus* sp. nov., isolated from a freshwater spring, reclassification of *Catellibacterium nectariphilum* as *Gemmobacter nectariphilus* comb. nov., *Catellibacterium changlense* as *Gemmobacter changlensis* comb. nov., *Catellibacterium aquatile* as *Gemmobacter aquaticus* nom. nov., *Catellibacterium caeni* as *Gemmobacter caeni* comb. nov., *Catellibacterium nanjingense* as *Gemmobacter nanjingensis* comb. nov., and emended description of the genus *Gemmobacter* and of *Gemmobacter aquatilis*. *Int. J. Syst. Evol. Microbiol.* 63, 470–478. doi: 10.1099/ijs.0.042051-0
- Chen, W.-M., Zhu, W.-F., Bontemps, C., Young, J. P. W., and Wei, G. H. (2010). *Mesorhizobium alhagi* sp. nov., isolated from wild *Alhagi sparsifolia* in north-western China. *Int. J. Syst. Evol. Microbiol.* 60, 958–962. doi: 10.1099/ijs.0.014043-0
- Chen, W.-X., Tan, Z.-Y., Gao, J.-L., Li, Y., and Wang, E.-T. (1997). *Rhizobium hainanense* sp. nov., isolated from tropical legumes. *Int. J. Syst. Evol. Microbiol.* 47, 870–873. doi: 10.1099/00207713-47-3-870
- Chen, X., Li, Q. L. G.-D., Lei, H., Jiang, Y., Han, L., Huang, X.-S., et al. (2017d). *Enterovirga rhinocerotis* gen. nov., sp. nov., isolated from *Rhinoceros unicornis* faeces. *Antonie Van Leeuwenhoek* 110, 553–562. doi: 10.1007/s10482-016-0823-1
- Chen, X., Wang, H., Xu, J., Song, D., Sun, G., and Xu, M. (2016). *Sphingobium hydrophobicum* sp. nov., a hydrophobic bacterium isolated from electronic-waste-contaminated sediment. *Int. J. Syst. Evol. Microbiol.* 66, 3912–3916. doi: 10.1099/ijs.0.001287
- Chen, Z., Liu, Y., Liu, L.-Z., Zhong, Z.-P., Liu, Z.-P., and Liu, Y. (2014). *Cribrihabitans marinus* gen. nov., sp. nov., isolated from a biological filter in a marine recirculating aquaculture system. *Int. J. Syst. Evol. Microbiol.* 64, 1257–1263. doi: 10.1099/ijs.0.059576-0
- Chen, Z., Zhang, J., Lei, X., Lai, Q., Yang, L., Zhang, H., et al. (2015). *Mameliella phaeodactyli* sp. nov., a member of the family Rhodobacteraceae isolated from the marine algae *Phaeodactylum tricorutum*. *Int. J. Syst. Evol. Microbiol.* 65, 1617–1621. doi: 10.1099/ijs.0.000146
- Chernikova, T. N., Dallimore, J., Lünsdorf, H., Heipieper, H. J., and Golyshin, P. N. (2017). *Monaibacterium marinum*, gen. nov., sp. nov., a new member of the Alphaproteobacteria isolated from seawater of Menai Straits, Wales, UK. *Int. J. Syst. Evol. Microbiol.* 67, 3310–3317. doi: 10.1099/ijs.0.002111
- Cho, J.-C., and Giovannoni, S. J. (2004). *Oceanicola granulosa* gen. nov., sp. nov. and *Oceanicola batsensis* sp. nov., poly- β -hydroxybutyrate-producing marine bacteria in the order 'Rhodobacterales'. *Int. J. Syst. Evol. Microbiol.* 54, 1129–1136. doi: 10.1099/ijs.0.03015-0
- Cho, J.-C., and Giovannoni, S. J. (2006). *Pelagibaca bermudensis* gen. nov., sp. nov., a novel marine bacterium within the *Roseobacter* clade in the order Rhodobacterales. *Int. J. Syst. Evol. Microbiol.* 56, 855–859. doi: 10.1099/ijs.0.64063-0
- Cho, Y.-J., Yi, H., Seo, B., Cho, K. H., and Chun, J. (2013). *Fretibacter rubidus* gen. nov., sp. nov., isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 63, 4633–4638. doi: 10.1099/ijs.0.053751-0
- Choi, D. H., and Cho, B. C. (2006). *Citreimonas salinaria* gen. nov., sp. nov., a member of the *Roseobacter* clade isolated from a solar saltern. *Int. J. Syst. Evol. Microbiol.* 56, 2799–2803. doi: 10.1099/ijs.0.64373-0
- Choi, D. H., Cho, J.-C., Lanoil, B. D., Giovannoni, S. J., and Cho, B. C. (2007). *Maribius salinus* gen. nov., sp. nov., isolated from a solar saltern and *Maribius pelagius* sp. nov., cultured from the Sargasso Sea, belonging to the *Roseobacter* clade. *Int. J. Syst. Evol. Microbiol.* 57(Pt 2), 270–275. doi: 10.1099/ijs.0.64552-0
- Choi, D. H., Hwang, C. Y., and Cho, B. C. (2009). *Pelagibius litoralis* gen. nov., sp. nov., a marine bacterium in the family Rhodospirillaceae isolated from coastal seawater. *Int. J. Syst. Evol. Microbiol.* 59, 818–823. doi: 10.1099/ijs.0.002774-0
- Choi, D. H., Yi, H., Chun, J., and Cho, B. C. (2006). *Jannaschia seosinensis* sp. nov., isolated from hypersaline water of a solar saltern in Korea. *Int. J. Syst. Evol. Microbiol.* 56, 45–49. doi: 10.1099/ijs.0.63835-0
- Choi, E. J., Lee, H. J., Kim, J. M., and Jeon, C. O. (2013). *Roseovarius lutimaris* sp. nov., isolated from a marine tidal flat. *Int. J. Syst. Evol. Microbiol.* 63(Pt 10), 3835–3840. doi: 10.1099/ijs.0.050807-0
- Choi, G., Gao, M., Lee, D., and Choi, H. (2017). *Mabikibacter ruber* gen. nov., sp. nov., a bacterium isolated from marine sediment, and proposal of Mabikibacteraceae fam. nov. in the class Alphaproteobacteria. *Int. J. Syst. Evol. Microbiol.* 67, 3375–3380. doi: 10.1099/ijs.0.002121
- Chu, C., Yuan, C., Liu, X., Yao, L., Zhu, J., He, J., et al. (2015). *Phenylobacterium kunshanense* sp. nov., isolated from the sludge of a pesticide manufacturing factory. *Int. J. Syst. Evol. Microbiol.* 65(Pt 2), 325–330. doi: 10.1099/ijs.0.063644-0
- Cleenwerck, I., Vandemeulebroecke, K., Janssens, D., and Swings, J. (2002). Re-examination of the genus *Acetobacter*, with descriptions of *Acetobacter cerevisiae* sp. nov. and *Acetobacter malorum* sp. nov. *Int. J. Syst. Evol. Microbiol.* 52(Pt 5), 1551–1558. doi: 10.1099/ijs.0.02064-0
- Coenye, T., Goris, J., Spilker, T., Vandamme, P., and LiPuma, J. J. (2002). Characterization of unusual bacteria isolated from respiratory secretions of cystic fibrosis patients and description of *Inquilinus limosus* gen. nov., sp. nov. *J. Clin. Microbiol.* 40, 2062–2069. doi: 10.1128/JCM.40.6.2062-2069.2002
- Coil, D. A., Flanagan, J. C., Stump, A., Alexiev, A., Lang, J. M., and Eisen, J. A. (2015). *Porphyrobacter mercurialis* sp. nov., isolated from a stadium seat and emended description of the genus *Porphyrobacter*. *PeerJ* 3:e1400. doi: 10.7717/peerj.1400
- Cole, J. K., Morton, B. R., Cardamone, H. C., Lake, H. R. R., Dohnalkova, A. C., Kim, Y. M., et al. (2018). *Salinivirga fredricksonii* gen. nov., sp. nov., a heterotrophic halophile isolated from a photosynthetic mat, a member of a novel lineage (Salinarimonadaceae fam. nov.) within the order Rhizobiales, and reclassification of the genus *Salinarimonas* Liu Y. et al., 2010 into Salinarimonadaceae. 2010 into Salinarimonadaceae. *Int. J. Syst. Evol. Microbiol.* 68, 1591–1598. doi: 10.1099/ijs.0.002715
- Cole, S. T., Brosch, R., Parkhill, J., Garnier, T., Churcher, C., Harris, D., et al. (1998). Deciphering the biology of mycobacterium tuberculosis from the complete genome sequence. *Nature* 393, 537–544. doi: 10.1038/31159
- Colwell, R. R. (1970). Polyphasic taxonomy of the genus vibrio: numerical taxonomy of *Vibrio cholerae*, *Vibrio parahaemolyticus*, and related *Vibrio* species. *J. Bacteriol.* 104, 410–433. doi: 10.1128/jb.104.1.410-433.1970
- Conn, H. J. (1938). Taxonomic relationships of certain non-sporeforming rods in soil. *J. Bacteriol.* 36, 320–321.
- Conn, H. J. (1942). Validity of the genus *Alcalignes*. *J. Bacteriol.* 44, 353–360.

- Cordeiro, A. B., Ribeiro, R. A., Helene, L. C. F., and Hungria, M. (2017). *Rhizobium esperanzae* sp. nov., a N₂-fixing root symbiont of *Phaseolus vulgaris* from Mexican soils. *Int. J. Syst. Evol. Microbiol.* 67, 3937–3945. doi: 10.1099/ijsem.0.002225
- Coton, M., Laplace, J. M., Auffray, Y., and Coton, E. (2006). Polyphasic study of *Zymomonas mobilis* strains revealing the existence of a novel subspecies *Z. mobilis* subsp. *francensis* subsp. nov., isolated from French cider. *Int. J. Syst. Evol. Microbiol.* 56, 121–125. doi: 10.1099/ijse.0.63732-0
- Cwyk, W. M., and Canale-Parola, E. (1979). *Treponema succinifaciens* sp. nov., an aerobic Spirochete from the swine intestine. *Arch. Microbiol.* 122, 231–239. doi: 10.1007/bf00411285
- da Rocha-Lima, H. (1916). Zur aetiologie des fleckfiebers. *Berliner Klin. Wochenschr.* 53, 567–569.
- Dadhwal, M., Jit, S., Kumari, H., and Lal, R. (2009). *Sphingobium chinhatense* sp. nov., a hexachlorocyclohexane (HCH)-degrading bacterium isolated from an HCH dumpsite. *Int. J. Syst. Evol. Microbiol.* 59, 3140–3144. doi: 10.1099/ijse.0.005553-0
- Dahal, R. H., Chaudhary, D. K., and Kim, J. (2018). *Pinisolibacter ravus* gen. nov., sp. nov., isolated from pine forest soil and allocation of the genera *Ancalomicrobium* and *pinisolibacter* to the family *ancalomicrobiaceae* fam. nov., and emendation of the genus *Ancalomicrobium* staley 1968. *Int. J. Syst. Evol. Microbiol.* 68, 1955–1962. doi: 10.1099/ijsem.0.002772
- Dai, X., Shi, X., Gao, X., Liang, J., and Zhang, X.-H. (2015). *Salipiger nanhaiensis* sp. nov., a bacterium isolated from deep sea water. *Int. J. Syst. Evol. Microbiol.* 65, 1122–1126. doi: 10.1099/ijse.0.000066
- Dai, X., Wang, B.-J., Yang, Q.-X., Jiao, N.-Z., and Liu, S.-J. (2006). *Yangia pacifica* gen. nov., sp. nov., a novel member of the *Roseobacter* clade from coastal sediment of the East China Sea. *Int. J. Syst. Evol. Microbiol.* 56, 529–533. doi: 10.1099/ijse.0.64013-0
- Daneshvar, M. I., Hollis, D. G., Weyant, R. S., Steigerwalt, A. G., Whitney, A. M., Douglas Michael, P., et al. (2003). *Paracoccus yeeii* sp. nov. (formerly CDC group EO-2), a novel bacterial species associated with human infection. *J. Clin. Microbiol.* 41, 1289–1294. doi: 10.1128/JCM.41.3.1289
- Das, S. K., Mishra, A. K., Tindall, B. J., Rainey, F. A., and Stackebrandt, E. (1996). Oxidation of Thiosulfate by a new bacterium, *Bosea thiooxidans* (strain BI-42) gen. nov., sp. nov.: analysis of phylogeny based on chemotaxonomy and 16S ribosomal DNA sequencing. *Int. J. Syst. Bacteriol.* 46, 981–987. doi: 10.1099/00207713-46-4-981
- Davis, D. H., Doudoroff, M., Stanier, R. Y., and Mandel, M. (1969). Proposal to reject the genus *Hydrogenomonas*: taxonomic implications. *Int. J. Syst. Bacteriol.* 19, 375–390. doi: 10.1099/00207713-19-4-375
- de Lajudie, P., Laurent-Fulele, E., Wüilers, A., Torck, U., Coopman, R., Collin, M. D., et al. (1998). *Allorhizobium undicola* gen. nov., sp. nov., nitrogen-fixing bacteria that efficiently nodulate *Neptunia natans* in Senegal. *Int. J. Syst. Evol. Microbiol.* 48, 1277–1290. doi: 10.1099/00207713-48-4-1277
- De Ley, J., and Frateur, J. (1974). “Genus *Acetobacter* Beijerinck, 1898,” in *Bergey’s Manual of Determinative Bacteriology*, 8th Edn, eds R. E. Buchanan and N. E. Gibbons (Baltimore, MD: The Williams & Wilkins Co), 276–278.
- De Ley, J., and Swings, J. (1976). Phenotypic description, numerical analysis, and proposal for an improved taxonomy and nomenclature of the genus *Zymomonas Kluyver* and van Niel 1936. *Int. J. Syst. Evol. Microbiol.* 26, 146–157. doi: 10.1099/00207713-26-2-146
- De Meyer, S. E., and Willems, A. (2012). Multilocus sequence analysis of *Bosea* species and description of *Bosea lupini* sp. nov., *Bosea lathyri* sp. nov. and *Bosea robiniae* sp. nov., isolated from legumes. *Int. J. Syst. Evol. Microbiol.* 62, 2505–2510. doi: 10.1099/ijse.0.035477-0
- Dedysh, S. N., Haupt, E. S., and Dunfield, P. F. (2016). Emended description of the family Beijerinckiaceae and transfer of the genera *Chelatococcus* and *Camelimonas* to the family Chelatococcaceae fam. nov. *Int. J. Syst. Evol. Microbiol.* 66, 3177–3182. doi: 10.1099/ijsem.0.001167
- Dedysh, S. N., Khmelenina, V. N., Suzina, N. E., Trotsenko, Y. A., Semrau, J. D., Liesack, W., et al. (2002). *Methylocapsa acidiphila* gen. nov., sp. nov., a novel methane-oxidizing and dinitrogen-fixing acidophilic bacterium from *Sphagnum bog*. *Int. J. Syst. Evol. Microbiol.* 52, 251–261. doi: 10.1099/00207713-52-1-251
- Defosse, D. L., Johnson, R. C., Paster, B. J., Dewhirst, F. E., and Fraser, G. J. (1995). *Brevinema andersonii* gen. nov., sp. nov., an infectious spirochete isolated from the short-tailed shrew (*Blarina brevicauda*) and the white-footed mouse (*Peromyscus leucopus*). *Int. J. Syst. Bacteriol.* 45, 78–84. doi: 10.1099/00207713-45-1-78
- Dehio, C., Lanz, C., Pohl, R., Behrens, P., Bermond, D., Piémont, Y., et al. (2001). *Bartonella schoenbuchii* sp. nov., isolated from the blood of wild roe deer. *Int. J. Syst. Evol. Microbiol.* 51, 1557–1565. doi: 10.1099/00207713-51-4-1557
- Delamuta, J. R. M., Ribeiro, R. A., Ormeño-Orillo, E., Parma, M. M., Melo, I. S., Martínez-Romero, E., et al. (2015). *Bradyrhizobium tropiciagri* sp. nov. and *Bradyrhizobium embrapense* sp. nov., nitrogen-fixing symbionts of tropical forage legumes. *Int. J. Syst. Evol. Microbiol.* 65, 4424–4433. doi: 10.1099/ijsem.0.000592
- Deng, Z.-S., Zhao, L.-F., Xu, L., Kong, Z.-Y., Zhao, P., Qin, W., et al. (2011). *Paracoccus sphaerophysae* sp. nov., a siderophore-producing, endophytic bacterium isolated from root nodules of *Sphaerophysa salsula*. *Int. J. Syst. Evol. Microbiol.* 61, 665–669. doi: 10.1099/ijse.0.021071-0
- Denner, E. B. M., Kämpfer, P., Busse, H.-J., and Moore, E. R. B. (1999). Reclassification of *Pseudomonas echinoides* Heumann 1962, 343AL, in the genus *Sphingomonas* as *Sphingomonas echinoides* comb. nov. *Int. J. Syst. Bacteriol.* 49, 1103–1109. doi: 10.1099/00207713-49-3-1103
- Denner, E. B. M., Paukner, S., Kämpfer, P., Moore, E. R. B., Abraham, W.-R., Busse, H.-J., et al. (2001). *Sphingomonas pituitosa* sp. nov., an exopolysaccharide-producing bacterium that secretes an unusual type of sphingane. *Int. J. Syst. Evol. Microbiol.* 51, 827–841. doi: 10.1099/00207713-51-3-827
- Derx, H. G. (1950). *Beijerinckia*, a new genus of nitrogen-fixing bacteria occurring in tropical soils. *Proc. K. Ned. Akad. van Wet. Ser. C* 53, 140–147.
- Desper, R., and Gascuel, O. (2004). Theoretical foundation of the balanced minimum evolution method of phylogenetic inference and its relationship to weighted least-squares tree fitting. *Mol. Biol. Evol.* 21, 587–598. doi: 10.1093/molbev/msh049
- Desper, R., and Gascuel, O. (2006). Getting a tree fast: neighbor joining, FastME, and distance-based methods. *Curr. Protoc. Bioinformatics* Chapter 6, Unit 6.3. doi: 10.1002/0471250953.bi0603s15
- Díaz-Cárdenas, C., Patel, B. K. C., and Baena, S. (2010). *Tistlia consotensis* gen. nov., sp. nov., an aerobic, chemoheterotrophic, free-living, nitrogen-fixing alphaproteobacterium, isolated from a Colombian saline spring. *Int. J. Syst. Evol. Microbiol.* 60, 1437–1443. doi: 10.1099/ijse.0.010926-0
- Donachie, S. P., Bowman, J. P., and Alam, M. (2006). *Nesiotobacter exalbescens* gen. nov., sp. nov., a moderately thermophilic alphaproteobacterium from an Hawaiian hypersaline lake. *Int. J. Syst. Evol. Microbiol.* 56, 563–567. doi: 10.1099/ijse.0.63440-0
- Dong, C., Lai, Q., Chen, L., Sun, F., Shao, Z., and Yu, Z. (2010). *Oceanibaculum pacificum* sp. nov., isolated from hydrothermal field sediment of the south-west Pacific Ocean. *Int. J. Syst. Evol. Microbiol.* 60, 219–222. doi: 10.1099/ijse.0.011932-0
- Doronina, N. V., Braus-Stromeier, S. A., Leisinger, T., and Trotsenko, Y. A. (1995). Isolation and characterization of a new facultatively methylotrophic bacterium: description of *Methylorhabdus multivorans* gen. nov., sp. nov. *Syst. Appl. Microbiol.* 18, 92–98. doi: 10.1016/S0723-2020(11)80454-6
- Doronina, N. V., Kaparullina, E. N., Trotsenko, Y. A., Nörtemann, B., Bucheli-Witschel, M., Weilenmann, H.-U., et al. (2010). *Chelativorans multitrophicus* gen. nov., sp. nov. and *Chelativorans oligotrophicus* sp. nov., aerobic EDTA-degrading bacteria. *Int. J. Syst. Evol. Microbiol.* 60, 1044–1051. doi: 10.1099/ijse.0.003152-0
- Doronina, N. V., Poroshina, M. N., Kaparullina, E. N., Ezhov, V. A., and Trotsenko, Y. A. (2013). *Methyloligella halotolerans* gen. nov., sp. nov. and *Methyloligella solikamskensis* sp. nov., two non-pigmented halotolerant obligately methylotrophic bacteria isolated from the Ural saline environments. *Syst. Appl. Microbiol.* 36, 148–154. doi: 10.1016/j.syapm.2012.12.001
- Doronina, N. V., Trotsenko, Y. A., and Tourova, T. P. (2000). *Methylarcula marina* gen. nov., sp. nov. and *Methylarcula terricola* sp. nov.: novel aerobic, moderately halophilic, facultatively methylotrophic bacteria from coastal saline environments. *Int. J. Syst. Evol. Microbiol.* 50, 1849–1859. doi: 10.1099/00207713-50-5-1849
- Douglas, H. C. (1957). “Order III. Hyphomicrobiales Douglas, ordo nov.,” in *Bergey’s Manual of Determinative Bacteriology*, 7th Edn, eds R. S. Breed, E. G. D. Murray, and N. R. Smith (Baltimore, MD: The Williams and Wilkins Co), 276.
- Dreyfus, B., Garcia, J. L., and Gillis, M. (1988). Characterization of *Azorhizobium caulinodans* gen. nov., sp. nov., a stem-nodulating nitrogen-fixing bacterium

- isolated from *Sesbania rostrata*. *Int. J. Syst. Bacteriol.* 38, 89–98. doi: 10.1099/00207713-38-1-89
- Droz, S., Chi, B., Horn, E., Steigerwalt, A. G., Whitney, A. M., and Brenner, D. J. (1999). *Bartonella koehlerae* sp. nov., isolated from cats. *J. Clin. Microbiol.* 37, 1117–1122. doi: 10.1128/jcm.37.4.1117-1122.1999
- Duchow, E., and Douglas, H. C. (1949). *Rhodomicrobium vannielii*, a new phototrophic bacterium. *J. Bacteriol.* 58, 409–416. doi: 10.1128/jb.58.4.409-416.1949
- Duh, D., Punda-Polic, V., Avsic-Zupanc, T., Bouyer, D., Walker, D. H., Popov, V. L., et al. (2010). *Rickettsia hoogstraalii* sp. nov., isolated from hard- and soft-bodied ticks. *Int. J. Syst. Evol. Microbiol.* 60, 977–984. doi: 10.1099/ijs.0.011049-0
- Dumler, J. S., Barbet, A. F., Bekker, C. P. J., Dasch, G. A., Palmer, G. H., Ray, S. C., et al. (2001). Reorganization of genera in the families Rickettsiaceae and Anaplasmataceae in the order Rickettsiales: unification of some species of *Ehrlichia* with *Anaplasma*, *Cowdria* with *Ehrlichia* and *Ehrlichia* with *Neorickettsia*, descriptions of six new species combinations and designation of *Ehrlichia equi* and 'HGE agent' as subjective synonyms of *Ehrlichia phagocytophila*. *Int. J. Syst. Evol. Microbiol.* 51, 2145–2165. doi: 10.1099/00207713-51-6-2145
- Dunfield, P. F., Khmelenina, V. N., Suzina, N. E., Trotsenko, Y. A., and Dedysh, S. N. (2003). *Methylocella silvestris* sp. nov., a novel methanotroph isolated from an acidic forest cambisol. *Int. J. Syst. Evol. Microbiol.* 53, 1231–1239. doi: 10.1099/ijs.0.02481-0
- Dutta, D., and Gachhui, R. (2006). Novel nitrogen-fixing *Acetobacter nitrogenifigens* sp. nov., isolated from Kombucha tea. *Int. J. Syst. Evol. Microbiol.* 56, 1899–1903. doi: 10.1099/ijs.0.64101-0
- Dziuba, M., Koziava, V., Grouzdev, D., Burganskaya, E., Baslerov, R., Kolganova, T., et al. (2016). *Magnetospirillum caucaseum* sp. nov., *Magnetospirillum marinigris* sp. nov. and *Magnetospirillum moscoviense* sp. nov., freshwater magnetotactic bacteria isolated from three distinct geographical locations in European Russia. *Int. J. Syst. Evol. Microbiol.* 66, 2069–2077. doi: 10.1099/ijs.0.000994
- Emerson, D., Rentz, J. A., Lilburn, T. G., Davis, R. E., Aldrich, H., Chan, C., et al. (2007). A novel lineage of *Proteobacteria* involved in formation of marine Fe-oxidizing microbial mat communities. *PLoS One* 2:e667. doi: 10.1371/journal.pone.0000667
- Enright, A. J., Van Dongen, S., and Ouzounis, C. A. (2002). An efficient algorithm for large-scale detection of protein families. *Nucleic Acids Res.* 30, 1575–1584. doi: 10.1093/nar/30.7.1575
- Eremeeva, M. E., Gerns, H. L., Lydy, S. L., Goo, J. S., Ryan, E. T., Mathew, S. S., et al. (2007). Bacteremia, fever, and splenomegaly caused by a newly recognized *Bartonella* species. *N. Engl. J. Med.* 356, 2381–2387. doi: 10.1056/nejmoa065987
- Faine, S., and Stallman, N. D. (1982). Amended descriptions of the genus *Leptospira* Noguchi 1917 and the species *L. interrogans* (Stimson 1907) Wenyon 1926 and *L. biflexa* (Wolbach and Binger 1914) Noguchi 1918. *Int. J. Syst. Bacteriol.* 32, 461–463. doi: 10.1099/00207713-32-4-461
- Falk, E. C., Döbereiner, J., Johnson, J. L., and Krieg, N. R. (1985). Deoxyribonucleic acid homology of *Azospirillum amazonense* Magalhães et al. 1984 and emendation of the description of the genus *Azospirillum*. *Int. J. Syst. Bacteriol.* 35, 117–118. doi: 10.1099/00207713-35-1-117
- Falush, D., Torpdahl, M., Didelot, X., Conrad, D. F., Wilson, D. J., and Achtman, M. (2006). Mismatch induced speciation in *Salmonella*: model and data. *Philos. Trans. R. Soc. B Biol. Sci.* 361, 2045–2053. doi: 10.1098/rstb.2006.1925
- Farrand, S. K., van Berkum, P. B., and Oger, P. (2003). *Agrobacterium* is a definable genus of the family Rhizobiaceae. *Int. J. Syst. Evol. Microbiol.* 53, 1681–1687. doi: 10.1099/ijs.0.02445-0
- Farris, J. S. (1974). Formal definitions of paraphyly and polyphyly. *Syst. Zool.* 23, 548–554. doi: 10.2307/2412474
- Farris, J. S. (1977). Phylogenetic analysis under Dollo's Law. *Syst. Zool.* 26, 77–88. doi: 10.1093/sysbio/26.1.77
- Farris, J. S. (1989). The retention index and homoplasy excess. *Syst. Biol.* 38, 406–407. doi: 10.2307/2992406
- Felföldi, T., Vengring, A., Márialigeti, K., András, J., Schumann, P., and Tóth, E. M. (2014). *Hephaestia caeni* gen. nov., sp. nov., a novel member of the family Sphingomonadaceae isolated from activated sludge. *Int. J. Syst. Evol. Microbiol.* 64, 738–744. doi: 10.1099/ijs.0.053736-0
- Feng, G., Da Yang, S. Z., Wang, Y. H., Zhang, X. X., Zhao, G. Z., Deng, M. R., et al. (2014). Description of a Gram-negative bacterium, *Sphingomonas guangdongensis* sp. nov. *Int. J. Syst. Evol. Microbiol.* 64, 1697–1702. doi: 10.1099/ijs.0.056853-0
- Feng, X.-M., Mo, Y.-X., Han, L., Nogi, Y., Zhu, Y.-H., and Lv, J. (2015). *Qipengyuania sediminis* gen. nov., sp. nov., a member of the family Erythrobacteraceae isolated from subterrestrial sediment. *Int. J. Syst. Evol. Microbiol.* 65, 3658–3665. doi: 10.1099/ijs.0.000472
- Flores-Félix, J. D., Carro, L., Velázquez, E., Valverde, Á., Cerda-Castillo, E., García-Fraile, P., et al. (2013). *Phyllobacterium endophyticum* sp. nov., isolated from nodules of *Phaseolus vulgaris*. *Int. J. Syst. Evol. Microbiol.* 63, 821–826. doi: 10.1099/ijs.0.038497-0
- Foesel, B. U., Drake, H. L., and Schramm, A. (2011). *Defluviimonas denitrificans* gen. nov., sp. nov., and *Pararhodobacter aggregans* gen. nov. sp. nov., non-phototrophic Rhodobacteraceae from the biofilter of a marine aquaculture. *Syst. Appl. Microbiol.* 34, 498–502. doi: 10.1016/j.syapm.2011.08.006
- Foesel, B. U., Größner, A. S., Drake, H. L., and Schramm, A. (2007). *Geminicoccus roseus* gen. nov., sp. nov., an aerobic phototrophic Alphaproteobacterium isolated from a marine aquaculture biofilter. *Syst. Appl. Microbiol.* 30, 581–586. doi: 10.1016/j.syapm.2007.05.005
- Foster, G., Osterman, B. S., Godfroid, J., Jacques, I., and Cloeckert, A. (2007). *Brucella ceti* sp. nov. and *Brucella pinnipedialis* sp. nov. for *Brucella* strains with cetaceans and seals as their preferred hosts. *Int. J. Syst. Evol. Microbiol.* 57, 2688–2693. doi: 10.1099/ijs.0.65269-0
- Fournier, P.-E., Dumler, J. S., Greub, G., Zhang, J., Wu, Y., and Raoult, D. (2003). Gene sequence-based criteria for identification of new *Rickettsia* isolates and description of *Rickettsia heilongjiangensis* sp. nov. *J. Clin. Microbiol.* 41, 5456–5465. doi: 10.1128/JCM.41.12.5456
- Fournier, P.-E., Grunnenberger, F., Jaulhac, B., Gastinger, G., and Raoult, D. (2000). Evidence of *Rickettsia helvetica* infection in Humans, eastern France. *Emerg. Infect. Dis.* 6, 389–392. doi: 10.3201/eid0604.000412
- Fournier, P.-E., Takada, N., Fujita, H., and Raoult, D. (2006). *Rickettsia tamurae* sp. nov., isolated from *Amblyomma testudinarium* ticks. *Int. J. Syst. Evol. Microbiol.* 56, 1673–1675. doi: 10.1099/ijs.0.64134-0
- Fox, J. E., Gullede, J., Engelhaupt, E., Burow, M. E., and McLachlan, J. A. (2007). Pesticides reduce symbiotic efficiency of nitrogen-fixing rhizobia and host plants. *PNAS* 104, 10282–10287. doi: 10.1073/pnas.0611710104
- Francis, I. M., Jochimsen, K. N., De Vos, P., and van Bruggen, A. H. C. (2014). Reclassification of rhizosphere bacteria including strains causing corky root of lettuce and proposal of *Rhizorhaphis suberificiens* gen. nov., comb. nov., *Sphingobium mellinum* sp. nov., *Sphingobium xanthum* sp. nov. and *Rhizorhaphis argentea* gen. nov., sp. nov. *Int. J. Syst. Evol. Microbiol.* 64, 1340–1350. doi: 10.1099/ijs.0.058909-0
- Frank, B. (1889). Über die pilzsymbiose der leguminosen. *Ber. Dtsch. Bot. Ges.* 7, 332–346.
- Frank, O., Goker, M., Pradella, S., and Petersen, J. (2015). Ocean's twelve: flagellar and biofilm chromids in the multipartite genome of *Marinovum algicola* DG898 exemplify functional compartmentalization. *Environ. Microbiol.* 17, 4019–4034. doi: 10.1111/1462-2920.12947
- Fritz, I., Strömpl, C., and Abraham, W.-R. (2004). Phylogenetic relationships of the genera *Stella*, *Labrys* and *Angulomicrobium* within the "Alphaproteobacteria" and description of *Angulomicrobium amanitifforme* sp. nov. *Int. J. Syst. Evol. Microbiol.* 54, 651–657. doi: 10.1099/ijs.0.02746-0
- Fuerst, J. A., Hawkins, J. A., Holmes, A., Sly, L. I., Moore, C. J., and Stackebrandt, E. (1993). *Porphyrobacter neustonensis* gen. nov., sp. nov., an aerobic bacteriochlorophyll-synthesizing budding bacterium from fresh water. *Int. J. Syst. Bacteriol.* 43, 125–134. doi: 10.1099/00207713-43-1-125
- Fujii, K., Satomi, M., Morita, N., Motomura, T., Tanaka, T., and Kikuchi, S. (2003). *Novosphingobium tardagens* sp. nov., an oestradiol-degrading bacterium isolated from activated sludge of a sewage treatment plant in Tokyo. *Int. J. Syst. Evol. Microbiol.* 53, 47–52. doi: 10.1099/ijs.0.02301-0
- Fukuda, W., Chino, Y., Araki, S., Kondo, Y., Imanaka, H., Kanai, T., et al. (2014). *Polymorphobacter multimanifer* gen. nov., sp. nov., a polymorphic bacterium isolated from antarctic white rock. *Int. J. Syst. Evol. Microbiol.* 64, 2034–2040. doi: 10.1099/ijs.0.050005-0
- Fukuda, W., Yamada, K., Miyoshi, Y., Okuno, H., Atomi, H., and Imanaka, T. (2012). *Rhodoligotrophos appendicifer* gen. nov., sp. nov., an appendaged bacterium isolated from a freshwater Antarctic lake. *Int. J. Syst. Evol. Microbiol.* 62, 1945–1950. doi: 10.1099/ijs.0.032953-0

- Fukui, Y., Abe, M., Kobayashi, M., Saito, H., Oikawa, H., Yano, Y., et al. (2013). *Algimonas porphyrae* gen. nov., sp. nov., a member of the family Hyphomonadaceae, isolated from the red alga *Porphyra yezoensis*. *Int. J. Syst. Evol. Microbiol.* 63, 314–320. doi: 10.1099/ijs.0.040485-0
- Furuhata, K., Miyamoto, H., Goto, K., Kato, Y., Hara, M., and Fukuyama, M. (2008). *Roseomonas stagni* sp. nov., isolated from pond water in Japan. *J. Gen. Appl. Microbiol.* 54, 167–171. doi: 10.2323/jgam.54.167
- Galatis, H., Martin, K., Kämpfer, P., and Glaeser, S. P. (2013). *Devosia epidermidihirudinis* sp. nov. isolated from the surface of a medical leech. *Antonie Van Leeuwenhoek* 103, 1165–1171. doi: 10.1007/s10482-013-9895-3
- Gallego, S., Vila, J., Nieto, J. M., Urdiain, M., Rosselló-Móra, R., and Grifoll, M. (2010). *Breoghania corrubedonensis* gen. nov. sp. nov., a novel alphaproteobacterium isolated from a Galician beach (NW Spain) after the prestige fuel oil spill, and emended description of the family Cohaesibacteraceae and the species *Cohaesibacter gelatinilyticus*. *Syst. Appl. Microbiol.* 33, 316–321. doi: 10.1016/j.syapm.2010.06.005
- Gao, J., Sun, P., Wang, X., Lv, F., Mao, X., and Sun, J. (2017). *Rhizobium wenxiniae* sp. nov., an endophytic bacterium isolated from maize root. *Int. J. Syst. Evol. Microbiol.* 67, 2798–2803. doi: 10.1099/ijsem.0.002025
- Gao, J.-L., Turner, S. L., Kan, F. L., Wang, E. T., Tan, Z. Y., Qiu, Y. H., et al. (2004). *Mesorhizobium septentrionale* sp. nov. and *Mesorhizobium temperatum* sp. nov., isolated from *Astragalus adsurgens* growing in the northern regions of China. *Int. J. Syst. Evol. Microbiol.* 54, 2003–2012. doi: 10.1099/ijs.0.02840-0
- García-Fraile, P., Rivas, R., Willems, A., Peix, A., Martens, M., Martínez-Molina, E., et al. (2007). *Rhizobium cellulosityticum* sp. nov., isolated from sawdust of *Populus alba*. *Int. J. Syst. Evol. Microbiol.* 57, 844–848. doi: 10.1099/ijs.0.64680-0
- Garg, N., Bala, K., and Lal, R. (2012). *Sphingobium lucknowense* sp. nov., a hexachlorocyclohexane (HCH)-degrading bacterium isolated from HCH-contaminated soil. *Int. J. Syst. Evol. Microbiol.* 62, 618–623. doi: 10.1099/ijs.0.028886-0
- Garrity, G. M., Bell, J. A., and Lilburn, T. (2005a). “Class I. Alphaproteobacteria class. nov,” in *Bergey’s Manual of Systematic Bacteriology: The Proteobacteria, (Part C)*, Vol. 2, eds D. J. Brenner, N. R. Krieg, J. T. Staley, and G. M. Garrity (New York, NY: Springer).
- Garrity, G. M., Bell, J. A., and Lilburn, T. (2005b). “Family I. Rhodobacteraceae fam. nov,” in *Bergey’s Manual of Systematic Bacteriology: The Proteobacteria, (Part C)*, Vol. 2, eds D. J. Brenner, N. R. Krieg, J. T. Staley, and G. M. Garrity (New York, NY: Springer), 161.
- Garrity, G. M., Bell, J. A., and Lilburn, T. (2005c). “Family IX. Methylobacteriaceae fam. nov,” in *Bergey’s Manual of Systematic Bacteriology: The Proteobacteria, (Part C)*, Vol. 2, eds D. J. Brenner, N. R. Krieg, J. T. Staley, and G. M. Garrity (New York, NY: Springer), 567.
- Garrity, G. M., Bell, J. A., and Lilburn, T. (2005d). “Family VI. Beijerinckiaceae fam. nov,” in *Bergey’s Manual of Systematic Bacteriology: The Proteobacteria, (Part C)*, Vol. 2, eds D. J. Brenner, N. R. Krieg, J. T. Staley, and G. M. Garrity (New York, NY: Springer), 422.
- Garrity, G. M., Bell, J. A., and Lilburn, T. (2005e). “Family VII. Bradyrhizobiaceae fam. nov,” in *Bergey’s Manual of Systematic Bacteriology: The Proteobacteria, (Part C)*, Vol. 2, eds D. J. Brenner, N. R. Krieg, J. T. Staley, and G. M. Garrity (New York, NY: Springer), 438.
- Garrity, G. M., Bell, J. A., and Lilburn, T. (2005f). “Family X. Rhodobiaceae fam. nov,” in *Bergey’s Manual of Systematic Bacteriology: The Proteobacteria, (Part C)*, Vol. 2, eds D. J. Brenner, N. R. Krieg, J. T. Staley, and G. M. Garrity (New York, NY: Springer), 571.
- Garrity, G. M., Bell, J. A., and Lilburn, T. G. (2003a). *Taxonomic Outline of the Prokaryotes*, 2nd Edn. New York, NY: Springer.
- Garrity, G. M., Bell, J. A., and Lilburn, T. G. (2003b). *Taxonomic Outline of the Prokaryotes, Bergey’s Manual of Systematic Bacteriology, Release 4.0*, 2nd Edn. New York, NY: Springer.
- Garrity, G. M., Lilburn, T. G., Cole, J. R., Harrison, S. H., Euzéby, J., and Tindall, B. J. (2007). *Taxonomic Outline of the Bacteria and Archaea, Release 7.7 March 6, 2007. Part 3 – the bacteria: phylum “Proteobacteria”, class Alphaproteobacteria* (East Lansing: Michigan State University).
- Geng, S., Pan, X. C., Mei, R., Wang, Y. N., Sun, J. Q., Liu, X. Y., et al. (2014). *Paradevosia shaoguanensis* gen. nov. sp. nov. isolated from a Coking Wastewater. *Curr. Microbiol.* 70, 110–118. doi: 10.1007/s00284-014-0689-2
- Gerpe, D., Buján, N., Diéguez, A. L., Lasa, A., and Romalde, J. L. (2017). *Kiloniella majae* sp. nov., isolated from spider crab (*Maja brachydactyla*) and pullet carpet shell clam (*Venerupis pullastra*). *Syst. Appl. Microbiol.* 40, 274–279. doi: 10.1016/j.syapm.2017.05.002
- Geueke, B., Busse, H.-J., Fleischmann, T., Kämpfer, P., and Kohler, H. E. (2007). Description of *Sphingosinicella xenopeptidilytica* sp. nov., a β -peptide-degrading species, and emended descriptions of the genus *Sphingosinicella* and the species *Sphingosinicella microcystinivorans*. *Int. J. Syst. Evol. Microbiol.* 57, 107–113. doi: 10.1099/ijs.0.64509-0
- Ghosh, W., Mandal, S., and Roy, P. (2006). *Paracoccus bengalensis* sp. nov., a novel sulfur-oxidizing chemolithoautotroph from the rhizospheric soil of an Indian tropical leguminous plant. *Syst. Appl. Microbiol.* 29, 396–403. doi: 10.1016/j.syapm.2005.10.004
- Gich, F., and Overmann, J. (2006). *Sandarakinorhabdus limnophila* gen. nov., sp. nov., a novel bacteriochlorophyll α -containing, obligately aerobic bacterium isolated from freshwater lakes. *Int. J. Syst. Evol. Microbiol.* 56, 847–854. doi: 10.1099/ijs.0.63970-0
- Giesberger, G. (1947). Some observations on the culture, physiology and morphology of some brown-red *Rhodospirillum*-species. *Antonie Van Leeuwenhoek* 13, 135–148. doi: 10.1007/bf02272755
- Gillis, M., and De Ley, J. (1980). Intra- and intergeneric similarities of the ribosomal ribonucleic acid cistrons of *Acetobacter* and *Gluconobacter*. *Int. J. Syst. Bacteriol.* 30, 7–27. doi: 10.1099/00207713-30-1-7
- Gillis, P., Vandamme, P., De Vos, P., Swings, J., and Kersters, K. (2005). “Polyphasic taxonomy,” in *Bergey’s Manual of Systematic Bacteriology: The Proteobacteria (Part A)*, Vol. 2, eds D. J. Brenner, N. R. Krieg, J. T. Staley, and G. M. Garrity (New York, NY: Springer Verlag), 43–48. doi: 10.1007/0-387-28021-9_7
- Girija, K. R., Sasikala, C., Ramana, C. V., Spröer, C., Takaichi, S., Thiel, V., et al. (2010). *Rhodobacter johrii* sp. nov., an endospore-producing cryptic species isolated from semi-arid tropical soils. *Int. J. Syst. Evol. Microbiol.* 60, 2099–2107. doi: 10.1099/ijs.0.011718-0
- Glaeser, J., and Overmann, J. (1999). Selective enrichment and characterization of *Roseospirillum parvum*, gen. nov. and sp. nov., a new purple nonsulfur bacterium with unusual light absorption properties. *Arch. Microbiol.* 11, 405–416. doi: 10.1007/s002030050727
- Glaeser, S. P., Galatis, H., Martin, K., and Kämpfer, P. (2013). *Niabella hirudinis* and *Niabella drilacis* sp. nov., isolated from the medicinal leech *Hirudo verbana*. *Int. J. Syst. Evol. Microbiol.* 63, 3487–3493. doi: 10.1099/ijs.0.050823-0
- Glaeser, S. P., and Kämpfer, P. (2015). Multilocus sequence analysis (MLSA) in prokaryotic taxonomy. *Syst. Appl. Microbiol.* 38, 237–245. doi: 10.1016/j.syapm.2015.03.007
- Glaeser, S. P., Kämpfer, P., Busse, H.-J., Langer, S., and Glaeser, J. (2009). *Novosphingobium acidiphilum* sp. nov., an acidophilic salt-sensitive bacterium isolated from the humic acid-rich Lake Grosse Fuchskuhle. *Int. J. Syst. Evol. Microbiol.* 59, 323–330. doi: 10.1099/ijs.0.65852-0
- Goloboff, P. A., Farris, J. S., and Nixon, K. C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786. doi: 10.1111/j.1096-0031.2008.00217.x
- González, J. M., Covert, J. S., Whitman, W. B., Henriksen, J. R., Mayer, F., Scharf, B., et al. (2003). *Silicibacter pomeroyi* sp. nov. and *Roseovarius nubinhibens* sp. nov., dimethylsulfoniopropionate-demethylating bacteria from marine environments. *Int. J. Syst. Evol. Microbiol.* 53, 1261–1269. doi: 10.1099/ijs.0.02491-0
- Gossling, J., and Moore, W. E. C. (1975). *Gemmiger formicilis*, n.gen., n.sp., an anaerobic budding bacterium from intestines. *Int. J. Syst. Bacteriol.* 25, 202–207. doi: 10.1099/00207713-25-2-202
- Gray, P. H. H., and Thornton, H. G. (1928). Soil bacteria that decompose certain aromatic compounds. *Zentralblatt für Bakteriologie, Parasitenkunde, Infekt. und Hyg. Abteilung II* 73, 74–96.
- Green, P. N., and Ardley, J. K. (2018). Review of the genus *Methylobacterium* and closely related organisms: a proposal that some *Methylobacterium* species be reclassified into a new genus, *Methylorubrum* gen. nov. *Int. J. Syst. Evol. Microbiol.* 68, 2727–2748. doi: 10.1099/ijsem.0.002856
- Green, P. N., and Bousfield, I. J. (1983). Emendation of *Methylobacterium* Patt, Cole, and Hanson 1976; *Methylobacterium rhodinum* (Heumann 1962) comb. nov. corrig.; *Methylobacterium radiotolerans* (Ito and Iizuka 1971) comb. nov. corrig.; and *Methylobacterium mesophilicum* (Austin and Goodfellow 1979) comb. nov. *Int. J. Syst. Bacteriol.* 33, 875–877. doi: 10.1099/00207713-33-4-875

- Gu, C. T., Wang, E. T., Tian, C. F., Han, T. X., Chen, W. F., Sui, X. H., et al. (2008). *Rhizobium miluonense* sp. nov., a symbiotic bacterium isolated from *Lespedeza* root nodules. *Int. J. Syst. Evol. Microbiol.* 58, 1364–1368. doi: 10.1099/ijs.0.656661-0
- Gu, T., Sun, L. N., Zhang, J., Sui, X. H., and Li, S. P. (2014). *Rhizobium flavum* sp. nov., a triazophos-degrading bacterium isolated from soil under the long-term application of triazophos. *Int. J. Syst. Evol. Microbiol.* 64, 2017–2022. doi: 10.1099/ijs.0.061523-0
- Gu, X., and Zhang, H. (2004). Genome phylogenetic analysis based on extended gene contents. *Mol. Biol. Evol.* 21, 1401–1408. doi: 10.1093/molbev/msh138
- Gundi, V. A. K. B., Taylor, C., Raoult, D., and La Scola, B. (2009). *Bartonella rattaustaliani* sp. nov., *Bartonella queenslandensis* sp. nov. and *Bartonella coopersplainsensis* sp. nov., identified in Australian rats. *Int. J. Syst. Evol. Microbiol.* 59, 2956–2961. doi: 10.1099/ijs.0.002865-0
- Guo, L.-L., Wu, Y.-H., Xu, X.-W., Huang, C.-J., Xu, Y.-Y., Cheng, H., et al. (2017). *Actibacterium pelagium* sp. nov., a novel alphaproteobacterium, and emended description of the genus *Actibacterium*. *Int. J. Syst. Evol. Microbiol.* 67, 5080–5086. doi: 10.1099/ijsem.0.002417
- Guo, P., Wang, B.-Z., Hang, B.-J., Li, L., Li, S.-P., and He, J. (2010). *Sphingobium faniae* sp. nov., a pyrethroid-degrading bacterium isolated from activated sludge treating wastewater from pyrethroid manufacture. *Int. J. Syst. Evol. Microbiol.* 60, 408–412. doi: 10.1099/ijs.0.009795-0
- Gupta, R. S., Mahmood, S., and Adeolu, M. (2013). A phylogenomic and molecular signature based approach for characterization of the phylum *Spirochaetes* and its major clades: proposal for a taxonomic revision of the phylum. *Front. Microbiol.* 4:217. doi: 10.3389/fmicb.2013.00217
- Gupta, S. K., Lal, D., and Lal, R. (2009). *Novosphingobium panipatense* sp. nov. and *Novosphingobium mathurensis* sp. nov., from oil-contaminated soil. *Int. J. Syst. Evol. Microbiol.* 59, 156–161. doi: 10.1099/ijs.0.65743-0
- Hahnke, R. L., Meier-Kolthoff, J. P., García-López, M., Mukherjee, S., Huntemann, M., Ivanova, N. N., et al. (2016). Genome-based taxonomic classification of Bacteroidetes. *Front. Microbiol.* 7:2003. doi: 10.3389/fmicb.2016.02003
- Hahnke, S., Tindall, B. J., Schumann, P., Simon, M., and Brinkhoff, T. (2013). *Pelagimonas varians* gen. nov., sp. nov., isolated from the southern North Sea. *Int. J. Syst. Evol. Microbiol.* 63, 835–843. doi: 10.1099/ijs.0.040675-0
- Hameed, A., Shahina, M., Lai, W.-A., Lin, S.-Y., Young, L.-S., Liu, Y.-C., et al. (2015). *Oricola cellulositytica* gen. nov., sp. nov., a cellulose-degrading bacterium of the family Phyllobacteriaceae isolated from surface seashore water, and emended descriptions of *Mesorhizobium loti* and *Phyllobacterium myrsinacearum*. *Antonie Van Leeuwenhoek* 107, 759–771. doi: 10.1007/s10482-014-0370-6
- Hameed, A., Shahina, M., Lin, S.-Y., Nakayan, P., Liu, Y.-C., Lai, W.-A., et al. (2014). *Youngimonas vesicularis* gen. nov., sp. nov., of the family Rhodobacteraceae, isolated from surface seawater, reclassification of *Donghicola xiamenensis* Tan et al. 2009 as *Pseudodonghicola xiamenensis* gen. nov., comb. nov. and emended description of the g. *Int. J. Syst. Evol. Microbiol.* 64, 2729–2737. doi: 10.1099/ijs.0.060962-0
- Hampson, D. J., and La, T. (2006). Reclassification of *Serpulina intermedia* and *Serpulina murdochii* in the genus *Brachyspira* as *Brachyspira intermedia* comb. nov. and *Brachyspira murdochii* comb. nov. *Int. J. Syst. Evol. Microbiol.* 56, 1009–1012. doi: 10.1099/ijs.0.64004-0
- Han, S.-B., Su, Y., Hu, J., Wang, R.-J., Sun, C., Wu, D., et al. (2016). *Terasakiella brassicae* sp. nov., isolated from the wastewater of a pickle-processing factory, and emended descriptions of *Terasakiella pusilla* and the genus *Terasakiella*. *Int. J. Syst. Evol. Microbiol.* 66, 1807–1812. doi: 10.1099/ijsem.0.000946
- Han, T. X., Wang, E. T., Wu, L. J., Chen, W. F., Gu, J. G., Gu, C. T., et al. (2008). *Rhizobium multihospitium* sp. nov., isolated from multiple legume species native of Xinjiang. *China. Int. J. Syst. Evol. Microbiol.* 58, 1693–1699. doi: 10.1099/ijs.0.65568-0
- Hansen, T. A., and Imhoff, J. F. (1985). *Rhodobacter veldkampii*, a new species of phototrophic purple nonsulfur bacteria. *Int. J. Syst. Bacteriol.* 35, 115–116. doi: 10.1099/00207713-35-1-115
- Harwati, T. U., Kasai, Y., and Kodama, Y. (2009a). *Tropicimonas isoalkanivorans* gen. nov., sp. nov., a branched-alkane-degrading bacterium isolated from Semarang Port in Indonesia. *Int. J. Syst. Evol. Microbiol.* 59, 388–391. doi: 10.1099/ijs.0.65822-0
- Harwati, T. U., Kasai, Y., Kodama, Y., Susilaningi, D., and Watanabe, K. (2009b). *Tropicibacter naphthalenivorans* gen. nov., sp. nov., a polycyclic aromatic hydrocarbon-degrading bacterium isolated from Semarang Port in Indonesia. *Int. J. Syst. Evol. Microbiol.* 59, 392–396. doi: 10.1099/ijs.0.65821-0
- Harwati, T. U., Kasai, Y., Kodama, Y., Susilaningi, D., and Watanabe, K. (2008). *Tranquillimonas alkanivorans* gen. nov., sp. nov., an alkane-degrading bacterium isolated from Semarang Port in Indonesia. *Int. J. Syst. Evol. Microbiol.* 58, 2118–2121. doi: 10.1099/ijs.0.65817-0
- Hedges, L. M., Brownlie, J. C., O'Neill, S. L., and Johnson, K. N. (2008). *Wolbachia* and virus protection in insects. *Science* 322:702. doi: 10.1126/science.1162418
- Helsel, L. O., Hollis, D., Steigerwalt, A. G., Morey, R. E., Jordan, J., Aye, T., et al. (2007). Identification of “*Haematobacter*,” a new genus of aerobic gram-negative rods isolated from clinical specimens, and reclassification of *Rhodobacter massiliensis* as “*Haematobacter massiliensis* comb. nov.”. *J. Clin. Microbiol.* 45, 1238–1243. doi: 10.1128/JCM.01188-06
- Helsel, L. O., Hollis, D. G., Steigerwalt, A. G., and Levett, P. N. (2006). Reclassification of *Roseomonas fauriae* Rihs et al. 1998 as a later heterotypic synonym of *Azospirillum brasiliense* Tarrand et al. 1979. *Int. J. Syst. Evol. Microbiol.* 56, 2753–2755. doi: 10.1099/ijs.0.64549-0
- Hennig, W. (1965). Phylogenetic systematics. *Annu. Rev. Entomol.* 10, 97–116.
- Henrici, A. T., and Johnson, D. E. (1935). Studies of freshwater bacteria: II. stalked bacteria, a new order of schizomycetes. *J. Bacteriol.* 30, 61–93.
- Henz, S. R., Huson, D. H., Auch, A. F., Nieselt-Struwe, K., and Schuster, S. C. (2005). Whole-genome prokaryotic phylogeny. *Bioinformatics* 21, 2329–2335. doi: 10.1093/bioinformatics/bth324
- Hildebrand, F., Meyer, A., and Eyre-Walker, A. (2010). Evidence of selection upon genomic GC-content in bacteria. *PLoS Genet.* 6:e1001107. doi: 10.1371/journal.pgen.1001107
- Hiraishi, A. (1997). Transfer of the bacteriochlorophyll β -containing phototrophic bacteria *Rhodospseudomonas viridis* and *Rhodospseudomonas sulfoviridis* to the genus *Blastochloris* gen. nov. *Int. J. Syst. Bacteriol.* 47, 217–219. doi: 10.1099/00207713-47-1-217
- Hiraishi, A., Kuraishi, H., and Kawahara, K. (2000). Emendation of the description of *Blastomonas natatoria* (Sly 1985) Sly and Cahill, 1997 as an aerobic photosynthetic bacterium and reclassification of *Erythromonas ursincola* Yurkov et al. 1997 as *Blastomonas ursincola* comb. nov. *Int. J. Syst. Evol. Microbiol.* 50, 1113–1118. doi: 10.1099/00207713-50-3-1113
- Hiraishi, A., Muramatsu, K., and Ueda, Y. (1996). Molecular genetic analyses of *Rhodobacter azotoformans* sp. nov. and related species of phototrophic bacteria. *Syst. Appl. Microbiol.* 19, 168–177. doi: 10.1016/S0723-2020(96)80042-7
- Hiraishi, A., and Ueda, Y. (1994a). Intrageneric structure of the genus *Rhodobacter*: transfer of *Rhodobacter sulfidophilus* and related marine species to the genus *Rhodovulum* gen. nov. *Int. J. Syst. Bacteriol.* 44, 15–23. doi: 10.1099/00207713-44-1-15
- Hiraishi, A., and Ueda, Y. (1994b). *Rhodoplanes* gen. nov., a new genus of phototrophic bacteria including *Rhodospseudomonas rosea* as *Rhodoplanes roseus* comb. nov. and *Rhodoplanes elegans* sp. nov. *Int. J. Syst. Bacteriol.* 44, 665–673. doi: 10.1099/00207713-44-4-665
- Hiraishi, A., Urata, K., and Satoh, T. (1995). A new genus of marine budding phototrophic bacteria, *Rhodobium* gen. nov., which includes *Rhodobium orientis* sp. nov. and *Rhodobium marinum* comb. nov. *Int. J. Syst. Bacteriol.* 45, 226–234. doi: 10.1099/00207713-45-2-226
- Hirsch, P. (1989). “Genus *Hyphomicrobium* Stutzer and Hartleb 1898, 76AL,” in *Bergey’s Manual of Systematic Bacteriology*, Vol. 3, eds J. T. Staley, M. P. Bryant, N. Pfennig, and J. G. Holt (Baltimore, MD: The Williams & Wilkins Co), 1895–1904.
- Hirsch, P., and Hoffmann, B. (1989). *Dichotomicrobium thermohalophilum*, gen. nov., spec. nov., budding prosthecate bacteria from the solar lake (Sinai) and some related strains. *Syst. Appl. Microbiol.* 11, 291–301. doi: 10.1016/S0723-2020(89)80027-X
- Holmes, B., Popoff, M., Kiredjian, M., and Kersters, K. (1988). *Ochrobractrum anthropi* gen. nov., sp. nov. from human clinical specimens and previously known as group Vd. *Int. J. Syst. Bacteriol.* 38, 406–416. doi: 10.1099/00207713-38-4-406
- Hong, Z., Lai, Q., Luo, Q., Jiang, S., Zhu, R., Liang, J., et al. (2015). *Sulfitobacter pseudonitzschiae* sp. nov., isolated from the toxic marine diatom *Pseudonitzschia* multiseriis. *Int. J. Syst. Evol. Microbiol.* 65, 95–100. doi: 10.1099/ijs.0.064972-0

- Hosokawa, T., Koga, R., Kikuchi, Y., Meng, X.-Y., and Fukatsu, T. (2010). *Wolbachia* as a bacteriocyte-associated nutritional mutualist. *PNAS* 107, 769–774. doi: 10.1073/pnas.0911476107
- Hosoya, S., and Yokota, A. (2007). *Loktanella atrilutea* sp. nov., isolated from seawater in Japan. *Int. J. Syst. Evol. Microbiol.* 57, 1966–1969. doi: 10.1099/ijs.0.64978-0
- Hou, L., Zhang, Y., Sun, J., and Xie, X. (2015). *Acuticoccus yangtzensis* gen. nov., sp. nov., a novel member in the family Rhodobacteraceae, isolated from the surface water of the Yangtze estuary. *Curr. Microbiol.* 70, 176–182. doi: 10.1007/s00284-014-0698-1
- Hovind-Hougen, K. (1979). Leptosprzaceae, a new family to include *Leptospira* Noguchi 1917 and *Leptonema* gen. nov. *Int. J. Syst. Bacteriol.* 29, 245–251. doi: 10.1099/00207713-29-3-245
- Hu, Q., Zhang, L., Hang, P., Zhou, X.-Y., Jia, W.-B., Li, S.-P., et al. (2018). *Xinfangfangia soli* gen. nov., sp. nov., isolated from a diuron-polluted soil. *Int. J. Syst. Evol. Microbiol.* 68, 2622–2626. doi: 10.1099/ijsem.0.002887
- Huang, M. M., Guo, L. L., Wu, Y. H., Lai, Q. L., Shao, Z. Z., Wang, C. S., et al. (2018). *Pseudoceanicola lipolyticus* sp. nov., a marine alphaproteobacterium, reclassification of *oceanicola* flagellates as *Pseudoceanicola flagellatus* comb. nov. and emended description of the genus *Pseudoceanicola*. *Int. J. Syst. Evol. Microbiol.* 68, 409–415. doi: 10.1099/ijsem.0.002521
- Huang, Z., Guo, F., Lai, Q., and Shao, Z. (2017). *Notoacmeibacter marinus* gen. nov., sp. nov., isolated from the gut of a limpet and proposal of notoacmeibacteraceae fam. nov. in the order rhizobiales of the class alphaproteobacteria. *Int. J. Syst. Evol. Microbiol.* 67, 2527–2531. doi: 10.1099/ijsem.0.001951
- Huber, B., Scholz, H. C., Kämpfer, P., Falsen, E., Langer, S., and Busse, H.-J. (2010). *Ochrobactrum pituitosum* sp. nov., isolated from an industrial environment. *Int. J. Syst. Evol. Microbiol.* 60, 321–326. doi: 10.1099/ijs.0.011668-0
- Huddleson, I. F. (1929). The differentiation of the species of the genus *Brucella*. *Michigan State Coll. Agric. Exp. Stn. Tech. Bull.* 100, 1–16.
- Humrighouse, B. W., Emery, B. D., Kelly, A. J., Metcalfe, M. G., Mbizo, J., and McQuiston, J. R. (2016). *Haematospirillum jordaniae* gen. nov., sp. nov., isolated from human blood samples. *Antonie Van Leeuwenhoek* 109, 493–500. doi: 10.1007/s10482-016-0654-0
- Hunter, W. J., Kuykendall, L. D., and Manter, D. K. (2007). *Rhizobium selenireducens* sp. nov.: a selenite-reducing α -Proteobacteria isolated from a bioreactor. *Curr. Microbiol.* 55, 455–460. doi: 10.1007/s00284-007-9020-9
- Huo, Y.-Y., Xu, X.-W., Liu, S.-P., Cui, H.-L., Li, X., and Wu, M. (2011). *Sphingomonas rubra* sp. nov., isolated from bioreactor wastewater. *Int. J. Syst. Evol. Microbiol.* 61, 1028–1032. doi: 10.1099/ijs.0.020958-0
- Huson, D. H., and Steel, M. (2004). Phylogenetic trees based on gene content. *Bioinformatics* 20, 2044–2049. doi: 10.1093/bioinformatics/bth198
- Hwang, C. Y., Bae, G. D., Yih, W., and Cho, B. C. (2009a). *Marivita cryptomonadis* gen. nov., sp. nov. and *Marivita litorea* sp. nov., of the family Rhodobacteraceae, isolated from marine habitats. *Int. J. Syst. Evol. Microbiol.* 59, 1568–1575. doi: 10.1099/ijs.0.005462-0
- Hwang, C. Y., and Cho, B. C. (2008a). *Cohaesibacter gelatinilyticus* gen. nov., sp. nov. a marine bacterium that forms a distinct branch in the order Rhizobiales, and proposal of Cohaesibacteraceae fam. nov. *Int. J. Syst. Evol. Microbiol.* 58, 267–277. doi: 10.1099/ijs.0.65016-0
- Hwang, C. Y., and Cho, B. C. (2008b). *Cucumibacter marinus* gen. nov., sp. nov., a marine bacterium in the family Hyphomicrobiaceae. *Int. J. Syst. Evol. Microbiol.* 58, 1591–1597. doi: 10.1099/ijs.0.65587-0
- Hwang, C. Y., Cho, K. D., Yih, W., and Cho, B. C. (2009b). *Maritalea myrionectae* gen. nov., sp. nov., isolated from a culture of the marine ciliate *Myrionecta rubra*. *Int. J. Syst. Evol. Microbiol.* 59, 609–614. doi: 10.1099/ijs.0.002881-0
- Hyatt, D., Chen, G.-L., LoCascio, P. F., Land, M. L., Larimer, F. W., and Hauser, L. J. (2010). Prodigal: prokaryotic gene recognition and translation initiation site identification. *BMC Bioinformatics* 11:119. doi: 10.1186/1471-2105-11-119
- Hyun, D.-W., Kim, M.-S., Shin, N.-R., Kim, J. Y., Kim, P. S., Whon, T. W., et al. (2013a). *Shimia haliotis* sp. nov., a bacterium isolated from the gut of an abalone, *Haliotis discus hannai*. *Int. J. Syst. Evol. Microbiol.* 63, 4248–4253. doi: 10.1099/ijs.0.053140-0
- Hyun, D.-W., Shin, N.-R., Kim, M.-S., Kim, P. S., Kim, J. Y., Whon, T. W., et al. (2013b). *Pseudoruegeria haliotis* sp. nov., isolated from the gut of the abalone *Haliotis discus hannai*. *Int. J. Syst. Evol. Microbiol.* 63, 4626–4632. doi: 10.1099/ijs.0.053892-0
- Iino, T., Suzuki, R., Kosako, Y., Ohkuma, M., Komagata, K., and Uchimura, T. (2012). *Acetobacter okinawensis* sp. nov., *Acetobacter papayae* sp. nov., and *Acetobacter persicus* sp. nov.; novel acetic acid bacteria isolated from stems of sugarcane, fruits, and a flower in Japan. *J. Gen. Appl. Microbiol.* 58, 235–243. doi: 10.2323/jgam.58.235
- Im, W.-T., Kim, S.-H., Kim, M. K., Ten, L. N., and Lee, S.-T. (2006). *Pleomorphomonas koreensis* sp. nov., a nitrogen-fixing species in the order Rhizobiales. *Int. J. Syst. Evol. Microbiol.* 56, 1663–1666. doi: 10.1099/ijs.0.63499-0
- Im, W.-T., Yokota, A., Kim, M.-K., and Lee, S.-T. (2004). *Kaistia adipata* gen. nov., sp. nov., a novel α -proteobacterium. *J. Gen. Appl. Microbiol.* 50, 249–254. doi: 10.2323/jgam.50.249
- Imhoff, J. F. (2001). Transfer of *Rhodopseudomonas acidophila* to the new genus *Rhodoblastus* as *Rhodoblastus acidophilus* gen. nov., comb. nov. *Int. J. Syst. Evol. Microbiol.* 51, 1863–1866. doi: 10.1099/00207713-51-5-1863
- Imhoff, J. F., Petri, R., and Süling, J. (1998). Reclassification of species of the spiral-shaped phototrophic purple non-sulfur bacteria of the α -Proteobacteria: description of the new genera *Phaeospirillum* gen. nov., *Rhodovibrio* gen. nov., *Rhodothalassium* gen. nov. and *Roseospira* gen. nov. as well as. *Int. J. Syst. Bacteriol.* 48, 793–798. doi: 10.1099/00207713-48-3-793
- Imhoff, J. F., Trüpper, H. G., and Pfenning, N. (1984). Rearrangement of the species and genera of the phototrophic “purple nonsulfur bacteria.” *Int. J. Syst. Bacteriol.* 34, 340–343. doi: 10.1099/00207713-34-3-340
- Imran, A., Hafeez, F. Y., Frühling, A., Schumann, P., Malik, K. A., and Stackebrandt, E. (2010). *Ochrobactrum ciceri* sp. nov., isolated from nodules of *Cicer arietinum*. *Int. J. Syst. Evol. Microbiol.* 60, 1548–1553. doi: 10.1099/ijs.0.013987-0
- Irgens, R. L., Kersters, K., Segers, P., Gillis, M., and Staley, J. T. (1991). *Aquabacter spiritalensis*, gen. nov., sp. nov. an aerobic, gas-vacuolate aquatic bacterium. *Arch. Microbiol.* 155, 137–142. doi: 10.1007/bf00248607
- Ivanova, E. P., Gorshkova, N. M., Sawabe, T., Zhukova, N. V., Hayashi, K., Kurilenko, V. V., et al. (2004). *Sulfitobacter delicatus* sp. nov. and *Sulfitobacter dubius* sp. nov., respectively from a starfish (*Stellaster equestris*) and sea grass (*Zostera marina*). *Int. J. Syst. Evol. Microbiol.* 54, 475–480. doi: 10.1099/ijs.0.02654-0
- Ivanova, E. P., Webb, H., Christen, R., Zhukova, N. V., Kurilenko, V. V., Kalinovskaya, N. I., et al. (2010). *Celeribacter neptunius* gen. nov., sp. nov., a new member of the class Alphaproteobacteria. *Int. J. Syst. Evol. Microbiol.* 60, 1620–1625. doi: 10.1099/ijs.0.014159-0
- Ivanova, E. P., Zhukova, N. V., Lysenko, A. M., Gorshkova, N. M., Sergeev, A. F., Mikhailov, V. V., et al. (2005). *Loktanella agnita* sp. nov. and *Loktanella rosea* sp. nov., from the north-west Pacific Ocean. *Int. J. Syst. Evol. Microbiol.* 55, 2203–2207. doi: 10.1099/ijs.0.63461-0
- Iwaki, H., Nishimura, A., and Hasegawa, Y. (2012). *Tropicibacter phthalicus* sp. nov., a phthalate-degrading bacterium from seawater. *Curr. Microbiol.* 64, 392–396. doi: 10.1007/s00284-012-0085-8
- Iwaki, H., Yasukawa, N., Fujioka, M., Takada, K., and Hasegawa, Y. (2013). Isolation and characterization of a marine cyclohexylacetate-degrading bacterium *Lutimaribacter litoralis* sp. nov., and reclassification of *Oceanicola pacificus* as *Lutimaribacter pacificus* comb. nov. *Curr. Microbiol.* 66, 588–593. doi: 10.1007/s00284-013-0321-x
- Jang, G. I., Hwang, C. Y., and Cho, B. C. (2011). *Nitratireductor aquimarinus* sp. nov., isolated from a culture of the diatom *Skeletonema costatum*, and emended description of the genus *Nitratireductor*. *Int. J. Syst. Evol. Microbiol.* 61, 2676–2681. doi: 10.1099/ijs.0.028373-0
- Jarvis, B. D. W., Van Berkum, P., Chen, W. X., Nour, S. M., Fernandez, M. P., Cleyet-Marel, J. C., et al. (1997). Transfer of *Rhizobium loti*, *Rhizobium huakuii*, *Rhizobium ciceri*, *Rhizobium mediterraneum*, and *Rhizobium tianshanense* to *Mesorhizobium* gen. nov. *Int. J. Syst. Bacteriol.* 47, 895–898. doi: 10.1099/00207713-47-3-895
- Jean, W. D., Huang, S. P., Chen, J. S., and Shieh, W. Y. (2016). *Tagaea marina* gen. nov., sp. nov., a marine bacterium isolated from shallow coastal water. *Int. J. Syst. Evol. Microbiol.* 66, 592–597. doi: 10.1099/ijsem.0.000756
- Jeffroy, O., Brinkmann, H., Delsuc, F., and Philippe, H. (2006). Phylogenomics: the beginning of incongruence? *Trends Genet.* 22, 225–231. doi: 10.1016/j.tig.2006.02.003
- Jeong, H. I., Jin, H. M., and Jeon, C. O. (2015). *Confluentimicrobium naphthalenivorans* sp. nov., a naphthalene-degrading bacterium isolated

- from sea-tidal-flat sediment, and emended description of the genus *Confluentimicrobium* Park et al. 2015. *Int. J. Syst. Evol. Microbiol.* 65, 4191–4195. doi: 10.1099/ijsem.0.000561
- Jia, X., Kim, H. R., Jia, B., Jeon, H. H., Baek, K., Choi, S. H., et al. (2017). *Roseovarius confluentis* sp. nov., isolated from estuary sediment. *Int. J. Syst. Evol. Microbiol.* 67, 346–351. doi: 10.1099/ijsem.0.001630
- Jiang, C.-Y., Dai, X., Wang, B.-J., Zhou, Y.-G., and Liu, S.-J. (2006). *Roseomonas lacus* sp. nov., isolated from freshwater lake sediment. *Int. J. Syst. Evol. Microbiol.* 56, 25–28. doi: 10.1099/ijms.0.63938-0
- Jiang, L., Xu, H., Shao, Z., and Long, M. (2014). *Defluviimonas indica* sp. nov., a marine bacterium isolated from a deep-sea hydrothermal vent environment. *Int. J. Syst. Evol. Microbiol.* 64, 2084–2088. doi: 10.1099/ijms.0.061614-0
- Jiao, Y. S., Yan, H., Ji, Z. J., Liu, Y. H., Sui, X. H., Zhang, X. X., et al. (2015). *Phyllobacterium sophora* sp. nov., a symbiotic bacterium isolated from root nodules of *Sophora flavescens*. *Int. J. Syst. Evol. Microbiol.* 65, 399–406. doi: 10.1099/ijms.0.067017-0
- Jin, H. M., Lee, H. J., Kim, J. M., Park, M. S., Lee, K., and Jeon, C. O. (2011). *Litorimicrobium taeanense* gen. nov., sp. nov., isolated from a sandy beach. *Int. J. Syst. Evol. Microbiol.* 61, 1392–1396. doi: 10.1099/ijms.0.025007-0
- Jindal, S., Dua, A., and Lal, R. (2013). *Sphingopyxis indica* sp. nov., isolated from a high dose point hexachlorocyclohexane (HCH)-contaminated dumpsite. *Int. J. Syst. Evol. Microbiol.* 63, 2186–2191. doi: 10.1099/ijms.0.040840-0
- Jogler, M., Chen, H., Simon, J., Rohde, M., Busse, H.-J., Klenk, H.-P., et al. (2013). Description of *Sphingorhabdus planktonica* gen. nov., sp. nov. and reclassification of three related members of the genus *Sphingopyxis* in the genus *Sphingorhabdus* gen. nov. *Int. J. Syst. Evol. Microbiol.* 63, 1342–1349. doi: 10.1099/ijms.0.043133-0
- Johnson, R. C., Burgdorfer, W., Lane, R. S., Barbour, A. G., Hayes Stanley, F., and Hyde, F. W. (1987). *Borrelia coriaceae* sp. nov.: putative agent of epizootic bovine abortion. *Int. J. Syst. Bacteriol.* 37, 72–74. doi: 10.1099/00207713-37-1-72
- Jojima, Y., Mihara, Y., Suzuki, S., Yokozeki, K., Yamanaka, S., and Fudou, R. (2004). *Saccharibacter floricola* gen. nov. sp. nov., a novel osmophilic acetic acid bacterium isolated from pollen. *Int. J. Syst. Evol. Microbiol.* 54, 2263–2267. doi: 10.1099/ijms.0.02911-0
- Jordan, D. C. (1982). Transfer of *Rhizobium japonicum* Buchanan 1980 to *Bradyrhizobium* gen. nov., a genus of slow-growing, root nodule bacteria from leguminous plants. *Int. J. Syst. Bacteriol.* 32, 136–139. doi: 10.1099/00207713-32-1-136
- Jordan, E. M., Thompson, F. L., Zhang, X. H., Li, Y., Vancanneyt, M., Kroppenstedt, R. M., et al. (2007). *Sneathiella chinensis* gen. nov., sp. nov., a novel marine alphaproteobacterium isolated from coastal sediment in Qingdao, China. *Int. J. Syst. Evol. Microbiol.* 57, 114–121. doi: 10.1099/ijms.0.64478-0
- Jourand, P., Giraud, E., Béna, G., Sy, A., Willems, A., Gillis, M., et al. (2004). *Methylobacterium nodulans* sp. nov., for a group of aerobic, facultatively methylotrophic, legume root-nodule-forming and nitrogen-fixing bacteria. *Int. J. Syst. Evol. Microbiol.* 54, 2269–2273. doi: 10.1099/ijms.0.02902-0
- Jung, J. Y., Kim, J. M., Jin, H. M., Kim, S. Y., Park, W., and Jeon, C. O. (2011). *Litorimonas taeanensis* gen. nov., sp. nov., isolated from a sandy beach. *Int. J. Syst. Evol. Microbiol.* 61, 1534–1538. doi: 10.1099/ijms.0.022129-0
- Jung, M.-Y., Shin, K.-S., Kim, S., Kim, S.-J., Park, S.-J., Kim, J.-G., et al. (2013). *Hoeflea halophila* sp. nov., a novel bacterium isolated from marine sediment of the East Sea, Korea. *Antonie Van Leeuwenhoek* 103, 971–978. doi: 10.1007/s10482-013-9876-6
- Jung, Y.-T., Kim, B.-H., Oh, T.-K., and Yoon, J.-H. (2010). *Pseudoruegeria lutimaris* sp. nov., isolated from a tidal flat sediment, and emended description of the genus *Pseudoruegeria*. *Int. J. Syst. Evol. Microbiol.* 60, 1177–1181. doi: 10.1099/ijms.0.015073-0
- Jung, Y.-T., Lee, J.-S., and Yoon, J.-H. (2014a). *Roseivivax jejudonensis* sp. nov., isolated from the junction between the ocean and a freshwater spring at Jeju island. *South Korea Antonie Van Leeuwenhoek* 106, 959–967. doi: 10.1007/s10482-014-0265-6
- Jung, Y. T., Lee, J. S., and Yoon, J. H. (2016). *Maliponia aquimaris* gen. nov., sp. nov., isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 66, 2271–2277. doi: 10.1099/ijsem.0.001021
- Jung, Y.-T., Oh, K.-H., Oh, T.-K., and Yoon, J.-H. (2012a). *Pseudorhodobacter aquimaris* sp. nov., isolated from seawater, and emended description of the genus *Pseudorhodobacter* Uchino et al., 2002. *Int. J. Syst. Evol. Microbiol.* 62, 100–105. doi: 10.1099/ijms.0.029769-0
- Jung, Y. T., Park, S., Lee, J. S., and Yoon, J. H. (2014b). *Defluviimonas aquaemixtae* sp. nov., isolated from the junction between a freshwater spring and the ocean. *Int. J. Syst. Evol. Microbiol.* 64, 4191–4197. doi: 10.1099/ijms.0.068767-0
- Jung, Y.-T., Park, S., Oh, T.-K., and Yoon, J.-H. (2012b). *Erythrobacter marinus* sp. nov., isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 62, 2050–2055. doi: 10.1099/ijms.0.034702-0
- Jung, Y.-T., and Yoon, J.-H. (2014). *Jannaschia faecimaris* sp. nov., isolated from a tidal flat sediment. *Int. J. Syst. Evol. Microbiol.* 64, 945–951. doi: 10.1099/ijms.0.057984-0
- Jung, Y. T., Yoon, J. H., Park, S., Lee, J.-S., and Oh, T.-K. (2012c). *Pseudahrensia aquimaris* gen. nov., sp. nov., isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 62, 2056–2061.
- Kaiya, S., Rubaba, O., Yoshida, N., Yamada, T., and Hiraishi, A. (2012). Characterization of *Rhizobium naphthalenivorans* sp. nov. with special emphasis on aromatic compound degradation and multilocus sequence analysis of housekeeping genes. *J. Gen. Appl. Microbiol.* 58, 211–224. doi: 10.2323/jgam.58.211
- Kämpfer, P., Arun, A. B., Busse, H.-J., Zhang, Z.-L., Young, C.-C., and Glaeser, S. P. (2015a). *Chelativorans intermedius* sp. nov. and proposal to reclassify *Thermovum composti* as *Chelativorans composti* comb. nov. *Int. J. Syst. Evol. Microbiol.* 65, 1646–1652. doi: 10.1099/ijms.0.000155
- Kämpfer, P., Arun, A. B., Rekha, P. D., Busse, H.-J., Young, C.-C., and Glaeser, S. P. (2013a). *Ruegeria intermedia* sp. nov., a moderately thermophilic bacterium isolated from a coastal hot spring. *Int. J. Syst. Evol. Microbiol.* 63, 2538–2544. doi: 10.1099/ijms.0.047910-0
- Kämpfer, P., Aurass, P., Karste, S., Flieger, A., and Glaeser, S. P. (2016). *Paracoccus contaminans* sp. nov., isolated from a contaminated water microcosm. *Int. J. Syst. Evol. Microbiol.* 66, 5101–5105. doi: 10.1099/ijsem.0.001478
- Kämpfer, P., Buczolits, S., Albrecht, A., Busse, H.-J., and Stackebrandt, E. (2003). Towards a standardized format for the description of a novel species (of an established genus): *Ochrobactrum gallinifaecis* sp. nov. *Int. J. Syst. Evol. Microbiol.* 53, 893–896. doi: 10.1099/ijms.0.02710-0
- Kämpfer, P., Busse, H.-J., Rossello-Mora, R., Kjellin, E., and Falsen, E. (2004). *Rhodovarius lipocyclicus* gen. nov. sp. nov., a new genus of the α -1 subclass of the *Proteobacteria*. *Syst. Appl. Microbiol.* 27, 511–516. doi: 10.1078/073202041748235
- Kämpfer, P., Glaeser, S., Busse, H. J., Eisenberg, T., and Scholz, H. (2013b). *Falsochrobactrum ovis* gen. nov., sp. nov., isolated from a sheep. *Int. J. Syst. Evol. Microbiol.* 63, 3841–3847. doi: 10.1099/ijms.0.049627-0
- Kämpfer, P., and Glaeser, S. P. (2012). Prokaryotic taxonomy in the sequencing era – the polyphasic approach revisited. *Environ. Microbiol.* 14, 291–317. doi: 10.1111/j.1462-2920.2011.02615.x
- Kämpfer, P., Huber, B., Busse, H.-J., Scholz, H. C., Tomaso, H., Hotzel, H., et al. (2011). *Ochrobactrum pecoris* sp. nov., isolated from farm animals. *Int. J. Syst. Evol. Microbiol.* 61, 2278–2283. doi: 10.1099/ijms.0.027631-0
- Kämpfer, P., Huber, B., Lidders, N., Warfolomeow, I., Busse, H. J., and Scholz, H. C. (2009a). *Pseudochrobactrum lubricantis* sp. nov., isolated from a metal-working fluid. *Int. J. Syst. Evol. Microbiol.* 59, 2464–2467. doi: 10.1099/ijms.0.008540-0
- Kämpfer, P., Jerzak, L., Wilharm, G., Golke, J., Busse, H.-J., and Glaeser, S. P. (2015b). *Gemmobacter intermedius* sp. nov., isolated from a white stork (*Ciconia ciconia*). *Int. J. Syst. Evol. Microbiol.* 65, 778–783. doi: 10.1099/ijms.0.000012
- Kämpfer, P., Martin, E., Lidders, N., and Jäckel, U. (2009b). Transfer of *Defluviobacter lusatiensis* to the genus *Aquamicrobium* as *Aquamicrobium lusatiense* comb. nov. and description of *Aquamicrobium aerolatum* sp. nov. *Int. J. Syst. Evol. Microbiol.* 59, 2468–2470. doi: 10.1099/ijms.0.008730-0
- Kämpfer, P., Martin, E., Lidders, N., Jäckel, U., Huber, B. E., Schumann, P., et al. (2010a). *Paenochrobactrum gallinarii* gen. nov., sp. nov., isolated from air of a duck barn, and reclassification of *Pseudochrobactrum glaciei* as *Paenochrobactrum glaciei* comb. nov. *Int. J. Syst. Evol. Microbiol.* 60, 1493–1498. doi: 10.1099/ijms.0.015842-0
- Kämpfer, P., Müller, C., Mau, M., Neef, A., Auling, G., Busse, H.-J., et al. (1999). Description of *Pseudaminobacter* gen. nov. with two new species,

- Pseudarninobacter salicylatoxidans* sp. nov. and *Pseudaminobacter defluvii* sp. nov. *Int. J. Syst. Bacteriol.* 49, 887–897. doi: 10.1099/00207713-49-2-887
- Kämpfer, P., Neef, A., Salkinoja-Salonen, M. S., and Busse, H.-J. (2002a). *Chelatobacter heintzii* (Auling et al., 1993) is a later subjective synonym of *Aminobacter aminovorans* (Urakami et al., 1992). *Int. J. Syst. Evol. Microbiol.* 52, 835–839. doi: 10.1099/ijs.0.01897-0
- Kämpfer, P., Poppel, M. T., Wilharm, G., Glaeser, S. P., and Busse, H. J. (2014). *Paenochrobactrum pullorum* sp. nov. isolated from a chicken. *Int. J. Syst. Evol. Microbiol.* 64, 1724–1728. doi: 10.1099/ijs.0.061101-0
- Kämpfer, P., Scholz, H. C., Huber, B., Falsen, E., and Busse, H.-J. (2007a). *Ochrobactrum haematophilum* sp. nov. and *Ochrobactrum pseudogrignonense* sp. nov., isolated from human clinical specimens. *Int. J. Syst. Evol. Microbiol.* 57, 2513–2518. doi: 10.1099/ijs.0.65066-0
- Kämpfer, P., Scholz, H., Huber, B., Thummes, K., Busse, H. J., Maas, E. W., et al. (2007b). Description of *Pseudochrobactrum kiredjianiae* sp. nov. *Int. J. Syst. Evol. Microbiol.* 57, 755–760. doi: 10.1099/ijs.0.64714-0
- Kämpfer, P., Scholz, H. C., Langer, S., Wernery, U., Wernery, R., Johnson, B., et al. (2010b). *Camelimonas lactis* gen. nov., sp. nov., isolated from the milk of camels. *Int. J. Syst. Evol. Microbiol.* 60, 2382–2386. doi: 10.1099/ijs.0.017806-0
- Kämpfer, P., Sessitsch, A., Schloter, M., Huber, B., Busse, H.-J., and Scholz, H. C. (2008). *Ochrobactrum rhizosphaerae* sp. nov. and *Ochrobactrum thiophenivorans* sp. nov., isolated from the environment. *Int. J. Syst. Evol. Microbiol.* 58, 1426–1431. doi: 10.1099/ijs.0.65407-0
- Kämpfer, P., Witzberger, R., Denner, E. B. M., Busse, H.-J., and Neef, A. (2002b). *Sphingopyxis wiflariensis* sp. nov., isolated from activated sludge. *Int. J. Syst. Evol. Microbiol.* 52, 2029–2034. doi: 10.1099/ijs.0.02217-0
- Kämpfer, P., Young, C. C., Arun, A. B., Shen, F. T., Jäckel, U., Rosselló-Mora, R., et al. (2006). *Pseudolabrys taiwanensis* gen. nov., sp. nov., an alphaproteobacterium isolated from soil. *Int. J. Syst. Evol. Microbiol.* 56, 2469–2472. doi: 10.1099/ijs.0.64124-0
- Kang, H. S., and Lee, S. D. (2009). *Ponticaulis koreensis* gen. nov., sp. nov., a new member of the family Hyphomonadaceae isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 59, 2951–2955. doi: 10.1099/ijs.0.011114-0
- Kang, J. Y., Kim, M.-J., Chun, J., Son, K. P., and Jahng, Y. (2017). *Gemmobacter straminiformis* sp. nov., isolated from an artificial fountain. *Class Quantum Gravity* 67, 5019–5025. doi: 10.1099/ijsem.0.002403
- Kang, Y.-S., Kim, J., Shin, H.-D., Nam, Y.-D., Bae, J.-W., Jeon, C. O., et al. (2007). *Methylobacterium platani* sp. nov., isolated from a leaf of the tree *Platanus orientalis*. *Int. J. Syst. Evol. Microbiol.* 57, 2849–2853. doi: 10.1099/ijs.0.65262-0
- Kanso, S., and Patel, B. K. C. (2003). *Microvirga subterranea* gen. nov., sp. nov., a moderate thermophile from a deep subsurface Australian thermal aquifer. *Int. J. Syst. Evol. Microbiol.* 53, 401–406. doi: 10.1099/ijs.0.02348-0
- Kathiravan, R., Jegan, S., Ganga, V., Prabavathy, V. R., Tushar, L., Sasikala, C., et al. (2013). *Ciceribacter lividus* gen. nov., sp. nov., isolated from rhizosphere soil of chick pea (*Cicer arietinum* L.). *Int. J. Syst. Evol. Microbiol.* 63, 4484–4488. doi: 10.1099/ijs.0.049726-0
- Kato, Y., Asahara, M., Goto, K., Kasai, H., and Yokota, A. (2008). *Methylobacterium persicinum* sp. nov., *Methylobacterium komagatae* sp. nov., *Methylobacterium brachiatum* sp. nov., *Methylobacterium tardum* sp. nov. and *Methylobacterium gregans* sp. nov., isolated from freshwater. *Int. J. Syst. Evol. Microbiol.* 58, 1134–1141. doi: 10.1099/ijs.0.65583-0
- Katoh, K., Kuma, K., Miyata, T., and Toh, H. (2005). Improvement in the accuracy of multiple sequence alignment program MAFFT. *Genome Inf.* 16, 22–33.
- Katsura, K., Yamada, Y., Uchimura, T., and Komagata, K. (2002). *Gluconobacter asaii* Mason and Claus, 1989 is a junior subjective synonym of *Gluconobacter cerinus* Yamada and Akita 1984. *Int. J. Syst. Evol. Microbiol.* 52, 1635–1640. doi: 10.1099/ijs.0.02093-0
- Kaur, J., Kaur, J., Niharika, N., and Lal, R. (2012). *Sphingomonas laterariae* sp. nov., isolated from a hexachlorocyclohexane-contaminated dump site. *Int. J. Syst. Evol. Microbiol.* 62, 2891–2896. doi: 10.1099/ijs.0.034686-0
- Kaur, J., Moskalikova, H., Niharika, N., Sedlackova, M., Hampl, A., Damborsky, J., et al. (2013). *Sphingobium baderi* sp. nov., isolated from a hexachlorocyclohexane dump site. *Int. J. Syst. Evol. Microbiol.* 63, 673–678. doi: 10.1099/ijs.0.039834-0
- Kawasaki, H., Hoshino, Y., Hirata, A., and Yamasato, K. (1993). Is intracytoplasmic membrane structure a generic criterion? It does not coincide with phylogenetic interrelationships among phototrophic purple nonsulfur bacteria. *Arch. Microbiol.* 160, 358–362.
- Kelly, D. P., McDonald, I. R., and Wood, A. P. (2000). Proposal for the reclassification of *Thiobacillus novellus* as *Starkeya novella* gen. nov., comb. nov., in the α -subclass of the *Proteobacteria*. *Int. J. Syst. Evol. Microbiol.* 50, 1797–1802. doi: 10.1099/00207713-50-5-1797
- Khammas, K. M., Ageron, E., Grimont, P. A. D., and Kaiser, P. (1989). *Azospirillum irakense* sp. nov., a nitrogen-fixing bacterium associated with rice roots and rhizosphere soil. *Res. Microbiol.* 140, 679–693. doi: 10.1016/0923-2508(89)90199-x
- Khan, I. U., Hussain, F., Habib, N., Wadaan, M. A. M., Ahmed, I., Im, W. T., et al. (2017). *Phenylobacterium deserti* sp. nov., isolated from desert soil. *Int. J. Syst. Evol. Microbiol.* 67, 4722–4727. doi: 10.1099/ijsem.0.002366
- Kim, B.-Y., Yoo, S.-H., Weon, H.-Y., Jeon, Y.-A., Hong, S.-B., Go, S.-J., et al. (2008). *Jannaschia pohangensis* sp. nov., isolated from seashore sand in Korea. *Int. J. Syst. Evol. Microbiol.* 58, 496–499. doi: 10.1099/ijs.0.65167-0
- Kim, D., Kang, K., and Ahn, T. Y. (2017). *Chthonobacter albigriseus* gen. nov., sp. nov., isolated from grass-field soil. *Int. J. Syst. Evol. Microbiol.* 67, 883–888. doi: 10.1099/ijsem.0.001695
- Kim, H. S., Srinivasan, S., and Lee, S. S. (2016). *Methyloterrigena soli* gen. nov., sp. nov., a methanol-utilizing bacterium isolated from chloroethylene-contaminated soil. *Int. J. Syst. Evol. Microbiol.* 66, 101–106. doi: 10.1099/ijsem.0.000680
- Kim, J. H., Konkitt, M., Yoon, J. H., and Kim, W. (2015). *Limibacillus halophilus* gen. nov., sp. nov., a moderately halophilic bacterium in the family Rhodospirillaceae isolated from reclaimed land. *Int. J. Syst. Evol. Microbiol.* 65, 3155–3161. doi: 10.1099/ijs.0.000346
- Kim, J. M., Jung, J. Y., Chae, H. B., Park, W., and Jeon, C. O. (2010). *Hwanghaeicola aestuarii* gen. nov., sp. nov., a moderately halophilic bacterium isolated from a tidal flat of the Yellow Sea. *Int. J. Syst. Evol. Microbiol.* 60, 2877–2881. doi: 10.1099/ijs.0.021048-0
- Kim, K. H., Cho, G. Y., Chun, B. H., Weckx, S., Moon, J. Y., Yeo, S. H., et al. (2018). *Acetobacter oryzifermentans* sp. nov., isolated from Korean traditional vinegar and reclassification of the type strains of *Acetobacter pasteurianus* subsp. ascendens (Henneberg 1898) and *Acetobacter pasteurianus* subsp. paradoxus (Frateur 1950) as *Acetobact. Syst. Appl. Microbiol.* 41, 324–332. doi: 10.1016/j.syapm.2018.03.003
- Kim, K. K., Lee, J.-S., Lee, K. C., Oh, H.-M., and Kim, S.-G. (2010). *Pontibacter methylaminivorans* gen. nov., sp. nov., a member of the family Rhodobacteraceae. *Int. J. Syst. Evol. Microbiol.* 60, 2170–2175. doi: 10.1099/ijs.0.020172-0
- Kim, K. K., Lee, K. C., Eom, M. K., Kim, J.-S., Kim, D.-S., Ko, S.-H., et al. (2014). *Variibacter gotjawalensis* gen. nov., sp. nov., isolated from soil of a lava forest. *Antonie Van Leeuwenhoek* 105, 915–924. doi: 10.1007/s10482-014-0146-z
- Kim, M., and Chun, J. (2014). 16S rRNA gene based identification of bacteria and Archaea using the EzTaxon server. *Meth. Microbiol.* 41, 61–74. doi: 10.1016/bs.mim.2014.08.001
- Kim, M. C., Kang, O. C., Zhang, Y., Ren, L., Chang, X., Jiang, F., et al. (2016). *Sphingourantiacus polygranulatus* gen. nov., sp. nov., isolated from high-Arctic tundra soil, and emended descriptions of the genera *Sandarakinorhabdus*, *Polymorphobacter* and *Rhizorhabdus* and the species *Sandarakinorhabdus limnophila*, *Rhizorhabdus argentea* and *Sphingomonas wittichii*. *Int. J. Syst. Evol. Microbiol.* 66, 91–100. doi: 10.1099/ijsem.0.000677
- Kim, M. K., Im, W.-T., Ohta, H., Lee, M., and Lee, S.-T. (2005). *Sphingopyxis granuli* sp. nov., a β -glucosidase-producing bacterium in the family Sphingomonadaceae in α -4 subclass of the *Proteobacteria*. *J. Microbiol.* 43, 152–157.
- Kim, S. J., Ahn, J. H., Lee, T. H., Weon, H. Y., Hong, S. B., Seok, S. J., et al. (2013). *Reyranella soli* sp. nov., isolated from forest soil, and emended description of the genus *Reyranella* Pagnier et al., 2011. *Int. J. Syst. Evol. Microbiol.* 63, 3164–3167. doi: 10.1099/ijs.0.045922-0
- Kim, Y.-G., Hwang, C. Y., and Cho, B. C. (2008). *Pelagicola litoralis* gen. nov., sp. nov., isolated from coastal water in Korea. *Int. J. Syst. Evol. Microbiol.* 58, 2102–2106. doi: 10.1099/ijs.0.65820-0
- Kim, Y. O., Park, I. S., Park, S., Nam, B. H., Park, J. M., Kim, D. G., et al. (2016a). *Octadecabacter ascidiaceicola* sp. nov., isolated from a sea squirt (*Halocynthia roretzi*). *Int. J. Syst. Evol. Microbiol.* 66, 296–301. doi: 10.1099/ijsem.0.000715
- Kim, Y.-O., Park, S., Nam, B.-H., Kang, S.-J., Hur, Y.-B., Kim, D.-G., et al. (2012a). Description of *Litoreibacter meonggei* sp. nov., isolated from the sea squirt

- Halocynthia roretzi*, reclassification of *Thalassobacter arenae* as *Litoreibacter arenae* comb. nov. and emended description of the genus *Litoreibacter* Romanenko et al. 2011. *Int. J. Syst. Evol. Microbiol.* 62, 1825–1831. doi: 10.1099/ijs.0.035113-0
- Kim, Y.-O., Park, S., Nam, B.-H., Kang, S.-J., Hur, Y. B., Lee, S.-J., et al. (2012b). *Ruegeria halocynthiae* sp. nov., isolated from the sea squirt *Halocynthia roretzi*. *Int. J. Syst. Evol. Microbiol.* 62, 925–930. doi: 10.1099/ijs.0.031609-0
- Kim, Y. O., Park, S., Nam, B. H., Park, J. M., Kim, D. G., and Yoon, J. H. (2016b). *Asciodiaceihabitans donghaensis* gen. nov., sp. nov., isolated from the golden sea squirt *Halocynthia aurantium*. *Int. J. Syst. Evol. Microbiol.* 64, 3970–3975. doi: 10.1099/ijs.0.000849
- Kimes, N. E., López-Pérez, M., Flores-Félix, J. D., Ramírez-Bahena, M.-H., Igual, J. M., Peix, A., et al. (2015). *Pseudorhizobium pelagicum* gen. nov., sp. nov. isolated from a pelagic Mediterranean zone. *Syst. Appl. Microbiol.* 38, 293–299. doi: 10.1016/j.syapm.2015.05.003
- Kishimoto, N., Kosako, Y., Wakao, N., Tano, T., and Hiraishi, A. (1995). Transfer of *Acidiphilium facilis* and *Acidiphilium aminolytica* to the genus *Acidocella* gen. nov., and emendation of the genus *Acidiphilium*. *Syst. Appl. Microbiol.* 18, 85–91. doi: 10.1016/S0723-2020(11)80453-4
- Klenk, H.-P., and Göker, M. (2010). En route to a genome-based classification of Archaea and Bacteria? *Syst. Appl. Microbiol.* 33, 175–182. doi: 10.1016/j.syapm.2010.03.003
- Klotz, F., Brinkhoff, T., Freese, H. M., Wietz, M., Teske, A., Simon, M., et al. (2018). *Tritonibacter horizontalis* gen. nov., sp. nov., a member of the rhodobacteraceae, isolated from the Deepwater Horizon oil spill. *Int. J. Syst. Evol. Microbiol.* 68, 736–744. doi: 10.1099/ijs.0.002573
- Kluyver, B., and van Niel, C. B. (1936). Prospects for a natural system of classification of bacteria. *Zentralblatt für Bakteriologie, Parasitenkunde, Infekt. und Hyg.* 94, 369–403.
- Knösel, D. H. (1984). “Genus IV, *Phyllobacterium*,” in *Bergey’s Manual of Systematic Bacteriology*, Vol. 1, eds N. R. Krieg and J. G. Holt (Baltimore, MD: The Williams and Wilkins Co.), 254–256.
- Koelschbach, J. S., Mouttaki, H., Pickl, C., Heipieper, H. J., Rache, R., Lawson, P. A., et al. (2017). *Rectinema cohabitans* gen. nov., sp. nov., a rod-shaped spirochaete isolated from an anaerobic naphthalene-degrading enrichment culture. *Int. J. Syst. Evol. Microbiol.* 67, 1288–1295. doi: 10.1099/ijs.0.001799
- Kommanee, J., Tanasupawat, S., Yukphan, P., Malimas, T., Muramatsu, Y., Nakagawa, Y., et al. (2011). *Gluconobacter nephelii* sp. nov., an acetic acid bacterium in the class Alphaproteobacteria. *Int. J. Syst. Evol. Microbiol.* 61, 2117–2122. doi: 10.1099/ijs.0.026385-0
- Kordick, D. L., Swaminathan, B., Greene, C. E., Wilson, K. H., Whitney, A. M., Connor, S. O., et al. (1996). *Bartonella vinsonii* subsp. berkhoffii subsp. nov., isolated from dogs; *Bartonella vinsonii* subsp. vinsonii; and emended description of *Bartonella vinsonii*. *Int. J. Syst. Bacteriol.* 46, 704–709. doi: 10.1099/00207713-46-3-704
- Kosako, Y., and Yabuuchi, E. (2005). “Order IV, Sphingomonadales ord. nov.” in *Bergey’s Manual of Systematic Bacteriology Part C*, Vol. 2, eds D. J. Brenner, N. R. Krieg, and J. T. Staley (Boston, MA: Springer), 230–233. doi: 10.1007/0-387-29298-5
- Kosako, Y., Yabuuchi, E., Naka, T., Fujiwara, N., and Kobayashi, K. (2000). Proposal of Sphingomonadaceae fam. nov., consisting of *Sphingomonas* Yabuuchi et al., 1990, *Erythrobacter* Shiba and Shimidu 1982, *Erythromicrobium* Yurkov et al., 1994, *Porphyrobacter* Fuerst et al., 1993, *Zymomonas* Kluyver and van Niel, 1936, and *Sandaracinobacter* Yurkov et al. 1997, with the type genus *Sphingomonas* Yabuuchi et al., 1990. *Microbiol. Immunol.* 44, 563–575. doi: 10.1111/j.1348-0421.2000.tb02535.x
- Kulichevskaya, I. S., Danilova, O. V., Tereshina, V. M., Kevbrin, V. V., and Dedysh, S. N. (2014). Descriptions of *Roseiarcus fermentans* gen. nov., sp. nov., a bacteriochlorophyll α -containing fermentative bacterium related phylogenetically to alphaproteobacterial methanotrophs, and of the family Roseiarcaceae fam. nov. *Int. J. Syst. Evol. Microbiol.* 64, 2558–2565. doi: 10.1099/ijs.0.064576-0
- Kulichevskaya, I. S., Guzev, V. S., Gorlenko, V. M., Liesack, W., and Dedysh, S. N. (2006). *Rhodoblastus sphagnicola* sp. nov., a novel acidophilic purple non-sulfur bacterium form *Sphagnum peat bog*. *Int. J. Syst. Evol. Microbiol.* 56, 1397–1402. doi: 10.1099/ijs.0.63962-0
- Kumar, B. V., Ramprasad, E. V. V., Sasikala, C., and Ramana, C. V. (2013). *Rhodopseudomonas pentothentaxigens* sp. nov. and *Rhodopseudomonas thermotolerans* sp. nov., isolated from paddy soils. *Int. J. Syst. Evol. Microbiol.* 63, 200–207. doi: 10.1099/ijs.0.038620-0
- Kumar, M., Verma, M., and Lal, R. (2008). *Devosia chinhatensis* sp. nov., isolated from a hexachlorocyclohexane (HCH) dump site in India. *Int. J. Syst. Evol. Microbiol.* 58, 861–865. doi: 10.1099/ijs.0.65574-0
- Kumari, H., Gupta, S. K., Jindal, S., Katoch, P., and Lal, R. (2009). *Sphingobium lactosutens* sp. nov., isolated from a hexachlorocyclohexane dump site and *Sphingobium abikonense* sp. nov., isolated from oil-contaminated soil. *Int. J. Syst. Evol. Microbiol.* 59, 2291–2296. doi: 10.1099/ijs.0.004739-0
- Kurahashi, M., Fukunaga, Y., Harayama, S., and Yokota, A. (2008). *Sneathiella glossodoripedis* sp. nov., a marine alphaproteobacterium isolated from the nudibranch *Glossodoris cincta*, and proposal of Sneathiellales ord. nov. and Sneathiellaceae fam. nov. *Int. J. Syst. Evol. Microbiol.* 58, 548–552. doi: 10.1099/ijs.0.65328-0
- Kurtti, T. J., Felsheim, R. F., Burkhardt, N. Y., Oliver, J. D., Heu, C. C., and Munderloh, U. G. (2015). *Rickettsia buchneri* sp. nov., a rickettsial endosymbiont of the blacklegged tick *Ixodes scapularis*. *Int. J. Syst. Evol. Microbiol.* 65, 965–970. doi: 10.1099/ijs.0.000047
- Kuykendall, L. D. (2005). “Order VI, Rhizobiales ord. nov.,” in *Bergey’s Manual of Systematic Bacteriology: The Proteobacteria, (Part C)*, Vol. 2, eds D. J. Brenner, N. R. Krieg, J. T. Staley, and G. M. Garrity (New York, NY: Springer), 324.
- Kuykendall, L. D., Saxena, B., Devine, T. E., and Udell, S. E. (1992). Genetic diversity in *Bradyrhizobium japonicum* Jordan, 1982 and a proposal for *Bradyrhizobium elkanii* sp. nov. *Can. J. Microbiol.* 38, 501–505. doi: 10.1139/m92-082
- Kwon, K. K., Lee, H. S., Yang, S. H., and Kim, S. J. (2005). *Kordiimonas gwangyangensis* gen. nov., sp. nov., a marine bacterium isolated from marine sediments that forms a distinct lineage (Kordiimonadales ord. nov.) in the “Alphaproteobacteria.” *Int. J. Syst. Evol. Microbiol.* 55, 2033–2037. doi: 10.1099/ijs.0.63684-0
- Kwon, K. K., Woo, J.-H., Yang, S.-H., Kang, J.-H., Kang, S. G., Kim, S.-J., et al. (2007). *Altererythrobacter epoxidivorans* gen. nov., sp. nov., an epoxide hydrolase-active, mesophilic marine bacterium isolated from cold-seep sediment, and reclassification of *Erythrobacter luteolus* Yoon et al. 2005 as *Altererythrobacter luteolus* comb. nov. *Int. J. Syst. Evol. Microbiol.* 57, 2207–2211. doi: 10.1099/ijs.0.64863-0
- La Scola, B., Mallet, M.-N., Grimont, P. A. D., and Raoult, D. (2002). Description of *Afpia birgiae* sp. nov. and *Afpia massiliensis* sp. nov. and recognition of *Afpia felis* genospecies A. *Int. J. Syst. Evol. Microbiol.* 52, 1773–1782. doi: 10.1099/ijs.0.02149-0
- La Scola, B., Mallet, M.-N., Grimont, P. A. D., and Raoult, D. (2003). *Bosea eneeae* sp. nov., *Bosea massiliensis* sp. nov. and *Bosea vestrisii* sp. nov., isolated from hospital water supplies, and emendation of the genus *Bosea* (Das et al., 1996). *Int. J. Syst. Evol. Microbiol.* 53, 15–20. doi: 10.1099/ijs.0.02127-0
- Labbé, N., Parent, S., and Villemur, R. (2004). *Nitratireductor aquibiodomus* gen. nov., sp. nov., a novel α -proteobacterium from the marine denitrification system of the Montreal Biodome (Canada). *Int. J. Syst. Evol. Microbiol.* 54, 269–273. doi: 10.1099/ijs.0.02793-0
- Labrenz, M., Collins, M. D., Lawson, P. A., Tindall, B. J., Schumann, P., and Hirsch, P. (1999). *Roseovarius tolerans* gen. nov., sp. nov., a budding bacterium with variable bacteriochlorophyll α production from hypersaline Ekho Lake. *Int. J. Syst. Bacteriol.* 49, 137–147. doi: 10.1099/00207713-49-1-137
- Labrenz, M., Lawson, P. A., Tindall, B. J., Collins, M. D., and Hirsch, P. (2005). *Roseisalinus antarcticus* gen. nov., sp. nov., a novel aerobic bacteriochlorophyll α -producing α -proteobacterium isolated from hypersaline Ekho Lake. *Antarctica. Int. J. Syst. Evol. Microbiol.* 55, 41–47. doi: 10.1099/ijs.0.63230-0
- Lagesen, K., Hallin, P., Rødland, E. A., Stærfeldt, H.-H., Rognes, T., and Ussery, D. W. (2007). RNAMmer: consistent and rapid annotation of ribosomal RNA genes. *Nucleic Acids Res.* 35, 3100–3108. doi: 10.1093/nar/gkm160
- Lai, Q., Cao, J., Yuan, J., Li, F., and Shao, Z. (2014). *Celeribacter indicus* sp. nov., a polycyclic aromatic hydrocarbon-degrading bacterium from deep-sea sediment and reclassification of *Huaishuia halophila* as *Celeribacter halophilus* comb. nov. *Int. J. Syst. Evol. Microbiol.* 64, 4160–4167. doi: 10.1099/ijs.0.069039-0

- Lai, Q., Fu, Y., Wang, J., Chen, S., Zhong, H., Sun, F., et al. (2011a). *Citricella marina* sp. nov., isolated from deep-sea sediment. *Int. J. Syst. Evol. Microbiol.* 61, 728–731. doi: 10.1099/ijs.0.022376-0
- Lai, Q., Li, G., Liu, X., Du, Y., Sun, F., and Shao, Z. (2015). *Pseudoceanicola atlanticus* gen. nov. sp. nov., isolated from surface seawater of the Atlantic Ocean and reclassification of *Oceanicola batsensis*, *Oceanicola marinus*, *Oceanicola nitratreducens*, *Oceanicola nanhaiensis*, *Oceanicola antarcticus* and *Oceanicola flagellatus*, as *Pseudoceanicola batsensis* comb. nov., *Pseudoceanicola marinus* comb. nov., *Pseudoceanicola nitratreducens* comb. nov., *Pseudoceanicola nanhaiensis* comb. nov., *Pseudoceanicola antarcticus* comb. nov., and *Pseudoceanicola flagellatus* comb. nov. *Antonie Van Leeuwenhoek* 107, 1065–1074. doi: 10.1007/s10482-015-0398-2
- Lai, Q., Yu, Z., Wang, J., Zhong, H., Sun, F., Wang, L., et al. (2011b). *Nitratreductor pacificus* sp. nov., isolated from a pyrene-degrading consortium. *Int. J. Syst. Evol. Microbiol.* 61, 1386–1391. doi: 10.1099/ijs.0.024356-0
- Lai, Q., Yu, Z., Yuan, J., Sun, F., and Shao, Z. (2011c). *Nitratreductor indicus* sp. nov., isolated from deep-sea water. *Int. J. Syst. Evol. Microbiol.* 61, 295–298. doi: 10.1099/ijs.0.022962-0
- Lai, Q., Yuan, J., Wu, C., and Shao, Z. (2009). *Oceanibaculum indicum* gen. nov., sp. nov., isolated from deep seawater of the Indian Ocean. *Int. J. Syst. Evol. Microbiol.* 59, 1733–1737. doi: 10.1099/ijs.0.004341-0
- Lake, J. A., and Rivera, M. C. (2004). Deriving the genomic tree of life in the presence of horizontal gene transfer: conditioned reconstruction. *Mol. Biol. Evol.* 21, 681–690. doi: 10.1093/molbev/msh061
- Lakshmi, K. V. N. S., Divyasree, B., Ramprasad, E. V. V., Sasikala, C., and Ramana, C. V. (2014). Reclassification of *Rhodospirillum photometricum* Molisch, 1907, *Rhodospirillum sulfurexigens* Anil Kumar et al., 2008 and *Rhodospirillum oryzae* Lakshmi et al. 2013 in a new genus, *Pararhodospirillum* gen. nov., as *Pararhodospirillum photometricum* comb. nov., *Pararhodospirillum sulfurexigens* comb. nov. and *Pararhodospirillum oryzae* comb. nov., respectively, and emended description of the genus *Rhodospirillum*. *Int. J. Syst. Evol. Microbiol.* 64, 1154–1159. doi: 10.1099/ijs.0.059147-0
- Lakshmi, K. V. N. S., Sasikala, C., Takaichi, S., and Ramana, C. V. (2011). *Phaeospirillum oryzae* sp. nov., a spheroplast-forming, phototrophic alphaproteobacterium from a paddy soil. *Int. J. Syst. Evol. Microbiol.* 61, 1656–1661. doi: 10.1099/ijs.0.025544-0
- Lassalle, F., Périan, S., Bataillon, T., Nesme, X., Duret, L., and Daubin, V. (2015). GC-content evolution in bacterial genomes: the biased gene conversion hypothesis expands. *PLoS Genet.* 11:e1004941. doi: 10.1371/journal.pgen.1004941
- Lau, S. C. K., Tsoi, M. M. Y., Li, X., Plakhotnikova, I., Wu, M., Wong, P.-K., et al. (2004). *Loktanella hongkongensis* sp. nov., a novel member of the α -Proteobacteria originating from marine biofilms in Hong Kong waters. *Int. J. Syst. Evol. Microbiol.* 54, 2281–2284. doi: 10.1099/ijs.0.63294-0
- Lavrinenko, K., Chernousova, E., Gridneva, E., Dubinina, G., Akimov, V., Kuever, J., et al. (2010). *Azospirillum thiophilum* sp. nov., a diazotrophic bacterium isolated from a sulfide spring. *Int. J. Syst. Evol. Microbiol.* 60, 2832–2837. doi: 10.1099/ijs.0.018853-0
- Lawson, P. A., and Collins, M. (1996). Description of *Bartonella clarridgeiae* sp. nov. isolated from the cat of a patient with *Bartonella henselae* septicemia. *Med. Microbiol. Lett.* 5, 64–73.
- Le Quesne, W. J. (1974). The uniquely evolved character concept and its cladistic application. *Syst. Biol.* 23, 513–517. doi: 10.1093/sysbio/23.4.513
- Lebuhn, M., Achouak, W., Schloter, M., Berge, O., Meier, H., Barakat, M., et al. (2000). Taxonomic characterization of *Ochrobactrum* sp. isolates from soil samples and wheat roots and description of *Ochrobactrum tritici* sp. nov. and *Ochrobactrum grignonense* sp. nov. *Int. J. Syst. Evol. Microbiol.* 50, 2207–2223. doi: 10.1099/00207713-50-6-2207
- Lee, H., Kim, D.-U., Lee, S., Park, S., Yoon, J.-H., Seong, C. N., et al. (2017). *Reyranella terrae* sp. nov., isolated from an agricultural soil, and emended description of the genus *Reyranella*. *Int. J. Syst. Evol. Microbiol.* 67, 2031–2035. doi: 10.1099/ijsem.0.001913
- Lee, H.-W., Yu, H.-S., Liu, Q.-M., Jung, H.-M., An, D.-S., Im, W.-T., et al. (2007a). *Kaistia granuli* sp. nov., isolated from anaerobic granules in an upflow anaerobic sludge blanket reactor. *Int. J. Syst. Evol. Microbiol.* 57, 2280–2283. doi: 10.1099/ijs.0.65023-0
- Lee, K., Choo, Y.-J., Giovannoni, S. J., and Cho, J.-C. (2007b). *Maritimibacter alkaliphilus* gen. nov., sp. nov., a genome-sequenced marine bacterium of the *Roseobacter* clade in the order Rhodobacterales. *Int. J. Syst. Evol. Microbiol.* 57, 1653–1658. doi: 10.1099/ijs.0.64960-0
- Lee, K., Choo, Y.-J., Giovannoni, S. J., and Cho, J.-C. (2007c). *Ruegeria pelagia* sp. nov., isolated from the Sargasso Sea, Atlantic Ocean. *Int. J. Syst. Evol. Microbiol.* 57, 1815–1818. doi: 10.1099/ijs.0.65032-0
- Lee, K., Lee, H. K., Choi, T.-H., and Cho, J.-C. (2007d). *Robiginotomaculum antarcticum* gen. nov., sp. nov., a member of the family Hyphomonadaceae, from Antarctic seawater. *Int. J. Syst. Evol. Microbiol.* 57, 2595–2599. doi: 10.1099/ijs.0.65274-0
- Lee, K.-B., Liu, C.-T., Anzai, Y., Kim, H., Aono, T., and Oyaizu, H. (2005). The hierarchical system of the 'Alphaproteobacteria': description of Hyphomonadaceae fam. nov., Xanthobacteraceae fam. nov. and Erythrobacteraceae fam. nov. *Int. J. Syst. Evol. Microbiol.* 55, 1907–1919. doi: 10.1099/ijs.0.63663-0
- Lee, M.-H., Lee, S.-Y., Jung, Y.-T., Park, S., and Yoon, J.-H. (2013). *Pseudorhodobacter wandonensis* sp. nov., isolated from wood falls, and emended description of the genus *Pseudorhodobacter*. *Int. J. Syst. Evol. Microbiol.* 63, 1479–1484. doi: 10.1099/ijs.0.042879-0
- Lee, S. D. (2012). *Loktanella tamensis* sp. nov., isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 62, 586–590. doi: 10.1099/ijs.0.029462-0
- Lee, S. D., Joung, Y., and Cho, J. C. (2017). *Phreatobacter stygius* sp. nov., isolated from pieces of wood in a lava cave and emended description of the genus *Phreatobacter*. *Int. J. Syst. Evol. Microbiol.* 67, 3296–3300. doi: 10.1099/ijsem.0.002106
- Lee, S. H., Shim, J. K., Kim, J. M., Choi, H.-K., and Jeon, C. O. (2011). *Henriciella litoralis* sp. nov., isolated from a tidal flat, transfer of *Maribaculum marinum* Lai et al., 2009 to the genus *Henriciella* as *Henriciella aquimarinum* nom. nov. and emended description of the genus *Henriciella*. *Int. J. Syst. Evol. Microbiol.* 61, 722–727. doi: 10.1099/ijs.0.020396-0
- Lee, S.-Y., Park, S., Oh, T.-K., and Yoon, J.-H. (2012). *Celeribacter baekdonensis* sp. nov., isolated from seawater, and emended description of the genus *Celeribacter* Ivanova et al., 2010. *Int. J. Syst. Evol. Microbiol.* 62, 1359–1364. doi: 10.1099/ijs.0.032227-0
- Lee, Y. M., Yang, J. Y., Baek, K., Han, S. J., Shin, S. C., Hwang, C. Y., et al. (2016). *Pseudorhodobacter psychrotolerans* sp. nov., a psychrotolerant bacterium isolated from terrestrial soil, and emended description of the genus *Pseudorhodobacter*. *Int. J. Syst. Evol. Microbiol.* 66, 1068–1073. doi: 10.1099/ijsem.0.000841
- Lee, Y. S., Lee, D.-H., Kahng, H.-Y., Kim, E. M., and Jung, J. S. (2010). *Erythrobacter gangjinensis* sp. nov., a marine bacterium isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 60, 1413–1417. doi: 10.1099/ijs.0.015743-0
- Lefort, V., Desper, R., and Gascuel, O. (2015). FastME 2.0: a comprehensive, accurate, and fast distance-based phylogeny inference program. *Mol. Biol. Evol.* 32, 2798–2800. doi: 10.1093/molbev/msv150
- Lei, X., Zhang, H., Chen, Y., Li, Y., Chen, Z., Lai, Q., et al. (2015). *Erythrobacter luteus* sp. nov., isolated from mangrove sediment. *Int. J. Syst. Evol. Microbiol.* 65, 2472–2478. doi: 10.1099/ijs.0.000283
- León-Barrios, M., Ramírez-Bahena, M. H., Igual, J. M., Peix, Á., and Velázquez, E. (2018). *Phyllobacterium salinisoli* sp. nov., isolated from a lotus lancerottensis root nodule in saline soil from lanzarote. *Int. J. Syst. Evol. Microbiol.* 68, 1085–1089. doi: 10.1099/ijsem.0.002628
- Letunic, I., and Bork, P. (2019). Interactive Tree Of Life (iTOL) v4: recent updates and new developments. *Nucleic Acids Res.* 47, W256–W259. doi: 10.1093/nar/gkz239
- Levett, P. N., Morey, R. E., Galloway, R., Steigerwalt, A. G., and Ellis, W. A. (2005). Reclassification of *Leptospira parva* Hovind-Hougen et al. 1982 as *Turneriella parva* gen. nov., comb. nov. *Int. J. Syst. Evol. Microbiol.* 55, 1497–1499. doi: 10.1099/ijs.0.63088-0
- Li, A.-H., Liu, H.-C., Hou, W.-G., and Zhou, Y.-G. (2016). *Pseudorhodobacter sinensis* sp. nov. and *Pseudorhodobacter aquaticus* sp. nov., isolated from crater lakes. *Int. J. Syst. Evol. Microbiol.* 66, 2819–2824. doi: 10.1099/ijsem.0.001601
- Li, A.-H., and Zhou, Y.-G. (2015). *Frigidibacter albus* gen. nov., sp. nov., a novel member of the family Rhodobacteraceae isolated from lake water. *Int. J. Syst. Evol. Microbiol.* 65, 1199–1206. doi: 10.1099/ijs.0.00080
- Li, G.-W., Zhang, X.-Y., Wang, C.-S., Zhang, Y.-J., Xu, X.-W., Liu, C., et al. (2013). *Albimonas pacifica* sp. nov., isolated from seawater of the Pacific, and emended

- description of the genus *Albimonas*. *Int. J. Syst. Evol. Microbiol.* 63, 3597–3601. doi: 10.1099/ijs.0.049742-0
- Li, L., Li, Y.-Q., Jiang, Z., Gao, R., Nimaichand, S., Duan, Y.-Q., et al. (2016). *Ochrobactrum endophyticum* sp. nov., isolated from roots of *Glycyrrhiza uralensis*. *Arch. Microbiol.* 198, 171–179. doi: 10.1007/s00203-015-1170-8
- Li, L., Stoeckert, C. J., and Roos, D. S. (2003). OrthoMCL: identification of ortholog groups for eukaryotic genomes. *Genome Res.* 13, 2178–2189. doi: 10.1101/gr.1224503
- Li, Q. Q., Wang, E. T., Chang, Y. L., Zhang, Y. Z., Zhang, Y. M., Sui, X. H., et al. (2011). *Ensifer sojae* sp. nov., isolated from root nodules of *Glycine max* grown in saline-alkaline soils. *Int. J. Syst. Evol. Microbiol.* 61, 1981–1988. doi: 10.1099/ijs.0.025049-0
- Li, Z., Qu, Z., Zhang, X., and Zhang, X.-H. (2012). *Lentibacter algarum* gen. nov., sp. nov., isolated from coastal water during a massive green algae bloom. *Int. J. Syst. Evol. Microbiol.* 62, 1042–1047. doi: 10.1099/ijs.0.029868-0
- Li, Z., Zhao, R., Ji, S., Shi, X., and Zhang, X.-H. (2013). *Roseovarius marisflavi* sp. nov., isolated from an amphioxus breeding zone in the coastal region of the Yellow Sea, China. *Antonie Van Leeuwenhoek* 104, 413–421. doi: 10.1007/s10482-013-9965-6
- Liang, J., Zhang, Z., Liu, Y., Wang, M., and Zhang, X.-H. (2015). *Loktanelia sediminum* sp. nov., isolated from marine surface sediment. *Int. J. Syst. Evol. Microbiol.* 65, 686–691. doi: 10.1099/ijs.0.070680-0
- Liao, H., Li, Y., Lin, X., Lai, Q., and Tian, Y. (2018). *Zhengella mangrovi* gen. nov., sp. nov., a novel member of family phyllobacteriaceae isolated from mangrove sediment. *Int. J. Syst. Evol. Microbiol.* 68, 2819–2825. doi: 10.1099/ijsem.0.002900
- Lienau, K. E., and DeSalle, R. (2009). Evidence, content and corroboration and the tree of life. *Acta Biotheor.* 57, 187–199. doi: 10.1007/s10441-008-9066-5
- Lin, S.-Y., Hameed, A., Shen, F.-T., Liu, Y.-C., Hsu, Y.-H., Shahina, M., et al. (2014). Description of *Niveispirillum fermenti* gen. nov., sp. nov., isolated from a fermentor in Taiwan, transfer of *Azospirillum irakense* (1989) as *Niveispirillum irakense* comb. nov., and reclassification of *Azospirillum amazonense* (1983) as *Nitrospirillum amazonense* gen. nov. *Antonie Van Leeuwenhoek* 105, 1149–1162. doi: 10.1007/s10482-014-0176-6
- Lin, S. Y., Hameed, A., Young, C. C., Liu, Y. C., Hsu, Y. H., Chung, W. C., et al. (2015). *Thalassocola ureilytica* gen. nov., sp. nov., of the family Phyllobacteriaceae isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 65, 4100–4106. doi: 10.1099/ijsem.0.000544
- Lin, S.-Y., Shen, F.-T., Young, L.-S., Zhu, Z.-L., Chen, W.-M., and Young, C.-C. (2012). *Azospirillum formosense* sp. nov., a diazotroph from agricultural soil. *Int. J. Syst. Evol. Microbiol.* 62, 1185–1190. doi: 10.1099/ijs.0.030585-0
- Lin, S.-Y., Young, C.-C., Hameed, A., Liu, Y.-C., Hsu, Y.-H., Chung, W.-C., et al. (2016). *Actibacterium ureilyticum* sp. nov., isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 66, 2769–2773. doi: 10.1099/ijsem.0.001052
- Lingens, F., Blecher, R., Blecher, H., Blobel, F., Eberspächer, J., Fröhner, C., et al. (1985). *Phenylobacterium immobile* gen. nov., sp. nov., a gran-negative bacterium that degrades the herbicide chloridazon. *Int. J. Syst. Bacteriol.* 35, 26–39. doi: 10.1099/00207713-35-1-26
- Lipski, A., and Kämpfer, P. (2012). *Aquamicrobium ahrensii* sp. nov. and *Aquamicrobium segne* sp. nov., isolated from experimental biofilters. *Int. J. Syst. Evol. Microbiol.* 62, 2511–2516. doi: 10.1099/ijs.0.038224-0
- Lipski, A., Reichert, K., Reuter, B., Spröer, C., and Altendorf, K. (1998). Identification of bacterial isolates from biofilters as *Paracoccus alkenifer* sp. nov. and *Paracoccus solventivorans* with emended description of *Paracoccus solventivorans*. *Int. J. Syst. Bacteriol.* 48, 529–536. doi: 10.1099/00207713-48-2-529
- Lisdiyanti, P., Kawasaki, H., Seki, T., Yamada, Y., Uchimura, T., and Kazuo, K. (2000). Systematic study of the genus *Acetobacter* with descriptions of *Acetobacter indonesiensis* sp. nov., *Acetobacter tropicalis* sp. nov., *Acetobacter orleanensis* (Henneberg 1906) comb. nov., *Acetobacter lovaniensis* (Fratreur 1950) comb. nov., and *Acetobacter estunensis* (Carr 1958) comb. nov. *J. Gen. Appl. Microbiol.* 46, 147–165. doi: 10.2323/jgam.46.147
- Lisdiyanti, P., Kawasaki, H., Seki, T., Yamada, Y., Uchimura, T., and Komagata, K. (2001). Identification of *Acetobacter* strains isolated from Indonesian sources, and proposals of *Acetobacter syzygii* sp. nov., *Acetobacter cibinongensis* sp. nov., and *Acetobacter orientalis* sp. nov. *J. Gen. Appl. Microbiol.* 47, 119–131. doi: 10.1016/S1043-2760(97)84344-5
- Liu, B. B., Wang, H. F., Li, Q. L., Zhou, X. K., Zhang, Y. G., Xiao, M., et al. (2016). *Aurantimonas endophytica* sp. nov., a novel endophytic bacterium isolated from roots of *Anabasis elatior* (C. A. Mey.) Schischk. *Int. J. Syst. Evol. Microbiol.* 66, 4112–4117. doi: 10.1099/ijsem.0.001320
- Liu, C., Wu, Y., Li, L., Ma, Y., and Shao, Z. (2007). *Thalassospira xiamenensis* sp. nov. and *Thalassospira profundimaris* sp. nov. *Int. J. Syst. Evol. Microbiol.* 57, 316–320. doi: 10.1099/ijs.0.64544-0
- Liu, J., Wang, Y., Liu, Y., and Zhang, X.-H. (2016). *Ahrensia marina* sp. nov., a dimethylsulfoniopropionate-cleaving bacterium isolated from seawater, and emended descriptions of the genus *Ahrensia* and *Ahrensia kielensis*. *Int. J. Syst. Evol. Microbiol.* 66, 874–880. doi: 10.1099/ijsem.0.000805
- Liu, J., Wang, Y., Yang, X., Sun, Z., Ren, Q., Zhang, Y., et al. (2017). *Roseibium sediminis* sp. nov., isolated from sea surface sediment. *Int. J. Syst. Evol. Microbiol.* 67, 2862–2867. doi: 10.1099/ijsem.0.002034
- Liu, J.-H., Wang, Y.-X., Zhang, X.-X., Wang, Z.-G., Chen, Y.-G., Wen, M.-L., et al. (2010). *Salinarimonas rosea* gen. nov., sp. nov., a new member of the α -2 subgroup of the *Proteobacteria*. *Int. J. Syst. Evol. Microbiol.* 60, 55–60. doi: 10.1099/ijs.0.006981-0
- Liu, J.-J., Zhang, X.-Q., Chi, F.-T., Pan, J., Sun, C., and Wu, M. (2014). *Gemmobacter megaterium* sp. nov., isolated from coastal planktonic seaweeds. *Int. J. Syst. Evol. Microbiol.* 64, 66–71. doi: 10.1099/ijs.0.050955-0
- Liu, K., Li, S., Jiao, N., and Tang, K. (2014). *Pacificamonas flava* gen. nov., sp. nov., a novel member of the family Sphingomonadaceae isolated from the Southeastern Pacific. *Curr. Microbiol.* 69, 96–101. doi: 10.1007/s00284-014-0560-5
- Liu, M., Dai, J., Liu, Y., Cai, F., Wang, Y., Rahman, E., et al. (2011). *Desertibacter roseus* gen. nov., sp. nov., a gamma radiation-resistant bacterium in the family Rhodospirillaceae, isolated from desert sand. *Int. J. Syst. Evol. Microbiol.* 61, 1109–1113. doi: 10.1099/ijs.0.021246-0
- Liu, X.-Z., Wang, Q.-M., Göker, M., Groenewald, M., Kachalkin, A. V., Lumsch, H. T., et al. (2015). Towards an integrated phylogenetic classification of the Tremellomycetes. *Stud. Mycol.* 81, 85–147. doi: 10.1016/j.simyco.2015.12.001
- Liu, Y., Jin, J. H., Liu, Y. H., Zhou, Y. G., and Liu, Z. P. (2010). *Dongia mobilis* gen. nov., sp. nov., a new member of the family Rhodospirillaceae isolated from a sequencing batch reactor for treatment of malachite green effluent. *Int. J. Syst. Evol. Microbiol.* 60, 2780–2785. doi: 10.1099/ijs.0.020347-0
- Liu, Y., Wang, R.-P., Ren, C., Lai, Q.-L., and Zeng, R.-Y. (2015). *Rhizobium marinum* sp. nov., a malachite-green-tolerant bacterium isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 65, 4449–4454. doi: 10.1099/ijsem.0.000593
- Liu, Y., Zhang, X., Lai, Q., and Shao, Z. (2018). Reclassification of *Mameliella phaeodactyli*, *Mameliella atlantica*, *Ponticoccus lacteus* and *Alkalimicrobium pacificum* as later heterotypic synonyms of *Mameliella alba* and an emended description of *Mameliella alba*. *Int. J. Syst. Evol. Microbiol.* 68, 1047–1051. doi: 10.1099/ijsem.0.002617
- Liu, Z.-P., Wang, B.-J., Liu, X.-Y., Dai, X., Liu, Y.-H., and Liu, S.-J. (2008). *Paracoccus halophilus* sp. nov., isolated from marine sediment of the South China Sea, China, and emended description of genus *Paracoccus* Davis 1969. *Int. J. Syst. Evol. Microbiol.* 58, 257–261. doi: 10.1099/ijs.0.65237-0
- López-López, A., Pujalte, M. J., Benlloch, S., Mata-Roig, M., Roselló-Mora, R., Garay, E., et al. (2002). *Thalassospira lucentensis* gen. nov., sp. nov., a new marine member of the α -*Proteobacteria*. *Int. J. Syst. Evol. Microbiol.* 52, 1277–1283. doi: 10.1099/ijs.0.01928-0
- Lucena, T., Ruvira, M. A., Garay, E., Macián, M. C., Arahál, D. R., and Pujalte, M. J. (2012). *Actibacterium mucosum* gen. nov., sp. nov., a marine alphaproteobacterium from Mediterranean seawater. *Int. J. Syst. Evol. Microbiol.* 62, 2858–2864. doi: 10.1099/ijs.0.038026-0
- Ludwig, W., Mittenhuber, G., and Friedrich, C. G. (1993). Transfer of *Thiosphaera pantotropha* to *Paracoccus denitrificans*. *Int. J. Syst. Bacteriol.* 43, 363–367. doi: 10.1099/00207713-43-2-363
- Luis-Pantoja, M., Ramos-González, P. L., Naranjo, M., Hernández-Rodríguez, L., Rodríguez, J., and Pérez-López, E. (2015). Rickettsia-related bacteria associated with papaya plants showing bunchy top disease in Cuba. *J. Gen. Plant. Pathol.* 81, 166–168. doi: 10.1007/s10327-014-0571-x
- Luo, G., Shi, Z., Wang, H., and Wang, G. (2012). *Skermanella stibiensis* sp. nov., a highly antimony-resistant bacterium isolated from coal-mining soil, and emended description of the genus *Skermanella*. *Int. J. Syst. Evol. Microbiol.* 62, 1271–1276. doi: 10.1099/ijs.0.033746-0

- Lv, H., Masuda, S., Fujitani, Y., Sahin, N., and Tani, A. (2017). *Oharaebacter diazotrophicus* gen. nov., sp. nov., a diazotrophic and facultatively methylotrophic bacterium, isolated from rice rhizosphere. *Int. J. Syst. Evol. Microbiol.* 67, 576–582. doi: 10.1099/ijsem.0.001660
- Lv, X.-L., Xie, B.-S., Cai, M., Geng, S., Tang, Y.-Q., Wang, Y.-N., et al. (2014). *Glycoaulis albus* sp. nov., a moderately halophilic dimorphic prosthecate bacterium isolated from petroleum-contaminated saline soil. *Int. J. Syst. Evol. Microbiol.* 64, 3181–3187. doi: 10.1099/ijms.0.063537-0
- Macián, M. C., Arahál, D. R., Garay, E., Ludwig, W., Schleifer, K. H., and Pujalte, M. J. (2005). *Jannaschia rubra* sp. nov., a red-pigmented bacterium isolated from sea water. *Int. J. Syst. Evol. Microbiol.* 55, 649–653. doi: 10.1099/ijms.0.63412-0
- Madhaiyan, M., Jin, T. Y., Roy, J. J., Kim, S. J., Weon, H. Y., Kwon, S. W., et al. (2013). *Pleomorphomonas diazotrophica* sp. nov., an endophytic N-fixing bacterium isolated from root tissue of *Jatropha curcas* L. *Int. J. Syst. Evol. Microbiol.* 63, 2477–2483. doi: 10.1099/ijms.0.044461-0
- Madhaiyan, M., Kim, B.-Y., Poonguzhali, S., Kwon, S.-W., Song, M.-H., Ryu, J.-H., et al. (2007). *Methylobacterium oryzae* sp. nov., and aerobic, pink-pigmented, facultatively methylotrophic, 1-aminocyclopropane-1-carboxylate deaminase-producing bacterium isolated from rice. *Int. J. Syst. Evol. Microbiol.* 57, 326–331. doi: 10.1099/ijms.0.64603-0
- Madhaiyan, M., and Poonguzhali, S. (2014). *Methylobacterium pseudosasicola* sp. nov. and *Methylobacterium phyllostachyos* sp. nov., isolated from bamboo leaf surfaces. *Int. J. Syst. Evol. Microbiol.* 64, 2376–2384. doi: 10.1099/ijms.0.057232-0
- Madhaiyan, M., Poonguzhali, S., Kwon, S.-W., and Sa, T.-M. (2009). *Methylobacterium phyllosphaerae* sp. nov., a pink-pigmented, facultative methylotroph from the phyllosphere of rice. *Int. J. Syst. Evol. Microbiol.* 59, 22–27. doi: 10.1099/ijms.0.001693-0
- Madhaiyan, M., Poonguzhali, S., Senthilkumar, M., Lee, J.-S., and Lee, K.-C. (2012). *Methylobacterium gossipiicola* sp. nov., a pink-pigmented, facultatively methylotrophic bacterium isolated from the cotton phyllosphere. *Int. J. Syst. Evol. Microbiol.* 62, 162–167. doi: 10.1099/ijms.0.030148-0
- Maina, A. N., Fogarty, C., Krueger, L., Macaluso, K. R., Odhiambo, A., Nguyen, K., et al. (2016). *Rickettsial* infections among *Ctenocephalides felis* and host animals during a flea-borne rickettsiosis outbreak in Orange County, California. *PLoS One* 11:e0160604. doi: 10.1371/journal.pone.0160604
- Malimas, T., Yukphan, P., Takahashi, M., Kaneyasu, M., Potacharoen, W., Tanasupawat, S., et al. (2007). *Gluconobacter kondonii* sp. nov., an acetic acid bacterium in the α -*Proteobacteria*. *J. Gen. Appl. Microbiol.* 53, 301–307. doi: 10.2323/jgam.53.301
- Mann, S., and Chen, Y.-P. P. (2010). Bacterial genomic G + C composition-eliciting environmental adaptation. *Genomics* 95, 7–15. doi: 10.1016/j.ygeno.2009.09.002
- Mantelin, S., Fischer-Le Saux, M., Zakhia, F., Béna, G., Bonneau, S., Jeder, H., et al. (2006). Emended description of the genus *Phyllobacterium* and description of four novel species associated with plant roots: *Phyllobacterium bourgognense* sp. nov., *Phyllobacterium ifriqiense* sp. nov., *Phyllobacterium leguminum* sp. nov. and *Phyllobacterium brassicacearum* sp. nov. *Int. J. Syst. Evol. Microbiol.* 56, 827–839. doi: 10.1099/ijms.0.63911-0
- Margesin, R., and Zhang, D.-C. (2013). *Humitalea rosea* gen. nov., sp. nov., an aerobic bacteriochlorophyll-containing bacterium of the family Acetobacteraceae isolated from soil. *Int. J. Syst. Evol. Microbiol.* 63, 1411–1416. doi: 10.1099/ijms.0.043018-0
- Margos, G., Lane, R. S., Fedorova, N., Koloczek, J., Piesman, J., Hojgaard, A., et al. (2016). *Borrelia bissettiae* sp. nov. and *Borrelia californiensis* sp. nov. prevail in diverse enzootic transmission cycles. *Int. J. Syst. Evol. Microbiol.* 66, 1447–1452. doi: 10.1099/ijsem.0.000897
- Margos, G., Wilske, B., Sing, A., Hizo-Teufel, C., Cao, W. C., Chu, C., et al. (2013). *Borrelia bavariensis* sp. nov. is widely distributed in Europe and Asia. *Int. J. Syst. Evol. Microbiol.* 63, 4284–4288. doi: 10.1099/ijms.0.052001-0
- Martens, M., Dawyndt, P., Coopman, R., Gillis, M., De Vos, P., and Willems, A. (2008). Advantages of multilocus sequence analysis for taxonomic studies: a case study using 10 housekeeping genes in the genus *Ensifer* (including former *Sinorhizobium*). *Int. J. Syst. Evol. Microbiol.* 58, 200–214. doi: 10.1099/ijms.0.65392-0
- Martens, T., Heidorn, T., Pukall, R., Simon, M., Tindall, B. J., and Brinkhoff, T. (2006). Reclassification of *Roseobacter gallaeciensis* Ruiz-Ponte et al. 1998 as *Phaeobacter gallaeciensis* gen. nov., comb. nov., description of *Phaeobacter inhibens* sp. nov., reclassification of *Ruegeria algicola* (Lafay et al. 1995) Uchino et al. 1999 as *Marinov*. *Int. J. Syst. Evol. Microbiol.* 56, 1293–1304. doi: 10.1099/ijms.0.63724-0
- Martínez-Cánovas, M. J., Quesada, E., Martínez-Checa, F., del Moral, A., and Béjar, V. (2004). *Salipiger mucescens* gen. nov., sp. nov., a moderately halophilic, exopolysaccharide-producing bacterium isolated from hypersaline soil, belonging to the α -*Proteobacteria*. *Int. J. Syst. Evol. Microbiol.* 54, 1735–1740. doi: 10.1099/ijms.0.63166-0
- Martínez-Hidalgo, P., Ramírez-Bahena, M. H., Flores-Félix, J. D., Rivas, R., Igual, J. M., Mateos, P. F., et al. (2015). Revision of the taxonomic status of type strains of *Mesorhizobium loti* and reclassification of strain USDA 3471T as the type strain of *Mesorhizobium erdmannii* sp. nov. and ATCC 33669T as the type strain of *Mesorhizobium jarvisii* sp. nov. *Int. J. Syst. Evol. Microbiol.* 65, 1703–1708. doi: 10.1099/ijms.0.000164
- Martínez-Romero, E., Segovia, L., Mercante, F. M., Franco, A. A., Graham, P., and Pardo, M. A. (1991). *Rhizobium tropici*, a novel species nodulating *Phaseolus vulgaris* L. Beans and *Leucaena* sp. trees. *Int. J. Syst. Bacteriol.* 41, 417–426.
- Maruyama, T., Park, H.-D., Ozawa, K., Tanaka, Y., Sumino, T., Hamana, K., et al. (2006). *Sphingosinicella microcystinivorans* gen. nov., sp. nov., a microcystin-degrading bacterium. *Int. J. Syst. Evol. Microbiol.* 56, 85–89. doi: 10.1099/ijms.0.63789-0
- Mason, L. M., and Claus, G. W. (1989). Phenotypic characteristics correlated with deoxyribonucleic acid sequence similarities for three species of *Gluconobacter*: *G. oxydans* (Henneberg 1897) De Ley 1961. *G. frateurii* sp. nov., and *G. asaii* sp. nov. *Int. J. Syst. Bacteriol.* 39, 174–184. doi: 10.1099/00207713-39-2-174
- Maszenan, A. M., Seviour, R. J., Patel, B. K. C., Janssen, P. H., and Wanner, J. (2005). *Deffluvicoccus vanus* gen. nov., sp. nov., a novel Gram-negative coccus/cocobacillus in the “*Alphaproteobacteria*” from activated sludge. *Int. J. Syst. Evol. Microbiol.* 55, 2105–2111. doi: 10.1099/ijms.0.02332-0
- Math, R. K., Jin, H. M., Jeong, S. H., and Jeon, C. O. (2013). *Deffluviomonas aestuarii* sp. nov., a marine bacterium isolated from a tidal flat, and emended description of the genus *Deffluviomonas* Foessel et al., 2011. *Int. J. Syst. Evol. Microbiol.* 63, 2895–2900. doi: 10.1099/ijms.0.048389-0
- Matsumoto, M., Iwama, D., Arakaki, A., Tanaka, A., Tanaka, T., Miyashita, H., et al. (2011). *Altererythrobacter ishigakiensis* sp. nov., an astaxanthin-producing bacterium isolated from a marine sediment. *Int. J. Syst. Evol. Microbiol.* 61, 2956–2961. doi: 10.1099/ijms.0.024729-0
- Matthias, M. A., Ricaldi, J. N., Cespedes, M., Diaz, M. M., Galloway, R. L., Saito, M., et al. (2008). Human Leptospirosis caused by a new, antigenically unique *Leptospira* associated with a *Rattus* species reservoir in the Peruvian Amazon. *PLoS Neglected Top. Dis.* 2:e213. doi: 10.1371/journal.pntd.0000213
- Mavromatis, K., Land, M. L., Brettin, T. S., Quest, D. J., Copeland, A., Clum, A., et al. (2012). The fast changing landscape of sequencing technologies and their impact on microbial genome assemblies and annotation. *PLoS One* 7:e48837. doi: 10.1371/journal.pone.0048837
- McCutcheon, J. P., McDonald, B. R., and Moran, N. A. (2009). Origin of an alternative genetic code in the extremely small and GC-rich genome of a bacterial symbiont. *PLoS Genet.* 5:e1000565. doi: 10.1371/journal.pgen.1000565
- McDonald, I. R., Doronina, N. V., Trotsenko, Y. A., McAnulla, C., and Murrell, J. C. (2001). *Hyphomicrobium chloromethanicum* sp. nov. and *Methylobacterium chloromethanicum* sp. nov., chloromethane-utilizing bacteria isolated from a polluted environment. *Int. J. Syst. Evol. Microbiol.* 51, 119–122. doi: 10.1099/00207713-51-1-119
- Mediannikov, O., Matsumoto, K., Samoylenko, I., Drancourt, M., Roux, V., Rydkina, E., et al. (2008). *Rickettsia raoultii* sp. nov., a spotted fever group rickettsia associated with *Dermacentor* ticks in Europe and Russia. *Int. J. Syst. Evol. Microbiol.* 58, 1635–1639. doi: 10.1099/ijms.0.64952-0
- Meier-Kolthoff, J. P., Auch, A. F., Klenk, H.-P., and Göker, M. (2013a). Genome sequence-based species delimitation with confidence intervals and improved distance functions. *BMC Bioinformatics* 14:60. doi: 10.1186/1471-2105-14-60
- Meier-Kolthoff, J. P., Auch, A. F., Klenk, H.-P., and Göker, M. (2014a). Highly parallelized inference of large genome-based phylogenies. *Concurr. Comput. Pract. Exp.* 26, 1715–1729. doi: 10.1002/cpe.3112
- Meier-Kolthoff, J. P., and Göker, M. (2019). TYGS is an automated high-throughput platform for state-of-the-art genome-based taxonomy. *Nat. Commun.* 10:2182. doi: 10.1038/s41467-019-10210-3

- Meier-Kolthoff, J. P., Göker, M., Spröer, C., and Klenk, H.-P. (2013b). When should a DDH experiment be mandatory in microbial taxonomy? *Arch. Microbiol.* 195, 413–418. doi: 10.1007/s00203-013-0888-4
- Meier-Kolthoff, J. P., Hahnke, R. L., Petersen, J., Scheuner, C., Michael, V., Fiebig, A., et al. (2014b). Complete genome sequence of DSM 30083T, the type strain (U5/41T) of *Escherichia coli*, and a proposal for delineating subspecies in microbial taxonomy. *Stand. Genomic Sci.* 9:2. doi: 10.1186/1944-3277-9-2
- Meier-Kolthoff, J. P., Klenk, H.-P., and Göker, M. (2014c). Taxonomic use of DNA G+C content and DNA-DNA hybridization in the genomic age. *Int. J. Syst. Evol. Microbiol.* 64, 352–356. doi: 10.1099/ijs.0.056994-0
- Meng, Y., Liu, H., Kang, Y., Zhou, Y., and Cai, M. (2017). *Blastomonas marina* sp. nov., a bacteriochlorophyll-containing bacterium isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 67, 3015–3019. doi: 10.1099/ijsem.0.002070
- Mergaert, J., and Swings, J. (2005). “Family IV. Phyllobacteriaceae fam. nov.” in *Bergey’s Manual of Systematic Bacteriology: The Proteobacteria, (Part C)*, Vol. 2, eds D. J. Brenner, N. R. Krieg, J. T. Staley, and G. M. Garrity (New York, NY: Springer), 393.
- Mesbah, M., Premachandran, U., and Whitman, W. B. (1989). Precise measurement of the G+C content of deoxyribonucleic acid by high-performance liquid chromatography. *Int. J. Syst. Bacteriol.* 39, 159–167. doi: 10.1099/00207713-39-2-159
- Meyer, K. F., and Shaw, E. B. (1920). A comparison of the morphologic, cultural and biochemical characteristics of *B. abortus* and *B. melitensis*: studies on the genus *Brucella* nov. gen. I. *J. Infect. Dis.* 27, 173–184. doi: 10.1093/infdis/27.3.173
- Meyer, O., Stackebrandt, E., and Auling, G. (1993). Reclassification of Ubiquinone Q-10 containing carboxydrotrophic bacteria: transfer of “[*Pseudomonas*] carboxydovorans” OM5T to *Oligotropha*, gen. nov., as *Oligotropha* carboxydovorans, comb. nov., transfer of “[*Alcaligenes*] carboxydus” DSM 1086T to *Carbophilus*, gen. nov., as *Carbophilus* carboxydus, comb. nov., transfer of “[*Pseudomonas*] compransoris” DSM 1231T to *Zavarzintia*, gen. nov., as *Zavarzintia* compransoris, comb. nov., and Amended Descriptions of the New Genera. *Syst. Appl. Microbiol.* 16, 390–395. doi: 10.1016/S0723-2020(11)80271-7
- Miyazaki, M., Sakai, S., Ritalahti, K. M., Saito, Y., Yamanaka, Y., Saito, Y., et al. (2014a). *Sphaerochaeta multiformis* sp. nov., an anaerobic, psychrophilic bacterium isolated from subseafloor sediment, and emended description of the genus *Sphaerochaeta*. *Int. J. Syst. Evol. Microbiol.* 64, 4147–4154. doi: 10.1099/ijs.0.068148-0
- Miyazaki, M., Sakai, S., Yamanaka, Y., Saito, Y., Takai, K., and Imachi, H. (2014b). *Spirochaeta psychrophila* sp. nov., a psychrophilic spirochaete isolated from subseafloor sediment offshore Shimokita, Japan, and emended description of the genus *Spirochaeta*. *Int. J. Syst. Evol. Microbiol.* 64(Pt 8), 2798–2804. doi: 10.1099/ijs.0.062463-0
- Mohd Nor, M. N., Sabaratnam, V., and Annie Tan, G. Y. (2017). *Devosia elaeis* sp. nov., isolated from oil palm rhizospheric soil. *Int. J. Syst. Evol. Microbiol.* 67, 851–855. doi: 10.1099/ijsem.0.001683
- Molisch, H. (1907). *Die Purpurbakterien Nach Neuen Untersuchungen*. Jena: G. Fischer. 1–95.
- Montero-Calasan, M., del, C., Meier-Kolthoff, J. P., Zhang, D. F., Yaramis, A., Rohde, M., et al. (2017). Genome-scale data call for a taxonomic rearrangement of Geodermatophilaceae. *Front. Microbiol.* 8:2501. doi: 10.3389/fmicb.2017.02501
- Moon, Y. G., Seo, S. H., Lee, S. D., and Heo, M. S. (2010). *Loktanella pyoseonensis* sp. nov., isolated from beach sand, and emended description of the genus *Loktanella*. *Int. J. Syst. Evol. Microbiol.* 60, 785–789. doi: 10.1099/ijs.0.011072-0
- Moore, R. L., Weiner, R. M., and Gebers, R. (1984). Genus *Hyphomonas* Pongratz 1957 nom. rev. emend., *Hyphomonas polymorpha* Pongratz 1957 nom. rev. emend., and *Hyphomonas neptunium* (Leifson 1964) comb. nov. emend. (*Hyphomicrobium neptunium*). *Int. J. Syst. Bacteriol.* 34, 71–73. doi: 10.1099/00207713-34-1-71
- Moreira, A. P. B., Pereira, N., Thompson, F. L., Pereira, N. Jr. and Thompson, F. L. (2011). Usefulness of a real-time PCR platform for G+C content and DNA-DNA hybridization estimations in vibrios. *Int. J. Syst. Evol. Microbiol.* 61, 2379–2383. doi: 10.1099/ijs.0.023606-0
- Moreira, F. M., de, S., Cruz, L., de Faria, S. M., Marsh, T., Martínez-Romero, E., et al. (2006). *Azorhizobium doebereineriae* sp. nov. microsymbiont of *Sesbania virgata* (caz.) pers. *Syst. Appl. Microbiol.* 29, 197–206. doi: 10.1016/j.syapm.2005.09.004
- Moshkovski, S. D. (1945). Cytotropic inducers of infection and the classification of the Rickettsiae within Chlamydozoa (original title in russian). *Adv. Mod. Biol.* 19, 1–44.
- Mousavi, S. A., Österman, J., Wahlberg, N., Nesme, X., Lavire, C., Vial, L., et al. (2014). Phylogeny of the *Rhizobium*–*Allorhizobium*–*Agrobacterium* clade supports the delineation of *Neorhizobium* gen. nov. *Syst. Appl. Microbiol.* 37, 208–215. doi: 10.1016/j.syapm.2013.12.007
- Mousavi, S. A., Willems, A., Nesme, X., de Lajudie, P., and Lindström, K. (2015). Revised phylogeny of *Rhizobiaceae*: proposal of the delineation of *Pararhizobium* gen. nov., and 13 new species combinations. *Syst. Appl. Microbiol.* 38, 84–90. doi: 10.1016/j.syapm.2014.12.003
- Mu, Y., Zhou, L., Zeng, X. C., Liu, L., Pan, Y., Chen, X., et al. (2016). *Arsenicitalea aurantiaca* gen. nov., sp. nov., a new member of the family Hyphomicrobiaceae, isolated from high-arsenic sediment. *Int. J. Syst. Evol. Microbiol.* 66, 5478–5484. doi: 10.1099/ijsem.0.001543
- Mukherjee, S., Seshadri, R., Varghese, N. J., Eloje-Fadros, E. A., Meier-Kolthoff, J. P., Göker, M., et al. (2017). 1,003 reference genomes of bacterial and archaeal isolates expand coverage of the tree of life. *Nat. Biotechnol.* 35, 676–685. doi: 10.1038/nbt.3886
- Muramatsu, Y., Uchino, Y., Kasai, H., Suzuki, K., and Nakagawa, Y. (2007). *Ruegeria mobilis* sp. nov., a member of the *Alphaproteobacteria* isolated in Japan and Palau. *Int. J. Syst. Evol. Microbiol.* 57, 1304–1309. doi: 10.1099/ijs.0.64572-0
- Nakagawa, Y., and Yokota, A. (1996). Transfer of “*Pseudomonas riboflavina*” (Foster 1944), a Gram-negative, motile rod with long-chain 3-hydroxy fatty acids, to *Devosia riboflavina* gen. nov., sp. nov., nom. rev. *Int. J. Syst. Bacteriol.* 46, 16–22. doi: 10.1099/00207713-46-1-16
- Nedashkovskaya, O. I., Kukhlevskiy, A. D., Zhukova, N. V., Kim, S.-J., and Rhee, S.-K. (2013). *Litorimonas cladophorae* sp. nov., a new Alphaproteobacterium isolated from the Pacific green alga *Cladophora stimpsoni*, and emended descriptions of the genus *Litorimonas* and *Litorimonas taeaeensis*. *Antonie Van Leeuwenhoek* 103, 1263–1269. doi: 10.1007/s10482-013-9906-4
- Nguyen, T. M., Pham, V. H. T., and Kim, J. (2015). *Mesorhizobium soli* sp. nov., a novel species isolated from the rhizosphere of *Robinia pseudoacacia* L. in South Korea by using a modified culture method. *Antonie Van Leeuwenhoek* 108, 301–310. doi: 10.1007/s10482-015-0481-8
- Nigam, A., Jit, S., and Lal, R. (2010). *Sphingomonas histidinilytica* sp. nov., isolated from a hexachlorocyclohexane dump site. *Int. J. Syst. Evol. Microbiol.* 60, 1038–1043. doi: 10.1099/ijs.0.008995-0
- Niharika, N., Jindal, S., Kaur, J., and Lal, R. (2012). *Sphingomonas indica* sp. nov., isolated from hexachlorocyclohexane (HCH)-contaminated soil. *Int. J. Syst. Evol. Microbiol.* 62, 2997–3002. doi: 10.1099/ijs.0.033845-0
- Niharika, N., Moskalikova, H., Kaur, J., Khan, F., Sedlackova, M., Hampl, A., et al. (2013a). *Sphingobium czechense* sp. nov., isolated from a hexachlorocyclohexane dump site. *Int. J. Syst. Evol. Microbiol.* 63, 723–728. doi: 10.1099/ijs.0.039396-0
- Niharika, N., Moskalikova, H., Kaur, J., Sedlackova, M., Hampl, A., Damborsky, J., et al. (2013b). *Novosphingobium barchaimii* sp. nov., isolated from hexachlorocyclohexane-contaminated soil. *Int. J. Syst. Evol. Microbiol.* 63, 667–672. doi: 10.1099/ijs.0.039826-0
- Nikoh, N., Hosokawa, T., Moriyama, M., Oshima, K., Hattori, M., and Fukatsu, T. (2014). Evolutionary origin of insect – *Wolbachia* nutritional mutualism. *Proc. Natl. Acad. Sci. U.S.A.* 111, 10257–10262. doi: 10.1073/pnas.1409284111
- Nogi, Y., Mori, K., Makita, H., and Hatada, Y. (2016). *Thalassobius abyssi* sp. nov., a marine bacterium isolated from cold-seep sediment. *Int. J. Syst. Evol. Microbiol.* 66, 574–579. doi: 10.1099/ijsem.0.000758
- Nogi, Y., Yoshizumi, M., and Miyazaki, M. (2014). *Thalassospira povalilytica* sp. nov., a polyvinyl-alcohol-degrading marine bacterium. *Int. J. Syst. Evol. Microbiol.* 64, 1149–1153. doi: 10.1099/ijs.0.058321-0
- Nordhoff, M., Taras, D., Macha, M., Tedin, K., Busse, H.-J., and Wieler, L. H. (2005). *Treponema berlinense* sp. nov. and *Treponema porcinum* sp. nov., novel spirochaetes isolated from porcine faeces. *Int. J. Syst. Evol. Microbiol.* 55, 1675–1680. doi: 10.1099/ijs.0.63388-0
- Nouioui, I., Carro, L., García-López, M., Meier-Kolthoff, J. P., Woyke, T., Kyrpides, N. C., et al. (2018). Genome-based taxonomic classification of the phylum actinobacteria. *Front. Microbiol.* 9:2007. doi: 10.3389/fmicb.2018.02007
- Nupur, P., Srinivas, T.N.R., Takaichi, S., AnilKumar, P. (2015). *Phaeobacterium nitrateducens* gen. nov., sp. nov., a phototrophic gammaproteobacterium

- isolated from a mangrove forest sediment sample. *Int. J. Syst. Evol. Microbiol.* 65, 2357–2364. doi: 10.1099/ijs.0.000263
- Ochiai, S., Adachi, Y., and Mori, K. (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. doi: 10.1111/j.1348-0421.1997.tb01877.x
- Oh, K.-H., Choi, W.-C., Jung, Y.-T., Kang, S.-J., Oh, T.-K., and Yoon, J.-H. (2012). *Tropicimonas aquimaris* sp. nov., isolated from seawater, and emended description of the genus *Tropicimonas* Harwati et al. 2009. *Int. J. Syst. Evol. Microbiol.* 62, 688–692. doi: 10.1099/ijs.0.029371-0
- Oh, K.-H., Jung, Y.-T., Oh, T.-K., and Yoon, J.-H. (2011). *Ruegeria faecimaris* sp. nov., isolated from a tidal flat sediment. *Int. J. Syst. Evol. Microbiol.* 61, 1182–1188. doi: 10.1099/ijs.0.025999-0
- Oh, M., Kim, J.-H., and Kim, W. (2016). *Tropicimonas arenosa* sp. nov., isolated from marine sand. *Int. J. Syst. Evol. Microbiol.* 66, 5514–5518. doi: 10.1099/ijs.0.001549
- Oh, Y.-S., Lim, H.-J., Cha, I.-T., Im, W.-T., Yoo, J.-S., Kang, U. G., et al. (2009). *Roseovarius halotolerans* sp. nov., isolated from deep seawater. *Int. J. Syst. Evol. Microbiol.* 59, 2718–2723. doi: 10.1099/ijs.0.002576-0
- Oren, A. (2017a). A plea for linguistic accuracy – also for *Candidatus taxa*. *Int. J. Syst. Evol. Microbiol.* 67, 1085–1094. doi: 10.1099/ijs.0.001715
- Oren, A. (2017b). On names of genera of prokaryotes that are later homonyms of generic names with standing in the zoological or the botanical nomenclature. proposal of *Neomegalonema* gen. nov. and *Neomegalonema perideroedes* comb. nov. as replacements for the prokaryotic generic name *Meganema* and the species name *Meganema perideroedes*. *Int. J. Syst. Evol. Microbiol.* 67, 4276–4278. doi: 10.1099/ijs.0.002349
- Pagnier, I., Raoult, D., and La Scola, B. (2011). Isolation and characterization of *Reyranella massiliensis* gen. nov., sp. nov. from freshwater samples by using an amoeba co-culture procedure. *Int. J. Syst. Evol. Microbiol.* 61, 2151–2154. doi: 10.1099/ijs.0.025775-0
- Pal, R., Bala, S., Dadhwal, M., Kumar, M., Dhingra, G., Prakash, O., et al. (2005). Hexachlorocyclohexane-degrading bacterial strains *Sphingomonas paucimobilis* B90A, UT26 and Sp+, having similar lin genes, represent three distinct species, *Sphingobium indicum* sp. nov., *Sphingobium japonicum* sp. nov. and *Sphingobium francense* sp. nov., and reclassification of [*Sphingomonas*] *chungbukensis* as *Sphingobium chungbukense* comb. nov. *Int. J. Syst. Evol. Microbiol.* 55, 1965–1972. doi: 10.1099/ijs.0.63201-0
- Pan, J., Sun, C., Zhang, X.-Q., Huo, Y.-Y., Zhu, X.-F., and Wu, M. (2014). *Paracoccus sediminis* sp. nov., isolated from Pacific Ocean marine sediment. *Int. J. Syst. Evol. Microbiol.* 64, 2512–2516. doi: 10.1099/ijs.0.051318-0
- Pan, X.-C., Geng, S., Lv, X.-L., Mei, R., Jiangyang, J.-H., Wang, Y.-N., et al. (2015). *Defluviimonas alba* sp. nov., isolated from an oilfield. *Int. J. Syst. Evol. Microbiol.* 65, 1805–1811. doi: 10.1099/ijs.0.000181
- Panday, D., and Das, S. K. (2010). *Chelatococcus sambhumathii* sp. nov., a moderately thermophilic alphaproteobacterium isolated from hot spring sediment. *Int. J. Syst. Evol. Microbiol.* 60, 861–865. doi: 10.1099/ijs.0.013466-0
- Paramasivam, N., Ben-Dov, E., Arotsker, L., and Kushmaro, A. (2013). *Eilatimonas milleporae* gen. nov., sp. nov., a marine bacterium isolated from the hydrocoral *Millepora dichotoma*. *Int. J. Syst. Evol. Microbiol.* 63, 1880–1884. doi: 10.1099/ijs.0.043976-0
- Park, J. R., Bae, J.-W., Nam, Y.-D., Chang, H.-W., Kwon, H.-Y., Quan, Z.-X., et al. (2007). *Sulfitobacter litoralis* sp. nov., a marine bacterium isolated from the East Sea, Korea. *Int. J. Syst. Evol. Microbiol.* 57, 692–695. doi: 10.1099/ijs.0.064267-0
- Park, M. S., Chung, B.-S., Lee, H. J., Jin, H. M., Lee, S.-S., Oh, Y. K., et al. (2011). *Citricella aestuarii* sp. nov., isolated from a tidal flat. *Int. J. Syst. Evol. Microbiol.* 61, 2595–2599. doi: 10.1099/ijs.0.028332-0
- Park, S., Jung, Y.-T., Won, S.-M., and Yoon, J.-H. (2014a). *Pseudoruegeria sabullitoris* sp. nov., isolated from seashore sand. *Int. J. Syst. Evol. Microbiol.* 64, 3276–3281. doi: 10.1099/ijs.0.066258-0
- Park, S., Jung, Y.-T., and Yoon, J.-H. (2013a). *Pelagicola litorisdiminis* sp. nov., a novel alphaproteobacterium isolated from tidal flat sediment. *Antonie Van Leeuwenhoek* 104, 103–110. doi: 10.1007/s10482-013-9930-4
- Park, S., Jung, Y.-T., and Yoon, J.-H. (2014b). *Wenxinia saemankumensis* sp. nov., isolated from a tidal flat sediment. *Int. J. Syst. Evol. Microbiol.* 64, 1958–1963. doi: 10.1099/ijs.0.062190-0
- Park, S., Kang, C.-H., Park, J.-M., and Yoon, J.-H. (2014c). *Aquimixticola soesokkakensis* gen. nov., sp. nov., a novel lipolytic alphaproteobacterium isolated from the junction between the ocean and a freshwater spring, and reclassification of *Roseovarius marinus* as *Pacificibacter marinus* comb. nov. and emended description of the genus *Pacificibacter*. *Antonie Van Leeuwenhoek* 106, 647–655. doi: 10.1007/s10482-014-0235-z
- Park, S., Kang, S.-J., Oh, T.-K., and Yoon, J.-H. (2010). *Roseivivax lentus* sp. nov., isolated from a tidal flat sediment, and emended description of the genus *Roseivivax* Suzuki et al. 1999. *Int. J. Syst. Evol. Microbiol.* 60, 1113–1117. doi: 10.1099/ijs.0.014795-0
- Park, S., Lee, J.-S., Lee, K.-C., and Yoon, J.-H. (2013b). *Lentilitoribacter donghaensis* gen. nov., sp. nov., a slowly-growing alphaproteobacterium isolated from coastal seawater. *Antonie Van Leeuwenhoek* 103, 457–464. doi: 10.1007/s10482-012-9825-9
- Park, S., Lee, M.-H., and Yoon, J.-H. (2013c). *Oceanicola litoreus* sp. nov., an alphaproteobacterium isolated from the seashore sediment. *Antonie Van Leeuwenhoek* 103, 859–866. doi: 10.1007/s10482-012-9867-z
- Park, S., Park, J.-M., Jung, Y.-T., Won, S.-M., and Yoon, J.-H. (2015a). *Primorskybacter insulae* sp. nov., isolated from the junction between the ocean and a freshwater spring. *Int. J. Syst. Evol. Microbiol.* 65, 3971–3976. doi: 10.1099/ijs.0.000522
- Park, S., Park, J. M., Kang, C. H., Kim, S. G., and Yoon, J. H. (2015b). *Pseudoseohaecicola caenipelagi* gen. nov., sp. nov., isolated from a tidal flat. *Int. J. Syst. Evol. Microbiol.* 65, 1819–1824. doi: 10.1099/ijs.0.000182
- Park, S., Park, J. M., Kang, C. H., and Yoon, J.-H. (2014d). *Aestuariaispira insulae* gen. nov., sp. nov., a lipolytic bacterium isolated from a tidal flat. *Int. J. Syst. Evol. Microbiol.* 64, 1841–1846. doi: 10.1099/ijs.0.062406-0
- Park, S., Park, J.-M., Kang, C.-H., and Yoon, J.-H. (2014e). *Confluentimicrobium lipolyticum* gen. nov., sp. nov., a novel lipolytic alphaproteobacterium isolated from the junction between the ocean and a freshwater spring, and emended description of *Actibacterium mucosum* Lucena et al., 2012. *Antonie Van Leeuwenhoek* 106, 969–977. doi: 10.1007/s10482-014-0266-5
- Park, S., Park, J. M., Kang, C. H., and Yoon, J. H. (2015c). *Aliiroseovarius pelagivivens* gen. nov., sp. nov., isolated from seawater, and reclassification of three species of the genus *Roseovarius* as *Aliiroseovarius crassostreae* comb. nov., *Aliiroseovarius halocynthiae* comb. nov. and *Aliiroseovarius sediminilitori*. *Int. J. Syst. Evol. Microbiol.* 65, 2646–2652. doi: 10.1099/ijs.0.000315
- Park, S., Won, S. M., Kim, H., Park, D. S., and Yoon, J. H. (2014f). *Aestuariaivita boseongensis* gen. nov., sp. nov., isolated from a tidal flat sediment. *Int. J. Syst. Evol. Microbiol.* 64, 2969–2974. doi: 10.1099/ijs.0.062406-0
- Park, S. C., Baik, K. S., Choe, H. N., Lim, C. H., Kim, H. J., Ka, J.-O., et al. (2011). *Altererythrobacter namhicola* sp. nov. and *Altererythrobacter aestuarii* sp. nov., isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 61, 709–715. doi: 10.1099/ijs.0.021196-0
- Parker, C. T., Tindall, B. J., and Garrity, G. M. (2019). International code of nomenclature of prokaryotes. *Int. J. Syst. Evol. Microbiol.* 69, S1–S111.
- Patt, T. E., Cole, G. C., and Hanson, R. S. (1976). *Methylobacterium*, a new genus of facultatively methyotrophic bacteria. *Int. J. Syst. Bacteriol.* 26, 226–229. doi: 10.1099/00207713-26-2-226
- Patwardhan, S., and Vetriani, C. (2016). *Varunaivibrio sulfuroxidans* gen. nov., sp. nov., a facultatively chemolithoautotrophic, mesophilic alphaproteobacterium from a shallow-water gas vent at Tor Caldara, Tyrrhenian Sea. *Int. J. Syst. Evol. Microbiol.* 66, 3579–3584. doi: 10.1099/ijs.0.001235
- Peix, A., Rivas, R., Trujillo, M. E., Vancanney, M., Velázquez, E., and Willems, A. (2005). Reclassification of *Agrobacterium ferrugineum* LMG 128 as *Hoeflea marina* gen. nov., sp. nov. *Int. J. Syst. Evol. Microbiol.* 55, 1163–1166. doi: 10.1099/ijs.0.63291-0
- Penesyan, A., Breider, S., Schumann, P., Tindall, B. J., Egan, S., and Brinkhoff, T. (2013). *Epibacterium ulvae* gen. nov., sp. nov., epibiotic bacteria isolated from the surface of a marine alga. *Int. J. Syst. Evol. Microbiol.* 63, 1589–1596. doi: 10.1099/ijs.0.042838-0
- Perolat, P., Chappel, R. J., Adler, B., Baranton, G., Bulacht, D. M., Billingham, M. L., et al. (1998). *Leptospira faimei* sp. nov., isolated from pigs in Australia. *Int. J. Syst. Bacteriol.* 48, 851–858. doi: 10.1099/00207713-48-3-851
- Pfennig, N., Lünsdorf, H., Süling, J., and Imhoff, J. F. (1997). *Rhodospira trueperi* gen. nov., spec. nov., a new phototrophic *Proteobacterium* of the alpha group. *Arch. Microbiol.* 168, 39–45. doi: 10.1007/s002030050467
- Pfennig, N., and Trüper, H. G. (1971). Higher taxa of the phototrophic bacteria. *Int. J. Syst. Bacteriol.* 21, 17–18. doi: 10.1099/00207713-21-1-17

- Philip, C. B. (1943). Nomenclature of the pathogenic rickettsiae. *Am. J. Hyg.* 37, 301–309.
- Philip, C. B. (1950). “Miscellaneous human rickettsioses,” in *Communicable Diseases*, ed. R. L. Pullen (Philadelphia, PA: Lea and Febiger Co.), 781–788.
- Philip, C. B. (1957). “Family IV. anaplasmataceae philip, fam. nov,” in *Bergey’s Manual of Systematic Bacteriology*, 7th Edn, eds R. S. Breed, E. G. D. Murray, and N. R. Smith (Baltimore, MD: The Williams and Wilkins Co.), 980–984.
- Philip, R. N., Casper, E. A., Anacker, R. L., Cory, J., Hayes, S. F., Burgdorfer, W., et al. (1983). *Rickettsia bellii* sp. nov.: a tick-borne *Rickettsia*, widely distributed in the United States, that is distinct from the spotted fever and typhus biogroups. *Int. J. Syst. Bacteriol.* 33, 94–106. doi: 10.1099/00207713-33-1-94
- Pikuta, E. V., Hoover, R. B., Bej, A. K., Marsic, D., Whitman, W. B., and Krader, P. (2009). *Spirochaeta dissipatitropha* sp. nov., an alkaliphilic, obligately anaerobic bacterium, and emended description of the genus *Spirochaeta* Ehrenberg 1835. *Int. J. Syst. Evol. Microbiol.* 59, 1798–1804. doi: 10.1099/ijs.0.016733-0
- Pini, F., Galardini, M., Bazzicalupo, M., and Mengoni, A. (2011). Plant-bacteria association and symbiosis: are there common genomic traits in *Alphaproteobacteria*? *Genes (Basel)* 2, 1017–1032. doi: 10.3390/genes2041017
- Poindexter, J. S. (1964). Biological properties and classification of the Caulobacter group. *Bacteriol. Rev.* 28, 231–295. doi: 10.1128/mbr.28.3.231-295.1964
- Poroshina, M. N., Trotsenko, Y. A., and Doronina, N. V. (2015). *Metylobrevia pamukkalensis* gen. nov., sp. nov., a halotolerant restricted facultative methylotroph isolated from saline water. *Int. J. Syst. Evol. Microbiol.* 65, 1321–1327. doi: 10.1099/ijs.0.000105
- Prakash, O., and Lal, R. (2006). Description of *Sphingobium fuliginis* sp. nov., a phenanthrene-degrading bacterium from a fly ash dumping site, and reclassification of *Sphingomonas cloacae* as *Sphingobium cloacae* comb. nov. *Int. J. Syst. Evol. Microbiol.* 56, 2147–2152. doi: 10.1099/ijs.0.64080-0
- Pritt, B. S., Respicio-Kingry, L. B., Sloan, L. M., Schriefer, M. E., Replogle, A. J., Bjork, J., et al. (2016). *Borrelia mayonii* sp. nov., a member of the *Borrelia burgdorferi* sensu lato complex, detected in patients and ticks in the upper midwestern United States. *Int. J. Syst. Evol. Microbiol.* 66, 4878–4880. doi: 10.1099/ijssem.0.001445
- Proença, D. N., Whitman, W. B., Varghese, N., Shapiro, N., Woyke, T., Kyrpidis, N. C., et al. (2018). *Arboriscoccus pini* gen. nov., sp. nov., an endophyte from a pine tree of the class *Alphaproteobacteria*, emended description of *Geminicoccus roseus*, and proposal of Geminicoccaceae fam. nov. *Syst. Appl. Microbiol.* 41, 94–100. doi: 10.1016/j.syapm.2017.11.006
- Pujalte, M. J., Lucena, T., Rodrigo-Torres, L., and Arahál, D. R. (2018). Comparative genomics of *Thalassobius* including the description of *Thalassobius activus* sp. nov., and *Thalassobius autumnalis* sp. nov. *Front. Microbiol.* 8:2645. doi: 10.3389/fmicb.2017.02645
- Pujalte, M. J., Macián, M. C., Arahál, D. R., Ludwig, W., Schleifer, K. H., and Garay, E. (2005). *Nereida ignava* gen. nov., sp. nov., a novel aerobic marine α -proteobacterium that is closely related to uncultured prionitis (alga) gall symbionts. *Int. J. Syst. Evol. Microbiol.* 55, 631–636. doi: 10.1099/ijs.0.63442-0
- Pukall, R., Laroche, M., Kroppenstedt, R. M., Schumann, P., Stackebrandt, E., and Ulber, R. (2003). *Paracoccus seriniphilus* sp. nov., an L-serine-dehydratase-producing coccus isolated from the marine bryozoan *Bugula plumosa*. *Int. J. Syst. Evol. Microbiol.* 53, 443–447. doi: 10.1099/ijs.0.02352-0
- Qu, L., Lai, Q., Zhu, F., Hong, X., Sun, X., and Shao, Z. (2011). *Cohaesibacter marisflavi* sp. nov., isolated from sediment of a seawater pond used for sea cucumber culture, and emended description of the genus *Cohaesibacter*. *Int. J. Syst. Evol. Microbiol.* 61, 762–766. doi: 10.1099/ijs.0.021972-0
- Quan, Z.-X., Zeng, D.-N., Xiao, Y.-P., Roh, S. W., Nam, Y.-D., Chang, H.-W., et al. (2009). *Henriciella marina* gen. nov., sp. nov., a novel member of the family Hyphomonadaceae isolated from the East Sea. *J. Microbiol.* 47, 156–161. doi: 10.1007/s12275-008-0290-0
- Radl, V., Simões-Araújo, J. L., Leite, J., Ribeiro Passos, S., Vieira Martins, L. M., Ribeiro Xavier, G., et al. (2014). *Microvirga vignae* sp. nov., a root nodule symbiotic bacterium isolated from cowpea grown in semi-arid Brazil. *Int. J. Syst. Evol. Microbiol.* 64, 725–730. doi: 10.1099/ijs.0.053082-0
- Rahalkar, M., Bahulikar, R. A., Deutzmann, J. S., Kroth, P. G., and Schink, B. (2012). *Elstera litoralis* gen. nov., sp. nov., isolated from stone biofilms of lake constance, Germany. *Int. J. Syst. Evol. Microbiol.* 62, 1750–1754. doi: 10.1099/ijs.0.026609-0
- Rahul, K., Azmatunnisa, M., Sasikala, C., and Ramana, C. V. (2015). *Hoeflea olei* sp. nov., a diesel-oil-degrading, anoxygenic, phototrophic bacterium isolated from backwaters and emended description of the genus *Hoeflea*. *Int. J. Syst. Evol. Microbiol.* 65, 2403–2409. doi: 10.1099/ijs.0.000277
- Rainey, F. A., Kelly, D. P., Stackebrandt, E., Burghardt, J., Hiraishi, A., Katayama, Y., et al. (1999). A re-evaluation of the taxonomy of *Paracoccus denitrificans* and a proposal for the combination *Paracoccus pantotrophus* comb. nov. *Int. J. Syst. Bacteriol.* 49, 645–651. doi: 10.1099/00207713-49-2-645
- Rainey, F. A., Silva, J., Nobre, M. F., Silva, M. T., and da Costa, M. S. (2003). *Porphyrobacter cryptus* sp. nov., a novel slightly thermophilic, aerobic, bacteriochlorophyll α -containing species. *Int. J. Syst. Evol. Microbiol.* 53, 35–41. doi: 10.1099/ijs.0.02308-0
- Raj, H. D. (1983). Proposal of *Ancylobacter* gen. nov. as a substitute for the bacterial genus microcycclus Ørskov 1928. *Int. J. Syst. Bacteriol.* 33, 397–398. doi: 10.1099/00207713-33-2-397
- Raj, P. S., Chakravarthy, S. K., Ramaprasad, E. V. V., Sasikala, C., and Ramana, C. V. (2012). *Phaeospirillum tilakii* sp. nov., a phototrophic *Alphaproteobacterium* isolated from aquatic sediments. *Int. J. Syst. Evol. Microbiol.* 62, 1069–1074. doi: 10.1099/ijs.0.032250-0
- Rajasabapathy, R., Mohandass, C., Dastager, S. G., Liu, Q., Khieu, T.-N., Son, C. K., et al. (2014). *Roseovarius azorensis* sp. nov., isolated from seawater at Espalamarca, Azores. *Antonie Van Leeuwenhoek* 105, 571–578. doi: 10.1007/s10482-013-0109-9
- Ramadass, P., Jarvis, B. D. W., Corner, R. J., Penny, D., and Marshall, R. B. (1992). Genetic characterization of pathogenic *Leptospira* species by DNA hybridization. *Int. J. Syst. Bacteriol.* 42, 215–219. doi: 10.1099/00207713-42-2-215
- Ramana, C. V., Parag, B., Girija, K. R., Ram, B. R., Ramana, V. V., and Sasikala, C. (2013). *Rhizobium subbaraonis* sp. nov., an endolithic bacterium isolated from beach sand. *Int. J. Syst. Evol. Microbiol.* 63, 581–585. doi: 10.1099/ijs.0.041442-0
- Ramana, V. V., Raj, P. S., Tushar, L., Sasikala, C., and Ramana, C. V. (2013). *Rhodomicrobium udaipurense* sp. nov., a psychrotolerant, phototrophic *Alphaproteobacterium* isolated from a freshwater stream. *Int. J. Syst. Evol. Microbiol.* 63, 2684–2689. doi: 10.1099/ijs.0.046409-0
- Ramírez-Bahena, M. H., García-Fraile, P., Peix, A., Valverde, A., Rivas, R., Mateos, P. F., et al. (2008). Revision of the taxonomic status of the species *Rhizobium leguminosarum* (Frank 1879) Frank, 1889AL, *Rhizobium phaseoli* Dangeard 1926AL and *Rhizobium trifolii* Dangeard 1926AL. *R. trifolii* is a later synonym of *R. leguminosarum*. Reclassification of the str. *Int. J. Syst. Evol. Microbiol.* 58, 2484–2490. doi: 10.1099/ijs.0.65621-0
- Ramírez-Bahena, M. H., Peix, A., Rivas, R., Camacho, M., Rodríguez-Navarro, D. N., Mateos, P. F., et al. (2009). *Bradyrhizobium pachyrhizi* sp. nov. and *Bradyrhizobium jicamae* sp. nov., isolated from effective nodules of *Pachyrhizus erosus*. *Int. J. Syst. Evol. Microbiol.* 59, 1929–1934. doi: 10.1099/ijs.0.006320-0
- Rathsack, K., Reitner, J., Stackebrandt, E., and Tindall, B. J. (2011). Reclassification of *Aurantimonas altamirensis* (Jurado et al. 2006), *Aurantimonas ureilytica* (Weon et al., 2007) and *Aurantimonas frigidaquae* (Kim Y.-G. et al., 2008) as members of a new genus, *Aureimonas* gen. nov., as *Aureimonas altamirensis* gen. nov., comb. nov. *Int. J. Syst. Evol. Microbiol.* 61, 2722–2728. doi: 10.1099/ijs.0.027029-0
- Reddy, G. S. N., and Garcia-Pichel, F. (2007). *Sphingomonas mucosissima* sp. nov. and *Sphingomonas desiccabilis* sp. nov., from biological soil crusts in the Colorado Plateau, USA. *Int. J. Syst. Evol. Microbiol.* 57(Pt 5), 1028–1034. doi: 10.1099/ijs.0.64331-0
- Reddy, G. S. N., Nagy, M., and Garcia-Pichel, F. (2006). *Belnapia moabensis* en. nov., sp. nov., an *Alphaproteobacterium* from biological soil crusts in the Colorado Plateau, USA. *Int. J. Syst. Evol. Microbiol.* 56, 51–58. doi: 10.1099/ijs.0.63764-0
- Rekha, P. D., Young, C.-C., Kämpfer, P., Martin, K., Arun, A. B., Chen, W.-M., et al. (2011). *Jhaorihella thermophila* gen. nov., sp. nov., a moderately thermophilic bacterium isolated from a coastal hot spring. *Int. J. Syst. Evol. Microbiol.* 61, 1544–1548. doi: 10.1099/ijs.0.025817-0
- Ren, D. W., Chen, W. F., Sui, X. H., Wang, E. T., and Chen, W. X. (2011). *Rhizobium vignae* sp. nov., a symbiotic bacterium isolated from multiple legume species. *Int. J. Syst. Evol. Microbiol.* 61, 580–586. doi: 10.1099/ijs.0.023143-0
- Ren, F., Zhang, L., Song, L., Xu, S., Xi, L., Huang, L., et al. (2014). *Fulvimarina manganoxydans* sp. nov., isolated from a deep-sea hydrothermal plume in

- the south-west Indian Ocean. *Int. J. Syst. Evol. Microbiol.* 64, 2920–2925. doi: 10.1099/ijs.0.060558-0
- Ribeiro, R. A., Rogel, M. A., López-López, A., Ormeño-Orillo, E., Barcellos, F. G., Martínez, J., et al. (2012). Reclassification of *Rhizobium tropici* type A strains as *Rhizobium leucaenae* sp. nov. *Int. J. Syst. Evol. Microbiol.* 62, 1179–1184. doi: 10.1099/ijs.0.032912-0
- Rihs, J. D., Brenner, D. J., Weaver, R. E., Steigerwalt, A. G., Hollis, D. G., and Yu, V. L. (1993). *Roseomonas*, a new genus associated with bacteremia and other human infections. *J. Clin. Microbiol.* 31, 3275–3283. doi: 10.1128/jcm.31.12.3275-3283.1993
- Rincón-Rosales, R., Villalobos-Escobedo, J. M., Rogel, M. A., Martínez, J., Ormeño-Orillo, E., and Martínez-Romero, E. (2013). *Rhizobium calliandrae* sp. nov., *Rhizobium mayense* sp. nov. and *Rhizobium jaguaris* sp. nov., rhizobial species nodulating the medicinal legume *Calliandra grandiflora*. *Int. J. Syst. Evol. Microbiol.* 63, 3423–3429. doi: 10.1099/ijs.0.048249-0
- Ritalahti, K. M., Justicia-Leon, S. D., Cusick, K. D., Ramos-Hernandez, N., Rubin, M., Dornbush, J., et al. (2012). *Sphaerochaeta globosa* gen. nov., sp. nov. and *Sphaerochaeta pleomorpha* sp. nov., free-living, spherical spirochaetes. *Int. J. Syst. Evol. Microbiol.* 62, 210–216. doi: 10.1099/ijs.0.023986-0
- Ritika, C., Suresh, K., and Anil Kumar, P. (2012). *Caenispirillum salinarum* sp. nov., a member of the family Rhodospirillaceae isolated from a solar saltern. *Int. J. Syst. Evol. Microbiol.* 62, 1698–1702. doi: 10.1099/ijs.0.035287-0
- Rivas, R., Abril, A., Trujillo, M. E., and Velázquez, E. (2004). *Sphingomonas phyllosphaerae* sp. nov., from the phyllosphere of *Acacia caven* in Argentina. *Int. J. Syst. Evol. Microbiol.* 54, 2147–2150. doi: 10.1099/ijs.0.63102-0
- Rivas, R., Martens, M., de Lajudie, P., and Willems, A. (2009). Multilocus sequence analysis of the genus *Bradyrhizobium*. *Syst. Appl. Microbiol.* 32, 101–110. doi: 10.1016/j.syapm.2008.12.005
- Rivas, R., Sánchez-Márquez, S., Mateos, P. F., Martínez-Molina, E., and Velázquez, E. (2005). *Martellella mediterranea* gen. nov., sp. nov., a novel α -proteobacterium isolated from a subterranean saline lake. *Int. J. Syst. Evol. Microbiol.* 55, 955–959. doi: 10.1099/ijs.0.63438-0
- Rivas, R., Willems, A., Subba-Rao, N. S., Mateos, P. F., Dazzo, F. B., Kroppenstedt, R. M., et al. (2003). Description of *Devosia neptuniae* sp. nov. that nodulates and fixes nitrogen in symbiosis with *Neptunia natans*, an aquatic legume from India. *Syst. Appl. Microbiol.* 26, 47–53. doi: 10.1078/072320203322337308
- Robinson, G. H. (1948). “Order V. Spirochaetales b Buchanan,” in *Bergey’s Manual of Determinative Bacteriology*, eds R. S. Breed, E. G. D. Murray, and A. P. Hitchens (Baltimore, MD: The Williams & Wilkins Co.), 1051–1058.
- Rocha, E. P. C., and Danchin, A. (2002). Base composition bias might result from competition for metabolic resources. *Trends Genet.* 18, 291–294. doi: 10.1016/S0168-9525(02)02690-2
- Roh, S. W., Kim, K.-H., Nam, Y.-D., Chang, H.-W., Kim, M.-S., Oh, H.-M., et al. (2009). *Sphingomonas aestuarii* sp. nov., isolated from tidal flat sediment. *Int. J. Syst. Evol. Microbiol.* 59, 1359–1363. doi: 10.1099/ijs.0.65528-0
- Romanenko, L. A., Tanaka, N., Frolova, G. M., and Mikhailov, V. V. (2008). *Pseudochrobactrum glaciei* sp. nov., isolated from sea ice collected from Peter the Great bay of the sea of Japan. *Int. J. Syst. Evol. Microbiol.* 58, 2454–2458. doi: 10.1099/ijs.0.65828-0
- Romanenko, L. A., Tanaka, N., Frolova, G. M., Svetashev, V. I., and Mikhailov, V. V. (2011a). *Litoreibacter albidus* gen. nov., sp. nov. and *Litoreibacter janthinus* sp. nov., members of the class Alphaproteobacteria isolated from the seashore. *Int. J. Syst. Evol. Microbiol.* 61, 148–154. doi: 10.1099/ijs.0.019513-0
- Romanenko, L. A., Tanaka, N., Svetashev, V. I., and Mikhailov, V. V. (2011b). *Primorskyibacter sedentarius* gen. nov., sp. nov., a novel member of the class Alphaproteobacteria from shallow marine sediments. *Int. J. Syst. Evol. Microbiol.* 61, 1572–1578. doi: 10.1099/ijs.0.025551-0
- Romanenko, L. A., Tanaka, N., Svetashev, V. I., and Mikhailov, V. V. (2011c). *Vadicella arenosi* gen. nov., sp. nov., a novel member of the class Alphaproteobacteria isolated from sandy sediments from the Sea of Japan seashore. *Curr. Microbiol.* 62, 795–801. doi: 10.1007/s00284-010-9780-5
- Romanenko, L. A., Tanaka, N., and Svetashev, V. I. (2013). *Devosia submarina* sp. nov., isolated from deepsea surface sediments. *Int. J. Syst. Evol. Microbiol.* 63, 3079–3085. doi: 10.1099/ijs.0.046607-0
- Rosselló-Mora, R., and Amann, R. (2001). The species concept for prokaryotes. *FEMS Microbiol. Rev.* 25, 39–67. doi: 10.1016/S0168-6445(00)00040-1
- Rothe, B., Fischer, A., Hirsch, P., Sittig, M., and Stackebrandt, E. (1987). The phylogenetic position of the budding bacteria *Blastobacter aggregatus* and *Gemmobacter aquatilis* gen., nov. sp. nov. *Arch. Microbiol.* 147, 92–99. doi: 10.1007/bf00492911
- Rüger, H.-J., and Höfle, M. G. (1992). Marine star-shaped-sggregate-forming bacteria: *Agrobacterium atlanticum* sp. nov.; *Agrobacterium meteori* sp. nov.; *Agrobacterium ferrugineum* sp. nov., nom. rev.; *Agrobacterium gelatinovorum* sp. nov., nom. rev.; and *Agrobacterium stellulatum* sp. nov., nom. *Int. J. Syst. Bacteriol.* 42, 133–143. doi: 10.1099/00207713-42-1-133
- Ryu, S. H., Chung, B. S., Le, N. T., Jang, H. H., Yun, P.-Y., Park, W., et al. (2008). *Devosia geojensis* sp. nov., isolated from diesel-contaminated soil in Korea. *Int. J. Syst. Evol. Microbiol.* 58, 633–636. doi: 10.1099/ijs.0.65481-0
- Ryu, S. H., Park, M., Lee, J. R., Yun, P.-Y., and Jeon, C. O. (2007). *Brevundimonas aveniformis* sp. nov., a stalked species isolated from activated sludge. *Int. J. Syst. Evol. Microbiol.* 57, 1561–1565. doi: 10.1099/ijs.0.64737-0
- Sánchez-Porro, C., Gallego, V., Busse, H.-J., Kämpfer, P., and Ventosa, A. (2009). Transfer of *Teichococcus ludipueritiae* and *Muricoccus roseus* to the genus *Roseomonas*, as *Roseomonas ludipueritiae* comb. nov. and *Roseomonas rosea* comb. nov., respectively, and emended description of the genus *Roseomonas*. *Int. J. Syst. Evol. Microbiol.* 59, 1193–1198. doi: 10.1099/ijs.0.004820-0
- Satomí, M., Kimura, B., Hamada, T., Harayama, S., and Fujii, T. (2002). Phylogenetic study of the genus *Oceanospirillum* based on 16S rRNA and gyrB genes: emended description of the genus *Oceanospirillum*, description of *Pseudospirillum* gen. nov., *Oceanobacter* gen. nov. and *Terasakiella* gen. nov. and transfer of *Oceanospirillum jannaschii* and *Pseudomonas stanieri* to *Marinobacterium* as *Marinobacterium jannaschii* comb. nov. and *Marinobacterium stanieri* comb. nov. *Int. J. Syst. Evol. Microbiol.* 52, 739–747. doi: 10.1099/ijs.0.01427-0
- Sawada, H., Ieki, H., Oyaizu, H., and Matsumoto, S. (1993). Proposal for rejection of *Agrobacterium tumefaciens* and revised descriptions for the genus *Agrobacterium* and for *Agrobacterium radiobacter* and *Agrobacterium rhizogenes*. *Int. J. Syst. Bacteriol.* 43, 694–702. doi: 10.1099/00207713-43-4-694
- Saxena, A., Anand, S., Dua, A., Sangwan, N., Khan, F., and Lal, R. (2013). *Novosphingobium lindaniclasticum* sp. nov., a hexachlorocyclohexane (HCH)-degrading bacterium isolated from an HCH dumpsite. *Int. J. Syst. Evol. Microbiol.* 63, 2160–2167. doi: 10.1099/ijs.0.045443-0
- Schaudinn, F. (1905). Korrespondenzen. *Dtsch. Med. Wochenschr.* 31:1728.
- Schiaffino, R., Sánchez, L., Gereá, M., Unrein, F., Balagué, V., Gasol, J. M., et al. (2016). Distribution patterns of the abundance of major bacterial and archaeal groups in Patagonian lakes. *J. Plankton Res.* 38, 64–82. doi: 10.1093/plankt/fbv105
- Schleheck, D., Tindall, B. J., Roselló-Mora, R., and Cook, A. M. (2004). *Parvibaculum lavamentivorans* gen. nov., sp. nov., a novel heterotroph that initiates catabolism of linear alkylbenzenesulfonate. *Int. J. Syst. Evol. Microbiol.* 54, 1489–1497. doi: 10.1099/ijs.0.03020-0
- Schleifer, H. K., Schüler, D., Spring, S., Weizenegger, M., Amann, R., Ludwig, W., et al. (1991). The genus *Magnetospirillum* gen. nov. description of *Magnetospirillum gryphiswaldense* sp. nov. and transfer of *Aquaspirillum magnetotacticum* to *Magnetospirillum magnetotacticum* comb. nov. *Syst. Appl. Microbiol.* 14, 379–385. doi: 10.1016/S0723-2020(11)80313-9
- Scholz, H. C., Hubalek, Z., Sedláček, I., Vergnaud, G., Tomaso, H., Al Dahouk, S., et al. (2008). *Brucella microti* sp. nov., isolated from the common vole *Microtus arvalis*. *Int. J. Syst. Evol. Microbiol.* 58, 375–382. doi: 10.1099/ijs.0.65356-0
- Scholz, H. C., Nöckler, K., Göllner, C., Bahn, P., Vergnaud, G., Tomaso, H., et al. (2010). *Brucella inopinata* sp. nov., isolated from a breast implant infection. *Int. J. Syst. Evol. Microbiol.* 60, 801–808. doi: 10.1099/ijs.0.011148-0
- Schrank, K., Choi, B.-K., Grund, S., Moter, A., Heuner, K., Nattermann, H., et al. (1999). *Treponema brennaborensis* sp. nov., a novel spirochaete isolated from a dairy cow suffering from digital dermatitis. *Int. J. Syst. Bacteriol.* 49, 43–50. doi: 10.1099/00207713-49-1-43
- Schüller, G., Hertel, C., and Hammes, W. P. (2000). *Gluconacetobacter entanii* sp. nov., isolated from submerged high-acid industrial vinegar fermentations. *Int. J. Syst. Evol. Microbiol.* 50, 2013–2020. doi: 10.1099/00207713-50-6-2013
- Segers, P., Vancanneyt, M., Pot, B., Torck, U., Hoste, B., Dewettinck, D., et al. (1994). Classification of *Pseudomonas diminuta* Leifson and Hugh 1954 and *Pseudomonas vesicularis* Büsing, Doll, and Freytag 1953 in *Brevundimonas* gen. nov. as *Brevundimonas diminuta* comb. nov. and *Brevundimonas vesicularis* comb. nov., respectively. *Int. J. Syst. Bacteriol.* 44, 499–510. doi: 10.1099/00207713-44-3-499

- Segovia, L., Young, J. P. W., and Martínez-Romero, E. (1993). Reclassification of American *Rhizobium leguminosarum* biovar phaseoli type I strains as *Rhizobium etli* sp. nov. *Int. J. Syst. Bacteriol.* 43, 374–377. doi: 10.1099/00207713-43-2-374
- Sekeyová, Z., Roux, V., Xu, W., Øehåæek, J., and Raoult, D. (1998). *Rickettsia slovacica* sp. nov., a member of the spotted fever group rickettsiae. *Int. J. Syst. Bacteriol.* 48, 1455–1462. doi: 10.1099/00207713-48-4-1455
- Seo, S. H., and Lee, S. D. (2010). *Altererythrobacter marensis* sp. nov., isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 60, 307–311. doi: 10.1099/ijs.0.011031-0
- Sha, S., Zhong, J., Chen, B., Lin, L., and Luan, T. (2017). *Novosphingobium guangzhouense* sp. nov., with the ability to degrade 1-methylphenanthrene. *Int. J. Syst. Evol. Microbiol.* 67, 489–497. doi: 10.1099/ijsem.0.001669
- Shalem Raj, P., Ramaprasad, E. V. V., Vaseef, S., Sasikala, C., and Ramana, C. V. (2013). *Rhodobacter viridis* sp. nov., a phototrophic bacterium isolated from mud of a stream. *Int. J. Syst. Evol. Microbiol.* 63, 181–186. doi: 10.1099/ijs.0.038471-0
- Sharma, P., Verma, M., Bala, K., Nigam, A., and Lal, R. (2010). *Sphingopyxis ummariensis* sp. nov., isolated from a hexachlorocyclohexane dump site. *Int. J. Syst. Evol. Microbiol.* 60, 780–784. doi: 10.1099/ijs.0.008805-0
- Shen, X., Li, Y., Zhao, Z., Han, Y. F., Zhang, W. W., Yu, X. Y., et al. (2018). Polyphasic taxonomic characterisation of a novel strain as *Pararhizobium haloflavum* sp. nov., isolated from soil samples near a sewage treatment tank. *Antonie van Leeuwenhoek* 111, 485–491. doi: 10.1007/s10482-017-0969-5
- Sheu, S. Y., Chen, Y. L., Young, C. C., and Chen, W. M. (2013). *Lacibacterium aquatile* gen. nov., sp. nov., a new member of the family Rhodospirillaceae isolated from a freshwater lake. *Int. J. Syst. Evol. Microbiol.* 63, 4797–4804. doi: 10.1099/ijs.0.055145-0
- Shi, B.-H., Arunparajana, V., Palakawong, S., and Yokota, A. (2002). *Tistrella mobilis* gen. nov., sp. nov., a novel polyhydroxyalkanoate-producing bacterium belonging to ALPHA-Proteobacteria. *J. Gen. Appl. Microbiol.* 48, 335–343. doi: 10.2323/jgam.48.335
- Shi, X., Li, C., Zhao, L., Si, M., Zhu, L., Xin, K., et al. (2016). *Rhizobium gei* sp. nov., a bacterial endophyte of *Geum aleppicum*. *Int. J. Syst. Evol. Microbiol.* 66, 4282–4288. doi: 10.1099/ijsem.0.001348
- Shiba, T. (1991). *Roseobacter litoralis* gen. nov., sp. nov., and *Roseobacter denitrificans* sp. nov., aerobic pink-pigmented bacteria which contain bacteriochlorophyll α . *Syst. Appl. Microbiol.* 14, 140–145. doi: 10.1016/s0723-2020(11)80292-4
- Shiba, T., and Smidu, U. (1982). *Erythrobacter longus* gen. nov., sp. nov., an aerobic bacterium which contains bacteriochlorophyll α . *Int. J. Syst. Bacteriol.* 32, 211–217. doi: 10.1099/00207713-32-2-211
- Shieh, W. Y., Lin, Y.-T., and Jean, W. D. (2004). *Pseudovibrio denitrificans* gen. nov., sp. nov., a marine, facultatively anaerobic, fermentative bacterium capable of denitrification. *Int. J. Syst. Evol. Microbiol.* 54, 2307–2312. doi: 10.1099/ijs.0.63107-0
- Shin, N.-R., Roh, S. W., Kim, M.-S., Yun, B., Whon, T. W., Kim, Y.-O., et al. (2012). *Tropicimonas sediminicola* sp. nov., isolated from marine sediment. *Int. J. Syst. Evol. Microbiol.* 62, 2424–2429. doi: 10.1099/ijs.0.037929-0
- Shivani, Y., Subhash, Y., Sasikala, C., and Ramana, C. V. (2016). Description of ‘*Candidatus Marispirochaeta associata*’ and reclassification of *Spirochaeta bajacaliforniensis*, *Spirochaeta smaragdinae* and *Spirochaeta sinaica* to a new genus *Sediminispirochaeta* gen. nov. as *Sediminispirochaeta bajacaliforniensis* comb. nov. *Int. J. Syst. Evol. Microbiol.* 66, 5485–5492. doi: 10.1099/ijsem.0.001545
- Shivani, Y., Subhash, Y., Tushar, L., Sasikala, C., and Ramana, C. V. (2015). *Spirochaeta lutea* sp. nov., isolated from marine habitats and emended description of the genus *Spirochaeta*. *Syst. Appl. Microbiol.* 38, 110–114. doi: 10.1016/j.syapm.2014.11.002
- Siddall, M. E. (2010). Unringing a bell: metazoan phylogenomics and the partition bootstrap. *Cladistics* 26, 444–452. doi: 10.1111/j.1096-0031.2009.00295.x
- Siddavattam, D., Karegoudar, T. B., Mudde, S. K., Kumar, N., Baddam, R., Avasthi, T. S., et al. (2011). Genome of a novel isolate of *Paracoccus denitrificans* capable of degrading N,N-dimethylformamide. *J. Bacteriol.* 193, 5598–5599. doi: 10.1128/JB.05667-11
- Simon, M., Scheuner, C., Meier-Kolthoff, J. P., Brinkhoff, T., Wagner-Döbler, I., Ulbrich, M., et al. (2017). Phylogenomics of *Rhodobacteraceae* reveals evolutionary adaptation to marine and non-marine habitats. *ISME J.* 11, 1483–1499. doi: 10.1038/ismej.2016.198
- Singh, A., and Lal, R. (2009). *Sphingobium ummariense* sp. nov., a hexachlorocyclohexane (HCH)-degrading bacterium, isolated from HCH-contaminated soil. *Int. J. Syst. Evol. Microbiol.* 59, 162–166. doi: 10.1099/ijs.0.65712-0
- Singh, P., Kim, Y.-J., Hoang, V.-A., Farh, M. E.-A., and Yang, D.-C. (2016). Erratum to: *Sphingomonas panacis* sp. nov., isolated from rhizosphere of rusty ginseng. *Antonie Van Leeuwenhoek* 109, 735–736. doi: 10.1007/s10482-016-0662-0
- Sizova, M. V., Panikov, N. S., Spiridonova, E. M., Slobodova, N. V., and Tourova, T. P. (2007). Novel facultative anaerobic acidotolerant *Telmatospirillum siberiense* gen. nov. sp. nov. isolated from mesotrophic fen. *Syst. Appl. Microbiol.* 30, 213–220. doi: 10.1016/j.syapm.2006.06.003
- Skerman, V. B. D., McGowan, V., and Sneath, P. H. A. (1980). Approved lists of bacterial names. *Int. J. Syst. Bacteriol.* 30, 225–420. doi: 10.1099/00207713-30-1-225
- Slack, A. T., Kalambaheti, T., Symonds, M. L., Dohnt, M. F., Galloway, R. L., Steigerwalt, A. G., et al. (2008). *Leptospira wolffii* sp. nov., isolated from a human with suspected leptospirosis in Thailand. *Int. J. Syst. Evol. Microbiol.* 58, 2305–2308. doi: 10.1099/ijs.0.64947-0
- Slack, A. T., Khairani-Bejo, S., Symonds, M. L., Dohnt, M. F., Galloway, R. L., Steigerwalt, A. G., et al. (2009). *Leptospira kmetyi* sp. nov., isolated from an environmental source in Malaysia. *Int. J. Syst. Evol. Microbiol.* 59, 705–708. doi: 10.1099/ijs.0.002766-0
- Sly, L. I., and Cahill, M. M. (1997). Transfer of *Blastobacter natatorius* (Sly 1985) to the genus *Blastomonas* gen. nov. as *Blastomonas natatoria* comb. nov. *Int. J. Syst. Bacteriol.* 47, 566–568. doi: 10.1099/00207713-47-2-566
- Sly, L. I., and Stackebrandt, E. (1999). Description of *Skermanella parooensis* gen. nov., sp. nov. to accommodate *Conglomeromonas largomobilis* subsp. *parooensis* following the transfer of *Conglomeromonas largomobilis* subsp. *largomobilis* to the genus *Azospirillum*. *Int. J. Syst. Bacteriol.* 49, 541–544. doi: 10.1099/00207713-49-2-541
- Smibert, R. M., Johnson, J. L., and Ranney, R. R. (1984). *Treponema socranskii* sp. nov., *Treponema socranskii* subsp. *socranskii* subsp. nov., *Treponema socranskii* subsp. *buccale* subsp. nov., and *Treponema socranskii* subsp. *paredis* subsp. nov. Isolated from the human periodontia. *Int. J. Syst. Evol. Microbiol.* 34, 457–462. doi: 10.1099/00207713-34-4-457
- Smythe, L., Adler, B., Hartskeerl, R. A., Galloway, R. L., Turenne, C. Y., and Levett, P. N. (2013). Classification of *Leptospira* genomospecies 1, 3, 4 and 5 as *Leptospira alstonii* sp. nov., *Leptospira vanthielii* sp. nov., *Leptospira terpstrae* sp. nov. and *Leptospira yanagawae* sp. nov., respectively. *Int. J. Syst. Evol. Microbiol.* 63, 1859–1862. doi: 10.1099/ijs.0.047324-0
- Sohn, J. H., Kwon, K. K., Kang, J.-H., Jung, H.-B., and Kim, S.-J. (2004). *Novosphingobium pentaromativorans* sp. nov. a high-molecular-mass polycyclic aromatic hydrocarbon-degrading bacterium isolated from estuarine sediment. *Int. J. Syst. Evol. Microbiol.* 54, 1483–1487. doi: 10.1099/ijs.0.02945-0
- Sorokin, D. Y. (1995). *Sulfobacter pontiacus* gen. nov., sp. nov. a new heterotrophic bacterium from the Black Sea, specialized on sulfite oxidation. *Microbiology* 64, 354–365.
- Sorokin, D. Y., Tourova, T. P., Kuznetsov, B. B., Bryantseva, I. A., and Gorlenko, V. M. (2000). *Roseinatronobacter thiooxidans* gen. nov., sp. nov., a new alkaliphilic aerobic bacteriochlorophyll α -containing bacterium isolated from a Soda Lake. *Microbiology* 69, 75–82. doi: 10.1007/bf02757261
- Sorokin, D. Y., Tourova, T. P., and Muyzer, G. (2005a). *Citricella thiooxidans* gen. nov., sp. nov., a novel lithoheterotrophic sulfur-oxidizing bacterium from the Black Sea. *Syst. Appl. Microbiol.* 28, 679–687. doi: 10.1016/j.syapm.2005.05.006
- Sorokin, D. Y., Tourova, T. P., Spiridonova, E. M., Rainey, F. A., and Muyzer, G. (2005b). *Thioclava pacifica* gen. nov., sp. nov., a novel facultatively autotrophic, marine, sulfur-oxidizing bacterium from a near-shore sulfidic hydrothermal area. *Int. J. Syst. Evol. Microbiol.* 55, 1069–1075. doi: 10.1099/ijs.0.63415-0
- Sorokina, A. Y., Chernousova, E. Y., and Dubinina, G. A. (2012). *Ferrovibrio denitrificans* gen. nov., sp. nov., a novel neutrophilic facultative anaerobic Fe(II)-oxidizing bacterium. *FEMS Microbiol. Lett.* 335, 19–25. doi: 10.1111/j.1574-6968.2012.02631.x
- Sravanthi, T., Tushar, L., Sasikala, C., and Ramana, C. V. (2016). *Alkalispicrochaeta cellulovorans* gen. nov., sp. nov., a cellulose-hydrolysing, alkaliphilic, halotolerant bacterium isolated from the gut of a wood-eating cockroach (*Cryptocercus punctulatus*), and reclassification of four species of *Spirochaeta* as new combinations within *Alkalispicrochaeta* gen. nov. *Int. J. Syst. Evol. Microbiol.* 66, 1612–1619. doi: 10.1099/ijsem.0.000865

- Srinivas, A., Vinay Kumar, B., Divya Sree, B., Tushar, L., Sasikala, C., and Ramana, C. V. (2014). *Rhodovulum salis* sp. nov. and *Rhodovulum viride* sp. nov., phototrophic Alphaproteobacteria isolated from marine habitats. *Int. J. Syst. Evol. Microbiol.* 64(Pt 3), 957–962. doi: 10.1099/ijfs.0.058974-0
- Srinivas, T. N. R., Anil Kumar, P., Sasikala, C., and Ramana, C. V. (2007a). *Rhodovulum imhoffii* sp. nov. *Int. J. Syst. Evol. Microbiol.* 57, 228–232. doi: 10.1099/ijfs.0.64470-0
- Srinivas, T. N. R., Kumar, P. A., Sasikala, C., Ramana, C. V., and Imhoff, J. F. (2007b). *Rhodobacter vinaykumarii* sp. nov., a marine phototrophic Alphaproteobacterium from tidal waters, and emended description of the genus *Rhodobacter*. *Int. J. Syst. Evol. Microbiol.* 57, 1984–1987. doi: 10.1099/ijfs.0.65077-0
- Srinivas, T. N. R., Kumar, P. A., Sasikala, C., Ramana, C. V., Stiling, J., and Imhoff, J. F. (2006). *Rhodovulum marinum* sp. nov., a novel phototrophic purple non-sulfur alphaproteobacterium from marine tides of Visakhapatnam, India. *Int. J. Syst. Evol. Microbiol.* 56, 1651–1656. doi: 10.1099/ijfs.0.64005-0
- Srinivas, T. N. R., Kumar, P. A., Sasikala, C., Spröer, C., and Ramana, C. V. (2008). *Rhodobacter ovatus* sp. nov., a phototrophic Alphaproteobacterium isolated from a polluted pond. *Int. J. Syst. Evol. Microbiol.* 58, 1379–1383. doi: 10.1099/ijfs.0.65619-0
- Stackebrandt, E. (1992). “Unifying phylogeny and phenotypic diversity,” in *The Prokaryotes*, eds A. Balows, H. G. Trueper, M. Dworkin, W. Harder, and K. H. Schleifer (New York, NY: Springer), 19–47.
- Staley, J. T. (1968). *Prosthecomicrobium* and *Ancalomicrobium*: new prosthecate freshwater bacteria. *J. Bacteriol.* 95, 1921–1942. doi: 10.1128/jb.95.5.1921-1942.1968
- Staley, J. T. (1984). *Prosthecomicrobium hirschii*, a new species in a redefined genus. *Int. J. Syst. Bacteriol.* 34, 304–308. doi: 10.1099/00207713-34-3-304
- Stamatakis, A. (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30, 1312–1313. doi: 10.1093/bioinformatics/btu033
- Stanton, T. B., Postic, D., and Jensenl, N. S. (1998). *Serpulina alvinipulli* sp. nov., a new *Serpulina* species that is enteropathogenic for chickens. *Int. J. Syst. Bacteriol.* 48, 669–676. doi: 10.1099/00207713-48-3-669
- Stenos, J., Roux, V., Walker, D., and Raoult, D. (1998). *Rickettsia honei* sp. nov., the aetiological agent of Flinders Island spotted fever in Australia. *Int. J. Syst. Bacteriol.* 48, 1399–1404. doi: 10.1099/00207713-48-4-1399
- Stoener, H. G., and Lackman, D. B. (1957). A new species of *Brucella* isolated from desert wood rat, *Neotoma lepida* Thomas. *Am. J. Vet. Res.* 69, 947–951.
- Strömpl, C., Hold, G. L., Lünsdorf, H., Graham, J., Gallacher, S., Abraham, W.-R., et al. (2003). *Oceanicaulis alexandrii* gen. nov., sp. nov., a novel stalked bacterium isolated from a culture of the dinoflagellate *Alexandrium tamarense* (Lebour) Balech. *Int. J. Syst. Evol. Microbiol.* 53, 1901–1906. doi: 10.1099/ijfs.0.02635-0
- Strong, R. P., Tyzzer, E. E., and Sellards, A. W. (1915). Oroya fever. Second report. *J. Am. Med. Assoc.* 64, 806–808.
- Stutzer, A., and Hartleb, R. (1899). *Untersuchungen über die bei der Bildung von Salpeter beobachteten Mikroorganismen*. Breslau: Abhandlungen und Mitteilungen des Landwirtschaftlichen Instituts der Königlichen Universität.
- Su, Y., Han, S., Wang, R., Yu, X., Fu, G., Chen, C., et al. (2017). *Microbaculum marinum* gen. nov., sp. nov., isolated from deep seawater. *Int. J. Syst. Evol. Microbiol.* 67, 812–817. doi: 10.1099/ijsem.0.001647
- Suarez, C., Ratering, S., Geissler-Plaum, R., and Schnell, S. (2014). *Hartmannibacter diazotrophicus* gen. nov., sp. nov., A phosphate-solubilizing and nitrogen-fixing alphaproteobacterium isolated from the rhizosphere of a natural salt-meadow plant. *Int. J. Syst. Evol. Microbiol.* 64, 3160–3167. doi: 10.1099/ijfs.0.064154-0
- Subhash, Y., Tushar, L., Sasikala, C., and Ramana, C. V. (2013). *Erythrobacter odishensis* sp. nov. and *Pontibacter odishensis* sp. nov. isolated from dry soil of a solar saltern. *Int. J. Syst. Evol. Microbiol.* 63, 4524–4532. doi: 10.1099/ijfs.0.052183-0
- Sultanpuram, V. R., Lodha, T. D., Chintalapati, V. R., and Chintalapati, S. (2013). *Cohaesibacter haloalkalitolerans* sp. nov., isolated from a soda lake, and emended description of the genus *Cohaesibacter*. *Int. J. Syst. Evol. Microbiol.* 63, 4271–4276. doi: 10.1099/ijfs.0.050112-0
- Sun, C., Pan, J., Zhang, X.-Q., Su, Y., and Wu, M. (2015). *Pseudoroseovarius zhejiangensis* gen. nov., sp. nov., a novel alpha-proteobacterium isolated from the chemical wastewater, and reclassification of *Roseovarius crassostreae* as *Pseudoroseovarius crassostreae* comb. nov., *Roseovarius sediminilitoris* as *Pseudoroseovarius sediminilitoris* comb. nov. and *Roseovarius halocynthiae* as *Pseudoroseovarius halocynthiae* comb. nov. *Antonie Van Leeuwenhoek* 108, 291–299. doi: 10.1007/s10482-015-0480-9
- Sun, C., Wang, R., Su, Y., Fu, G., Zhao, Z., Yu, X., et al. (2017). *Hyphobacterium vulgare* gen. nov., sp. nov., a novel Alphaproteobacterium isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 67, 1169–1176. doi: 10.1099/ijsem.0.001780
- Sun, L., Liu, H., Chen, W., Huang, K., Lyu, W., and Gao, X. (2018). *Alsobacter soli* sp. nov., a novel bacterium isolated from paddy soil, emended description of the genus *Alsobacter* and description of the family *Alsobacteraceae* fam. nov. *Int. J. Syst. Evol. Microbiol.* 68, 3902–3907. doi: 10.1099/ijsem.0.003088
- Suresh, G., Sasikala, C., and Ramana, C. V. (2015). Reclassification of *Gemmobacter changlensis* to a new genus as *Cereibacter changlensis* gen. nov., comb. nov. *Int. J. Syst. Evol. Microbiol.* 65, 794–798. doi: 10.1099/ijfs.0.000016
- Suzuki, R., Zhang, Y., Iino, T., Kosako, Y., Komagata, K., and Uchimura, T. (2010). *Asaia astilbes* sp. nov., *Asaia platycodi* sp. nov. and *Asaia prunellae* sp. nov., novel acetic acid bacteria isolated from flowers in Japan. *J. Gen. Appl. Microbiol.* 56, 339–346. doi: 10.2323/jgam.56.339
- Suzuki, T., Mori, Y., and Nishimura, Y. (2006). *Roseibacterium elongatum* gen. nov., sp. nov., sp. nov., an aerobic, bacteriochlorophyll-containing bacterium isolated from the west coast of Australia. *Int. J. Syst. Evol. Microbiol.* 56, 417–421. doi: 10.1099/ijfs.0.02094-0
- Suzuki, T., Muroga, Y., Takahama, M., and Nishimura, Y. (1999a). *Roseivivax holodurans* gen. nov., sp. nov. and *Roseivivax halotolerans* sp. nov., aerobic bacteriochlorophyll-containing bacteria isolated from a saline lake. *Int. J. Syst. Bacteriol.* 49, 629–634. doi: 10.1099/00207713-49-2-629
- Suzuki, T., Muroga, Y., Takahama, M., and Nishimura, Y. (2000). *Roseibium denhamense* gen. nov., sp. nov. and *Roseibium hamelinense* sp. nov., aerobic bacteriochlorophyll-containing bacteria isolated from the east and west coasts of Australia. *Int. J. Syst. Evol. Microbiol.* 50, 2151–2156. doi: 10.1099/00207713-50-6-2151
- Suzuki, T., Muroga, Y., Takahama, M., Shiba, T., and Nishimura, Y. (1999b). *Rubrimonas cliftonensis* gen. nov., sp. nov., an aerobic bacteriochlorophyll-containing bacterium isolated from a saline lake. *Int. J. Syst. Bacteriol.* 49, 201–205. doi: 10.1099/00207713-49-1-201
- Swellingrebel, N. H. (1907). Sur la cytologie comparée des spirochètes et des spirilles. *Ann. Institut Pasteur* 21, 562–586.
- Takeuchi, M., Hamana, K., and Hiraishi, A. (2001). Proposal of the genus *Sphingomonas* sensu stricto and three new genera, *Sphingobium*, *Novosphingobium* and *Sphingopyxis*, on the basis of phylogenetic and chemotaxonomic analyses. *Int. J. Syst. Evol. Microbiol.* 51, 1405–1417. doi: 10.1099/00207713-51-4-1405
- Takeuchi, M., Katayama, T., Yamagishi, T., Hanada, S., Tamaki, H., Kamagata, Y., et al. (2014). *Methyloceanibacter caenitepidi* gen. nov., sp. nov., a facultatively methylotrophic bacterium isolated from marine sediments near a hydrothermal vent. *Int. J. Syst. Evol. Microbiol.* 64, 462–468. doi: 10.1099/ijfs.0.053397-0
- Takeuchi, M., Kawai, F., Shimada, Y., and Yokota, A. (1993). Taxonomic study of polyethylene glycol-utilizing bacteria: emended description of the genus *Sphingomonas* and new descriptions of *Sphingomonas macrogoltabidus* sp. nov., *Sphingomonas sanguis* sp. nov. and *Sphingomonas terrae* sp. nov. *Syst. Appl. Microbiol.* 16, 227–238. doi: 10.1016/S0723-2020(11)80473-X
- Takeuchi, M., Sakane, T., Yanagi, M., Yamasato, K., Hamana, K., and Yokota, A. (1995). Taxonomic study of bacteria isolated from plants: proposal of *Sphingomonas rosa* sp. nov., *Sphingomonas pruni* sp. nov., *Sphingomonas asaccharolytica* sp. nov., and *Sphingomonas mali* sp. nov. *Int. J. Syst. Bacteriol.* 45, 334–341. doi: 10.1099/00207713-45-2-334
- Takeuchi, M., Yamagishi, T., Kamagata, Y., Oshima, K., Hattori, M., Katayama, T., et al. (2015). *Tepidicaulis marinus* gen. nov., sp. nov., a marine bacterium that reduces nitrate to nitrous oxide under strictly microaerobic conditions. *Int. J. Syst. Evol. Microbiol.* 65, 1749–1754. doi: 10.1099/ijfs.0.000167
- Tamura, A., Ohashi, N., Urakami, H., and Miyamura, S. (1995). Classification of *Rickettsia tsutsugamushi* in a new genus, *Orientia* gen. nov., as *Orientia tsutsugamushi* comb. nov. *Int. J. Syst. Evol. Microbiol.* 45, 589–591. doi: 10.1099/00207713-45-3-589
- Tanaka, N., Romanenko, L. A., Kurilenko, V. V., Svetashev, V. I., Kalinovskaya, N. I., and Mikhailov, V. V. (2014). *Loktanelia maritima* sp. nov. isolated from

- shallow marine sediments. *Int. J. Syst. Evol. Microbiol.* 64, 2370–2375. doi: 10.1099/ijs.0.061747-0
- Tanaka, Y., Hanada, S., Manome, A., Tsuchida, T., Kurane, R., Nakamura, K., et al. (2004). *Catellibacterium nectarophilum* gen. nov., sp. nov., which requires a diffusible compound from a strain related to the genus *Sphingomonas* for vigorous growth. *Int. J. Syst. Evol. Microbiol.* 54, 955–959. doi: 10.1099/ijs.0.02750-0
- Tarhriz, V., Thiel, V., Nematzadeh, G., Hejazi, M. A., Imhoff, J. F., and Hejazi, M. S. (2013). *Tabrizicola aquatica* gen. nov. sp. nov., a novel *Alphaproteobacterium* isolated from Qurugöl Lake nearby Tabriz city, Iran. *Antonie Van Leeuwenhoek* 104, 1205–1215. doi: 10.1007/s10482-013-0042-y
- Tarrand, J., Krieg, N., and Döbereiner, J. (1978). A taxonomic study of the *Spirillum lipoferum* group, with descriptions of a new genus, *Azospirillum* gen. nov. and two species, *Azospirillum lipoferum* (Beijerinck) comb. nov. and *Azospirillum brasilense* sp. nov. *Can. J. Microbiol.* 24, 967–980. doi: 10.1139/m78-160
- Taylor, D. J., and Piel, W. H. (2004). An assessment of accuracy, error, and conflict with support values from genome-scale phylogenetic data. *Mol. Biol. Evol.* 21, 1534–1537. doi: 10.1093/molbev/msh156
- Teixeira, L., Ferreira, Á, and Ashburner, M. (2008). The bacterial symbiont *Wolbachia* induces resistance to RNA viral infections in *Drosophila melanogaster*. *PLoS Biol.* 6:e1000002. doi: 10.1371/journal.pbio.1000002
- Teramoto, M., and Nishijima, M. (2014). *Temperatibacter marinus* gen. nov., sp. nov., a mesophilic bacterium isolated from surface seawater and description of *Temperatibacteraceae* fam. nov. in the class *Alphaproteobacteria*. *Int. J. Syst. Evol. Microbiol.* 64, 3075–3080. doi: 10.1099/ijs.0.063685-0
- Teyssier, C., Marchandin, H., Jean-Pierre, H., Masnou, A., Dusart, G., and Jumas-Bilak, E. (2007). *Ochrobactrum pseudintermedium* sp. nov., a novel member of the family Brucellaceae, isolated from human clinical samples. *Int. J. Syst. Evol. Microbiol.* 57, 1007–1013. doi: 10.1099/ijs.0.64416-0
- Thomsen, T. R., Blackall, L. L., Aquino, de Muro, Marilena Nielsen, J. L., and Nielsen, P. H. (2006). *Meganema perideroedes* gen. nov., sp. nov., a filamentous *Alphaproteobacterium* from activated sludge. *Int. J. Syst. Evol. Microbiol.* 56, 1865–1868. doi: 10.1099/ijs.0.02916-0
- Tindall, B. J. (2019a). The name *Bradyrhizobiaceae* Garrity et al. 2006 contains *Nitrobacter* Winogradsky, 1892 (Approved Lists 1980), the nomenclatural type of the family *Nitrobacteraceae* Buchanan, 1917 (Approved Lists 1980), is illegitimate and proposals to alter the wording of Rule 54 of the International Code of Nomenclature of Prokaryotes to clarify the fact that the family name *Bradyrhizobiaceae* Garrity et al. 2006 is replaced by the family name *Nitrobacteraceae* Buchanan, 1917 (Approved Lists 1980) the only correct name. *Int. J. Syst. Evol. Microbiol.* 69, 2609–2611. doi: 10.1099/ijsem.0.003253
- Tindall, B. J. (2019b). The role of incorrect citation of the international code of nomenclature of prokaryotes and subsequent misinterpretation in causing unnecessary nomenclatural confusion. *Int. J. Syst. Evol. Microbiol.* 69, 2621–2625. doi: 10.1099/ijsem.0.003529
- Tirandaz, H., Mehdi, S. M. D., Amoozegar, M. A., Shavandi, M., de la Haba, R. R., and Ventosa, A. (2015). *Pseudorhodoplanes sinuspersici* gen nov sp. nov. isolated from oil-contaminated soil. *Int. J. Syst. Evol. Microbiol.* 65, 4743–4748. doi: 10.1099/ijsem.0.000643
- To, T. H., Jung, M., Lycett, S., and Gascuel, O. (2016). Fast dating using least-squares criteria and algorithms. *Syst. Biol.* 65, 82–97. doi: 10.1093/sysbio/syv068
- Tóth, E. M., Vengring, A., Homonnay, Z. G., Kéki, Z., Spröer, C., Borsodi, A. K., et al. (2014). *Phreatobacter oligotrophus* gen. nov., sp. nov., an *Alphaproteobacterium* isolated from ultrapure water of the water purification system of a power plant. *Int. J. Syst. Evol. Microbiol.* 64, 839–845. doi: 10.1099/ijs.0.053843-0
- Tripathi, A. K., Verma, S. C., Chowdhury, S. P., Lebuhn, M., Gattinger, A., and Schlöter, M. (2006). *Ochrobactrum oryzae* sp. nov., an endophytic bacterial species isolated from deep-water rice in India. *Int. J. Syst. Evol. Microbiol.* 56, 1677–1680. doi: 10.1099/ijs.0.63934-0
- Trujillo, M. E., Willems, A., Abril, A., Luden, D., Mateos, P. F., and Vela, E. (2005). Nodulation of *Lupinus albus* by strains of *Ochrobactrum lupini* sp. nov. *Society* 71, 1318–1327. doi: 10.1128/AEM.71.3.1318
- Tsubouchi, T., Ohta, Y., Haga, T., Usui, K., Shimane, Y., Mori, K., et al. (2014). *Thalassospira alkalitolerans* sp. nov. and *Thalassospira mesophila* sp. nov., isolated from a decaying bamboo sunken in the marine environment, and emended description of the genus *Thalassospira*. *Int. J. Syst. Evol. Microbiol.* 64, 107–115. doi: 10.1099/ijs.0.056028-0
- Tsubouchi, T., Shimane, Y., Mori, K., Miyazaki, M., Tame, A., Uematsu, K., et al. (2013). *Loktanelle cinnabarina* sp. nov., isolated from a deep seafloor sediment, and emended description of the genus *Loktanelle*. *Int. J. Syst. Evol. Microbiol.* 63, 1390–1395. doi: 10.1099/ijs.0.043174-0
- Uchida, T., Uchiyama, T., Kumano, K., and Walker, D. H. (1992). *Rickettsia japonica* sp. nov., the etiological agent of spotted fever group rickettsiosis in Japan. *Int. J. Syst. Bacteriol.* 42, 303–305. doi: 10.1099/00207713-42-2-303
- Uchino, Y., Hamada, T., and Yokota, A. (2002). Proposal of *Pseudorhodobacter ferrugineus* gen. nov., comb. nov., for a non-photosynthetic marine bacterium, *Agrobacterium ferrugineum*, related to the genus *Rhodobacter*. *J. Gen. Appl. Microbiol.* 48, 309–319. doi: 10.2323/jgam.48.309
- Uchino, Y., Hirata, A., Yokota, A., and Sugiyama, J. (1998). Reclassification of marine *Agrobacterium* species: proposals of *Stappia stellulata* gen. nov., comb. nov., *Stappia aggregata* sp. nov., nom. rev., *Ruegeria atlantica* gen. nov., comb. nov., *Ruegeria gelatinovora* comb. nov., *Ruegeria algicola* comb. nov., and *Ahrensia kieliense* gen. nov., sp. nov., nom. rev. *J. Gen. Appl. Microbiol.* 44, 201–210. doi: 10.2323/jgam.44.201
- Ueki, A., Kodama, Y., Kaku, N., Shiromura, T., Satoh, A., Watanabe, K., et al. (2010). *Rhizomicrobium palustre* gen. nov., sp. nov., a facultatively anaerobic, fermentative stalked bacterium in the class *Alphaproteobacteria* isolated from rice plant roots. *J. Gen. Appl. Microbiol.* 56, 193–203. doi: 10.2323/jgam.56.193
- Umamoto, T., Nakazawa, F., Hoshino, E., Okada, K., Fukunaga, M., and Namikawa, I. (1997). *Treponema medium* sp. nov., isolated from human subgingival dental plaque. *Int. J. Syst. Bacteriol.* 47, 67–72. doi: 10.1099/00207713-47-1-67
- Urakami, T., Araki, H., Oyanagi, H., Suzuki, K., and Komagata, K. (1992). Transfer of *Pseudomonas aminovorans* (den Dooren de Jong 1926) to *Aminobacter* gen. nov. as *Arminobacter aminovorans* comb. nov. and description of *Aminobacter aganoensis* sp. nov. and *Aminobacter niigataensis* sp. nov. *Int. J. Syst. Bacteriol.* 42, 84–92. doi: 10.1099/00207713-42-1-84
- Urakami, T., and Komagata, K. (1984). *Protomonas*, a new genus of facultatively methylotrophic bacteria. *Int. J. Syst. Bacteriol.* 34, 188–201. doi: 10.1099/00207713-34-2-188
- Urakami, T., Oyanagi, H., Araki, H., Suzuki, K.-I., and Komagata, K. (1990). Recharacterization and emended description of the genus *Mycoplana* and description of two new species, *Mycoplana ramosa* and *Mycoplana segnis*. *Int. J. Syst. Bacteriol.* 40, 434–442. doi: 10.1099/00207713-40-4-434
- Urakami, T., Tamaoka, J., Suzuki, K.-I., and Komagata, K. (1989). *Paracoccus alcaliphilus* sp. nov., an alkaliphilic and facultatively methylotrophic bacterium. *Int. J. Syst. Bacteriol.* 39, 116–121. doi: 10.1099/00207713-39-2-116
- Urbance, J. W., Bratina, B. J., Stoddard, S. F., and Schmidt, T. M. (2001). Taxonomic characterization of *Ketogulonigenium vulgare* gen. nov., sp. nov. and *Ketogulonigenium robustum* sp. nov., which oxidize L-sorbose to 2-keto-L-gulonic acid. *Int. J. Syst. Evol. Microbiol.* 51, 1059–1070. doi: 10.1099/00207713-51-3-1059
- Urdiain, M., López-López, A., Gonzalo, C., Busse, H.-J., Langer, S., Kämpfer, P., et al. (2008). Reclassification of *Rhodobium marinum* and *Rhodobium pfennigii* as *Afifella marina* gen. nov. comb. nov. and *Afifella pfennigii* comb. nov., a new genus of photoheterotrophic *Alphaproteobacteria* and emended descriptions of *Rhodobium*, *Rhodobium orientis* and *Rhodobium gokarnense*. *Syst. Appl. Microbiol.* 31, 339–351. doi: 10.1016/j.syapm.2008.07.002
- Urios, L., Michotey, V., Intertaglia, L., Lesongeur, F., and Lebaron, P. (2010). *Thalassobaculum salexigens* sp. nov., a new member of the family *Rhodospirillaceae* from the NW Mediterranean Sea, and emended description of the genus *Thalassobaculum*. *Int. J. Syst. Evol. Microbiol.* 60, 209–213. doi: 10.1099/ijs.0.011460-0
- Urios, L., Michotey, V., Intertalia, L., Lesongeur, F., and Lebaron, P. (2008). *Nisaea denitrificans* gen. nov., sp. nov. and *Nisaea nitritireducens* sp. nov., two novel members of the class *Alphaproteobacteria* from the Mediterranean Sea. *Int. J. Syst. Evol. Microbiol.* 58, 2336–2341. doi: 10.1099/ijs.0.64592-0
- Ushiba, Y., Takahara, Y., and Ohta, H. (2003). *Sphingobium amiense* sp. nov., a novel nonylphenol-degrading bacterium isolated from a river sediment. *Int. J. Syst. Evol. Microbiol.* 53, 2045–2048. doi: 10.1099/ijs.0.02581-0
- Vaas, L. A. I., Sikorski, J., Hofner, B., Fiebig, A., Buddrhu, N., Klenk, H.-P., et al. (2013). oprn: an R package for analysing OmniLog\$phenotype microarray data. *Bioinformatics* 29, 1823–1824. doi: 10.1093/bioinformatics/btt291

- Valverde, A., Igual, J. M., Peix, A., Cervantes, E., and Velázquez, E. (2006). *Rhizobium lusitanum* sp. nov. a bacterium that nodulates *Phaseolus vulgaris*. *Int. J. Syst. Evol. Microbiol.* 56, 2631–2637. doi: 10.1099/ijs.0.64402-0
- van Berkum, P., Beyene, D., Bao, G., Campbell, T. A., and Eardly, B. D. (1998). *Rhizobium mongolense* sp. nov. is one of three rhizobial genotypes identified which nodulate and form nitrogen-fixing symbioses with *Medicago ruthenica* [(L.) Ledebour]. *Int. J. Syst. Bacteriol.* 48, 13–22. doi: 10.1099/00207713-48-1-13
- van Niel, C. B. (1944). The culture, general physiology, morphology, and classification of the non-sulfur purple and brown bacteria. *Bacteriol. Rev.* 8, 1–118. doi: 10.1128/mmmbr.8.1.1-118.1944
- Van Trappen, S., Mergaert, J., and Swings, J. (2004). *Loktanelia salsilacus* gen. nov., sp. nov., *Loktanelia fryxellensis* sp. nov. and *Loktanelia vestfoldensis* sp. nov., new members of the *Rhodobacter* group, isolated from microbial mats in Antarctic lakes. *Int. J. Syst. Evol. Microbiol.* 54, 1263–1269. doi: 10.1099/ijs.0.03006-0
- Vandamme, P., Pot, B., Gillis, M., De Vos, P., Kersters, K., and Swings, J. (1996). Polyphasic taxonomy, a consensus approach to bacterial systematics. *Microbiol. Rev.* 60, 407–438. doi: 10.1128/mmmbr.60.2.407-438.1996
- Vandecastelaere, I., Nercessian, O., Segart, E., Achouak, W., Faimali, M., and Vandamme, P. (2008a). *Ruegeria scottomollicae* sp. nov., isolated from a marine electroactive biofilm. *Int. J. Syst. Evol. Microbiol.* 58, 2726–2733. doi: 10.1099/ijs.0.65843-0
- Vandecastelaere, I., Nercessian, O., Segart, E., Achouak, W., Mollica, A., Faimali, M., et al. (2009). *Nautella italica* gen. nov., sp. nov., isolated from a marine electroactive biofilm. *Int. J. Syst. Evol. Microbiol.* 59, 811–817. doi: 10.1099/ijs.0.002683-0
- Vandecastelaere, I., Segart, E., Mollica, A., Faimali, M., and Vandamme, P. (2008b). *Leisingera aquimarina* sp. nov., isolated from a marine electroactive biofilm, and emended descriptions of *Leisingera methylohalidivorans* Schaefer et al. 2002, *Phaeobacter daeponenensis* Yoon et al. 2007 and *Phaeobacter inhibens* Martens et al., 2006. *Int. J. Syst. Evol. Microbiol.* 58, 2788–2793. doi: 10.1099/ijs.0.65844-0
- Vasil'eva, L. V., Lafitskaya, T. N., and Namsaraev, B. B. (1980). *Angulomicrobium tetraedrale*, a new genus of budding bacteria with radial cell symmetry. *Mikrobiologiya* 48, 843–849.
- Vasilyeva, L. V. (1985). *Stella*, a new genus of soil prosthecobacteria, with proposals for *Stella humosa* sp. nov. and *Stella vacuolata* sp. nov. *Int. J. Syst. Evol. Microbiol.* 35, 518–521. doi: 10.1099/00207713-35-4-518
- Vasilyeva, L. V., Omelchenko, M. V., Berestovskaya, Y. Y., Lysenko, A. M., Abraham, W.-R., Dedysh, S. N., et al. (2006). *Asticcacaulis benevestitus* sp. nov., a psychrotolerant, dimorphic, prosthecate bacterium from tundra wetland soil. *Int. J. Syst. Evol. Microbiol.* 56, 2083–2088. doi: 10.1099/ijs.0.64122-0
- Vekeman, B., Kerckhof, F. M., Cremers, G., de Vos, P., Vandamme, P., Boon, N., et al. (2016). New methyloceanibacter diversity from North Sea sediments includes methanotroph containing solely the soluble methane monooxygenase. *Environ. Microbiol.* 18, 4523–4536. doi: 10.1111/1462-2920.13485
- Velasco, J., Romero, C., Leiva, J., Diaz, R., Moriyon, I., and Lopez-Goni, I. (1998). Evaluation of the relatedness of *Brucella* spp. and *Ochrobactrum anthropi* and description of *Ochrobactrum intermedium* sp. nov., a new species with a closer relationship to *Brucella* spp. *Int. J. Syst. Bacteriol.* 48, 759–768. doi: 10.1099/00207713-48-3-759
- Vences, M., Guayasamin, J. M., Miralles, A., and De La Riva, I. (2013). To name or not to name: criteria to promote economy of change in Linnaean classification schemes. *Zootaxa* 3636, 201–244. doi: 10.11646/zootaxa.3636.2.1
- Venkata Ramana, V., Anil Kumar, P., Srinivas, T. N. R., Sasikala, C., and Ramana, C. V. (2009). *Rhodobacter aestuarii* sp. nov., a phototrophic Alphaproteobacterium isolated an estuarine environment. *Int. J. Syst. Evol. Microbiol.* 59, 1133–1136. doi: 10.1099/ijs.0.004507-0
- Venkata Ramana, V., Chakravarthy, S. K., Raj, P. S., Kumar, B. V., Shobha, E., Ramaprasad, E. V. V., et al. (2012). Descriptions of *Rhodopseudomonas parapalustris* sp. nov., *Rhodopseudomonas harwoodiae* sp. nov. and *Rhodopseudomonas pseudopalustris* sp. nov., and emended description of *Rhodopseudomonas palustris*. *Int. J. Syst. Evol. Microbiol.* 62, 1790–1798. doi: 10.1099/ijs.0.026815-0
- Venkata Ramana, V., Sasikala, C., and Ramana, C. V. (2008). *Rhodobacter maris* sp. nov., a phototrophic Alphaproteobacterium isolated from a marine habitat of India. *Int. J. Syst. Evol. Microbiol.* 58, 1719–1722. doi: 10.1099/ijs.0.65838-0
- Venkata Ramana, V., Sasikala, C., Takaichi, S., and Ramana, C. V. (2010). *Roseomonas aestuarii* sp. nov., a bacteriochlorophyll-a containing alphaproteobacterium isolated from an estuarine habitat of India. *Syst. Appl. Microbiol.* 33, 198–203. doi: 10.1016/j.syapm.2009.09.004
- Verger, J.-M., Grimont, F., Grimont, P. A. D., and Grayon, M. (1985). *Brucella*, a monospecific genus as shown by deoxyribonucleic acid hybridization. *Int. J. Syst. Bacteriol.* 35, 292–295. doi: 10.1099/00207713-35-3-292
- Verma, M., Kumar, M., Dadhwal, M., Kaur, J., and Lal, R. (2009). *Devosia albugilva* sp. nov. and *Devosia crocina* sp. nov., isolated from a hexachlorocyclohexane dump site. *Int. J. Syst. Evol. Microbiol.* 59, 795–799. doi: 10.1099/ijs.0.005447-0
- Veyisoglu, A., Camas, M., Tatar, D., Guven, K., Sazak, A., and Sahin, N. (2013). *Methylobacterium tarhaniae* sp. nov., isolated from arid soil. *Int. J. Syst. Evol. Microbiol.* 63, 2823–2828. doi: 10.1099/ijs.0.049551-0
- Vidal, C., Chantreuil, C., Berge, O., Mauré, L., Escarré, J., Béna, G., et al. (2009). *Mesorhizobium metallidurans* sp. nov., a metal-resistant symbiont of *Anthyllis vulneraria* growing on metallicolous soil in Languedoc, France. *Int. J. Syst. Evol. Microbiol.* 59, 850–855. doi: 10.1099/ijs.0.003327-0
- Visser't Hooft, F. (1925). *Biochemische Onderzoekingen over het geslacht Acetobacter*. Delft: Meinema.
- Vorobev, A. V., Baani, M., Doronina, N. V., Brady, A. L., Liesack, W., Dunfield, P. F., et al. (2011). *Methyloferula stellat* gen. nov., sp. nov., an acidophilic, obligately methanotrophic bacterium that possesses only a soluble methane monooxygenase. *Int. J. Syst. Evol. Microbiol.* 61, 2456–2463. doi: 10.1099/ijs.0.028118-0
- Wagner-Döbler, I., Rheims, H., Felske, A., El-Ghezal, A., Flade-Schröder, D., Laatsch, H., et al. (2004). *Oceanibulbus indolifex* gen. nov., sp. nov., a North Sea Alphaproteobacterium that produces bioactive metabolites. *Int. J. Syst. Evol. Microbiol.* 54, 1177–1184. doi: 10.1099/ijs.0.02850-0
- Wakao, N., Nagasawa, N., Matsuura, T., Matsukura, H., Matsumoto, T., Hiraishi, A., et al. (1994). *Acidiphilium multivorum* sp. nov., an acidophilic chemoorganotrophic bacterium from pyritic acid mine drainage. *J. Gen. Appl. Microbiol.* 40, 143–159. doi: 10.2323/jgam.40.143
- Wang, B., Sun, F., Lai, Q., Du, Y., Liu, X., Li, G., et al. (2010). *Roseovarius nanhaiticus* sp. nov., a member of the *Roseobacter* clade isolated from marine sediment. *Int. J. Syst. Evol. Microbiol.* 60, 1289–1295. doi: 10.1099/ijs.0.012930-0
- Wang, D., Liu, H., Zheng, S., and Wang, G. (2014). *Paenirhodobacter enshiensis* gen. nov., sp. nov., a non-photosynthetic bacterium isolated from soil, and emended descriptions of the genera *Rhodobacter* and *Haematobacter*. *Int. J. Syst. Evol. Microbiol.* 64, 551–558. doi: 10.1099/ijs.0.050351-0
- Wang, F. Q., Wang, E. T., Liu, J., Chen, Q., Sui, X. H., Chen, W. F., et al. (2007). *Mesorhizobium albiziae* sp. nov., a novel bacterium that nodulates *Albizia kalkora* in a subtropical region of China. *Int. J. Syst. Evol. Microbiol.* 57, 1192–1199. doi: 10.1099/ijs.0.64363-0
- Wang, G., Tang, M., Wu, H., Dai, S., Li, T., Chen, C., et al. (2016). *Pyruvibacter mobilis* gen. nov., sp. nov., a marine bacterium from the culture broth of *Picochlorum* sp. 122. *Int. J. Syst. Evol. Microbiol.* 66, 184–188. doi: 10.1099/ijs.0.000692
- Wang, G., van Dam, A. P., Le Fleche, A., Postic, D., Peter, O., Baranton, G., et al. (1997). Genetic and phenotypic analysis of *Bowelia valaisiana* sp. nov. (*Bowelia* genomic groups VS116 and M19). *Int. J. Syst. Bacteriol.* 47, 926–932. doi: 10.1099/00207713-47-4-926
- Wang, G., Wang, Y., Su, H., Wu, H., Li, T., Liang, J., et al. (2017). *Butyratibacter algicola* gen. nov., sp. nov., a marine bacterium from the culture broth of *Picochlorum* sp. 122. *Int. J. Syst. Evol. Microbiol.* 67, 3209–3213. doi: 10.1099/ijs.0.002081
- Wang, J., Zhang, J., Ding, K., Xin, Y., and Pang, H. (2012). *Brevundimonas viscosa* sp. nov., isolated from saline soil. *Int. J. Syst. Evol. Microbiol.* 62, 2475–2479. doi: 10.1099/ijs.0.035352-0
- Wang, L., Liu, Y., Shi, X., Wang, Y., Zheng, Y., Dai, X., et al. (2016). *Xuhuaishuia manganoxidans* gen. nov., sp. nov., a manganese-oxidizing bacterium isolated from deep-sea sediments from the Pacific Polymetallic Nodule Province. *Int. J. Syst. Evol. Microbiol.* 66, 1521–1526. doi: 10.1099/ijs.0.000912

- Wang, L., Liu, Y., Wang, Y., Dai, X., and Zhang, X.-H. (2015). *Celeribacter manganoxidans* sp. nov., a manganese-oxidizing bacterium isolated from deep-sea sediment of a polymetallic nodule province. *Int. J. Syst. Evol. Microbiol.* 65, 4180–4185. doi: 10.1099/ijsem.0.000558
- Wang, R., Chang, Y. L., Zheng, W. T., Zhang, D., Zhang, X. X., Sui, X. H., et al. (2013). *Bradyrhizobium arachidis* sp. nov., isolated from effective nodules of *Arachis hypogaea* grown in China. *Syst. Appl. Microbiol.* 36, 101–105. doi: 10.1016/j.syapm.2012.10.009
- Wang, Y., Tang, S.-K., Lou, K., Mao, P.-H., Jin, X., Jiang, C.-L., et al. (2009). *Paracoccus saliphilus* sp. nov., a halophilic bacterium isolated from a saline soil. *Int. J. Syst. Evol. Microbiol.* 59, 1924–1928. doi: 10.1099/ijms.0.005918-0
- Wang, Y. C., Wang, F., Hou, B. C., Wang, E. T., Chen, W. F., Sui, X. H., et al. (2013). Proposal of *Ensifer psoraleae* sp. nov., *Ensifer sesbaniae* sp. nov., *Ensifer morelense* comb. nov. and *Ensifer americanum* comb. nov. *Syst. Appl. Microbiol.* 36, 467–473. doi: 10.1016/j.syapm.2013.05.001
- Wang, Y. X., Huang, F. Q., Nogi, Y., Pang, S. J., Wang, P. K., and Lv, J. (2015). *Youhaella tibetensis* gen. nov., sp. nov., isolated from subsurface sediment. *Int. J. Syst. Evol. Microbiol.* 65, 2048–2055. doi: 10.1099/ijms.0.000219
- Wang, Y.-X., Liu, J.-H., Zhang, X.-X., Chen, Y.-G., Wang, Z.-G., Chen, Y., et al. (2009). *Fodinicurvata sediminis* gen. nov., sp. nov. and *Fodinicurvata fenggangensis* sp. nov., poly- β -hydroxybutyrate-producing bacteria in the family Rhodospirillaceae. *Int. J. Syst. Evol. Microbiol.* 59, 2575–2581. doi: 10.1099/ijms.0.009340-0
- Wayne, L. G., Brenner, D. J., Colwell, R. R., Grimont, P. A. D., Kandler, O., Krichevsky, M. I., et al. (1987). Report of the ad hoc committee on reconciliation of approaches to bacterial systematics. *Int. J. Syst. Bacteriol.* 37, 463–464. doi: 10.1099/00207713-37-4-463
- Wei, G. H., Tan, Z. Y., Zhu, M. E., Wang, E. T., Han, S. Z., and Chen, W. X. (2003). Characterization of rhizobia isolated from legume species within the genera *Astragalus* and *Lespedeza* grown in the Loess Plateau of China and description of *Rhizobium loessense* sp. nov. *Int. J. Syst. Evol. Microbiol.* 53, 1575–1583. doi: 10.1099/ijms.0.02031-0
- Wei, S., Wang, T., Liu, H., Zhang, C., Guo, J., Wang, Q., et al. (2015). *Sphingomonas hengshuiensis* sp. nov., isolated from lake wetland. *Int. J. Syst. Evol. Microbiol.* 65, 4644–4649. doi: 10.1099/ijsem.0.000626
- Weiner, R. M., Devine, R. A., Powell, D. M., Dagan, L., and Moore, R. L. (1985). *Hyphomonas oceanitis* sp. nov., *Hyphomonas hirschiensis* sp. nov., and *Hyphomonas jannaschiana* sp. nov. *Int. J. Syst. Bacteriol.* 35, 237–243. doi: 10.1007/s10482-014-0236-y
- Weiner, R. M., Melick, M., O'Neill, K., and Quintero, E. (2000). *Hyphomonas adhaerens* sp. nov., *Hyphomonas johnsonii* sp. nov. and *Hyphomonas rosenbergii* sp. nov., marine budding and prosthecate bacteria. *Int. J. Syst. Evol. Microbiol.* 50, 459–469. doi: 10.1099/00207713-50-2-459
- Welch, D. F., Carroll, K. C., Hofmeister, E. K., Persing, D. H., Robison, D. A., Steigerwalt, A. G., et al. (1999). Isolation of a new subspecies, *Bartonella vinsonii* subsp. arupensis, from a cattle rancher: identity with isolates found in conjunction with *Borrelia burgdorferi* and *Babesia microti* among naturally infected mice. *J. Clin. Microbiol.* 37, 2598–2601. doi: 10.1128/jcm.37.8.2598-2601.1999
- Weon, H.-Y., Kim, B.-Y., Hong, S.-B., Joa, J.-H., Nam, S.-S., Lee, K. H., et al. (2007). *Skermanella aerolata* sp. nov., isolated from air, and emended description of the genus *Skermanella*. *Int. J. Syst. Evol. Microbiol.* 57, 1539–1542. doi: 10.1099/ijms.0.064676-0
- Weon, H.-Y., Kim, B.-Y., Kwon, S.-W., Go, S.-J., Koo, B.-S., and Stackebrandt, E. (2008a). *Phenylobacterium composti* sp. nov., isolated from cotton waste compost in Korea. *Int. J. Syst. Evol. Microbiol.* 58, 2301–2304. doi: 10.1099/ijms.0.065530-0
- Weon, H.-Y., Kim, B.-Y., Yoo, S.-H., Kim, J.-S., Kwon, S.-W., Go, S.-J., et al. (2006). *Loktanella koreensis* sp. nov., isolated from sea sand in Korea. *Int. J. Syst. Evol. Microbiol.* 56, 2199–2202. doi: 10.1099/ijms.0.064276-0
- Weon, H.-Y., Lee, C.-M., Hong, S.-B., Kim, B.-Y., Yoo, S.-H., Kwon, S.-W., et al. (2008b). *Kaistia soli* sp. nov., isolated from a wetland in Korea. *Int. J. Syst. Evol. Microbiol.* 58, 1522–1524. doi: 10.1099/ijms.0.065366-0
- Wichlacz, P. L., Unz, R. F., and Langworthy, T. A. (1986). *Acidiphilium angustum* sp. nov., *Acidiphilium facilis* sp. nov., and *Acidiphilium rubrum* sp. nov.: acidophilic heterotrophic bacteria isolated from acidic coal mine drainage. *Int. J. Syst. Bacteriol.* 36, 197–201. doi: 10.1099/00207713-36-2-197
- Wiegel, J., Wilke, D., Baumgarten, J., Opitz, R., and Schlegel, H. G. (1978). Transfer of the nitrogen-fixing hydrogen bacterium *Corynebacterium autotrophicum* Baumgarten et al. to *Xanthobacter* gen. nov. *Int. J. Syst. Evol. Microbiol.* 28, 573–581. doi: 10.1099/00207713-28-4-573
- Wiese, J., Thiel, V., Gärtner, A., Schmaljohann, R., and Imhoff, J. F. (2009). *Kiloniella laminariae* gen. nov., sp. nov., an Alphaproteobacterium from the marine macroalga *Laminaria saccharina*. *Int. J. Syst. Evol. Microbiol.* 59, 350–356. doi: 10.1099/ijms.0.001651-0
- Wiley, E. O., and Lieberman, B. S. (2011). *Phylogenetics: Theory and Practice of Phylogenetic Systematics*, 2nd Edn. Hoboken, NJ: John Wiley & Sons, Inc.
- Willems, A. (2006). The taxonomy of rhizobia: an overview. *Plant Soil* 287, 3–14. doi: 10.1007/s11104-006-9058-7
- Williams, K. P., Sobral, B. W., and Dickerman, A. W. (2007). A robust species tree for the Alphaproteobacteria. *J. Bacteriol.* 189, 4578–4586. doi: 10.1128/JB.00269-07
- Williams, T. J., Lefèvre, C. T., Zhao, W., Beveridge, T. J., and Bazylinski, D. A. (2012). *Magnetospira thiophila* gen. nov., sp. nov., a marine magnetotactic bacterium that represents a novel lineage within the Rhodospirillaceae (Alphaproteobacteria). *Int. J. Syst. Evol. Microbiol.* 62, 2443–2450. doi: 10.1099/ijms.0.037697-0
- Winogradsky, S. (1892). Contributions à la morphologie des organismes de la nitrification. *Arkiv Biol. Nauk* 1, 87–137.
- Winslow, C.-E. A., Broadhurst, J., Buchanan, R. E., Krumwiede, C., Rogers, L. A., and Smith, G. H. (1917). The families and genera of the bacteria: preliminary report of the committee of the society of american bacteriologist on characterization and classification of bacterial types. *J. Bacteriol.* 2, 505–566. doi: 10.1128/jb.2.5.505-566.1917
- Wirth, J. S., and Whitman, W. B. (2018). Phylogenomic analyses of a clade within the roseobacter group suggest taxonomic reassignments of species of the genera *Aestuaria*, *Citricella*, *Loktanella*, *Nautella*, *Pelagibaca*, *Ruegeria*, *Thalassobius*, *Thiobacimonas* and *Tropicibacter*, and the proposal. *Int. J. Syst. Evol. Microbiol.* 68, 2393–2411. doi: 10.1099/ijsem.0.002833
- Wolf, Y. I., Rogozin, I. B., Grishin, N. V., Tatusov, R. L., and Koonin, E. V. (2001). Genome trees constructed using five different approaches suggest new major bacterial clades. *BMC Evol. Biol.* 1:8. doi: 10.1186/1471-2148-1-8
- Wolf, Y. I., Rogozin, I. B., Grishin, N. V., and Koonin, E. V. (2002). Genome trees and the tree of life. *Trends Genet.* 18, 472–479. doi: 10.1016/S0168-9525(02)02744-0
- Wong, S. K., Yoshizawa, S., Nakajima, Y., Cuadra, M. J., Nogi, Y., Nakamura, K., et al. (2018). *Amylibacter kogurei* sp. nov., a novel marine Alphaproteobacterium isolated from the coastal sea surface microlayer of a marine inlet. *Int. J. Syst. Evol. Microbiol.* 68, 2872–2877. doi: 10.1099/ijsem.0.002911
- Woo, S. G., Ten, L. N., Park, J., and Lee, M. (2011). *Ochrobactrum daejeonense* sp. nov., a nitrate-reducing bacterium isolated from sludge of a leachate treatment plant. *Int. J. Syst. Evol. Microbiol.* 61, 2690–2696. doi: 10.1099/ijms.0.025510-0
- Wood, S. (1994). Monophyly and comparison between trees. *Cladistics* 10, 339–346. doi: 10.1006/clad.1994.1024
- Wu, X.-L., Yu, S.-L., Gu, J., Zhao, G.-F., and Chi, C.-Q. (2009). *Filomicrobium insigne* sp. nov., isolated from an oil-polluted saline soil. *Int. J. Syst. Evol. Microbiol.* 59, 300–305. doi: 10.1099/ijms.0.065758-0
- Wu, Y.-H., Jian, S.-L., Meng, F.-X., Maripatay, Tohty, D., Wang, C.-S., et al. (2016). *Kordiimonas lipolytica* sp. nov., isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 66, 2198–2204. doi: 10.1099/ijsem.0.001007
- Wu, Y.-H., Meng, F.-X., Xu, L., Zhang, X.-Q., Wang, C.-S., Oren, A., et al. (2013). *Roseivivax pacificus* sp. nov., isolated from deep-sea sediment. *Int. J. Syst. Evol. Microbiol.* 63, 4574–4579. doi: 10.1099/ijms.0.052274-0
- Wu, Y.-H., Xu, L., Meng, F.-X., Zhang, D.-S., Wang, C.-S., Oren, A., et al. (2014). *Altererythrobacter atlanticus* sp. nov., isolated from deep-sea sediment. *Int. J. Syst. Evol. Microbiol.* 64, 116–121. doi: 10.1099/ijms.0.052951-0
- Wu, Y.-H., Xu, L., Zhou, P., Wang, C.-S., Oren, A., and Xu, X.-W. (2015). *Brevirhabdus pacifica* gen. nov., sp. nov., isolated from deep-sea sediment in a hydrothermal vent field. *Int. J. Syst. Evol. Microbiol.* 65, 3645–3651. doi: 10.1099/ijsem.0.000469
- Wu, Z.-G., Wang, F., Gu, C.-G., Zhang, Y.-P., Yang, Z.-Z., Wu, X.-W., et al. (2014). *Aquamicrobium terrae* sp. nov., isolated from the polluted soil near a chemical factory. *Antonie Van Leeuwenhoek* 105, 1131–1137. doi: 10.1007/s10482-014-0174-8

- Wyss, C., Choi, B. K., Schüpbach, P., Guggenheim, B., and Göbel, U. B. (1996). *Treponema maltophilum* sp. nov., a small oral Spirochete isolated from human periodontal lesions. *Int. J. Syst. Bacteriol.* 46, 745–752. doi: 10.1099/00207713-46-3-745
- Wyss, C., Choi, B.-K., Schüpbach, P., Moter, A., Guggenheim, B., and Göbel, U. B. (1999). *Treponema lecithinolyticum* sp. nov., a small saccharolytic spirochaete with phospholipase A and C activities associated with periodontal diseases. *Int. J. Syst. Bacteriol.* 49, 1329–1339. doi: 10.1099/00207713-49-4-1329
- Wyss, C., Moter, A., Choi, B.-K., Dewhirst, F. E., Xue, Y., Schüpbach, P., et al. (2004). *Treponema putidum* sp. nov., a medium-sized proteolytic spirochaete isolated from lesions of human periodontitis and acute necrotizing ulcerative gingivitis. *Int. J. Syst. Evol. Microbiol.* 54, 1117–1122. doi: 10.1099/ijs.0.02806-0
- Xi, J., Wang, Y., Yang, X., Tao, Y., Shao, Y., and Feng, F. (2017). *Mongoliimonas terrestris* gen. nov., sp. nov., isolated from desert soil. *Int. J. Syst. Evol. Microbiol.* 67, 3010–3014. doi: 10.1099/ijsem.0.002067
- Xi, X.-D., Dong, W.-J., Zhang, J., Huang, Y., and Cui, Z.-J. (2013). *Taonella mepensis* gen. nov., sp. nov., a member of the family Rhodospirillaceae isolated from activated sludge. *Int. J. Syst. Evol. Microbiol.* 63, 2472–2476. doi: 10.1099/ijs.0.047803-0
- Xie, C.-H., and Yokota, A. (2005). *Pleomorphomonas oryzae* gen. nov., sp. nov., a nitrogen-fixing bacterium isolated from paddy soil of *Oryza sativa*. *Int. J. Syst. Evol. Microbiol.* 55, 1233–1237. doi: 10.1099/ijs.0.63406-0
- Xie, C.-H., and Yokota, A. (2006). *Sphingomonas azotifigens* sp. nov., a nitrogen-fixing bacterium isolated from the roots of *Oryza sativa*. *Int. J. Syst. Evol. Microbiol.* 56, 889–893. doi: 10.1099/ijs.0.64056-0
- Xu, H., Jiang, L., Li, S., Zeng, X., and Shao, Z. (2015). *Mameliella atlantica* sp. nov., a marine bacterium of the *Roseobacter* clade isolated from deep-sea sediment of the South Atlantic Ocean. *Int. J. Syst. Evol. Microbiol.* 65, 2255–2259. doi: 10.1099/ijs.0.000248
- Xu, H. Y., Chen, L. P., Fu, S. Z., Fan, H. X., Zhou, Y. G., Liu, S. J., et al. (2009). *Zhangella mobilis* gen. nov., sp. nov., a new member of the family Hyphomicrobiaceae isolated from coastal seawater. *Int. J. Syst. Evol. Microbiol.* 59, 2297–2301. doi: 10.1099/ijs.0.004366-0
- Xu, M., Xin, Y., Yu, Y., Zhang, J., Zhou, Y., Liu, H., et al. (2010). *Erythrobacter nanhaisediminis* sp. nov., isolated from marine sediment of the South China Sea. *Int. J. Syst. Evol. Microbiol.* 60, 2215–2220. doi: 10.1099/ijs.0.014027-0
- Xu, X.-W., Huo, Y.-Y., Wang, C.-S., Oren, A., Cui, H.-L., Vedler, E., et al. (2011). *Pelagibacterium halotolerans* gen. nov. sp. nov. and *Pelagibacterium luteolum* sp. nov., novel members of the family Hyphomicrobiaceae. *Int. J. Syst. Evol. Microbiol.* 61, 1817–1822. doi: 10.1099/ijs.0.023325-0
- Xu, X.-W., Wu, M., and Oren, A. (2014). “The family kordiimonadaceae,” in *The Prokaryotes*, eds E. Rosenberg, E. F. DeLong, S. Lory, E. Stackebrandt, and F. Thompson (Berlin: Springer Berlin Heidelberg), 307–312. doi: 10.1007/978-3-642-30197-1_261
- Xu, X.-W., Wu, Y.-H., Wang, C.-S., Wang, X.-G., Oren, A., and Wu, M. (2009). *Croceicoccus marinus* gen. nov., sp. nov. a yellow-pigmented bacterium from deep-sea sediment, and emended description of the family Erythrobacteraceae. *Int. J. Syst. Evol. Microbiol.* 59, 2247–2253. doi: 10.1099/ijs.0.004267-0
- Xue, H., Piao, C., Guo, M., Wang, L., Fang, W., and Li, Y. (2016). Description of *Altererythrobacter aerius* sp. nov., isolated from air, and emended description of the genus *Altererythrobacter*. *Int. J. Syst. Evol. Microbiol.* 66, 4543–4548. doi: 10.1099/ijsem.0.001388
- Xue, X., Zhang, K., Cai, F., Dai, J., Wang, Y., Rahman, E., et al. (2012). *Altererythrobacter xinjiangensis* sp. nov., isolated from desert sand, and emended description of the genus *Altererythrobacter*. *Int. J. Syst. Evol. Microbiol.* 62, 28–32. doi: 10.1099/ijs.0.025437-0
- Yabuuchi, E., Kosako, Y., Naka, T., Suzuki, S., and Yano, I. (1999). Proposal of *Sphingomonas suberifaciens* (van Bruggen, Jochimsen and Brown 1990) comb. nov., *Sphingomonas natatoria* (Sly 1985) comb. nov., and Emendation of the Genus *Sphingomonas*. *Microbiol. Immunol.* 43, 339–349. doi: 10.1111/j.1348-0421.1999.tb02414.x
- Yabuuchi, E., Yamamoto, H., Terakubo, S., Okamura, N., Naka, T., Fujiwara, N., et al. (2001). Proposal of *Sphingomonas wittichii* sp. nov. for strain RW1T, known as a dibenzo-p-dioxin metabolizer. *Int. J. Syst. Evol. Microbiol.* 51, 281–292. doi: 10.1099/00207713-51-2-281
- Yabuuchi, E., Yano, I., Oyaizu, H., Hashimoto, Y., Ezaki, T., and Yamamoto, H. (1990). Proposals of *Sphingomonas paucimobilis* gen. nov. and comb. nov., *Sphingomonas parapaucimobilis* sp. nov., *Sphingomonas yanoikuyae* sp. nov., *Sphingomoas adhaesiva* sp. nov., *Sphingomonas capsulata* comb. nov. and two genospecies of the genus *Sphingomonas*. *Microbiol. Immunol.* 34, 99–119. doi: 10.1111/j.1348-0421.1990.tb00996.x
- Yamada, K., Fukuda, W., Kondo, Y., Miyoshi, Y., Atomi, H., and Imanaka, T. (2011). *Constrictibacter antarcticus* gen. nov., sp. nov., a cryptoendolithic micro-organism from Antarctic white rock. *Int. J. Syst. Evol. Microbiol.* 61, 1973–1980. doi: 10.1099/ijs.0.026625-0
- Yamada, Y., Hoshino, K., and Ishikawa, T. (1997). The phylogeny of acetic acid bacteria based on the partial sequences of 16S ribosomal RNA: the elevation of the subgenus *Gluconoacetobacter* to the generic level. *Biosci. Biotechnol. Biochem.* 61, 1244–1251. doi: 10.1271/bbb.61.1244
- Yamada, Y., Yukphan, P., Vu, H. T. L., Muramatsu, Y., Ochaikul, D., Tanasupawat, S., et al. (2012). Description of *Komagataeibacter* gen. nov., with proposals of new combinations (Acetobacteraceae). *J. Gen. Appl. Microbiol.* 58, 397–404. doi: 10.2323/jgam.58.397
- Yamashita, S. I., Uchimura, T., and Komagata, K. (2004). Emendation of the genus *Acidomonas* Urakami, Tamaoka, Suzuki and Komagata 1989. *Int. J. Syst. Evol. Microbiol.* 54, 865–870. doi: 10.1099/ijs.0.02946-0
- Yang, D.-C., Im, W.-T., Kim, M. K., Ohta, H., and Lee, S.-T. (2006). *Sphingomonas soli* sp. nov., a β -glucosidase-producing bacterium in the family Sphingomonadaceae in the α -4 subgroup of the *Proteobacteria*. *Int. J. Syst. Evol. Microbiol.* 56, 703–707. doi: 10.1099/ijs.0.63839-0
- Yang, S., Doolittle, R. F., and Bourne, P. E. (2005). Phylogeny determined by protein domain content. *Proc. Natl. Acad. Sci. U.S.A.* 102, 373–378. doi: 10.1073/pnas.0408810102
- Yang, S.-H., Kim, M.-R., Seo, H.-S., Lee, S. H., Lee, J.-H., Kim, S.-J., et al. (2013). Description of *Kordiimonas aquimaris* sp. nov., isolated from seawater, and emended descriptions of the genus *Kordiimonas* Kwon et al., 2005 emend. Xu et al., 2011 and of its existing species. *Int. J. Syst. Evol. Microbiol.* 63, 298–302. doi: 10.1099/ijs.0.038893-0
- Yang, S.-H., Seo, H.-S., Lee, J.-H., Kim, S.-J., and Kwon, K. K. (2015). *Kiloniella spongiae* sp. nov., isolated from a marine sponge and emended description of the genus *Kiloniella* Wiese et al., 2009 and *Kiloniella laminariae*. *Int. J. Syst. Evol. Microbiol.* 65, 230–234. doi: 10.1099/ijs.0.069773-0
- Yang, S.-Z., Xiong, X., Feng, G.-D., Li, H.-P., and Zhu, H.-H. (2017). Reclassification of *Sphingopyxis contaminans* as *Sphingorhabdus contaminans* comb. nov. and emended description of the genus *Sphingorhabdus*. *Int. J. Syst. Evol. Microbiol.* 67, 4328–4331. doi: 10.1099/ijsem.0.002201
- Yang, Y., Sun, J., Tang, K., Lin, D., Li, C., and Lin, Y. (2015). *Ponticoccus lacteus* sp. nov. of the family Rhodobacteraceae, isolated from surface seawater. *Int. J. Syst. Evol. Microbiol.* 65, 1247–1250. doi: 10.1099/ijs.0.000086
- Yao, L., Zhang, J. J., Yu, L. L., Chen, Q., Zhu, J. C., He, J., et al. (2016). *Rhizorhabdus dicambivorans* sp. nov., a dicamba-degrading bacterium isolated from compost. *Int. J. Syst. Evol. Microbiol.* 66, 3317–3323. doi: 10.1099/ijsem.0.001194
- Yao, L. J., Shen, Y. Y., Zhan, J. P., Xu, W., Cui, G. L., and Wei, G. H. (2012). *Rhizobium taibaihanense* sp. nov., isolated from a root nodule of *Kummerowia striata*. *Int. J. Syst. Evol. Microbiol.* 62, 335–341. doi: 10.1099/ijs.0.029108-0
- Yarza, P., and Munoz, R. (2014). The all-species living tree project. *Meth. Microbiol.* 41, 45–59. doi: 10.1016/bs.mim.2014.07.006
- Yarza, P., Spröer, C., Swiderski, J., Mroczek, N., Spring, S., Tindall, B. J., et al. (2013). Sequencing orphan species initiative (SOS): Filling the gaps in the 16S rRNA gene sequence database for all species with validly published names. *Syst. Appl. Microbiol.* 36, 69–73. doi: 10.1016/j.syapm.2012.12.006
- Yarza, P., Yilmaz, P., Pruesse, E., Glöckner, F. O., Ludwig, W., Schleifer, K. H., et al. (2014). Uniting the classification of cultured and uncultured bacteria and archaea using 16S rRNA gene sequences. *Nat. Rev. Microbiol.* 12, 635–645. doi: 10.1038/nrmicro3330
- Yasir, M., Aslam, Z., Song, G. C., Jeon, C. O., and Chung, Y. R. (2010). *Sphingosinicella vermicomposti* sp. nov., isolated from vermicompost, and emended description of the genus *Sphingosinicella*. *Int. J. Syst. Evol. Microbiol.* 60, 580–584. doi: 10.1099/ijs.0.010777-0
- Yasuda, P. H., Steigerwalt, A. G., Sulzer, K. R., Kaufmann, A. F., Rogers, F., and Brenner, D. J. (1987). Deoxyribonucleic acid relatedness between serogroups and serovars in the family leptospiraceae with proposals for seven new *Leptospira* species. *Int. J. Syst. Bacteriol.* 37, 407–415. doi: 10.1099/00207713-37-4-407
- Yee, B., Oertli, G. E., Fuerst, J. A., and Staley, J. T. (2010). Reclassification of the polyphyletic genus *Prosthecomicrobium* to form two novel genera, *Vasilyevaeva*

- gen. nov. and *Bauldia* gen. nov. with four new combinations: *Vasilyevaea enhydra* comb. nov., *Vasilyevaea mishustinii* comb. nov., *Bauldia consociata* comb. nov. and *Bauldia litoralis* comb. nov. *Int. J. Syst. Evol. Microbiol.* 60, 2960–2966. doi: 10.1099/ijs.0.018234-0
- Yi, H., Lim, Y. W., and Chun, J. (2007). Taxonomic evaluation of the genera *Ruegeria* and *Silicibacter*: a proposal to transfer the genus *Silicibacter* Petursdottir and Kristjansson 1999 to the genus *Ruegeria* Uchino et al. 1999. *Int. J. Syst. Evol. Microbiol.* 57, 815–819. doi: 10.1099/ijs.0.64568-0
- Yin, D., Xiao, J., Ao, J., Ai, C., and Chen, X. (2012). *Albidovulum xiamenense* sp. nov., a moderately thermophilic bacterium from a terrestrial hot spring. *Int. J. Syst. Evol. Microbiol.* 62, 1609–1612. doi: 10.1099/ijs.0.034454-0
- Ying, J.-Y., Wang, B.-J., Dai, X., Yang, S.-S., Liu, S.-J., and Liu, Z.-P. (2007). *Wenxinia marina* gen. nov., sp. nov., a novel member of the *Roseobacter* clade isolated from oilfield sediments of the South China Sea. *Int. J. Syst. Evol. Microbiol.* 57, 1711–1716. doi: 10.1099/ijs.0.64825-0
- Yoo, S.-H., Weon, H.-Y., Kim, B.-Y., Hong, S.-B., Kwon, S.-W., Cho, Y.-H., et al. (2006). *Devosia soli* sp. nov., isolated from greenhouse soil in Korea. *Int. J. Syst. Evol. Microbiol.* 56, 2689–2692. doi: 10.1099/ijs.0.64214-0
- Yoo, S.-H., Weon, H.-Y., Noh, H.-J., Hong, S.-B., Lee, C.-M., Kim, B.-Y., et al. (2008). *Roseomonas aerilata* sp. nov., isolated from an air sample. *Int. J. Syst. Evol. Microbiol.* 58, 1482–1485. doi: 10.1099/ijs.0.65385-0
- Yoon, J., and Kang, D.-H. (2018). *Terasakiella salincola* sp. nov., a marine *Alphaproteobacterium* isolated from seawater, and emended description of the genus *Terasakiella*. *Int. J. Syst. Evol. Microbiol.* 68, 2048–2053. doi: 10.1099/ijs.0.002788
- Yoon, J.-H., Kang, S.-J., Im, W.-T., Lee, S.-T., and Oh, T.-K. (2008). *Chelatococcus daeguensis* sp. nov., isolated from wastewater of a textile dye works, and emended description of the genus *Chelatococcus*. *Int. J. Syst. Evol. Microbiol.* 58, 2224–2228. doi: 10.1099/ijs.0.65291-0
- Yoon, J.-H., Kang, S.-J., Lee, J.-S., and Oh, T.-K. (2009). *Lutimaribacter saemankumensis* gen. nov., sp. nov., isolated from a tidal flat of the Yellow Sea. *Int. J. Syst. Evol. Microbiol.* 59, 48–52. doi: 10.1099/ijs.0.000109-0
- Yoon, J.-H., Kang, S.-J., Lee, M.-H., and Oh, T.-K. (2007a). Description of *Sulfitobacter donghicola* sp. nov., isolated from seawater of the East Sea in Korea, transfer of *Staleyia guttiformis* Labrenz et al. 2000 to the genus *Sulfitobacter* as *Sulfitobacter guttiformis* comb. nov. and emended description of the genus. *Int. J. Syst. Evol. Microbiol.* 57, 1788–1792. doi: 10.1099/ijs.0.65071-0
- Yoon, J.-H., Kang, S.-J., Lee, S.-Y., Jung, Y.-T., Lee, J.-S., and Oh, T.-K. (2012). *Marivita hallyeoneensis* sp. nov., isolated from seawater, reclassification of *Gaetbulicola byunsanensis* as *Marivita byunsanensis* comb. nov. and emended description of the genus *Marivita* Hwang et al. 2009. *Int. J. Syst. Evol. Microbiol.* 62, 839–843. doi: 10.1099/ijs.0.032086-0
- Yoon, J. H., Kang, S. J., Park, S., Lee, S. Y., and Oh, T. K. (2007b). Reclassification of *Aquaspirillum itersonii* and *Aquaspirillum peregrinum* as *Novispirillum itersonii* gen. nov., comb. nov. and *Insolitispirillum peregrinum* gen. nov., comb. nov. *Int. J. Syst. Evol. Microbiol.* 57, 2830–2835. doi: 10.1099/ijs.0.65340-0
- Yoon, J. H., Kang, S. J., Park, S., and Oh, T. K. (2007c). *Devosia insulae* sp. nov., isolated from soil, and emended description of the genus *Devosia*. *Int. J. Syst. Evol. Microbiol.* 57, 1310–1314. doi: 10.1099/ijs.0.65028-0
- Yoon, J.-H., Lee, C.-H., Yeo, S.-H., and Oh, T.-K. (2005a). *Sphingopyxis baekryunensis* sp. nov., an orange-pigmented bacterium isolated from sea water of the Yellow Sea in Korea. *Int. J. Syst. Evol. Microbiol.* 55, 1223–1227. doi: 10.1099/ijs.0.63495-0
- Yoon, J.-H., Oh, T.-K., and Park, Y.-H. (2005b). *Erythrobacter seohaensis* sp. nov. and *Erythrobacter gaetbuli* sp. nov., isolated from a tidal flat of the Yellow Sea in Korea. *Int. J. Syst. Evol. Microbiol.* 55, 71–75. doi: 10.1099/ijs.0.63233-0
- Young, J. M. (2003). The genus name *Ensifer* Casida, 1982 takes priority over *Sinorhizobium* Chen et al. 1988, and *Sinorhizobium morelense* Wang et al. 2002 is a later synonym of *Ensifer adhaerens* Casida, 1982. Is the combination “*Sinorhizobium adhaerens*” (Casida, 1982) Willems et. *Int. J. Syst. Evol. Microbiol.* 53, 2107–2110. doi: 10.1099/ijs.0.02665-0
- Young, J. M., Kuykendall, L. D., Martínez-Romero, E., Kerr, A., and Sawada, H. (2001). A revision of *Rhizobium* Frank, 1889, with an emended description of the genus, and the inclusion of all species of *Agrobacterium* Conn, 1942 and *Allorhizobium undicola* de Lajudie et al., 1998 as new combinations: *Rhizobium radiobacter*, *R. rhizogenes*, *R. rubi*, *R. undicola* and *R. vitis*. *Int. J. Syst. Evol. Microbiol.* 51, 89–103.
- Young, J. M., Kuykendall, L. D., Martínez-Romero, E., Kerr, A., and Sawada, H. (2003). Classification and nomenclature of *Agrobacterium* and *Rhizobium* – A reply to Farrand et al. (2003). *Int. J. Syst. Evol. Microbiol.* 53, 1689–1695. doi: 10.1099/ijs.0.02762-0
- Yu, X., Cloutier, S., Tambong, J. T., and Bromfield, E. S. P. (2014). *Bradyrhizobium ottawaense* sp. nov., a symbiotic nitrogen fixing bacterium from root nodules of soybeans in Canada. *Int. J. Syst. Evol. Microbiol.* 64, 3202–3207. doi: 10.1099/ijs.0.065540-0
- Yu, X. Y., Tao, T. Y., Fu, G. Y., Su, Y., Han, S. B., Wang, R. J., et al. (2016). *Marinibaculum pumilum* gen. nov., sp. nov., isolated from seawater. *Int. J. Syst. Evol. Microbiol.* 66, 4844–4849. doi: 10.1099/ijs.0.001439
- Yukphan, P., Malimas, T., Muramatsu, Y., Potacharoen, W., Tanasupawat, S., Nakagawa, Y., et al. (2011). *Neokomagataea* gen. nov., with descriptions of *Neokomagataea thailandica* sp. nov. and *Neokomagataea tanensis* sp. nov., osmotolerant acetic acid bacteria of the α -*Proteobacteria*. *Biosci. Biotechnol. Biochem.* 75, 419–426. doi: 10.1271/bbb.100344
- Yukphan, P., Malimas, T., Muramatsu, Y., Takahashi, M., Kaneyasu, M., Tanasupawat, S., et al. (2008). *Tanticharoenia sakaeratisensis* gen. nov., sp. nov., a new osmotolerant acetic acid bacterium in the α -*Proteobacteria*. *Biosci. Biotechnol. Biochem.* 72, 672–676. doi: 10.1271/bbb.70319
- Yukphan, P., Malimas, T., Potacharoen, W., Tanasupawat, S., Tanticharoen, M., and Yamada, Y. (2005). *Neoasaia chiangmaiensis* gen. nov., sp. nov., a novel osmotolerant acetic acid bacterium in the α -*Proteobacteria*. *J. Gen. Appl. Microbiol.* 51, 301–311. doi: 10.2323/jgam.51.301
- Yurkov, V., Stackebrandt, E., Buss, O., Vermegl, A., Gorlenk, V., and Beatty, J. T. (2017). Reorganization of the Genus *Eythromicrobium*: description of “*Eythromicrobium sibiricum*” as *Sandaracinobacter sibiricus* gen. nov., sp. nov., and of “*Eythromicrobium ursincola*” as *Eythromonas ursincola* gen. nov., sp. nov. *Int. J. Syst. Bacteriol.* 47, 1172–1178. doi: 10.1099/00207713-47-4-1172
- Yurkov, V., Stackebrandt, E., Holmes, A., Fuerst, J. A., Hugenholtz, P., Golecki, J., et al. (1994). Phylogenetic positions of novel aerobic, bacteriochlorophyll α -containing bacteria and description of *Roseococcus thiosulfatophilus* gen. nov., sp. nov., *Erythromicrobium ramosum* gen. nov., sp. nov., and *Erythrobacter litoralis* sp. nov. *Int. J. Syst. Bacteriol.* 44, 427–434. doi: 10.1099/00207713-44-3-427
- Zdrodovskii, P. F. (1948). *Rickettsiae and Rickettsioses*. Moscow: Academy of Medical Sciences.
- Zeevi Ben, Yosef, D., Ben-Dov, E., and Kushmaro, A. (2008). *Amorphus coralli* gen. nov., sp. nov., a marine bacterium isolated from coral mucus, belonging to the order Rhizobiales. *Int. J. Syst. Evol. Microbiol.* 58, 2704–2709. doi: 10.1099/ijs.0.65462-0
- Zhang, D.-C., Liu, H.-C., Xin, Y.-H., Zhou, Y.-G., Schinner, F., and Margesin, R. (2010). *Sphingopyxis bauzanensis* sp. nov., a psychrophilic bacterium isolated from soil. *Int. J. Syst. Evol. Microbiol.* 60, 2618–2622. doi: 10.1099/ijs.0.018218-0
- Zhang, D.-C., Neuner, K., Wu, J., Yao, J., and Margesin, R. (2015). *Punicibacterium sediminis* sp. nov., from intertidal sediment. *Int. J. Syst. Evol. Microbiol.* 65, 1462–1466. doi: 10.1099/ijs.0.000119
- Zhang, D. C., Redzic, M., Liu, H. C., Zhou, Y. G., Schinner, F., and Margesin, R. (2012). *Devosia psychrophila* sp. nov. and *Devosia glacialis* sp. nov., from alpine glacier cryoconite, and an emended description of the genus *Devosia*. *Int. J. Syst. Evol. Microbiol.* 62, 710–715. doi: 10.1099/ijs.0.023937-0
- Zhang, G., Yang, Y., Wang, S., Sun, Z., and Jiao, K. (2015). *Alkalimicrobium pacificum* gen. nov., a marine bacterium in the family Rhodobacteraceae. *Int. J. Syst. Evol. Microbiol.* 65, 2453–2458. doi: 10.1099/ijs.0.000282
- Zhang, G. I., Hwang, C. Y., and Cho, B. C. (2008). *Thalassobaculum litoreum* gen. nov., sp. nov., a member of the family Rhodospirillaceae isolated from coastal seawater. *Int. J. Syst. Evol. Microbiol.* 58, 479–485. doi: 10.1099/ijs.0.65344-0
- Zhang, J., Song, F., Xin, Y. H., Zhang, J., and Fang, C. (2009). *Microvirga guangxiensis* sp. nov., a novel *Alphaproteobacterium* from soil, and emended description of the genus *Microvirga*. *Int. J. Syst. Evol. Microbiol.* 59, 1997–2001. doi: 10.1099/ijs.0.007997-0
- Zhang, J. J., Liu, T. Y., Chen, W. F., Wang, E. T., Sui, X. H., Zhang, X. X., et al. (2012). *Mesorhizobium muleiense* sp. nov., nodulating with *Cicer arietinum* L. *Int. J. Syst. Evol. Microbiol.* 62, 2737–2742. doi: 10.1099/ijs.0.038265-0
- Zhang, L., Li, X., Zhang, F., and Wang, G. (2014a). Genomic analysis of *Agrobacterium radiobacter* DSM 30147T and emended description of *A. radiobacter* (Beijerinck and van Delden 1902) Conn, 1942 (Approved Lists

- 1980) emend. Sawada et al., 1993. *Stand. Genom. Sci.* 9, 574–584. doi: 10.4056/sig
- Zhang, L., Shi, X., Si, M., Li, C., Zhu, L., Zhao, L., et al. (2014b). *Rhizobium smilacinae* sp. nov., an endophytic bacterium isolated from the leaf of *Smilacina japonica*. *Antonie Van Leeuwenhoek* 106, 715–723. doi: 10.1007/s10482-014-0241-1
- Zhang, L., Wang, K. L., Yin, Q., Liang, J. Y., and Xu, Y. (2018). *Ruegeria kandeliae* sp. nov., isolated from the rhizosphere soil of a mangrove plant *kandelia candel*. *Int. J. Syst. Evol. Microbiol.* 68, 2653–2658. doi: 10.1099/ijsem.0.002894
- Zhang, S., Yang, S., Chen, W., Chen, Y., Zhang, M., Zhou, X., et al. (2017). *Rhizobium arenae* sp. nov., isolated from the sand of Desert Mu Us, China. *Int. J. Syst. Evol. Microbiol.* 67, 2098–2103. doi: 10.1099/ijsem.0.001810
- Zhang, X.-Y., Li, G.-W., Wang, C.-S., Zhang, Y.-J., Xu, X.-W., Li, H., et al. (2013). *Marinicauda pacifica* gen. nov., sp. nov., a prosthecate *Alphaproteobacterium* of the family Hyphomonadaceae isolated from deep seawater. *Int. J. Syst. Evol. Microbiol.* 63, 2248–2253. doi: 10.1099/ijms.0.046656-0
- Zhang, Y., Jiang, F., Chang, X., Qiu, X., Ren, L., Qu, Z., et al. (2016). *Pseudorhodobacter collinsensis* sp. nov., isolated from a till sample of an icecap front. *Int. J. Syst. Evol. Microbiol.* 66, 178–183. doi: 10.1099/ijsem.0.000693
- Zhang, Y., Xu, Y., Fang, W., Wang, X., Fang, Z., and Xiao, Y. (2017). *Pseudoruegeria marinistellae* sp. nov., isolated from an unidentified starfish in Sanya, China. *Antonie Van Leeuwenhoek* 110, 187–194. doi: 10.1007/s10482-016-0789-z
- Zhang, Y.-J., Liu, X.-F., Kuang, B.-Z., Zhang, X.-Y., Zhou, M.-Y., and Chen, S. (2018). *Neptunicoccus sediminis* gen. nov., sp. nov., a member of the family Rhodobacteraceae isolated from the Yellow Sea. *Int. J. Syst. Evol. Microbiol.* 68, 1702–1706. doi: 10.1099/ijsem.0.002728
- Zhang, Y.-Q., Lee, J.-C., Park, D.-J., Lu, X.-X., Mou, X.-Z., and Kim, C.-J. (2014c). *Roseivivax roseus* sp. nov., an *Alphaproteobacterium* isolated from a solar saltern soil sample. *Int. J. Syst. Evol. Microbiol.* 64, 1743–1746. doi: 10.1099/ijms.0.061630-0
- Zhang, Y.-Q., Yu, L.-Y., Wang, D., Liu, H.-Y., Sun, C.-H., Jiang, W., et al. (2008). *Roseomonas vinacea* sp. nov., a Gram-negative coccobacillus isolated from a soil sample. *Int. J. Syst. Evol. Microbiol.* 58, 2070–2074. doi: 10.1099/ijms.0.65789-0
- Zhao, J.-J., Zhang, J., Sun, L., Zhang, R.-J., Zhang, C.-W., Yin, H.-Q., et al. (2017). *Rhizobium oryziradicis* sp. nov., isolated from rice roots. *Int. J. Syst. Evol. Microbiol.* 67, 963–968. doi: 10.1099/ijsem.0.001724
- Zheng, Q., Chen, C., Yan, X.-J., Wang, Y.-N., Zeng, Y.-H., Hao, L.-K., et al. (2010). *Mameliella alba* gen. nov., sp. nov., a marine bacterium of the *Roseobacter* clade in the order Rhodobacterales. *Int. J. Syst. Evol. Microbiol.* 60, 953–957. doi: 10.1099/ijms.0.011437-0
- Zheng, W. T., Li, Y., Wang, R., Sui, X. H., Zhang, X. X., Zhang, J. J., et al. (2013). *Mesorhizobium qingshengii* sp. nov., isolated from effective nodules of *Astragalus sinicus*. *Int. J. Syst. Evol. Microbiol.* 63, 2002–2007. doi: 10.1099/ijms.0.044362-0
- Zhilina, T. N., Zavarzin, G. A., Rainey, F., Kevbrin, V. V., Kostrikina, N. A., and Lysenko, A. M. (1996). *Spirochaeta alkalica* sp. nov., *Spirochaeta africana* sp. nov., and *Spirochaeta asiatica* sp. nov., alkaliphilic anaerobes from the continental soda lakes in central Asia and the East African Rift. *Int. J. Syst. Bacteriol.* 46, 305–312. doi: 10.1099/00207713-46-1-305
- Zhong, Z.-P., Liu, Y., Liu, H.-C., Wang, F., Zhou, Y.-G., and Liu, Z.-P. (2014). *Roseibium aquae* sp. nov., isolated from a saline lake. *Int. J. Syst. Evol. Microbiol.* 64, 2812–2818. doi: 10.1099/ijms.0.065508-0
- Zhu, C., Delmont, T. O., Vogel, T. M., and Bromberg, Y. (2015). Functional basis of microorganism classification. *PLoS Comput. Biol.* 11:e1004472. doi: 10.1371/journal.pcbi.1004472
- Zhuang, L., Liu, Y., Wang, L., Wang, W., and Shao, Z. (2015). *Erythrobacter atlanticus* sp. nov., a bacterium from ocean sediment able to degrade polycyclic aromatic hydrocarbons. *Int. J. Syst. Evol. Microbiol.* 65, 3714–3719. doi: 10.1099/ijsem.0.000481
- Zurdo-Piñeiro, J. L., Rivas, R., Trujillo, M. E., Vizcaíno, N., Carrasco, J. A., Chamber, M., et al. (2007). *Ochrobactrum cytisi* sp. nov., isolated from nodules of *Cytisus scoparius* in Spain. *Int. J. Syst. Evol. Microbiol.* 57, 784–788. doi: 10.1099/ijms.0.64613-0

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Copyright © 2020 Hördt, López, Meier-Kolthoff, Schleuning, Weinhold, Tindall, Gronow, Kyrpides, Woyke and Göker. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.