18 The Family *Phyllobacteriaceae*

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Abstract
The family *Phyllobacteriaceae* belongs to the order *Rhizobiales* in the *Alphaproteobacteria* and currently comprises the 72 species in 13 genera: *Ahrensia*, *Aliihoeflea*, *Aminobacter* (including *Chelatobacter*), *Aquamicrobium* (including *Defluvibacter*), *Chelativorans*, *Hoeflea*, *Lentilitoribacter*, *Mesorhizobium*, *Nitratireductor*, *Phyllobacterium*, *Pseudahrensia*, *Pseudaminobacter*, and *Thermovum*. They form a single cluster within the 16S rRNA gene phylogeny. The family consists of environmental (soil, water) and plant-associated bacteria that have a heterotrophic respiratory metabolism with oxygen as terminal electron acceptor. One *Aquamicrobium* species can use nitrate as an alternative terminal electron acceptor. One *Mesorhizobium* species is facultatively chemolithotrophic using thiosulfate or elemental sulfur as sole energy source. *Candidatus Liberibacter*, a group of uncultivated phloem-inhabiting bacteria that are associated with various plant diseases in citrus and *Solanaceae* or are endophytic in pear plants, is also associated with the family. However, comprehensive phylogenetic analyses indicate the position of this group as a member of the *Phyllobacteriaceae* is uncertain.

Taxonomy, Historical and Current

Short Description of the Family

Phyl.lo.bac.te.ri.a'ce.ae. N.L. neut. n. *Phyllobacterium*, type genus of the family; suff. *-aceae*, suffix to denote a family; N.L. fem. pl. n. *Phyllobacteriaceae*, the *Phyllobacterium* family.

The family *Phyllobacteriaceae* belongs to the *Rhizobiales* order in the *Alphaproteobacteria* class of the phylum Proteobacteria. It was proposed by Mergaert and Swings (2005a) in *Bergey's Manual of Systematic Bacteriology* and was validated in 2006. At the time the family comprised six genera and one *Candidatus* genus: *Phyllobacterium*, *Aminobacter*, *Aquamicrobium*, *Defluvibacter*, *Candidatus Liberibacter*, *Mesorhizobium*, and *Pseudaminobacter*. *Defluvibacter* has since been transferred to *Aquamicrobium* (Kämpfer et al. 2009). *Aminobacter* includes *Chelatobacter heintzii* which is regarded as a later subjective synonym of *Aminobacter aminovorans* (Kämpfer et al. 2002). The basis for the proposal of this family was that these genera form a cluster in the 16S rRNA gene phylogeny. The description of the family (Mergaert and Swings 2005a) is rather brief: "Rod-shaped, ovoid, or reniform cells when cultured in vitro. Nonsporeforming. Gram negative. Aerobic. Cells cultured in vitro are motile by means of polar, subpolar, or lateral flagella. Strains grow well on complex solid media at 28 °C. Occur in leaf nodules and the rhizosphere of higher plants. The mol % G+C of the DNA is 60–62". With the inclusion of the additional genera *Ahrensia*, *Chelativorans*, *Hoeflea*, *Lentilitoribacter*, *Nitratireductor*, *Pseudahrensia*, and *Thermovum* to the *Phyllobacteriaceae* cluster, most of this definition still applies except that cells can also be nonmotile and members of the family can also occur in seawater, marine sediments, activated sludge, and soil and

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thermophilic members are found in compost. The range of the G+C content of DNA is 48–65 %. Comprehensive phylogenetic analysis reveals that the position of *Candidatus Liberibacter* as a member of the *Phyllobacteriaceae* cluster is uncertain (see below).

Phylogenetic Structure of the Family and Its Genera

In the 16S rRNA gene phylogeny, the *Phyllobacteriaceae* family forms a single cluster in the phylum Alphaproteobacteria, and inside this large cluster, the different species generally group together per genus, in support of the current taxonomy (➋ *Fig. 18.1*).

An important exception is the genus *Mesorhizobium*: these species make up several groups and separate lineages grouping in between the other genus clusters (➋ *Fig. 18.1*). The type species *Mesorhizobium loti* forms tight subcluster with *Mesorhizobium ciceri*, *Mesorhizobium australicum*, *Mesorhizobium shangrilense*, *Mesorhizobium sangaii*, and *Mesorhizobium qingshengii*. *Mesorhizobium chacoense* forms a separate but related lineage, and the *Aminobacter* cluster is their nearest neighbor. Nineteen species form the largest subcluster: *Mesorhizobium metallidurans*, *Mesorhizobium temperatum*, *Mesorhizobium mediterraneum*, *Mesorhizobium gobiense*, *Mesorhizobium tarimense*, *Mesorhizobium caraganae*, *Mesorhizobium robiniae*, *Mesorhizobium muleiense*, *Mesorhizobium tianshanense*, *Mesorhizobium tamadayense*, *Mesorhizobium amorphae*, *Mesorhizobium septentrionale*, *Mesorhizobium huakuii*, *Mesorhizobium plurifarium*, *Mesorhizobium silamurunense*, *Mesorhizobium opportunistum*, *Mesorhizobium abyssinicae*, *Mesorhizobium hawassense*, and *Mesorhizobium shonense*. *Mesorhizobium albiziae* groups at the periphery of this subcluster as does *Mesorhizobium thiogangeticum*. The position of the two latter species, however, varied depending on the filter applied. In most trees, it constitutes a separate lineage at some distance from other *Mesorhizobium* subclusters or other genera of the family. *Mesorhizobium thiogangeticum* was not recovered from legume nodules but was isolated from soil by enrichment using reduced sulfur compounds as sole electron sources; it is the only *Mesorhizobium* species reported to be facultatively chemolithoautotrophic. Two other species, *Mesorhizobium camelthorni* and *Mesorhizobium alhagi*, make up a further subcluster that groups most closely to the *Chelativorans* cluster. The 16S rRNA gene phylogeny of *Mesorhizobium* is thus polyphyletic, and the genus may in the future require taxonomic rearrangements if further evidence would support these observations.

Ahrensia and *Lentilitoribacter* group together with *Hoeflea* species, but, according to branch length, are clearly distinct.

Nitratireductor species form a single cluster, except for *Nitratireductor basaltis* which is located separately.

Candidatus Liberibacter, consisting of psyllid-transmitted, as yet uncultured, phloem-limited bacteria associated with greening disease or huanglongbing disease of citrus and yellows disease of various *Solanaceae* plants or endophytic in pear plants, was initially placed inside the *Phyllobacteriaceae* based on a limited phylogenetic indications (Mergaert and Swings 2005a; Garnier 2005). A more comprehensive analysis performed for this chapter revealed that the position of *Candidatus Liberibacter* as a member of the *Phyllobacteriaceae* cluster is uncertain. Although it does group on a long branch inside the *Phyllobacteriaceae* cluster in ➋ *Fig. 18.1*, in most other trees calculated using other filters and including other neighboring taxa, *Candidatus Liberibacter* grouped outside the family and occupied a separate position in the *Alphaproteobacteria*. Its membership of the family therefore seems not strongly supported by 16S rRNA phylogeny.

Comments on the Membership of the Family

Although the genus *Ahrensia* is was classified in the *Rhodobacteraceae* in *Bergey's Manual of Systematic Bacteriology* (Garrity et al. 2005) based on the phylogenetic analysis of 16S rRNA genes, since then more taxa have been described in the *Rhizobiales*, and current 16S rRNA gene phylogeny places *Ahrensia* in the *Phyllobacteriaceae* (Living Tree Project, release 111). It is therefore included in this chapter.

"*Aliihoeflea aestuarii*" gen. nov., sp. nov. was described for a bacterium isolated from tidal flat sediments (Roh et al. 2008). Its 16S rRNA gene sequence was reported to cluster with members of the *Phyllobacteriaceae*. Fatty acid data, quinone, and DNA G+C content data are also in agreement with the family characteristics; therefore, although *Aliihoeflea aestuarii* has as yet not been included in a validation list, it is included here in the chapter on *Phyllobacteriaceae*.

Molecular Analyses

DNA-DNA Hybridization Studies

In all multispecies genera of the family, DNA-DNA hybridizations with existing species have been performed to justify proposals of new species.

Other Sequence Analyses

Genes other than the 16S rRNA gene have been reported in *Mesorhizobium* where recA sequences are available for all species and a number of other genes including *atpD*, *gyrB*, *dnaK*, and *rpoB* have also been reported for several of the *Mesorhizobium* species. However, for other *Phyllobacteriaceae* genera, only in a few cases have other genes been reported and used for phylogenetic purposes: for three of six *Aminovorans* species sequences are available for *atpD*, *dnaK*, and *recA* (Maynaud et al. 2012); for four of eight *Phyllobacterium* species, an *atpD* sequence has been reported, as well as a *recA* sequence for one species

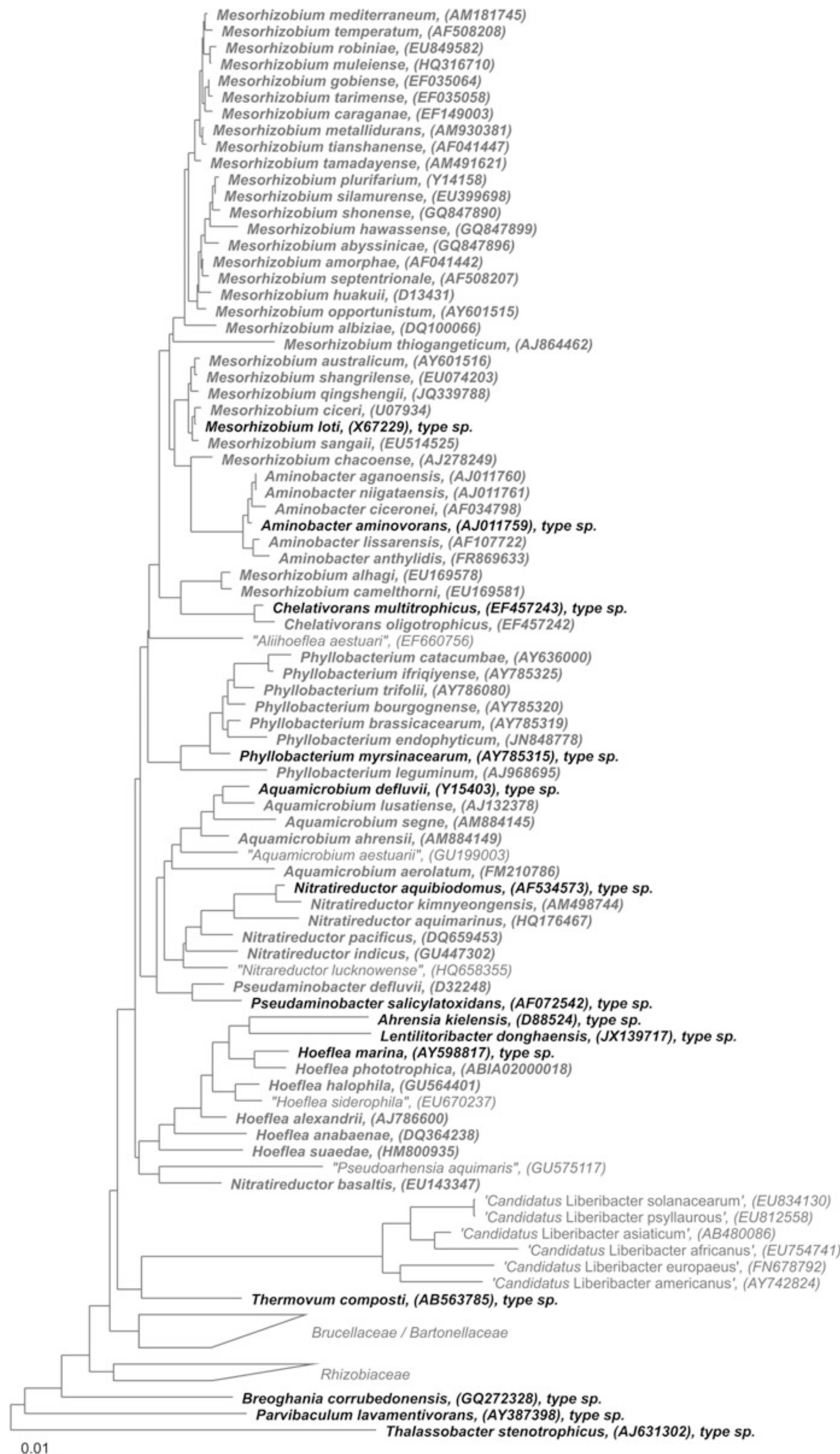

Fig. 18.1

Phylogenetic reconstruction of the family *Phyllobacteriaceae* based on 16S rRNA and created using the neighbor-joining algorithm with the Jukes-Cantor correction. The sequence datasets and alignments were used according to the All-Species Living Tree Project (*LTP*) database (Yarza et al. 2010; http://www.arb-silva.de/projects/living-tree). The tree topology was stabilized with the use of a representative set of nearly 750 high-quality type strain sequences proportionally distributed among the different bacterial and archaeal phyla. In addition, a 40 % maximum frequency filter was applied in order to remove hypervariable positions and potentially misplaced bases from the alignment. Scale bar indicates estimated sequence divergence

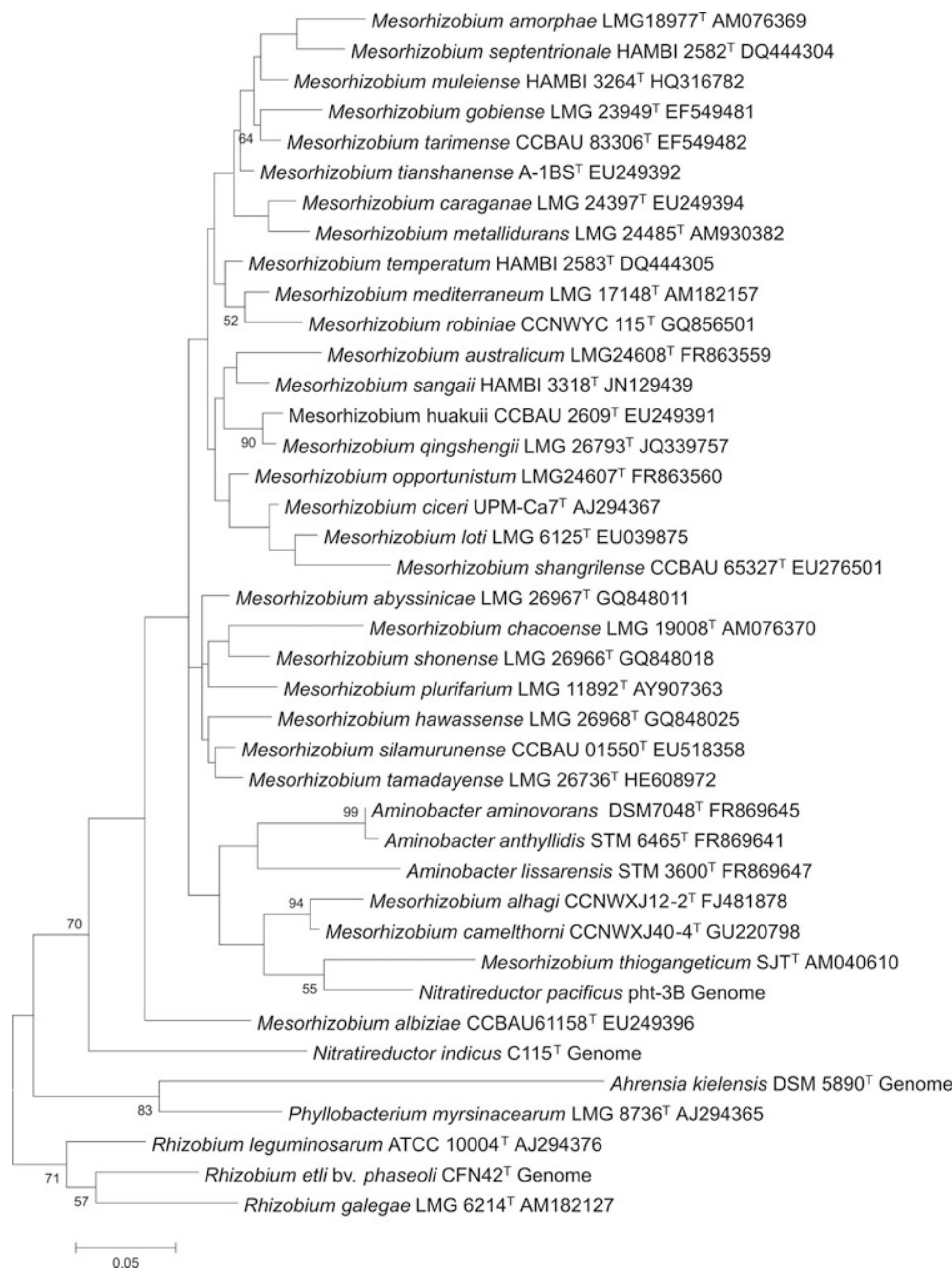

Fig. 18.2

Phylogenetic reconstruction of the family *Phyllobacteriaceae* based *recA* sequences. The tree was constructed using the maximum likelihood method and general time-reversible model in MEGA (Tamura et al. 2011). A bootstrap analysis with 500 replicates was performed to assess the support of the clusters; values above 50 % are shown at the nodes

(Mantelin et al. 2006b), and for two of six *Nitratireductor* species, an *rpoD* sequence is available (unpublished data available through NCBI dataportal). Given this lack of data for all genera, it is currently not possible to comprehensively assess the phylogeny of the family using a housekeeping gene other than the 16S rRNA gene. At present most data are available for *recA* where 6 of the 13 genera are represented (three of these are extracted from total genome information). Given that *Mesorhizobium* is represented with 30 species versus only 8 species from other genera, this tree (➲ *Fig. 18.2*) does not permit a comprehensive comparison with the 16S rRNA gene phylogeny (➲ *Fig. 18.1*). It thus remains to be established whether the subclusters of *Mesorhizobium* in the latter phylogeny are confirmed by *recA* or other gene phylogenies.

Table 18.1
Overview of genome sequences available for type strains of the *Phyllobacteriaceae*

Organism	Genome structure	Size (Mb)	GC%	Genes	Proteins	GenBank	Reference
Ahrensia kielensis DSM 5890^T	16 Contigs	3.36	48.0	3,287	3,233	ARFW01000000	JGI Project ID: 406534
Candidatus Liberibacter asiaticus psy62	1 Ch.	0.99	36.5	1,162	1,109	NC_012985	Duan et al. 2009
Candidatus Liberibacter solanacearum CLso-ZC1	1 Ch.	1.26	35.2	1,246	1,192	NC_014774	Lin et al. 2011
Chelativorans sp. NBC1	1 Ch., 3 pl.	4.94	61.1	4,684	4,543	CP000390.1, CP000389.1, CP000391.1, CP000392.1	JGI Project ID: 10690
Hoeflea phototrophica DFL-43 (DSM 17068)	22 Contigs	4.46	59.8	4,407	4,357	ABIA02000000	The Gordon and Betty Moore Foundation Marine Microbial Genome Sequencing Project; J. Craig Venter Institute
Mesorhizobium alhagi CCNWXJ12-2^T	375 Contigs	6.97	62.6	7,244	7,195	AHAM00000000	Zhou et al. 2012
Mesorhizobium amorphae CCNWGS0123	274 Contigs	7.29	62.9	7,136	7,084	AGSN00000000	Hao et al. 2012
Mesorhizobium australicum WSM2073^T	1 Ch.	6.2	62.8	6,075	5,792	CP003358.1	JGI Project ID: 47287
Mesorhizobium ciceri bv. *biserrulae* WSM1271	1 Ch., 1 pl.	6.69	62.6	6,532	6,264	CP002447.1, CP002448.1	JGI Project ID: 48991
Mesorhizobium loti MAFF303099	1 Ch., 2 pl.	7.6	62.5	7,333	7,272	BA000012.4, BA000013.4, AP003017.1	Kaneko et al. 2000
Mesorhizobium opportunistum WSM2075^T	1 Ch.	6.88	62.9	6,746	6,508	CP002279.1	JGI Project ID: 33861
Nitratireductor aquibiodomus RA22	95 Contigs	4.59	61.3	4,293	4,241	AJXZ00000000	Singh et al. 2012
Nitratireductor indicus C115^T	75 Contigs	4.99	60.8	4,872	4,824	AMSI01000000	Lai et al. 2012b
Nitratireductor pacificus pht-3B^T	51 Contigs	4.47	65.5	4,246	4,197	AMRM01000000	Lai et al. 2012a

Data obtained from the NCBI genome pages (http://www.ncbi.nlm.nih.gov/genome)

Genome Comparisons

Only in recent years have some complete genome sequences been reported or drafts made available. An overview of the type strains and a few other strains is given in *Table 18.1*. Unpublished draft genomes are available in public database online for *Ahrensia kielensis*, *Chelativorans* sp., *Hoeflea phototrophica*, *Mesorhizobium australicum*, *Mesorhizobium ciceri* bv. *biserrulae*, and *Mesorhizobium opportunistum* (*Table 18.1*).

The genome of *Mesorhizobium loti* MAFF303099 was reported more than 10 years ago (Kaneko et al. 2000); however, later this strain was shown to be a representative of another *Lotus* symbiont, *Mesorhizobium huakuii* bv. *loti* (Turner et al. 2002). Its genome consists of one chromosome (7 Mb) and two megaplasmids (352 kb and 208 kb); a transmissible symbiotic island containing 580 protein-encoding genes including genes for nodulation and nitrogen fixation was identified on the chromosome, inserted into the phe-tRNA gene as in other *Mesorhizobium loti* strains (Kaneko et al. 2000). The genomes of several other *Mesorhizobium* strains have been sequenced and had a similar size between 6.2 and 7.6 Mb with one circular chromosome and either no, one or two megaplasmids (*Table 18.1*). *Mesorhizobium amorphae* CCNWGS0123 is a copper-resistant rhizobium that contributes to survival of the

host plant in copper-, zinc-, and chromium-containing environments. Its genome was found to harbor numerous genes involved in copper resistance including a copper efflux system and multicopper oxidases, as well as various genes for plant growth promotion that most rhizobia share. In addition genes involved in the biosynthesis of a number of antibiotics and in chloramphenicol resistance were present (Hao et al. 2012). *Mesorhizobium alhagi* CCNWXJ12-2^T is very resistant to salt (0.8 M) and alkali (pH 12). Its genome was found to encode various systems contributing to salt resistance and osmoregulation including multiple membrane transport system (Zhou et al. 2012).

The genomes have been reported for three *Nitratireductor* strains. For the type species, *Nitratireductor aquibiodomus* strain RA22 from a marine water sample in India has been sequenced; its 16S rRNA gene was reported as 100 % identical to that of the type strain. Annotation revealed genes for iron acquisition, ammonia and sulfur assimilation, biosynthesis of ectoine and betaine, and uptake of choline and betaine, indicative of its marine habitat requiring osmotic stress tolerance. Genes for catabolism of aromatic compounds, including genes for the chloroaromatic degradation pathway, correspond with the observation that many *Nitratireductor* strains were obtained from sources contaminated with pyrene, crude oil, or pesticide (Singh et al. 2012). *Nitratireductor pacificus* pht-3B^T, although isolated from a pyrene-degrading consortium from deep-sea sediments, is unable to utilize pyrene, and this was confirmed by the absence of polycyclic aromatic hydrocarbon (PAH)-degrading dioxygenase in its genome (Lai et al. 2012a). *Nitratireductor indicus* C115^T originates from a crude oil-degrading consortium from deep seawater; however, it cannot degrade *n*-alkanes or PAHs as sole carbon source. Also here, the genome sequence confirmed the absence of any alkane-degrading monooxygenase or PAH-degrading dioxygenase (Lai et al. 2012b).

Two complete genomes have been reported representing *Candidatus Liberibacter*, a group of uncultured bacteria associated with *citrus* and *Solanaceae* plant diseases; genomes were obtained from DNA isolated from the phloem-feeding psyllid vectors that transmit the pathogen (Duan et al. 2009; Lin et al. 2011). As can be expected for obligate intracellular endophytes, the genomes are small and have a low GC content: 0.99 Mb and 36.5 mol % and 1.26 Mb and 35.2 mol % for *Candidatus Liberibacter asiaticus* psy62 and *Candidatus Liberibacter solanacearum* CLso-ZC1, respectively. *Candidatus Liberibacter asiaticus* psy62 harbored few genes for the biosynthesis of compounds that can be obtained from the host and more genes for motility such as type IV pili and flagellar genes; it had no transposons or insertion elements but did have some phage-related genes (Duan et al. 2009). Its genome also revealed the absence of several key components required for oxidative phosphorylation and several terminal oxidases, pointing to a limited potential for aerobic respiration; genome analysis suggests that the organism cannot reduce sulfur compound, but instead anaerobic respiration is coupled to nitrogen metabolism. The presence of an active TCA cycle suggests that a range of amino acids (present in phloem fluid) may serve as energy sources (Duan et al. 2009). *Candidatus Liberibacter solanacearum* shares 884 protein-encoding genes with *Candidatus Liberibacter asiaticus*. Comparison of both genomes revealed many rearrangements and gene losses/gains (Lin et al. 2011). *Candidatus Liberibacter solanacearum* also contained several small and two large phage-derived segments, one of which was similar to a segment in *Candidatus Liberibacter asiaticus*. The analysis of its gene repertoire suggests it can take up glucose but not sucrose or fructose and has limited capacity for aerobic respiration and for the biosynthesis of amino acids and lacks a complete restriction-modification system. It has several transport systems for amino acids and a system (NttA) for the uptake of ATP and ADP from the host. The comparison further revealed that *Candidatus Liberibacter solanacearum* has reduced capacity for nucleic acid modification, increased potential for amino acid and vitamin biosynthesis, and a high-affinity iron transport system (Lin et al. 2011). Lin et al. (2011) point out that the approach of extracting bacterial genome information from the vector does not exclude that other genetic components such as plasmids or linear chromosomes could be present.

Based on the complete genome (Duan et al. 2009; Tyler et al. 2009), a computational analysis of the *Candidatus Liberibacter asiaticus* proteome has been performed, and the results predicting 3D structure, function, cellular localization, and potential virulence factors are publically available (http://prodata.swmed.edu/liberibacter_asiaticus/curated/) as a tool for further study of this pathogen (Cong et al. 2012).

Phenotypic Analyses

A comparison of some general features of the members of the *Phyllobacteriaceae* is given in *Table 18.2*.

Ahrensia Uchino et al. 1999, 1^{VL}

Ah.ren'si.a. N.L. fem. n. *Ahrensia*, named in honor of R. Ahrens, a German microbiologist, for his contribution to the taxonomy of marine species of *Agrobacterium*.

The genus *Ahrensia* comprises rod-shaped cells that do not form spores. They are motile with polar flagella. Aerobic and oxidase and catalase positive. The major quinone is ubiquinone Q10; the major fatty acid is C18:1; the main hydroxy fatty acid is C12:0 3-OH. No 2-hydroxy fatty acids are present. The G+C content of the DNA is 48 mol %. The type species is *Ahrensia kielensis*.

The following description of *Ahrensia kielensis* is based on those from Uchino et al. (1998) and from Rüger and Höfle (1992). The species is able to grow at 5 °C, but not at 37 °C. Na^+ is required. Cells are motile rods, 0.6–1.0 × 2.0–4.0 μm. Hardly any carbon sources are used: the type strain tested negative for 12 carbohydrates, 11 carboxylic acids, 3 alcohols, 7 amino acids, and putrescine (Rüger and Höfle 1992). H_2S is produced from cysteine; hydrolysis of gelatin and starch is negative. Nitrate is not reduced to nitrite or gas. Acids are

Table 18.2
Morphological and chemotaxonomic characteristics of the genera of *Phyllobacteriaceae*

Genus	Source	# species	Morphology	Motility	Metabolism	Temperature preference	Major fatty acids	Major hydroxy fatty acids	G+C content
Ahrensia	Seawater	1	Rods	Polar flagella	Aerobic respiration	Mesophilic	C18:1 ω7c	C12:0 3-OH	48
Aliihoeflea	Tidal flat sediment	1	Rods	Not reported	Aerobic respiration	Mesophilic	C18:1 ω7c, C19:cyclo ω8c	–	53.4
Aminobacter	Soil, root nodules	6	Rods	Subpolar flagella	Aerobic respiration	Mesophilic	SF7 (C18 :1 ω7c/C18:1 ω9t/C18:1 ω12t)	C12:0 3-OH	62.5–63.8
Aquamicrobium	Air from a duck shed, biofilter for the treatment of animal rendering waste gas, activated sludge	6	Rods	+	Aerobic respiration; one species also uses nitrate as respiratory electron acceptor	Mesophilic	C18:1 ω7*c*	–	58.7–61.7
Chelativorans	Soil, activated sludge, sewage sludge	2	Rods	+/–	Aerobic respiration	Mesophilic	SF7 (C18:1 ω7c/C18:1 ω9t/C18:1 ω12t), C19:0 cyclo ω8c	–	60.8–63.1
Hoeflea	Seawater, in cultures of marine dinoflagellates or cyanobacteria, root surface of a halophyte	7	Rods	One polar flagellum or nonmotile	Aerobic or microaerophilic respiration	Mesophilic	C18:1 ω7*c*	None or C12:0 3-OH	53.1–59.7
Lentilitoribacter	Seawater	1	Rods, short rods	–	Aerobic respiration	Mesophilic	C18 :1 ω7*c*, 11-methyl-C18:1 ω7c, SF3 (iso-C15:0 2-OH and/or C16:1 ω7c)	C10:0 3-OH	49.3
Mesorhizobium	Nodules of legume plants or soil	30	Rods	+	Aerobic respiration; one species is fac. chemolithotrophic using thiosulfate or elemental sulfur	Mesophilic	C18:1 ω7c		57.9–65.1
Nitratireductor	Marine sediment, seawater, beach sand, dried seaweed sample	7	Rods or coccoid cells	+/–	Aerobic respiration	Mesophilic	C18:1 ω7c/ω6c	–	56.7–63
Phyllobacterium	Root or leaf nodules, tuff volcanic rock	8	Rods	+	Aerobic respiration	Mesophilic	C16:0, C18:1 ω7c, C18:1 ω7c 11-Me, C19:0 cyclo ω8c	C16:0 3-OH, C18:1 2-OH	52–58.5
Pseudahrensia	Seawater	1	Ovoid to rod shaped	–	Aerobic respiration	Mesophilic	C18:1 ω7c	C18:0 3-OH, iso-C13:0 3-OH	60.1
Pseudaminobacter	River water, activated sludge	2	Coccoid to rod shaped	+	Aerobic respiration	Mesophilic	C18:1 (ω7c/ω9t/ω12t), C19:0 cyclo ω8c	C15:0 iso 3-OH	62.9–63.9
Thermovum	Compost	1	Ovoid	–	Aerobic respiration	Thermophilic	C18:1 ω7c, C19:0 ω8c and C18:0	–	63.4

Data taken from the original descriptions and references as given in the main text

produced from fructose, maltose, xylose, and glycerol after 4–6 weeks of incubation. Negative in the following tests: indole production, methyl red, Voges-Proskauer, lysine and ornithine decarboxylase, and hydrolysis of casein, chitin, and alginate.

The major fatty acid is C18:1 ω7c; C12:0 3-OH and iso-C13:0 3-OH are present, but 2-hydroxy fatty acids are absent (Uchino et al. 1998; Park et al. 2013). The G+C content of the DNA is 48 mol %.

The type strain IAM 12618^T was isolated from seawater of the Baltic Sea.

Aliihoeflea Roh et al. 2008

A.li.i.ho.e.fle'a, L. adj. and pronoun *alius*, other, another, different; N.L. fem. n. *Hoeflea*, a bacterial genus name; N.L. fem. n. *Aliihoeflea*, the other *Hoeflea*.

Aliihoeflea comprises rod-shaped cells that are catalase and oxidase positive. The major quinone is ubiquinone Q10; the major fatty acids are C18:1 ω7c and C19:0 cyclo ω8c. G+C content is approximately 53 mol %. The type species is *Aliihoeflea aestuarii.*

The following description of the phenotype is based on the description of the strain N8^T, thus far the only strain of *Aliihoeflea aestuarii* (Roh et al. 2008). Cells are rod shaped (0.50–0.75 μm × 1.25–1.50 μm). Colonies on MA are circular with entire margin, convex, shiny, and cream colored. Growth is also possible on Trypticase soy agar, SA, LA, and yeast mannitol agar, but not on R2A. Temperature range for growth is 17–37 °C; the optimal growth temperature is 30 °C. Optimal NaCl concentration is 1 % (w/v), although NaCl is not required and up to 8 % is tolerated during growth. Nitrates are not reduced to nitrites or nitrogen. Indole is not produced. Glucose is not fermented, and hydrolysis of starch, esculin, gelatin, and PNPG (*p*-nitrophenyl-β-D-galactopyranoside) is negative. Urease positive and arginine dihydrolase negative. Glycogen, Tween 80, L-arabinose, D-fructose, pyruvic acid methyl ester, succinic acid monomethyl ester, acetic acid, α-hydroxybutyric acid, β-hydroxybutyric acid, γ-hydroxybutyric acid, α-ketobutyric acid, α-ketoglutaric acid, α-ketovaleric acid, D,L-lactic acid, succinic acid, succinamic acid, L-alaninamide, D-alanine, L-alanine, L-glutamic acid, glycyl-L-glutamic acid, L-leucine, L-serine, inosine, uridine, and thymidine can be used as sole carbon sources. Positive for alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, naphthol-AS-BI-phosphohydrolase. Negative for lipase (C14), acid phosphatase, α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, N-acetyl-β-glucosaminidase, α-mannosidase, and α-fucosidase. The genomic DNA G+C content is 53.4 mol %. The type strain KCTC 22052^T was isolated from tidal flat sediment in Yeosu (34°47′26″ N 127°34′01″ E), Republic of Korea.

Aminobacter Urakami et al. 1992, 90^{VP}

Am.i.no.bac'ter, N.L. n. *aminum*, amine; N.L. masc. n. *bacter*, rod; N.L. masc.n. *Aminobacter*, amine rod.

The genus *Aminobacter* comprises non-spore-forming rod-shaped cells that can utilize methylamine. Cells are motile by means of subpolar flagella. They multiply by budding. Poly-β-hydroxybutyrate granules are accumulated in the cells. Good growth in nutrient broth and PYG broth. No water-soluble fluorescent pigment is produced. No growth factors are required. Oxidase and catalase positive and urease negative. Aerobic respiratory metabolism, not fermentative (Urakami et al. 1992).

The following tests are negative: methyl red, Voges-Proskauer, indole production, hydrogen sulfide production, hydrolysis of gelatin and starch, denitrification, litmus milk, and fermentation of sugars.

Ammonia is produced. Acids are produced from sugars oxidatively. Monomethylamine, trimethylamine, trimethylamine-N-oxide, and sugars are utilized. Methanol, methane, and hydrogen are not utilized. Ammonia, nitrate, urea, peptone, and methylamine are utilized as nitrogen sources.

Good growth occurs at pH 6.0–8.0 and at 30–37 °C. No growth above pH 9.0 and below pH 5.0 at 42 °C and in the presence of 3 % NaCl (Urakami et al. 1992).

The type strains of all species can utilize L-arabinose and L-alanine; none can use adonitol (McDonald et al. 2005; Maynaud et al. 2012). McDonald et al. (2005) performed a biochemical characterization of all *Aminobacter* species except *Aminobacter anthyllidis* and found that all type strains could utilize *N*-acetyl-D-glucosamine, D-cellobiose, D-fructose, D-galactose, D-glucose, D-mannose, D-maltose, D-ribose, D-xylose, i-inositol, D-mannitol, D-sorbitol, acetate, 4-aminobutyrate, DL-3-hydroxybutyrate, DL-lactate, oxoglutarate, L-histidine, L-leucine, L-ornithine, and L-proline and hydrolyze bis-*para*-nitrophenyl (pNP)-phosphate, pNP-phenyl-phosphonate, L-alanine-*para*-nitroanilide (pNA), and L-proline-pNA. None of the strains could utilize *p*-arbutin, α-D-melibiose, salicin, maltitol, putrescine, cis-aconitate, trans-aconitate, adipate, azelate, citrate, fumarate, itaconate, mesaconate, suberate, L-phenylalanine, 3-hydroxybenzoate, and phenylacetate. All type strains used sucrose. None of the strains could hydrolyze esculin, pNP-β-D-galactopyranoside, pNP-β-D-glucuronide, 2-deoxythymidine-5′-pNP-phosphate, and L-glutamate-γ-3-carboxy-pNA and none produced acid from lactose, adonitol, rhamnose, methyl D-glucoside, erythritol, and melibiose. Additional features and differentiating characteristics of the species are shown in ➋ *Table 18.3*.

Only strains of *Aminobacter ciceronei* and *Aminobacter lissarensis* utilize several methyl halides as sole carbon sources (➋ *Table 18.3*). Of all *Aminobacter* strains tested, two strains of *Aminobacter ciceronei* (ER2 and C147; not the type strain) were the sole *Aminobacter* strains that could degrade atrazine and carbofuran (McDonald et al. 2005). *Aminobacter anthyllidis*, which is capable of nodulation and was isolated from a Zn-Pb

Table 18.3
Comparison of selected characters of the species of *Aminobacter*

Characteristic	*Aminobacter anthyllidis* LMG 26462[T]	*Aminobacter aganoensis* DSM 7051[T]	*Aminobacter aminovorans* LMG 2122[T]	*Aminobacter ciceronei* CCUG 50580[T]	*Aminobacter lissarensis* CCUG 50579[T]	*Aminobacter niigataensis* DSM 7050[T]
References	Maynaud et al. 2012	Urakami et al. 1992; McDonald et al. 2005	Urakami et al. 1992; McDonald et al. 2005	McDonald et al. 2005	McDonald et al. 2005; Maynaud et al. 2012	Urakami et al. 1992; McDonald et al. 2005
Source	Soil from a Zn-Pb mine, after trapping with *Anthyllis vulneraria* subsp. *pyrenaica*	Soil enrichment on trimethylammonium hydroxide	Soil enrichment cultures containing various amines	CH_3Br-fumigated soil	Soil from beech woodland	Soil enrichment on *N,N*-dimethylformamide
Motility		Subpolar flagella	Subpolar flagella	Motile	Motile	Subpolar flagella
Cell shape	Rods	Rods with rounded ends	Rods with rounded ends	Rods	Rods	Rods with rounded ends
Cell size		0.5–0.9 × 1.0–3.0 μm	0.5–0.9 × 1.0–3.0 μm	0.6 × 1.3 μm	0.5–0.6 × 1.3–1.5 μm	0.5–0.9 × 1.0–3.0 μm
Colony pigmentation	Cream	White to light yellow	White to light yellow	Unpigmented	Faint pink	White to light yellow
Metabolism		Aerobic respiration	Aerobic respiration	Aerobic	Aerobic	Aerobic respiration
Temperature range for growth (°C)	Up to 37	30–37	30–37			30–37
Growth at 42 °C	–	–	–			–
Optimal growth (°C)	28			28–30	25	
Growth below pH 5 and above pH 9	+ (5–11)	–	–			–
Optimal pH		6.0–8.0	6.0–8.0	6.5–7.5	6.7–7.2	6.0–8.0
Growth with 3 % NaCl	–	–	–		+	–
Oxidase		+	+			+
Catalase		+	+			+
Urease		–	–			–
Major fatty acids (>10 %)		SF7 (C18:1 ω7c/C18:1 ω9t/C18:1 ω12t), unknown (ECL 18.081)	SF7 (C18:1 ω7c/C18:1 ω9t/C18:1 ω12t), C19:0 cyclo ω8c, unknown (ECL 18.081)	11-Me-C18:1 ω7t, SF7 (C18:1 ω7c/C18:1 ω9t/C18:1 ω12t)	11-Me-C18:1 ω7t, SF7 (C18:1 ω7c/C18:1 ω9t/C18:1 ω12t)	SF7 (C18:1 ω7c/C18:1 ω9t/C18:1 ω12t), C19:0 cyclo ω8c, unknown (ECL 18.081)
Important fatty acids (5–10 %)		C16:0		C16:0, C19:0 cyclo ω8c	C16:0, C19:0 cyclo ω8c	C16:0
Hydroxy fatty acids		C12:0 3-OH	C12:0 3-OH	C12:0 3-OH	C12:0 3-OH	C12:0 3-OH
DNA G+C content (mol %)	62.6	63.8	62.5	62.0–63.7	62.5	63.2
Reduction nitrate to nitrite		w	–			w
Indole production = tryptophanase		–	–			–
Hydrolysis of:						

Table 18.3 (continued)

Characteristic	*Aminobacter anthyllidis* LMG 26462^T	*Aminobacter aganoensis* DSM 7051^T	*Aminobacter aminovorans* LMG 2122^T	*Aminobacter ciceronei* CCUG 50580^T	*Aminobacter lissarensis* CCUG 50579^T	*Aminobacter niigataensis* DSM 7050^T
Gelatin, starch		–	–			–
pNP-α-D-glucopyranoside		+	+	w	–	+
pNP-β-D-glucopyranoside		w	w	–	–	w
pNP-phosphorylcholine		w	+	w	–	–
Acid production from:						
Glucose		w	w	w	w	w
D-Mannitol	+	w	w	w	w	w
Sucrose		w	w	–	w	w
Dulcitol, salicin		–	w	–	–	w
Inositol	+	w	–[a]	–	–[a]	w
Sorbitol	+	w	–[a]	–	w	w
L-Arabinose		–	w	w	w	w
Raffinose, cellobiose		–	w	–	–	–
Maltose	–	w	w	w	–	w
D-Xylose	–	w	w	w	w	w
Trehalose		–	w	–	–	w
D-Arabitol	w	w	w	–	w	w
M-Mannose	+	w	w[b]	w	w	w
Erythritol, L-xylose, L-sorbose, D-tyranose, D-lyxose	–		–		+	
D-Adonitol, D-lactose	–		–		–	
D-Galactose, D-fructose	+		+		+	
Fucose	w		+		+	
L-Rhamnose	+		–		+	

Utilization of:						
Gluconate		–	–	w	–	–
L-Rhamnose		–	+	+	+	+
D-Trehalose		+	–	+	+	+
Propionate	–	+	+[b]	+	+[b]	–
Glutarate		+	+	+	+	–
L-Malate	+	+	–	–	–	–
Pyruvate	+	+	–	+	+	+
L-Aspartate	w	+	+[b]	+	+	+
L-Serine	w	+	+[b]	+	+[b]	+
β-Alanine		+	–	+	+	+
L-Tryptophan		–	–	+	+	–
4-Hydroxybenzoate		+	–	–	–	+
H_2S production		–	–			–
Methyl red		–	–			–
Voges-Proskauer		–	–			–
Denitrification		–	–			–
Utilization as sole carbon and energy source of:						
CH_3Br, CH_3Cl		–	–	+	+[c]	–
CH_3I				+	–	
CH_3F				–	–	
Methylamine				+	+[c]	
PHB accumulation		+	+			+

Data taken from the descriptions in the references that are listed in the table. Fatty acid data from McDonald et al. (2005)
[a]Positive according to Maynaud et al. (2012)
[b]Negative according to Maynaud et al. (2012)
[c]Requires the presence of cyanocobalamin (1 $mg.l^{-1}$)

mining site through trapping with *Anthyllis vulneraria*, can tolerate 1–2 mM of Zn and 0.3–1 mM of Cd in YEM broth after 1 week (Maynaud et al. 2012).

The DNA base composition ranges from 62 to 64 mol % G + C. The main cellular fatty acids include C18:1, and the main hydroxy fatty acids include C12:0 3-OH. The ubiquinone system is ubiquinone Q10.

The type species is *Aminobacter aminovorans*, originally described as *Pseudomonas aminovorans* (Urakami et al. 1992).

Aquamicrobium Bambauer et al. 1998, 631[VL] emend. Lipski and Kämpfer 2012

A.qua.mi.cro'bi.um, L. n. *aqua*, water; N.L. neut. n. *microbium*, a microbe; N.L. neut. n. *Aquamicrobium*, a bacterium living in water/wastewater.

This description is based on the emended description of Lipski and Kämpfer (2012). *Aquamicrobium* consists of pleomorphic or regularly shaped short rods that are mesophilic and grow best at pH 6–9. They can tolerate up to 7 % NaCl (w/v) and utilize sugars, carbonic acids, amino acids, and alcohols for growth. Major quinone is Q10, major fatty acid is C18:1 *cis*-11, major polyamine is spermidine, and main polar lipids are phosphatidylglycerol, phosphatidylcholine, and phosphatidylethanolamine. G+C content of the DNA is 57–65 mol %. The type species is *Aquamicrobium defluvii*.

A number of phenotypic and other characteristics of the *Aquamicrobium* type strains are listed in ➋ *Table 18.4*. All species are oxidase and catalase positive. *Aquamicrobium defluvii* is able to utilize thiophene-2-carboxylate as sole carbon source in the presence of molybdate (Bambauer et al. 1998). In addition, acetate, propionate, butyrate, crotonate, glucose, fructose, mannose, xylose, mannitol, and sorbitol are used for growth with oxygen or nitrate as electron acceptors. Nitrate is reduced to nitrite. No growth was observed with thiophene-2-acetate, thiophene-3-carboxylate, thiophene-3-acetate, thiophene-2-carbaldehyde, thiophene-2-methanol, thiophene-2-mandelate, thiophene-2-acrylate, thiophene, benzothiophene, dibenzothiophene, pyrrole-2-carboxylate, furan-2-carboxylate, pyridine, nicotinate, benzoate, phenylacetate, phthalate, galactose, ribose, sorbose, maltose, saccharose, cellobiose, and lactose. Hydrolysis of gelatin, arginine dihydrolase, lysine decarboxylase, and urease is negative (Bambauer et al. 1998). *Aquamicrobium lusatiense* is able to degrade 4-chlorophenol, 2,4-dichlorophenol, and phenol, and this capacity was not lost over repeated transfers and attempts at curing. Indeed, genes for chlorocatechol 1,2-dioxygenase and 2,4-dichlorophenol hydroxylase were shown to be located on the chromosome rather than on a megaplasmid (Fritsche et al. 1999). Hydrolysis of urea, starch, gelatin, casein, DNA, Tween 80, and esculin is negative (Fritsche et al. 1999). *Aquamicrobium aerolatum* is positive for phosphatase and L-alanine aminopeptidase (Kämpfer et al. 2009).

Small amounts of 12:0 3-OH were reported for *Aquamicrobium defluvii* and *Aquamicrobium lusatiense* and iso-15:0 3-OH for *Aquamicrobium aerolatum* by Kämpfer et al. (2009), but a later study comprising all species did not find hydroxy fatty acids (Lipski and Kämpfer 2012).

Chelativorans Doronina et al. 2010, 1047[VP]

Che.la'ti.vo.rans. N.L. n. *chelatum*, a chelate; L. part. adj. *vorans*, devouring; N.L. masc. n. *Chelativorans*, a bacterium digesting metal chelates.

Chelativorans strains are non-spore-forming rods. The genus was described as nonmotile (Doronina et al. 2010), although flagella were later reported for *Chelativorans multitrophicus* DSM 9103^T and several *Chelativorans* sp. strains (Kaparullina et al. 2011). They often occur as pairs and multiply by binary fission. They form small white colonies on EDTA/mineral salt agar (diameter 0.1–0.3 mm after 7 days at 30 °C). Optimal NaCl concentration for growth is 1.5 %. No PHB inclusions; electron dense inclusions are thought to consist of calcium and magnesium phosphates and are absent in cells grown on fumarate. Oxidase and catalase positive; indole is produced; no nitrate reduction to nitrite; no nitrogen fixation. Optimal temperature and pH for growth are 25–35 °C and 6.5–7.5. Aerobic respiratory metabolism; able to use EDTA as carbon, nitrogen and energy source, either facultatively (*Chelativorans multivorans*) or obligately (*Chelativorans oligotrophicus*). No autotrophic or methylotrophic growth; unable to use methanol or methylated amines as carbon, nitrogen, or energy source (Doronina et al. 2010). Unable to use alcohols, amines, malate, pyruvate, L-alanine, and L-serine as carbon and energy sources (Kaparullina et al. 2011). *Chelativorans oligotrophicus* has several defective or missing enzymes in the central carbon metabolism. The tricarboxylic acid cycle lacks α-ketoglutarate dehydrogenase activity, and 6-phosphofructokinase (ATP/PPi) is also absent (Doronina et al. 2010). The major cellular fatty acids are summed feature 7 (C18:1 ω7c, C18:1 ω9t and/or C18:1 ω12t) and C19:0 cyclo ω8c. Hydroxy fatty acids C12:0 3-OH, C13:0 3-OH, and C15:0 iso 3-OH are absent. The major ubiquinone is Q10. Predominant polar lipids are phosphatidylcholine, phosphatidylglycerol, phosphatidylethanolamine, phosphatidyldimethylethanolamine, phosphatidylmonomethylethanolamine, and diphosphatidylglycerol. *Mesorhizobium*-specific ornithine lipid is absent. sym-Homospermidine is the main polyamine with small amounts of spermidine and putrescine present. The DNA G+C content is 60–64 mol %. The type species is *Chelativorans multitrophicus* (Doronina et al. 2010).

Additional characters and differentiating features of both species are shown in ➋ *Table 18.5*.

Hoeflea Peix et al. 2005, 1165[VP]

Hoef.le.a'. N.L. fem. n. *Hoeflea* honoring Manfred Höfle, German microbiologist, in recognition of his contribution to the taxonomy of marine bacteria.

Table 18.4
Comparison of selected characters of the species of *Aquamicrobium*

Characteristic	*Aquamicrobium aerolatum* DSM 7051[T]	*Aquamicrobium aestuarii* KACC 14931[T]	*Aquamicrobium ahrensii* DSM 19730[T]	*Aquamicrobium defluvii* CCUG 50580[T]	*Aquamicrobium lusatiense* CCUG 50579[T]	*Aquamicrobium segne* DSM 19714[T]
References	Kämpfer et al. 2009; Lipski and Kämpfer 2012	Jin et al. 2013	Lipski and Kämpfer 2012	Bambauer et al. 1998; Lipski and Kämpfer 2012	Fritsche et al. 1999; Kämpfer et al. 2009; Lipski and Kämpfer 2012	Lipski and Kämpfer 2012
Source	Air collected in a duck shed	Crude oil-contaminated tidal flat	Biofilter for the treatment of animal rendering waste gas	Activated sludge from the municipal sewage plant of Regensburg (Germany)	Activated sludge of an industrial wastewater treatment plant	Biofilter for the treatment of animal rendering waste gas
Cell shape	Rods	Ovoid rods	Rods	Rods	Short rods	Rods
Cell size	0.3–0.5 × 1.5–2.0 μm	0.5–07 × 0.8–1.4 μm		0.5–0.8 × 1.5–2.5 μm	0.6–0.8 × 1.5–3 μm	
Motility	Motile	Two polar flagella		Motile	Polar flagellum	
Colony morphology	Smooth, greyish white, translucent, shiny with entire margin	Round, entire margin, convex, ivory	Circular, whitish	Circular, white, convex	Circular, white-greyish	Circular, whitish
Metabolism	Aerobic	Aerobic	Aerobic	Respiration with oxygen or nitrate electron acceptor	Aerobic	Aerobic
Temperature range for growth (°C)		15–45			12–44	
Growth at 41 °C		+		+		
Optimal growth (°C)		30–35	30	30–37	30–37	30
pH range	5.5–10	5.5–9.0			6.0–9.2	
Optimal pH		6.5–7.5	6–9	7.5–8.5	7.0–7.5	6–9
Growth with 2 % NaCl	+	+		+		
Nitrate reduction		+		+	–	
Vitamins required				+	+	
Major fatty acids (>10 %)	C18:1 ω7*c*, C17:0, C19:0 cyclo 11–12	C18:1 ω7*c*/ω6*c*	C18:1 ω7*c*	C18:1 ω7*c*	C18:1 ω7*c*	C18:1 ω7*c*, C16:0, C19 :0 cyclo ω8c
Important fatty acids (5–10 %)		C19:0 cyclo ω8c			C19:0 cyclo ω8c	C18:0
Polyamines	Putrescine, spermidine, spermine	Putrescine, spermidine, *sym*-homospermidine	Putrescine, spermidine, *sym*-homospermidine, spermine		Spermidine	Putrescine, spermidine, spermine
Polar lipids[a]	PG, PC, DPG, PE, UAL	PG, DPG, PE, PC, PME, UAL, UPL	PG, PC, DPG, PE, PME, UAL	PG, PC, DPG, PE, PME, UAL	PG, PC, DPG, PE, PME, UAL	PG, PC, DPG, PE, UAL
DNA G+C content (mol %)		56.9	60.6	61.7	61.4	58.7

Table 18.4 (continued)

Characteristic	*Aquamicrobium aerolatum* DSM 7051^T	*Aquamicrobium aestuarii* KACC 14931^T	*Aquamicrobium ahrensii* DSM 19730^T	*Aquamicrobium defluvii* CCUG 50580^T	*Aquamicrobium lusatiense* CCUG 50579^T	*Aquamicrobium segne* DSM 19714^T
Reaction in Biolog GN tests:						
Tween 40	–	+	w	–	–	–
Tween 80	–	–	w	w	w	–
N-Acetyl-D-galactosamine, adonitol, L-ornithine	–	–	–	–	+	–
α-Ketoglutaric acid	–	+	–	–	+	–
N-Acetyl-D-glucosamine, D-mannose, formic acid, L-alanine, L-threonine	–	–	–	+	+	–
myo-Inositol	–	+	–	+	+	–
D-Arabitol, D-mannitol	–	–	–	+	–	–
α-Ketobutyric acid	–	+	–	+	–	–
D-Fructose, D-alanine, L-glutamic acid, L-histidine, L-leucine, γ-Aminobutyric acid	–	–	+	+	+	–
α-D-Glucose, DL-lactic acid, L-proline	–	+	+	+	+	–
Gentiobiose	–	–	–	–	w	–
D-Sorbitol	–	–	–	w	–	–

Methylpyruvate	+	+	+	+	–	–
Inosine, uridine, thymidine	+	–	–	–	–	–
Monomethyl succinate, succinamic acid	+	+	–	–	–	–
Acetic acid, L-aspartic acid, 2-aminoethanol	–	–	–	w	+	–
D-Gluconic acid	+	–	+	+	+	–
Urocanic acid, glycerol	+	+	+	+	+	–
α-Hydroxybutyric acid	–	+	+	w	w	–
β-Hydroxybutyric acid	w	+	–	+	+	–
γ-Hydroxybutyric acid	w	+	–	–	–	–
α-Ketovaleric acid, hydroxy L-proline	–	–	w	+	+	–
L-Alanyl glycine, L-asparagine, L-serine	–	–	w	w	+	–
Propionic acid	–	+	w	w	+	–
Succinic acid	–		+	–	+	–
L-Alaninamide	+	+	–	–	+	–
Glycyl-L-aspartic acid	–		w	–	+	–
Glycyl-L-glutamic acid	+		w	–	+	–
DL-Carnitine	–		w	w	–	–

Data taken from the descriptions in the references is listed in the table. Fatty acid data were taken from Lipski and Kämpfer (2012). This study did not detect hydroxy fatty acids
[a]*PG* phosphatidylglycerol, *PC* phosphatidylcholine, *DPG* diphosphatidylglycerol, *PE* phosphatidylethanolamine, *PME* phosphatidylmonomethylethanolamine, *UAL* unidentified aminolipid, *UPL* unidentified phospholipid

Table 18.5
Characteristics of the species of *Chelativorans*

Characteristic	*Chelativorans multitrophicus* DSM 9103^T	*Chelativorans oligotrophicus* DSM 19276^T
Source	Mixture of soil extracts and activated sludge samples taken from various industrial wastewater treatment plants	Municipal sewage sludge samples
Cell size	0.5–1.0 × 0.7–2.0 μm	0.4–0.5 × 1.0–2.0 μm
Utilization of EDTA	Facultative	Obligate
Optimal growth temperature (°C)	30	32–34
Optimal pH	7.0	6.8–7.2
Vitamin requirements	Biotin, thiamine	Biotin
DNA G+C content (mol %)	63.1	60.8
Utilization as sole carbon and energy source:		
Glucose, lactate, glutamate, fumarate, succinate, acetate, nitrilotriacetate, iminodiacetate, N,N9-ethylenediaminediacetate, and ethylenediamine disuccinate	+	–
Diethylenetriamine pentaacetate, hydroxyethylethylene-diaminetriacetate	–	
Generation time on EDTA under optimal growth conditions	14h	7h
Degradation of uncomplexed EDTA, Ca^{2+}-, Ba^{2+}-, Mg^{2+}-, Mn^{2+}-, or Zn^{2+}-EDTA complexes	+	+
Degradation of Pb^{2+}- and Cu^{2+}-EDTA complexes	+	–
Degradation of Fe^{3+}-EDTA complexes	–	–
Growth on dilute complex media	Good but slow	–
Resistance to oxacillin, ampicillin, and lincomycin	+	+
Resistance to novobiocin, nalidixic acid, and neomycin	–	+
Resistance to gentamicin and streptomycin	–	–
α-Ketoglutarate dehydrogenase	+	–

Data from Doronina et al. (2010) and Kaparullina et al. (2011)

Cells are non-spore-forming, motile short rods. They are aerobic chemoorganotrophs and are oxidase and catalase positive except for *Hoeflea alexandrii* which was described as oxidase negative. Cells do not require NaCl; however, they can grow in the presence of up to 5 % NaCl. Growth is possible at a temperature of 18–33°C although some species can grow at higher and lower temperatures (Table 18.6). pH range for growth is 6–8 or 9, and *Hoeflea suaedae* has a more wide pH range of 5–10. No nitrate reduction to nitrite or nitrogen except for *Hoeflea suaedae* which was reported to reduce nitrate to nitrite.

The main fatty acid is C18:1 ω7c, and other important fatty acids (>3 %) are C16:0, 11-Me C18:1 ω7c, and C19:0 cyclo ω8c. Only small amounts of hydroxy fatty acid are present. Ubiquinone Q10 is the major quinone; the main polar lipids are phosphatidylglycerol, phosphatidylethanolamine, phosphatidylmonomethylethanolamine, and sulfoquinovosyldiacylglyceride, although the latter polar lipid was not reported from *Hoeflea anabaenae*. The G+C content of the DNA ranges from 53 to 60 mol %. The type species is *Hoeflea marina*.

Additional characters and differentiating features of the five *Hoeflea* species are shown in Table 18.6.

Hoeflea anabaenae cells attach to *Anabaena* heterocysts; of the other *Hoeflea* species, only *Hoeflea phototrophica* has been observed to do this, although at a much lower frequency (Stevenson et al. 2011). *Hoeflea siderophila* is the only species reported to be iron oxidizing, using FeS, $FeSO_4$, or $FeCO_3$ for lithotrophic growth while depositing iron oxides on the cell surface. It also has a facultative anaerobic metabolism. In anaerobic, iron-oxidizing conditions, it uses nitrate or N_2O as terminal electron acceptor. Nitrate is converted to nitrite which inhibits growth as it accumulates. In those conditions, nitrite can chemically oxidize up to 20 % of Fe(II). When N_2O is given as an electron acceptor, there is virtually no chemical Fe(II) oxidation, and N_2 is formed. The organism is also able to grow mixotrophically or

Table 18.6
Characteristics of *Hoeflea* species

Characteristic	*Hoeflea alexandrii* DSM 16655^T	*Hoeflea anabaenae* CCUG 56626^T	*Hoeflea halophila* KTCT 23107^T	*Hoeflea marina* LMG 128^T	*Hoeflea phototrophica* DSM 17068^T	*Hoeflea siderophila* DSM 21587^T	*Hoeflea suaedae* KACC 14911^T
References	Palacios et al. 2006; Stevenson et al. 2011	Stevenson et al. 2011	Jung et al. 2013	Peix et al. 2005; Stevenson et al. 2011; Chung et al. 2013	Biebl et al. 2006; Stevenson et al. 2011; Chung et al. 2013	Sorokina et al. 2012	Chung et al. 2013
Source	A culture of *Alexandrium minutum* AL1V (marine planktonic dinoflagellate)	Culture of *Anabaena*, attached to heterocysts	Marine sediment	Baltic Sea, water	A culture of *Prorocentrum lima* (marine dinoflagellate)	Brackish, iron-rich spring	Root surface of the halophyte *Suaeda maritima*
Shape	Rods	Irregular club-shaped rods; star-shaped aggregates	Straight to curved rods	Short rods	Small rods	Thin, slightly curved rods	Short rods
Cell size	0.8 × 2.5 μm	0.2 × 2–5 μm	0.7–0.8 × 2.5 μm	0.7–0.9 × 1.1–1.4 μm	0.3–0.5 × 0.7–2.0 μm	0.4 × 0.9–2.2 μm	0.3–0.5 × 1.3–1.4 μm
Motility	+, single polar flagellum	–	+, polar flagellum	+	+, single polar flagellum or single bipolar flagella	+, single polar flagellum	+, single polar flagellum
Pigmentation colonies	Light brown (marine agar)	None	Beige	White-cream (nutrient agar)	Light beige (marine agar) to wine red (1/10 marine agar)	Orange (due to Fe oxides)	White-cream (marine agar)
Bacteriochlorophyll a	–	–	–	–	+	–	–
Carotenoid pigment	–	–	–		+		
Metabolism	Aerobic respiration	Aerobic to microaerophilic respiration	Aerobic respiration	Aerobic respiration	Microaerophilic respiration	Fac. iron oxidizing; fac. mixo- or heterotrophic in anaerobic or microaerobic conditions	Aerobic respiration
Temperature range for growth (°C)	10–42	18–34	15–30	4–37	15–33	9–38	10–42
Optimal growth temperature (°C)	30	30	25–28	28	31	30	30–37
pH range for growth	6–9	6–8	6–9	6–8	6–9	6.2–8.5	5.0–10.0
Optimal pH	7	6.5	7.5	7		7.5	6.5–7.5

Table 18.6 (continued)

Characteristic	*Hoeflea alexandrii* DSM 16655[T]	*Hoeflea anabaenae* CCUG 56626[T]	*Hoeflea halophila* KTCT 23107[T]	*Hoeflea marina* LMG 128[T]	*Hoeflea phototrophica* DSM 17068[T]	*Hoeflea siderophila* DSM 21587[T]	*Hoeflea suaedae* KACC 14911[T]
Optimal salt conc. (% w/v)	0–6.8	1.25–1.75	0.5–1	3	ND	1	0–7
Salt range (%)	0–11.8	0.5–2.5	0–5	Up to 5	0.5–7	0.1–8.5	0–9.5
Growth on NaCl instead of sea salt		–					
Growth factors required		Yeast extract	Yeast extract		Yeast extract		
Major fatty acids (>10 %)	C18:1 ω7c	C18:1 ω7c/ω9t/ω12t, ECL 17.603	C18:1 ω7c 11Me, C18:1 ω7c/ω6c	C18:1 ω7c	C18:1 ω7c, C18:1 ω7c 11Me	C18:1ω7c, C16:0, C18:1ω7c 11Me	C16:0, C18:1 ω7c
Important fatty acids (5–10 %)	C16:0	C18:1 ω9c, ECL 18.846/ C19:1 ω6c	C16:0	C18:1 ω7c 11Me, C19:0 cyclo ω8c	C16:0		C18:1 ω7c 11Me, C19:0 cyclo ω8c
Hydroxy fatty acids	–	–	–	–	–	–	C12:0 3-OH
Polar lipids[a]	PG, DPG, PEA, PMMEA, PC, SQVDG, UPGL, UAL, UGL	PG, DPG, PEA, PMMEA, PC, UPL1, UPL2, UAL	PG, PEA, SQVDG, PC, PMMEA	PG, PEA, PMMEA, SQVDG, DPG, UPL, UPGL, PC	PG, PEA, PMMEA, PC, SQVDG, DPG, UAL		PG, PEA, PMMEA, SQVDG, PC, UGL, UL
Polyamines	2-Hydroxyputrescine, putrescine	2-Hydroxyputrescine, putrescine, spermidine		ND	ND		ND
DNA G+C content (mol %)	59.7	58.1	57.8	53.1	59.3	57.5	53.7
Oxidase	–		+	+	+	+	+
Catalase	+		+	+	+	w	+
Inhibition of *Pythium ultimum* and *Phytophtora capsici*	–	ND		–	–		+
Nitrate reduction to nitrite	–	ND		–	–	+	+
Nitrate reduction to nitrogen	–	ND		–	–	–	ND
Arginine dihydrolase	–			–			

Indole production	–				–		
Hydrolysis of gelatin	–			Weak, slow	–		–
Hydrolysis of esculin	+			+			+
Hydrolysis of starch					–		–
Hydrolysis of alginate					–		
Hydrolysis of Tween 80	+			+	–[f]		–
Hydrolysis of Tween 20	+			+	–		–
Urease	–			+	ND		+
β-Galactosidase	+	+	+	+[c]	+[c]		–
Alkaline phosphatase, leucine arylamidase, α-glucosidase	+	+	+	+	+		+
Esterase (C4)	+	+	+	+	+		–
Esterase lipase (C8)	+	–	+	+	+		–
Naphthol-AS-BI-phosphohydrolase	+[c]	–	–	–	–		+
Valine arylamidase	+[c]	–	+	–	–		–
Cystine arylamidase	+	–	+	–	–		–
β-Glucosidase	+	+	+	+	–		–
Trypsin	–	+	–	–	–		+
Acid phosphatase	–[d]	–	–	–	–		+
α-Galactosidase	–[d]	–	+	–	–		+
Lipase (C14), α-chymotrypsin, α-mannosidase, α-fucosidase	–	–	–	–	–		–
N-Acetyl-β-glucosaminidase,	–	–	–	–	–		+
β-Glucuronidase	–	–	–	–	–		

Table 18.6 (continued)

Characteristic	*Hoeflea alexandrii* DSM 16655^T	*Hoeflea anabaenae* CCUG 56626^T	*Hoeflea halophila* KTCT 23107^T	*Hoeflea marina* LMG 128^T	*Hoeflea phototrophica* DSM 17068^T	*Hoeflea siderophila* DSM 21587^T	*Hoeflea suaedae* KACC 14911^T
Growth in mineral medium plus:							
Yeast extract			+		+	+	
Succinate					w	+	
Citrate			+		w	+	
Acetate, pyruvate	+	+	–	+	+	+	
Malate	+	+		+	+	+	
Fumarate	+	+	+	+	+	+	
Fructose	+	–		+	+	+	
Sucrose	+	–	+	+	+	+	
Glucose, lactate	+	–	–	+	+	+	
L-Arabinose	+	–	+	+	+		
Glutamate	+	–	–	+	+	–	
Glycerol	–	–	–	+	–[b]	+	
Butyrate	–	–	–	–	+	+	
Ethanol	–	–		–	–	–	
Methanol	–	–		–	–		
Utilization of:							
Salicin, L-fucose	+[e]			–	–		+
D-Xylose	+[e]		–	–	–	+	+

D-Arabinose	–	+	+	–	–		+
Erythritol	–			–	–		+
D-Glucose	–		–	+	w	+	
D-Mannose	–		+	+		+	
L-Arabinose	–		+	+			
D-Mannitol	–		+	+			
D-Maltose	–		+	+		+	
N-Acetylglucosamine	–			–		+	
Malate	–			+	+	+	
Gluconate	–						
Gentiobiose	+			–			
Caproate	–			–			
Adipate	–			–			
Citrate	–			–		+	
Phenylacetate	–			–			

[a] *PEA* Phosphatidylethanolamine, *PG* phosphatidylglycerol, *DPG* diphosphatidylglycerol, *PMMEA* phosphatidylmonomethylethanolamine, *PC* phosphatidylcholine, *SQVDG* sulfoquinovosyldiacylglyceride, *UAL* unidentified aminolipid, *UPL* unidentified phospholipids, *UPGL* unidentified phosphoglycolipid

[b] Weak positive according to Biebl et al. (2006)

[c] Negative according to Stevenson et al. (2011)

[d] Positive according to Stevenson et al. (2011)

[e] Negative according to Chung et al. (2013)

[f] Positive according to Chung et al. (2013)

organotrophically in microaerobic or anaerobic condition, using nitrate or N_2O as electron acceptors. Nitrite, ClO_4^-, S^0, thiosulfate, and $Fe(OH)_3$ are not used as electron acceptors, and H_2 oxidation is not possible (Sorokina et al. 2012).

Lentilitoribacter Park et al. 2013, 2365[VL]

Len.ti.li.to.ri.bac'ter. L. masc. adj. *lentus*, slow, delayed; L. n. *litus-oris*, the seashore, coast; N.L. masc. n. *bacter*, rod; N.L. masc. n. *Lentilitoribacter*, slowly growing rod from the coast).

Lentilitoribacter cells are non-spore-forming, nonmotile, and rods to short rods. They are catalase and oxidase positive and do not reduce nitrate to nitrite. Aerobic. The predominant ubiquinone is Q10. The major fatty acids are C18:1 ω7c, 11-methyl-C18:1 ω7c, and summed feature 3 (iso-C15:0 2-OH and/or C16:1 ω7c). The major polar lipids are phosphatidylglycerol and phosphatidylmonomethylethanolamine. The DNA G+C content is 49.3 mol %. The type species is *Lentilitoribacter donghaensis*.

Lentilitoribacter donghaensis cells are rods, 0.3–0.6 × 0.6–4.0 μm. Colonies on marine agar are circular, slightly convex, smooth, whitish yellow and less than 0.5 mm in diameter after 10 days at 25 °C. Optimal growth temperature is 25 °C; growth occurs at 4 and 30 °C, but not at 35 °C. Optimal pH is between 7.0 and 7.5; growth occurs at pH 5.5, but not at pH 5.0. Grows in the presence of 1.0–5.0 % NaCl (bstl growth with 2.0 % NaCl). Requires Mg^{2+} ions for growth. Hydrolyzes Tween 20, 40, 60, and 80, but not esculin, casein, gelatin, hypoxanthine, L-tyrosine, starch, and xanthine. Acid is produced from D-xylose, but not from L-arabinose, D-cellobiose, D-fructose, D-galactose, D-glucose, myo-inositol, lactose, maltose, D-mannitol, D-mannose, D-melezitose, melibiose, D-raffinose, L-rhamnose, D-ribose, D-sorbitol, sucrose, and D-trehalose. In the API ZYM tests, alkaline phosphatase, esterase lipase (C8), and leucine arylamidase are positive, while esterase (C4), trypsin, and acid phosphatase activities are weakly present, and lipase (C14), valine arylamidase, cysteine arylamidase, α-chymotrypsin, naphthol-AS-BI-phosphohydrolase, α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, N-acetyl-β-glucosaminidase, α-mannosidase, or α-fucosidase activities are negative. The major fatty acids (>10 %) are C18:1 ω7c, 11-methyl-C18:1 ω7c, and summed feature 3 (iso-C15:0 2-OH and/or C16:1 ω7c). C10:0 3-OH is the only hydroxy fatty acid detected.

The type strain CCUG 62792[T] was isolated from seawater from the coast around Baekdo harbor in the East Sea, South Korea. Its DNA G+C content is 49.3 mol %.

Mesorhizobium Jarvis et al. 1997, 897[VP]

Me.so.rhi.zo'bi.um. Gr. adj. *mesos*, middle; N.L. neut. n. *Rhizobium*, bacterial genus name; N.L. neut.n. *Mesorhizobium*, rhizobia, phylogenetically intermediate between the genera *Bradyrhizobium* and *Rhizobium*. This etymology is given in the original description (Jarvis et al. 1997); alternatively in the List of Prokaryotic names with Standing in Nomenclature (www.bacterio.cict.fr), the name *Mesorhizobium* is said to refer to the growth rate of the bacteria which is intermediate between that of the genera *Rhizobium* and *Bradyrhizobium*.

The genus *Mesorhizobium* comprises 30 species, most occurring as nitrogen-fixing endosymbionts in root nodules of various legume plants. The species *Mesorhizobium thiogangeticum* was isolated from the soil adjacent to the roots of the legume *Clitoria ternatea*, by enrichment using reduced sulfur compounds as sole carbon and energy source (Ghosh and Roy 2006).

All species comprise rod-shaped cells that form creamy, white, or colorless colonies on agar media. They are aerobic organotrophs; only *Mesorhizobium thiogangeticum* is capable of facultative chemolithotrophic growth using thiosulfate or elemental sulfur as energy source (Ghosh and Roy 2006). Optimal temperature for growth is around 28 °C, and optimal pH is about 7. Three species have been reported to grow at 4°C: *Mesorhizobium ciceri*, *Mesorhizobium sangaii*, and *Mesorhizobium shonense* (Zhou et al. 2013); *Mesorhizobium ciceri* is the only species reported to grow at 40 °C (Jarvis et al. 1997; Zhou et al. 2013). Several species can grow in the presence of 1 or 2 % NaCl (➲ *Table 18.7*); for *Mesorhizobium shangrilense*, even growth with 3 % NaCl was reported (Lu et al. 2009).

The fatty acid C18:1 ω7c is present in all species in large amounts (at least 10 % detected in itself or as part of a summed feature), while C16:0, 11-Me C18:1 ω7c, and C19:0 cyclo ω8c are also important (at least 5 %) in more than two thirds to half of the species. Hydroxy fatty acids have been reported at more than 1 % in 7 of the 30 species and comprise mostly C12:0 3-OH and/or iso-C13:0 3-OH; only in *Mesorhizobium albiziae* and *Mesorhizobium temperatum* has iso-C15:0 3-OH been reported at more than 1 % (Wang et al. 2007). Polar lipids have been reported for six of the species (➲ *Table 18.7*): all comprised phosphatidylethanolamine, phosphatidylglycerol, and phosphatidylcholine, while five also contained diphosphatidylglycerol and several unidentified phospholipids (Zhang et al. 2012; Zheng et al. 2013). The DNA G+C content ranges from 57.9 % to 65.1 %.

The type species is *Mesorhizobium loti*. Additional characters and differentiating features of *Mesorhizobium* species are shown in ➲ *Table 18.7*.

Nitratireductor Labbé et al. 2004, 54[VP]

Ni.tra.ti.re.duc'tor. N.L. masc. n. *nitras*, nitrate; L. v. *reducere*, to bring back, to reduce; N.L. masc. n. *nitratireductor*, nitrate-reducing bacterium.

The genus *Nitratireductor* comprises six species that occur in various marine habitats. All species are aerobic chemoorganotrophs; nitrate reduction varies between strains. Cells are rods, short rods, or coccoid. Motility is variable. Optimum temperature for growth is 25–35 °C. No growth below 10 °C. pH range is 5–12. All species are oxidase and catalase positive. Major quinone is ubiquinone Q10. The main fatty acid is C18:1 ω7c/ω6c. DNA G+C content is 56.7–63 mol %. The type species is *Nitratireductor aquibiodomus*.

Table 18.7
Characteristics of the type strains of species of *Mesorhizobium*

(Part 1)								
Characteristic	*Mesorhizobium abyssinicae* LMG 26967^T	*Mesorhizobium albiziae* LMG 23507^T	*Mesorhizobium alhagi* HAMBI 3019^T	*Mesorhizobium amorphae* LMG 18977^T	*Mesorhizobium australicum* LMG 24608^T	*Mesorhizobium camelthorni* HAMBI 3020^T	*Mesorhizobium caraganae* LMG 24397^T	*Mesorhizobium chacoense* LMG 19008^T
References	Degefu et al. 2013	Wang et al. 2007	Chen et al. 2010	Wang et al. 1999	Nandasena et al. 2009	Chen et al. 2011	Guan et al. 2008	Velazquez et al. 2001
Source	Root nodules of *Acacia abyssinica* and *Acacia tortilis*	Root nodules of *Albizia kalkora*	Root nodules of *Alhagi sparsifolia*	Root nodules of *Amorpha fruticosa*	Root nodules *Biserrula pelecinus*	Root nodules of *Alhagi sparsifolia*	Root nodules of *Caragana microphylla*	Root nodules of *Prosopis alba*
Motility	+	+	+			+	+	+
Cell size (µm)	0.3–0.4 × 2.2–3.0	0.3–0.5 × 1–3	0.5–0.7 × 1.3–1.5	0.4–0.7 × 0.5–1.7		0.3–0.6 × 1.0–1.2	0.5 × 2–3	
Growth with 1 % (w/v) NaCl	–	v	+	v			v	–
Growth with 2 % (w/v) NaCl			+	–		+	–	
Growth at pH 5		–	–	v		–	–	–
Growth at pH 9				–				
Growth at pH 10		–	+	–		–	+	–
Growth at 4 °C								
Growth at 10 °C						–	+	
Growth at 37 °C	–			–			+	
Growth at 39 °C							+	
Growth at 40 °C							+	
Survival at 60 °C (10 min)							+	
Temperature range (°C)	Max. 35			<37			Max. 40	
pH range	4,5–9,0			< 9	5,5–9,0	6–11		
Major fatty acids (>10 %)	C16:0, C18:1 ω7c	C18:1 ω7c/ω9c/ω9t/ω12t	11-Me C18:1 ω7c, C18:1 ω7c, C19:0 cyclo ω8c	C16:0, 11-Me C18:1 ω7c, C18:1 ω7c/ω9t/ω9c/ω12t, C19:0 cyclo ω8c	C16:0, C18:1 ω7c, 19:0 cyclo ω8c	11-Me C18:1 ω7c, C18: ω7c	C16:0, C18:1 ω7c/w6c	C16:0, C19:0 cyclo ω8c, C18:1 ω7c/ω9c/ω12t
Important fatty acids (5–10 %)		iso-C15:0, 11-Me C18:1 ω7c	iso-C17:0	C18:0		iso-C17:0, C19:0 cyclo ω8c	C18:0	C18:0, 11-Me C18:1 ω7c
Important hydroxy fatty acids (>1 %)	C12:0 3-OH, iso-C13:0 3-OH	iso-C15:0 3-OH						
DNA G+C content (mol %)	63.5	59.0	60.4	64	63.0	63.7	59.7	61.7

Table 18.7 (continued)

(Part 1)

Characteristic	*Mesorhizobium abyssinicae* LMG 26967^T	*Mesorhizobium albiziae* LMG 23507^T	*Mesorhizobium alhagi* HAMBI 3019^T	*Mesorhizobium amorphae* LMG 18977^T	*Mesorhizobium australicum* LMG 24608^T	*Mesorhizobium camelthorni* HAMBI 3020^T	*Mesorhizobium caraganae* LMG 24397^T	*Mesorhizobium chacoense* LMG 19008^T
Polar lipids[a]								
Nitrate reduction							+	
Catalase								
Oxidase				+				
Urease								
Reduction of nile blue								
Reduction of methyl blue				–				
Utilization as sole carbon source:								
L-Arabinose		–	+	+				+
D-Arabinose		–	+	–		+	+	–
D-Galactose			+					
Glucose				+				
D-Fructose		v	+	+		+	+	v
Lactose		+		v				–
D-Mannose				–				
L-Rhamnose		–	+	v		+	+	v
D-Ribose		–		–			+	–
Sucrose		+		+	+		+	v
Sorbose		v		–	–		v	–
Trehalose		+		+	+		+	–
L-Xylose		+		+				
D-Xylose		–	+	v		+	+	–
D-Maltose		v	+	+	+	+	+	v
D-Raffinose		+		+			+	+
D-Melibiose	+	v	v	+	+	–	–	v
Turanose								
Melezitose				–				
Calcium gluconate				–			–	

Inulin		+		–			+	+
D-Sorbitol		–	+	+		+	+	–
Dulcitol		–		v	–		–	–
Inositol		+	+	+		+	+	+
Glycerol	+							
Sodium pyruvate		–		–			+	–
Salicin		–		–			v	–
Dextrin	+	–		–			+	–
Amygdalin		–		–			+	–
Sodium formate	+	–		–			–	–
Sodium acetate		–		–			+	–
Sodium citrate	+	–	+	v		+	–	–
Sodium D-gluconate	+			–			–	
Sodium hippurate		–	–	–		–	+	v
Sodium tartrate		–	v	–		–	–	v
L-Malate		+		+				+
DL-Sodium malate		+		+			+	–
Succinate	+	+	+	+		+	+	–
Adipic acid								
Malonate	+	–		v				+
Itaconate	+							
Soluble starch							–	
Vanillic acid							–	
Glycine		+		–			–	–
L-Serine	+							
L-Methionine		–		–			+	–
L-Histidine	+							
L-Arginine		–		–			–	–
DL-Asparagine							–	
L-Proline								
L-Glycine							–	
L-Threonine	+	–		–			+	–
N-Acetyl-D-glucosamine	+							

Table 18.7 (continued)

(Part 1)								
Characteristic	*Mesorhizobium abyssinicae* LMG 26967^T	*Mesorhizobium albiziae* LMG 23507^T	*Mesorhizobium alhagi* HAMBI 3019^T	*Mesorhizobium amorphae* LMG 18977^T	*Mesorhizobium australicum* LMG 24608^T	*Mesorhizobium camelthorni* HAMBI 3020^T	*Mesorhizobium caraganae* LMG 24397^T	*Mesorhizobium chacoense* LMG 19008^T
Utilization as sole nitrogen source								
L-Phenylalanine	+	+	+	v		+	+	–
L-Valine		+		v			+	+
L-Methionine		+		+			+	+
D-Arginine		+	+	+		–	+	–
L-Arginine		+		+				
L-Cystine		v	+	v			+	–
DL-α-Alanine		+		–				
DL-Histidine		–	–	–		–		–
Glycine		–	+	–		+		–
DL-α-Aminopropionate		–		+			+	–
Hypoxanthine		–		+			+	–
L-Isoleucine		+		+			+	+
L-Lysine		+	+	+		+	+	+
D-Threonine		+		–			–	–
L-Threonine		+		+			+	–
D-Aspartate		+	–	+			+	–
L-Aspartic acid	+		–	–		–		
D-Glutamic acid		–		v			+	–
L-Glutamic acid	+	v		+			+	–
Resistance to (μg/ml)								
Ampicillin (5)				v			–	
Ampicillin (50)		+	–	–	–	–	–	–
Ampicillin (100)		+		–			–	–
Ampicillin (300)		+		–			–	–
Ampicillin sodium (5)		+		–				–
Ampicillin sodium (50)		+		–				–
Ampicillin sodium (300)		+		–				–

Bacitracin (5)		+		+			+	–
Bacitracin (50)		+		+			+	–
Bacitracin (100)		–		–			–	–
Chloramphenicol (5)		+	–	v			–	–
Chloromycetin (100)		+		–			–	+
Chloromycetin (50)		+		–			–	+
Chloromycetin (5)		+	+	+		+		+
Erythromycin (5)		+	+	+		+	+	–
Erythromycin (50)		+	–	+		–	+	–
Erythromycin (100)		+		v			–	–
Erythromycin (300)		+		+			v	–
Gentamicin (50)							–	
Gentamicin (5)		+	–	+		–	–	–
Kanamycin sulfate (50)	–	–		–	+		v	–
Kanamycin (100)		–		–				–
Kanamycin (50)		+		–				–
Kanamycin sulfate (5)		+		+			+	–
Neomycin (50)							+	
Neomycin sulfate (5)		+		+			+	–
Spectinomycin (5)	–	+		–			+	–
Spectinomycin (50)					–		+	
Streptomycin (50)	–			–				
Streptomycin (5)			–	–		–		
Streptomycin sulfate (5)		+	–	–			+	–
Streptomycin sulfate (50)		+		–			–	–
Streptomycin sulfate (100)		+		–			–	–
Streptomycin sulfate (300)				–			–	–
Dihydrostreptomycin (5)		+		–				+

Table 18.7 (continued)

(Part 1)								
Characteristic	*Mesorhizobium abyssinicae* LMG 26967^T	*Mesorhizobium albiziae* LMG 23507^T	*Mesorhizobium alhagi* HAMBI 3019^T	*Mesorhizobium amorphae* LMG 18977^T	*Mesorhizobium australicum* LMG 24608^T	*Mesorhizobium camelthorni* HAMBI 3020^T	*Mesorhizobium caraganae* LMG 24397^T	*Mesorhizobium chacoense* LMG 19008^T
Dihydrostreptomycin (50)		+		–				–
Dihydrostreptomycin (100)		+		–				–
Dihydrostreptomycin (300)		–		–				–
Bromothymol blue (0.2 %)		+	–	+		–		+
Neutral red (0.2 %)		–	v	–		–		–

(Part 2)								
Characteristic	*Mesorhizobium ciceri* LMG 14989^T	*Mesorhizobium gobiense* LMG 23949^T	*Mesorhizobium hawassense* LMG 26968^T	*Mesorhizobium huakuii* LMG 14107^T	*Mesorhizobium loti* LMG 6125^T	*Mesorhizobium mediterraneum* LMG 17148^T	*Mesorhizobium metallidurans* LMG 24485^T	*Mesorhizobium muleiense* HAMBI 3264^T
Reference	Nour et al. 1994; Jarvis et al. 1997	Han et al. 2008	Degefu et al. 2013	Chen et al. 1991; Jarvis et al. 1997	Jarvis et al. 1982, 1997	Nour et al. 1995; Jarvis et al. 1997	Vidal et al. 2009	Zhang et al. 2012
Source	Root nodules of *Cicer arietinum*	Root nodules of *Oxytropis glabra*	Root nodules of *Sesbania sesban*	Root nodules of *Astragalus sinicus*	Root nodules of *Lotus corniculatus*	Root nodules of *Cicer arietinum*	Root nodules of *Anthyllis vulneraria*	Root nodules *Cicer arietinum*, China
Motility			+	One polar or subpolar flagellum	One polar or subpolar flagellum			+
Cell size (μm)		0.3–0.6 × 1–3	0.28–0.32 × 2.25–3.15	0.5–0.9 × 1.2–3.0				0.46–0.61 × 0.91–2.40
Growth with 1 % (w/v) NaCl	+	+		+	v	v	+	–
Growth with 2 % (w/v) NaCl	+	v			–	v	–	–
Growth at pH 5	+	+		–	–	–		
Growth at pH 9		+			+	+		
Growth at pH 10	v	v		v	v	v	+	–
Growth at 4 °C					–		–	–
Growth at 10 °C		–				–	+	–
Growth at 37 °C		+	–		–	v	+	–
Growth at 39 °C				–		+	–	
Growth at 40 °C	+				–	+		

Survival at 60 °C (10 min)		–				–	–	–
Temperature range (°C)	Max. 40		Max. 35			Max. 40	Max. 37	
pH range	5.0–10.0	5–9	4.5–10.0	5.0–9.5	4.0 to <10.0	5.0–9.5	5–11	6–9
Major fatty acids (>10 %)	C16:0, C19:0 cyclo ω8c, 11-Me C18:1 ω7c, C18:1 ω7c/ω6c	C16:0, C19:0 cyclo ω8c, 11-Me C18:1 ω7c, C18:1ω7c/ω6c	C16:0, C18:1 ω7c	C16:0, C18:1 ω7c, C19:0 cyclo ω8c	C16:0, C19:0 cyclo ω8c, 11-Me C18:1 ω7c, C18:1 ω7c/ω6c	C16:0, C19:0 cyclo ω8c, C18:1ω7c/iso-C17:1ω9c	C16:0, C19:0 cyclo ω8c, C18:1ω7c/iso-C17:1ω9c	C16:0, C19:0 cyclo ω8c, C18:1ω7c/iso-C17:1ω9c
Important fatty acids (5–10 %)		iso-C17:0	iso-C17:0	iso-C17:0		C18:0, 11-Me C18:1 ω7c	C18:0, 11-Me C18:1 ω7c	C18:0, 11-Me C18:1 ω7c
Important hydroxy fatty acids (> = 1 %)			iso-C13:0 3-OH	C12:0 3-OH, iso-C13:0 3-OH				
DNA G+C content (mol %)	63.0	57.9	62.5	63.5	62.7	62.5		61.2
Polar lipids[a]	DPG, PEA, PG, PC, 6UPL				DPG, PEA, PG, PC, 5UPL		DPG, PEA, PG, PC, 6UPL	PC, PEA, PG
Nitrate reduction	+	v			+	–	+	–
Catalase		+						+
Oxidase	+	+			+	+		+
Urease	–	–			–			
Reduction of Nile blue	–	–			–			
Reduction of methyl blue	–	+			v	–		
Utilization as sole carbon source:								
L-Arabinose	+			+	+	+	+	+
D-Arabinose	+	+		v	v	v		+
D-Galactose	+	+		+	+	+	+	+
Glucose	v	+		+	+	+	+	+
D-Fructose	+	+		+	v	+	+	+
Lactose	v	+	+	v	+	+	+	+
D-Mannose	+	+		+	+	+		+
L-Rhamnose	v	+		+	+	+	+	+
D-Ribose	+			+	v	v	v	+
Sucrose	+	+		+	+	+		+
Sorbose	–	–		–	–	–	+	–
Trehalose	v	+		+	+	+		+
L-Xylose	+			+	–	–	+	
D-Xylose	v	+		+	v	v		+
D-Maltose	+	+		+	+	+	+	
D-Raffinose	–	–		+	v	–	v	–

Table 18.7 (continued)

(Part 2)

Characteristic	*Mesorhizobium ciceri* LMG 14989^T	*Mesorhizobium gobiense* LMG 23949^T	*Mesorhizobium hawassense* LMG 26968^T	*Mesorhizobium huakuii* LMG 14107^T	*Mesorhizobium loti* LMG 6125^T	*Mesorhizobium mediterraneum* LMG 17148^T	*Mesorhizobium metallidurans* LMG 24485^T	*Mesorhizobium muleiense* HAMBI 3264^T
D-Melibiose	v		+	v	v	–	+	
Turanose	+	+			+	+	+	
Melezitose	–	–			–	–	–	–
Calcium gluconate	–	v			–	–	–	v
Inulin	v	–		v	–	–	–	+
D-Sorbitol	v			+	v	v	–	+
Dulcitol	v	+		v	–	v	v	–
Inositol	+	v		v	+	+	+	–
meso-Erythritol	+	+		–	v	v	–	+
Glycerol	+		+	w	+	+	+	
Sodium pyruvate	v	+		v	v	v	–	–
Salicin	–	–		v	–	v	v	–
Dextrin	v	+	+	+	v	v	–	
Amygdalin	v	–		–	–	–	–	
Sodium formate	v	v	w	v	v	v	–	–
Sodium acetate	v	–		v	v	v	–	+
Sodium citrate	v	+	+	v	v	–	–	
Sodium D-gluconate	v	v	+	+	v	v	–	–
Sodium hippurate	–	–		v	–	–	–	
Sodium tartrate	–	–		v	–	–	–	
L-Malate	+			+	+	+		
DL-Sodium malate	v	+		+	+	–		
Succinate	+	+	+	v	v	v	–	
Adipic acid	–	–			–	–		–
Malonate	v		w	v	v	–	–	
Itaconate	v		+	w	v	–	–	
Soluble starch	–	–		–	–	–	–	W
Vanillic acid		–		–		–	–	–
Glycine	–	–		+	–	–	+	–
L-Serine	v		w	w	v	–	–	
L-Methionine	–	–		+	–	v		

L-Histidine	+		+	w	+	+		
L-Arginine	–			+	–	–	–	
DL-Asparagine		–		–		–	–	–
L-Proline	+			–	v	+	v	+
L-Glycine	+	–			–	–	v	–
L-Threonine	v	+	+	v	v	–	–	–
N-Acetyl-D-glucosamine	+		+	w	+	+		
Utilization as sole nitrogen source:								
L-Phenylalanine	v	v	+	v	+	+	+	–
L-Valine	v	v		v	v	v	–	+
L-Methionine	+	–		+	+	v	+	+
D-Arginine	+			+	+	–		
L-Arginine	–	+		+	–	+	–	+
L-Cystine	v	+		+	v	v		+
DL-α-Alanine	–	+			–	–	–	+
DL-Histidine	–			–	–	–		
Glycine	–	+		–	–	+		
DL-α-Aminopropionate	+			+	+	–		
Hypoxanthine	v	+		+	v	+	–	+
L-Isoleucine	+	+		+	v	v	–	+
L-Lysine	+	+		+	v	v	–	+
D-Threonine	–	+		+	–	v	–	
L-Threonine	+	+		+	+	–		+
D-Aspartate	+			+	+	–		
L-Aspartic acid	v	+	+	+	+			–
D-Glutamic acid	+	+		+	v	v	–	–
L-Glutamic acid	v	+	+	+	v	+	–	–
Resistance to (μg/ml):								
Ampicillin (5)	v	+		–	+	+	v	–
Ampicillin (50)	v	–		–	v	v	+	–
Ampicillin (100)	–			–	v	–	–	
Ampicillin (300)	–			–	–	–		
Ampicillin sodium (5)	–			–	+	–		
Ampicillin sodium (50)	–			–	+	–		
Ampicillin sodium (300)	–			–	–	–		
Bacitracin (5)	+			+	+	+		

Table 18.7 (continued)

(Part 2)								
Characteristic	*Mesorhizobium ciceri* LMG 14989^T	*Mesorhizobium gobiense* LMG 23949^T	*Mesorhizobium hawassense* LMG 26968^T	*Mesorhizobium huakuii* LMG 14107^T	*Mesorhizobium loti* LMG 6125^T	*Mesorhizobium mediterraneum* LMG 17148^T	*Mesorhizobium metallidurans* LMG 24485^T	*Mesorhizobium muleiense* HAMBI 3264^T
Bacitracin (50)	+			+	+	–		
Bacitracin (100)	–			+	–	–		
Chloramphenicol (5)	v	+		v	v	v		
Chloromycetin (100)	–	+		–	–	v	+	–
Chloromycetin (50)	–	+		–	–	v	+	–
Chloromycetin (5)	+			+	–	–		+
Erythromycin (5)	+	+		+	v	+		
Erythromycin (50)	+			+	v	v		
Erythromycin (100)	+			+	+	–		
Erythromycin (300)	+	–		+	+	–	+	+
Gentamicin (50)		–				+	+	–
Gentamicin (5)	+			+	+	–		+
Kanamycin sulfate (50)	–	–		v	+	v	+	–
Kanamycin (100)	–			+	+	–		
Kanamycin (50)	–			+	+	–		
Kanamycin sulfate (5)	+			+	+	–		+
Neomycin (50)		–				+	+	–
Neomycin sulfate (5)	+			+	+	–		
Spectinomycin (5)	–	+	–	+	+	v	+	–
Spectinomycin (50)		–				–	+	–
Streptomycin (50)	–	–	–		+	–		
Streptomycin (5)	+	+			+	+		
Streptomycin sulfate (5)	v	–		+	+	v	+	–
Streptomycin sulfate (50)	–			+	+	–		
Streptomycin sulfate (100)	–			+	+	–		
Streptomycin sulfate (300)	–				+	–		
Dihydrostreptomycin (5)	+			+	+	–		
Dihydrostreptomycin (50)	–			–	+	–		

Dihydrostreptomycin (100)	–			–	+	–		
Dihydrostreptomycin (300)	–			–	+	–		
Bromothymol blue (0.2 %)	+			+	–	+		
Neutral red (0.2 %)	–			–	+	+		
(Part 3)								
Characteristic	*Mesorhizobium opportunistum* LMG 24607^T	*Mesorhizobium plurifarium* LMG 11892^T	*Mesorhizobium qingshengii* LMG 26793^T	*Mesorhizobium robiniae* HAMBI 3082^T	*Mesorhizobium sangaii* HAMBI 3318^T	*Mesorhizobium septentrionale* HAMBI 2582^T	*Mesorhizobium shangrilense* LMG 24762^T	*Mesorhizobium shonense* LMG 26966^T
Reference	Nandasena et al. 2009	de Lajudie et al. 1998	Zheng et al. 2013	Zhou et al. 2010	Zhou et al. 2013	Gao et al. 2004	Lu et al. 2009	Degefu et al. 2013
Source	Root nodules of *Biserrula pelecinus*	Root nodules of *Acacia senegal*	Root nodules of *Astragalus sinicus*, China	Root nodules of *Robinia pseudoacacia*	Root nodules of *Astragalus luteolus*, China	Root nodules of *Astragalus adsurgens*	Root nodules of *Caragana bicolor*	Root nodules of *Acacia abyssinica*
Motility		+		+	+			+
Cell size		0.5–0.7 × 1–3	0.38–0.52 × 1.75–2.12	0.3–0.6 × 1–2.5	0.3–0.6 × 1–3		0.3–0.6 × 1–3	0.3–0.4 × 2.1–3.1
Growth with 1 % (w/v) NaCl		v	+	+	+	v	+	–
Growth with 2 % (w/v) NaCl		+		+	–		v	
Growth at pH 5		–				–	+	
Growth at pH 9				+		–		
Growth at pH 10		v		v	–	–	+	
Growth at 4 °C			–				–	
Growth at 10 °C			+	+			+	
Growth at 37 °C		+	–	+		–	+	–
Growth at 39 °C							–	
Growth at 40 °C		+		+	–			
Survival at 60 °C (10 min)				+				
Temperature range (°C)		Max. 42	10–35				10–37	Max. 35
pH range	5.5–9.0	4.5–9.0	5.5–9.0	6–11	5–9		5–10	4.5–10.5
Major fatty acids (>10 %)	C16:0, C18:1ω7c	C16:0, C18:1 ω7c, C19:0 cyclo ω8c	C16:0, 11-Me C18:1 ω7c, C18:1 ω7c/ω6c	C19:0 cyclo ω8c, C18:1 ω7c/ω9c/ω9t/ω12t	C16 :0, C18:1 ω7c/ω9c/ω9t/ω12t, 11-Me C18:1 ω7c, C19:0 cyclo ω8c	C16:0, 11-Me C18:1 ω7c, C18:1 ω7c/ω9t/ω9c/ω12t	C16:0, 11-Me C18:1 ω7c, C19:0 cyclo ω8c, C18:1ω7c/ω6c	C16:0, C18:1 ω7c
Important fatty acids (5–10 %)	11-Me C18:1 ω7c	iso-C17:0		C16:0, iso-C17:0, 11-Me C18:1 ω7c		C18:0		C19:0 cyclo ω8c
Important hydroxy fatty acids (> = 1 %)		iso-C13:0 3-OH	iso-C13:0 3-OH	iso-C13 3-OH				C12:0 3-OH, iso-C13:0 3-OH

Table 18.7 (continued)

(Part 3)

Characteristic	*Mesorhizobium opportunistum* LMG 24607[T]	*Mesorhizobium plurifarium* LMG 11892[T]	*Mesorhizobium qingshengii* LMG 26793[T]	*Mesorhizobium robiniae* HAMBI 3082[T]	*Mesorhizobium sangaii* HAMBI 3318[T]	*Mesorhizobium septentrionale* HAMBI 2582[T]	*Mesorhizobium shangrilense* LMG 24762[T]	*Mesorhizobium shonense* LMG 26966[T]
DNA G+C content (mol %)	63.2	64.4 or 62.8	59.5	61.5	58.3	59.4 or 63.12	61.4	62.2
Polar lipids[a]			DPG, PEA, PG, PC, 5UPL					
Nitrate reduction				+	–		v	
Catalase			+		+		+	
Oxidase					+	+	v	
Urease			+		+		–	
Reduction of Nile blue					–		–	
Reduction of methyl blue					–	–	+	
Utilization as sole carbon source:								
L-Arabinose		+		+		+		
D-Arabinose		+	+		+	–	+	
D-Galactose			+	+			–	
Glucose		+	+	+	+	v	+	
D-Fructose		v	+	+	+	v	+	
Lactose	+	v	–	+	+	+	–	
D-Mannose		+	+	+	+	v	+	
L-Rhamnose		+	–	+	+	+	+	
D-Ribose		+	+	+	+	+	–	
Sucrose	+	+	+	+	+	+	v	
Sorbose	–	+	–	v		–	–	
Trehalose	+	+				+	+	
L-Xylose		+				+		
D-Xylose		+	+	+	+	v	+	
D-Maltose	+	+	+	+	+	+	+	
D-Raffinose	–	+	–	+	+	+	–	
D-Melibiose	+	v	+		+	v	–	+
Turanose	+					+	–	
Melezitose						–	–	
Calcium gluconate			–	+		–	–	
Inulin		+	–			+	+	

D-Sorbitol		+	–		+	+	+	
Dulcitol	–	–	+	+	+	+	–	
Inositol		+	+	+		+	+	
meso-Erythritol		–	+			v	–	
Glycerol		w						+
Sodium pyruvate		v		+		v	+	
Salicin		+	–	+		–	–	
Dextrin		v	–			v	–	+
Amygdalin		–	–			v	–	
Sodium formate		v	–	+		v	–	+
Sodium acetate		+	–			v	–	
Sodium citrate		+	–		–	–	+	+
Sodium D-gluconate		w	–	+		–	–	+
Sodium hippurate		+	–	+	–	+		
Sodium tartrate		–	–	–	–	–	–	
L-Malate		+				+		
DL-Sodium malate		+	+			–	+	
Succinate		+	+	+		v	+	+
Adipic acid			–				–	
Malonate		v	–	+	–	–		+
Itaconate		w						+
Soluble starch			–	+	–		–	
Vanillic acid				+	–		–	
Glycine		–		+		–	–	
L-Serine		w						+
L-Methionine		–	–			–	–	
L-Histidine		w						+
L-Arginine		v	+			–	–	
DL-Asparagine			–	+			–	
L-Proline		+	+				–	
L-Glycine			+	+	–			
L-Threonine		+	+	+		+		+
N-Acetyl-D-glucosamine	+	w						+
Utilization as sole nitrogen source:								
L-Phenylalanine		+		+	+	v	+	+

Table 18.7 (continued)

(Part 3)

Characteristic	*Mesorhizobium opportunistum* LMG 24607^T	*Mesorhizobium plurifarium* LMG 11892^T	*Mesorhizobium qingshengii* LMG 26793^T	*Mesorhizobium robiniae* HAMBI 3082^T	*Mesorhizobium sangaii* HAMBI 3318^T	*Mesorhizobium septentrionale* HAMBI 2582^T	*Mesorhizobium shangrilense* LMG 24762^T	*Mesorhizobium shonense* LMG 26966^T
L-Valine		+	+	+	+	v	+	
L-Methionine		+	+	+	+	+	+	
D-Arginine		+				–		
L-Arginine			–	+	+	+	+	
L-Cystine		+	+	+	–	v	+	
DL-α-Alanine			–		–	–	–	
DL-Histidine		–				+		
Glycine		–			–	+	v	
DL-α-Aminopropionate		+				–		
Hypoxanthine		+	–	+		v	+	
L-Isoleucine		+	+			+	–	
L-Lysine		+	+		–	v		
D-Threonine		+	–			v	–	
L-Threonine		+		+	+	+	+	
D-Aspartate		+		+		+		
L-Aspartic acid		+				–	+	+
D-Glutamic acid		+	+			v		
L-Glutamic acid		+	+	+	–	–	+	+
Resistance to (μg/ml):								
Ampicillin (5)		+	–	+	–	v	+	
Ampicillin (50)	–	–		+	–	+	+	
Ampicillin (100)		–	–	+		+		
Ampicillin (300)		–		+		+		
Ampicillin sodium (5)		+				–		
Ampicillin sodium (50)		–				–		
Ampicillin sodium (300)		–				–		
Bacitracin (5)		+				–		
Bacitracin (50)		+				–		
Bacitracin (100)		+				–		
Chloramphenicol (5)		–	+			v	+	
Chloromycetin (100)		–	+	+		–		

Chloromycetin (50)		–		+		–		
Chloromycetin (5)		–				–		
Erythromycin (5)		+				v	+	
Erythromycin (50)		+				v	–	
Erythromycin (100)		+				–		
Erythromycin (300)		+	+	+		–		
Gentamicin (50)				+				
Gentamicin (5)		+				–		
Kanamycin sulfate (50)	+	v		+		–	–	
Kanamycin (100)		–				–		
Kanamycin (50)		+				–		
Kanamycin sulfate (5)		+				–	+	
Neomycin (50)				+				
Neomycin sulfate (5)		+				–		
Spectinomycin (5)		–		+		+		–
Spectinomycin (50)	–			+				
Streptomycin (50)					–	–	–	–
Streptomycin (5)				+		–		
Streptomycin sulfate (5)		+		+	–	v	+	
Streptomycin sulfate (50)		–				–	+	
Streptomycin sulfate (100)		–				–		
Streptomycin sulfate (300)		–				–		
Dihydrostreptomycin (5)		+				–		
Dihydrostreptomycin (50)		–				–		
Dihydrostreptomycin (100)		–				–		
Dihydrostreptomycin (300)		–				–		
Bromothymol blue (0.2 %)		+		+		+		
Neutral red (0.2 %)		–				–		

(Part 4)

Characteristic	*Mesorhizobium silamurunense* LMG 24822^T	*Mesorhizobium tamadayense* LMG 26736^T	*Mesorhizobium tarimense* LMG 24338^T	*Mesorhizobium temperatum* HAMBI 2583^T	*Mesorhizobium thiogangeticum* LMG 22697^T	*Mesorhizobium tianshanense* LMG 18976^T
Reference	Zhao et al. 2012	Ramirez-Bahena et al. 2012	Han et al. 2008	Gao et al. 2004	Ghosh and Roy 2006	Chen et al. 1995; Jarvis et al. 1997
Source	Root nodules of *Astragalus membranaceus*	Root nodules of *Anagyris latifolia*	Root nodules of *Lotus frondosus*	Root nodules of *Astragalus adsurgens*	Soil, by enrichment using reduced S compounds as sole C and energy source	Root nodules of *Glycyrrhiza pallidiflora*

Table 18.7 (continued)

(Part 4)						
Characteristic	*Mesorhizobium silamurunense* LMG 24822[T]	*Mesorhizobium tamadayense* LMG 26736[T]	*Mesorhizobium tarimense* LMG 24338[T]	*Mesorhizobium temperatum* HAMBI 2583[T]	*Mesorhizobium thiogangeticum* LMG 22697[T]	*Mesorhizobium tianshanense* LMG 18976[T]
Motility	+	One subpolar flagellum				Peritrichous flagella
Cell size	1.2–1.8 × 2.1–4.2	0.6–0.7 × 1.1–1.2	0.3–0.6 × 1–3		0.2–0.4 × 1.2–1.5	0.2–0.9 × 1.2–3.0
Growth with 1 % (w/v) NaCl	–	+	v	v		v
Growth with 2 % (w/v) NaCl		–	+	–		–
Growth at pH 5			+	–		–
Growth at pH 9			+	+		–
Growth at pH 10	+		+	–		v
Growth at 4 °C						
Growth at 10 °C		–	–	–		+
Growth at 37 °C		–	v	v	–	–
Growth at 39 °C						
Growth at 40 °C	+					
Survival at 60 °C (10 min)	+		–	–		–
Temperature range (°C)	Max. 40	11–36				
pH range		5–9			5.5–8.5	
Major fatty acids (>10 %)	C16:0, C18:1 ω7c/ω6c		C16:0, C18:1 ω7c/ω6c	C16:0, C18:0, C19:0 cyclo ω8c, C18:1ω7c/iso-C17:1ω9c	C18:1 ω7c	C16:0, C19:0 cyclo ω8c, 11-Me C18:1 ω7c, C18:1ω7c/iso-C17:1ω9c
Important fatty acids (5–10 %)	C19:0 cyclo ω8c		C18:0, 11-Me C18:1 ω7c	C18:1 ω9c, 11-Me C18:1 ω7c	iso-C15:0	C18:0
Important hydroxy fatty acids (> = 1 %)				iso-C15:0 3-OH		
DNA G+C content (mol %)	62.4	60.3	57.9	65.1 or 62.22	59.6 or 60.72	61 or 62.51
Polar lipids[a]						DPG, PEA, PG, PC, 12UPL
Nitrate reduction	–	–	v	+		+
Catalase	+		+		+	
Oxidase	–		–	+	–	+

Urease	–	+	–			
Reduction of Nile blue	+		–			
Reduction of methyl blue	+		–	–		–
Utilization as sole carbon source:						
L-Arabinose		+		–	+	
D-Arabinose	–		v	+		v
D-Galactose	+		v		+	v
Glucose	+	+	+	–	+	+
D-Fructose	+		+	v	–	+
Lactose	–		v	+	–	+
D-Mannose	+	+	+	–	–	v
L-Rhamnose	+	+	v	+	–	v
D-Ribose		+	–	+		v
Sucrose	+	+	+	v	–	+
Sorbose	–		v	v		–
Trehalose	+		+	–		+
L-Xylose				–	–	+
D-Xylose	+		v	+	–	v
D-Maltose	+	+	+	v	–	–
D-Raffinose	–		v	v	–	–
D-Melibiose	+	+		v		v
Turanose			+	–		
Melezitose	–		–	–		–
Calcium gluconate	–		v	–		v
Inulin	–		–	+		v
D-Sorbitol	+	+	+	v		v
Dulcitol			+	v		v
Inositol	+	+	+	v		v
meso-Erythritol	+		v	v	–	v
Glycerol					–	+
Sodium pyruvate	–		+	v		v
Salicin	–	w	v	–		v
Dextrin	–		+	–		v
Amygdalin	–		–	–		–
Sodium formate	–		–	v		v

Table 18.7 (continued)

(Part 4)						
Characteristic	*Mesorhizobium silamurunense* LMG 24822^T	*Mesorhizobium tamadayense* LMG 26736^T	*Mesorhizobium tarimense* LMG 24338^T	*Mesorhizobium temperatum* HAMBI 2583^T	*Mesorhizobium thiogangeticum* LMG 22697^T	*Mesorhizobium tianshanense* LMG 18976^T
Sodium acetate	+	–	–	+	–	v
Sodium citrate	–	–	–	v	–	v
Sodium D-gluconate	–	–	v	v		v
Sodium hippurate	–		–	–		v
Sodium tartrate			–	–		–
L-Malate				–	–	–
DL-Sodium malate	+	+	+	–		v
Succinate	+		v	–	+	+
Adipic acid	–	–	–			
Malonate		–	–	+		v
Itaconate		–				
Soluble starch	–		v	–		–
Vanillic acid			v	–		–
Glycine			+	–		–
L-Serine		–			–	
L-Methionine	–		–	–		–
L-Histidine		v			+	
L-Arginine	–		–	–	–	v
DL-Asparagine	–		+	–		–
L-Proline	–	+	+			+
L-Glycine	–		v	–		v
L-Threonine			v	v	–	v
N-Acetyl-D-glucosamine		+				
Utilization as sole nitrogen source:						
L-Phenylalanine	+		v	v		v
L-Valine	+		v	–		v
L-Methionine			–	+		v
D-Arginine				–		+
L-Arginine	+		+	+		+
L-Cystine	+		–	–		+

DL-α-Alanine			–	–		v
DL-Histidine				–		–
Glycine			–	+		+
DL-α-Aminopropionate				–		+
Hypoxanthine	+		v	v		+
L-Isoleucine	+		–	v		+
L-Lysine	+		+	v		v
D-Threonine			–	v		v
L-Threonine	+		+	+		+
D-Aspartate				–		–
L-Aspartic acid	+		+			v
D-Glutamic acid	+		–	–		v
L-Glutamic acid	+		v	–		+
Resistance to (μg/ml):						
Ampicillin (5)	+		v	v		v
Ampicillin (50)	–		+	–		–
Ampicillin (100)			–	–		–
Ampicillin (300)				–		–
Ampicillin sodium (5)				+		–
Ampicillin sodium (50)				–		–
Ampicillin sodium (300)				–		–
Bacitracin (5)				–		+
Bacitracin (50)				–		+
Bacitracin (100)				–		–
Chloramphenicol (5)	–		–	v		v
Chloromycetin (100)			+	–		–
Chloromycetin (50)			+	–		–
Chloromycetin (5)				+		+
Erythromycin (5)			+	v		+
Erythromycin (50)				–		v
Erythromycin (100)	+			–		v
Erythromycin (300)	–		–	–		v
Gentamicin (50)	–		+	–		–

Table 18.7 (continued)

(Part 4)						
Characteristic	*Mesorhizobium silamurunense* LMG 24822^T	*Mesorhizobium tamadayense* LMG 26736^T	*Mesorhizobium tarimense* LMG 24338^T	*Mesorhizobium temperatum* HAMBI 2583^T	*Mesorhizobium thiogangeticum* LMG 22697^T	*Mesorhizobium tianshanense* LMG 18976^T
Gentamicin (5)	+			–		–
Kanamycin sulfate (50)	–		–	v		v
Kanamycin (100)				–		–
Kanamycin (50)				–		–
Kanamycin sulfate (5)	+			–		+
Neomycin (50)	–		+	+		–
Neomycin sulfate (5)				–		–
Spectinomycin (5)			+	v		v
Spectinomycin (50)			+	–		+
Streptomycin (50)			–	–		–
Streptomycin (5)			–	–		–
Streptomycin sulfate (5)	–		+	v		v
Streptomycin sulfate (50)				–		–
Streptomycin sulfate (100)				–		–
Streptomycin sulfate (300)				–		–
Dihydrostreptomycin (5)				+		–
Dihydrostreptomycin (50)				–		–
Dihydrostreptomycin (100)				–		–
Dihydrostreptomycin (300)				–		–
Bromothymol blue (0.2 %)				+		+
Neutral red (0.2 %)				–		+

For substrate utilization and resistance, only characters with data for at least 10 species are listed; data were compiled from the original descriptions; *v* different report differ in this character, *w* weak positive. Empty cells indicate no data available

[a]*PEA* Phosphatidylethanolamine, *PG* phosphatidylglycerol, *DPG* diphosphatidylglycerol, *PC* phosphatidylcholine, *UPL* unidentified phospholipids

All species are positive for leucine arylamidase (API ZYM tests) and for the use of D-glucose and N-acetyl-glucosamine (API 20NE); all are negative for indole production (API 20NE). Further characteristics and differentiating features of the species are given in *Table 18.8*.

Phyllobacterium (*ex* Knösel 1962) Knösel 1984, 356[VP]

Phyl.lo.bac.te'ri.um. Gr. neut. n. *phyllon*, leaf; L. neut. n. *bacterium*, rod; N.L. neut. n. *phyllobacterium*, leaf bacterium (occurring in leaf nodules of higher plants).

Cells are rods and motile by means of polar, subpolar, or lateral flagella. The optimal growth temperature is 28 °C, and there is no growth at 40 °C. Growth occurs in 1 % NaCl. Glucose metabolism is oxidative. Oxidase positive; urease is positive except for *Phyllobacterium endophyticum*. Indole production, β-galactosidase, and gelatinase are negative for all species. Some other enzyme activities that were originally included in the genus description, however, have not been reported for all species. These include DNase (negative, but no data for *P. endophyticum* and *P. trifolii*), hydrolysis of Tween 80 (negative, but not tested for *P. catacumbae*, *P. endophyticum*, and *P. trifolii*), starch (negative for *P. myrsinacearum* and *P. catacumbae*), pectin and cellulose (both only reported as negative for *P. myrsinacearum*), nitrate reduction (positive for *P. myrsinacearum*, negative for *P. catacumbae*, *P. endophyticum* and *P. trifolii*). Esculin is hydrolyzed (weak reaction for *P. trifolii*). 3-Ketolactose test is negative (no data for *P. endophyticum* and *P. trifolii*). Assimilation of D-glucose, D-mannose, L-arabinose, D-mannitol, and N-acetylglucosamine is positive for all species. Maltose is used by all species except *P. endophyticum*. Quinones have only been reported for *Phyllobacterium endophyticum* and comprised Q10 (88 %) and Q9 (12 %) (Flores-Felix et al. 2013). Additional characteristics of the *Phyllobacterium* species are given in *Table 18.9*.

The G+C content of the DNA ranges from 51 to 61 mol % (Tm). The type species is *Phyllobacterium myrsinacearum*.

Pseudahrensia Jung et al. 2012, 2059[VP]

Pseu.dah.ren'si.a. Gr. adj. *pseudes*, false; N.L. fem. n. *Ahrensia*, a bacterial genus name; N.L. fem. n. *Pseudahrensia*, the false *Ahrensia*.

Pseudahrensia cells are aerobic, non-spore-forming, nonmotile, and ovoid to rod shaped. Catalase, oxidase, and nitrate reduction are positive. The predominant ubiquinone is Q10. The major fatty acid is C18:1 ω7c. The major polar lipids are phosphatidylcholine, phosphatidylglycerol, diphosphatidylglycerol, and phosphatidylethanolamine. The DNA G+C content of the type strain of the type species is 60.1 mol %. The type species is *Pseudahrensia aquimaris*.

Pseudahrensia aquimaris cells are nonmotile, ovoid to rod shaped, and 0.5–1.0 × 1.0–7.0 μm. Colonies on MA are circular, convex, smooth, glistening, cream colored and 1.0–1.5 mm in diameter after 5 days at 30 °C. Temperature range for growth is 4–32 °C; optimal growth at 30 °C, pH 7–8, and 2–3 % NaCl. Grows at pH 5.5, but not pH 5. Can grow in 10 % NaCl, but not in 11 % or without NaCl. Na^+ and Mg^{2+} ions are required for growth. No anaerobic growth on marine agar. Nitrate is reduced to nitrite. Gelatin is hydrolyzed. H_2S is not produced. Esculin; casein; hypoxanthine; starch; Tween 20, 40, 60, and 80; L-tyrosine; urea; and xanthine are not hydrolyzed. Acid is positive from D-fructose, D-galactose, D-glucose, lactose, maltose, D-mannose, D-ribose, and sucrose; no acid production from L-arabinose, cellobiose, myo-inositol, D-mannitol, melezitose, melibiose, raffinose, L-rhamnose, D-sorbitol, trehalose, or D-xylose. Susceptible to ampicillin, cephalothin, chloramphenicol, gentamicin, kanamycin, neomycin, novobiocin, penicillin G, polymyxin B, and streptomycin; resistant to carbenicillin, lincomycin, oleandomycin, and tetracycline. The following enzymes are present (API ZYM): alkaline phosphatase, esterase (C4), leucine arylamidase, acid phosphatase, esterase lipase (C8) (weak), and trypsin (weak); the following enzymes are absent: lipase (C14), valine arylamidase, cystine arylamidase, α-chymotrypsin, naphthol-AS-BI-phosphohydrolase, α- and β-galactosidase, β-glucuronidase, α- and β-glucosidase, N-acetyl-β-glucosaminidase, α-mannosidase, and α-fucosidase (Jung et al. 2012).

Major fatty acid (>10 %) is C18:1 ω7c; no other fatty acids are present at more than 5 %; the only hydroxy fatty acid detected is C18:0 3-OH, apart from the possible presence of C14:0 3-OH as part of summed feature 2 (Jung et al. 2012). However, Park et al. (2013) report the presence of iso-C13:0 3-OH and the absence of C18:0 3-OH.

The type strain (CCUG 60023[T]) was isolated from seawater, Yellow Sea of the island of Hwang-do, Korea.

Pseudaminobacter Kämpfer et al. 1999, 894[VP]

Pseud.ami.no.bac'ter. Gr. adj. *pseudos*, false; N.L. masc.n. *Aminobacter*, bacterial genus name; N.L. masc. n. *Pseudaminobacter*, false *Aminobacter*.

Pseudaminobacter cells are rod shaped and motile. Obligate aerobic heterotrophs. They have an oxidative metabolism and can use D-glucose, D-ribose, D-xylose, acetate, propionate, pyruvate, β-alanine, N-acetyl-D-glucosamine, 4-aminobutyrate, DL-3-hydroxybutyrat, DL-lactate, oxoglutarate, L-alanine, L-histidine, L-leucine, and L-proline as sole carbon source. Growth occurs on nutrient agar (Oxoid), Caso agar, R2A agar (Oxoid), and TSB agar (BBL). Colonies are circular, entire, slightly convex and smooth, glistening, and pale beige on nutrient agar at 25 °C. Oxidase and catalase positive. Main ubiquinone is Q10. The major polyamines are spermidine, sym-homospermidine, and putrescine. Polar lipids include phosphatidylcholine, phosphatidylglycerol, phosphatidyldimethylethanolamine, phosphatidylmonomethylethanolamine, phosphatidylethanolamine, and diphosphatidylglycerol in nearly the same amounts. Main fatty acids are C18:1 and C19:0 cyclo ω8c. The only hydroxy fatty acid is C15:O iso 3-OH. The G+C content of the

Table 18.8
Characteristics of the type strains of *Nitratireductor* species

Characteristic	*Nitratireductor aquibiodomus* DSM 15645^T	*Nitratireductor aquimarinus* JCM 17288^T	*Nitratireductor basaltis* JCM 14935^T	*Nitratireductor indicus* LMG 25540^T	*Nitratireductor kimnyeongensis* JCM 14851^T	*Nitratireductor lucknowense* DSM 24322^T	*Nitratireductor pacificus* LMG 25541^T
Reference	Labbé et al. 2004	Jang et al. 2011	Kim et al. 2009	Lai et al. 2011b	Kang et al. 2009	Manickam et al. 2012	Lai et al. 2011a
Source	Marine denitrification system	Culture of the marine diatom *Skeletonema costatum*	Black beach sand	Deep seawater crude oil enrichment culture	Dried seaweed samples	Lindane-contaminated soil	Deep-sea sediment pyrene-degrading consortium
Shape	Rods	Rods	Coccoid cells or rods	Rods	Rods	Rods	Short rods
Motility		1 polar flagellum	Nonmotile	1 polar flagellum	Motile		Motile
Cell size	1 × 2–3 μm	0.4–0.7 × 1.3–2.0 μm	0.6–0.7 × 0.6–2.0 μm	1.3 × 3.0 μm	0.4–0.5 × 1.2–2.7 μm		0.8–0.9 × 1.4–1.5 μm
Colonies	White	Cream	Cream	Gray	Light yellow	Straw yellow	Gray
Temperature range		20–40	15–45	10–43	10–40	20–42	10–41
Optimal temperature for growth (°C)	30–35	30–35		25–30	30	30	25–30
pH range		6.5–9.0	5.5–10.0		6.1–12.1	5.2–11.0	
Optimal pH for growth	7–7.5	7.7–8.2				8.0	
NaCl range for growth (%)		1–7	0–8	0–7	1–7	0–5	0–7
Optimal NaCl range for growth (%)		3–4		3	ND	2	3
Major cellular fatty acids (>10 %)	C18:1 ω7c/ω6c, C19:0 ω8c cyclo	C18:1 ω7c/ω6c, C19:0 ω8c cyclo	C18:1 ω7c/ω6c	C18:1 ω7c/ω6c	C18:1 ω7c/ω6c, C19:0 ω8c cyclo	C18:1 ω11c/ω9t/ω6t	SF8 (C18:1 ω7c/ω6c), C19:0 ω8c cyclo
Important fatty acids (5–10 %)	–	–	C18:0	C18:0	–	C16:0, C18:0, C19:0 ω8c cyclo	–
Hydroxy fatty acids (Jang et al. 2011)	–	iso-C15:0 3-OH, C18:0 3-OH	–	–	–	–	–
Major polar lipids[a]	PC, PG, DPG, PEA, UAPL1, UAPL2, UAL, UL1, UL2, UL3	PC, PG, DPG, PEA, UAPL1, UAPL2, UAL, UL1, UL2, UL3				PMMEA, PEA, DPG, PG, PC	
DNA G+C content (mol %)	57	56.7	56.7	59	60.4	62.4	63
Nitrate reduction	+	+	+	+	–	+	+
API ZYM tests:							
Alkaline phosphatase	+	+	+	+	+	–	+

Esterase C4, valine arylamidase, phosphoamidase	+	+	+	+	+		+
Lipase C8	+	+	+	–	+	+	+
Lipase C14	–	–	–	+	–	–	+
Cystine arylamidase	+	w	–	+	+	+	+
Trypsin	+	+	w	+	+		+
Chymotrypsin	–	–	–	+	–		–
Acid phosphatase	+	+	–	+	+		+
α-Galactosidase, β-galactosidase	–	–	+	–	–	–	w
β-Glucuronidase	–	–	w	–	–		–
α-Glucosidase	+	–	–	+	+	–	+
β-Glucosidase	–	–	–	–	–		+
N-Acetyl-β-glucosaminidase	+	+	–	–	–	–	+
α-Mannosidase, α-fucosidase	–	–	–	–	–		–
API 20 NE tests:							
Reduction nitrate to nitrite	+		+				
Reduction nitrate to nitrogen	–		–			+	
Fermentation of glucose	–	–	–	–	–		–
Hydrolysis of gelatin	–	–	–	–	–	+	–
Arginine dihydrolase	w	–	–	+	–	–	–
Urease	–	+	–	+	–	+	–
Hydrolysis of esculin	–	–	–	+	–	–	+
β-Galactosidase	–	+	+	+	–	–	w
Use of:							
L-Arabinose	+	+	+	–	–		–
D-Mannose	+	+	–	+	–	w	w
D-Mannitol	–	–	+	–	+		–
D-Maltose, potassium gluconate	–	–	+	–	–		–
Capric acid	–	–	–	–	–	–	+
Adipic acid	w	–	–	+	–	–	w

Table 18.8 (continued)

Characteristic	*Nitratireductor aquibiodomus* DSM 15645^T	*Nitratireductor aquimarinus* JCM 17288^T	*Nitratireductor basaltis* JCM 14935^T	*Nitratireductor indicus* LMG 25540^T	*Nitratireductor kimnyeongensis* JCM 14851^T	*Nitratireductor lucknowense* DSM 24322^T	*Nitratireductor pacificus* LMG 25541^T
Malic acid	w	–	–	+	–	–	–
Trisodium citrate	+	+	–	+	–	–	+
Phenylacetate	–	–	–	+	–	–	–
Biolog GN2:							
Acetic acid	w		+	w	–	–	+
Bromosuccinic acid, turanose	–		–	w	–	–	–
cis-Aconitic acid, succinic acid	–		w	+	–	–	–
DL-α-Glycerol phosphate, propionic acid	–		–	+	–	–	–
D-Alanine, L-alanine	+		+	+	–	–	+
D-Arabitol, D-mannose	–		–	–	+		–
Dextrin, itaconic acid	–		w	–	–		–
Thymidine	–		w	–	–	–	–
D-Fructose, D-mannitol	–		+	–	+		–
D-Galactose	+		w	–	+		–
D-Glucosaminic acid	+		–	–	–		–
D-Sorbitol, inosine, L-arabinose, uridine	–		+	–	–		–
Tween 40	–		+	–	–	+	–
Glycogen, γ-hydroxybutyric acid	–		+	–	–	–	–
Trehalose	+		–	+	+	–	w
Glycerol	+		+	w	+	–	+

Glycyl-L-aspartic acid, L-alanyl glycine	+		w	–	w	–	+
Glycyl-L-glutamic acid	w		+	+	w	–	+
Hydroxyl-L-proline	+		+	w	+	–	w
L-Alaninamide	+		+	–	–	–	+
L-Asparagine	+		w	+	+	–	+
L-Aspartic acid	–		+	w	+	–	–
L-Fucose	+		w	–	–		–
L-Histidine, L-ornithine	+		–	w	+	–	–
L-Leucine	–		+	w	–	–	+
L-Phenylalanine	+		–	–	–	–	+
L-Threonine	+		+	w	+	–	–
Maltose	–		+	–	+	–	w
Pyruvic acid methyl ester	+		w	+	+		w
myo-Inositol	+		–	+	w	–	–
Succinic acid monomethyl ester	+		–	+	+		+
N-Acetyl-D-glucosamine	+		–	+	+	–	+
N-Acetyl-D-galactosamine	+		–	–	w		–
Succinamic acid	–		+	+	w	–	–
Tween 80	–		+	–	–	+	w
Urocanic acid	–		–	+	+	–	+
α-D-Glucose	+		+	+	+	+	–
α-Hydroxybutyric acid	+		w	+	w	–	–
α-Ketobutyric acid	–		–	w	–	+	w
α-Ketoglutaric acid	w		w	+	+		+
γ-Aminobutyric acid	w		+	+	w	–	w

[a]*PEA* Phosphatidylethanolamine, *PG* phosphatidylglycerol, *DPG* diphosphatidylglycerol, *PMMEA* phosphatidylmonomethylethanolamine, *PC* phosphatidylcholine, *UAPL* unidentified aminophospholipid, *UAL* unidentified aminolipid, *UL* unidentified lipids

Table 18.9
Comparison of selected characters of the species of *Phyllobacterium*

Characteristic	*Phyllobacterium bourgognense* LMG 22837^T	*Phyllobacterium brassicacearum* LMG 22836^T	*Phyllobacterium catacumbae* LMG 22520^T	*Phyllobacterium endophyticum* LMG 26470^T	*Phyllobacterium ifriqiyense* LMG 22831^T	*Phyllobacterium leguminum* LMG 22833^T	*Phyllobacterium myrsinacearum* LMG 8736^T	*Phyllobacterium trifolii* LMG 22712^T
Reference	Mantelin et al. 2006b; Flores-Felix et al. 2013	Mantelin et al. 2006b; Flores-Felix et al. 2013	Jurado et al. 2005	Flores-Félix et al. 2013	Mantelin et al. 2006b	Mantelin et al. 2006b	Mergaert et al. 2002; Mergaert and Swings 2005b	Valverde et al. 2005
Source	Root of *Brassica napus* cv. Eurol	Root of *Brassica napus* cv. Eurol	Tuff volcanic rock in catacombs	Root nodule of *Phaseolus vulgaris*	Root nodule of *Lathyrus numidicus*	Root nodule of *Astragalus algerianus*	Leaf nodules of *Rubiaceae* and *Myrsinaceae*	Root nodule of *Trifolium repens*
Shape	Rods	Rods	Rods	Rods	Rods	Rods	Rods	Rods
Motility	Motile with flagella	Motile with flagella	Motile with a polar tuft of flagella	Motile with a polar flagellum	Motile with flagella	Motile with flagella	Motile with flagella	Motile with a polar flagellum
Cell size			0.4–0.7 × 0.4–1.9 µm				0.4–0.8 × 0.8–2.0 µm	
Colonies	White/cream	White/cream	Beige	Pearly white	White/cream	White, highly convex	Beige	Small, pearly white
Temperature range (°C)				5–39				
Temperature max (°C)	Below 35	Below 35		39	37	37	36	4–37
Optimal temperature for growth (°C)	28	28	28	28	28	28	28–34	28
Growth at 37 °C	–	–	+	+	+	+	–	+
pH range	5–10	5–10		6–8	5–10	5–10	4–10	6–8
Optimal pH for growth				7				7
Growth with 1 % NaCl	+	+			+	+	+	
Growth with 2 % NaCl	–	+	–	+	+	+	+	+
Growth with 3 % NaCl	–	–			+	–	+	+
NaCl max for growth (%)	1	2		2	3	2		0–3
Major cellular fatty acids (>10 %) (Jang et al. 2011)	C16:0, SF8 (C18:1 ω6c/C18:1 ω7c), C19:0 cyclo ω8c	C16:0, SF8 (C18:1 ω6c/C18:1 ω7c)	C16:0, C18:1 ω7c, C18:1 ω7c 11-Me, C19:0 cyclo ω8c	C16:0, C19:0 cyclo ω8c, SF8 (C18:1 ω6c/C18:1 ω7c)			C16:0 3-OH, C18:1 ω7c, C18:1 2-OH	C16:0, C18:1 ω7c, C18:1 ω7c 11-Me, C19:0 cyclo ω8c
Important fatty acids (5–10 %)	C18:1 ω7c 11-Me, C18:0	C19:0 cyclo ω8c, C18:1 ω7c 11-Me		C18:1 ω7c 11-Me			C16:0, C20:0	
Hydroxy fatty acids	C16:0 3-OH	C16:0 3-OH, C18:0 3-OH	C16:0 3-OH, C18:1 2-OH	C16:0 3-OH, C18:1 2-OH, C18:0 3-OH			C15:0 3-OH, C16:0 2-OH, C16:0 3-OH, C18:1 2-OH, C18:0 3-OH	C16:0 3-OH, C18:1 2-OH

DNA G+C content (mol %)	54	55.5	55.9	52	52	57	58.5	56.4
Oxidase	+	+	+		+	+	+	
Urease	+	+	+	–	+	+	–[a]	w
Growth in LB broth	–	+			+	+	+	
Arginine dihydrolase			+	–			–	–
Hydrolysis of esculin				+				w
Use of:								
3-O-Methyl-D-glucopyranose	–	–			–	–	–	
3-Phenylpropionate	–	–			–	–	–	
5-Keto-D-gluconate	+	+	+	+	+	–	+	+
Adonitol	+	–			+	–	+	
Esculin	+	+			+	+	+	
α-Ketoglutarate	–	+			–	–	+	
Benzoate	–	–			–	–	–	
Betaine	+	+			+	–	+	
β-Gentiobiose	+	+			+	+	+	w
β-Glucuronide	–	–			–	–	–	
Caprylate	–	–			–	–	–	
cis-Aconitate	+	+			+	–	+	
Citrate	+	+	–	–	–	–	+	–
D-Alanine	–	–			–	–	–	
D-Arabitol	+	+			+	+	+	
D-Cellobiose	+	+			+	+	+	
D-Galactose	+	+			+	+	+	
D-Galacturonate	–	–			+	+	+	
D-Gluconate	+[b]	+[b]	+	–	+	+	+	+
D-Glucosamine	+	+			+	+	+	
D-Glucuronate	–	–			+	+	+	
DL-α-Amino-n-butyrate	–	+			+	–	+	
DL-β-Hydroxybutyrate	+	+	+	+	+	–	+	+
DL-Glycerate	–	+			+	–	+	
DL-Lactate	+	+		+	+	+	+	
D-Lyxose	+	+			+	+	+	
D-Malate	+	+	+	+	+	–	+	+
D-Melezitose	–	–			–	–	–	

Table 18.9 (continued)

Characteristic	*Phyllobacterium bourgognense* LMG 22837^{T}	*Phyllobacterium brassicacearum* LMG 22836^{T}	*Phyllobacterium catacumbae* LMG 22520^{T}	*Phyllobacterium endophyticum* LMG 26470^{T}	*Phyllobacterium ifriqiyense* LMG 22831^{T}	*Phyllobacterium leguminum* LMG 22833^{T}	*Phyllobacterium myrsinacearum* LMG 8736^{T}	*Phyllobacterium trifolii* LMG 22712^{T}
D-Melibiose	–	–		–	–	–	–	
D-Raffinose	–	–			–	–	–	
D-Saccharate	+	–			–	+	–	
D-Sorbitol	+	+		+	+	+	+	
D-Tagatose	+	–			+	–	+	
D-Tartrate	–	–			–	–	–	
D-Trehalose	+	+			+	+	+	
Dulcitol	+	+			+	–	+	
D-Xylose	+	+			+	+	+	
Ethanolamine	–	+			+	–	+	
Fructose	+	+			+	+	+	
Fumarate	+	+			+	–	+	
Gentisate	–	–			–	–	–	
Glutarate	–	–			–	–	+	
Histamine	–	–			–	–	–	
Hydroxyquinoline	–	–			–	–	–	
i-Erythritol	–	–			+	–	–	
L-Alanine	+[b]	+	+	+	+[b]	–	+	w
L-Arabitol	+	–			+	–	+	
L-Aspartate	+	+			+	–	+	
L-Malate	+	+			+	–	+	
L-Serine	–	+		–	+	–	+	
L-Tartrate	–	–			–	–	–	
L-Tryptophan	–	–			–	–	–	
L-Tyrosine	–	–			–	–	+	
Malonate	–	+	w	w	+	–	–	–
Maltitol	+	+			+	–	+	
Maltotriose	+	+			–	–	+	

m-Coumarate	–	–			–	–	–	
meso-Tartrate	–	–			–	–	–	
Methyl α-D-glucopyranoside	+	–			–	–	+	
Methyl β-D-galactopyranoside	–	+			+	+	+	
Mucate	–	–			–	+	–	
Palatinose	+	+			+	–	+	
Phenylacetate	–	–		–	–	–	–	–
p-Hydroxybenzoate	–	+	–	–	–	–	+	–
Propionate	–	–		–	–	–	–	
Protocatechuate	+	+			–	–	+	
Putrescine	–	–			–	–	–	
Quinate	+	+			–	–	+	
Succinate	+	+			+	–	+	
trans-Aconitate	+	+			+	–	+	
Tricarballylate	–	–			–	–	–	
Trigonelline	+	+			–	–	+	
Tryptamine	–	–			–	–	–	
Xylitol	–	–			+	–	+	
3-Hydroxybenzoate	–	–		–	–	–	–	
Itaconate	–	–		–	–	–	–	
L-Fucose	+	+		+	+	+	+	
L-Histidine	–	–		w	–	–	–	
L-Proline	+	+		+	+	+	+	
L-Rhamnose	+	+		+	+	+	+	
Sucrose	+	+	+	–		–	+	+
Valerate	+	+	+	–	v	–	+	+
Capric acid	–	–		–	–	–	–	
D-Maltose	+	+	+	–	+	v	+	+

[a]Positive according to Mantelin et al. (2006b)
[b]Negative according to Flores-Felix et al. (2013)

Table 18.10

Characteristics of the two *Pseudaminobacter* species. Data taken from Kämpfer et al. (1999)

Characteristic	*Pseudaminobacter defluvii* NBRC 14570^T	*Pseudaminobacter salicylatoxidans* DSM 6986^T
Source	Activated sludge	6-Aminonaphthalene-2-sulfonate-degrading consortium from river water
Cell shape	Coccoid to rod shaped	Rods
Cell size	0.8–0.8 × 0.8–1.2 μm	0.5–0.8 × 1–1.5 μm
Temperature range	10–40	20–40
Major fatty acids (>10 %)	C18:1 (ω7c/ω9t/ω12t), C19:0 cyclo ω8c	C18:1 (ω7c/ω9t/ω12t), C19:0 cyclo ω8c
Important fatty acid (5–10 %)		C17:0
Hydroxy fatty acids	C15:0 iso 3-OH	C15:0 iso 3-OH
DNA G+C content (mol %)	62.9	63.9
Acid produced from D-mannitol, dulcitol, and melibiose	–	w
Assimilation of D-maltose, D-trehalose, adonitol, D-mannitol, D-sorbitol, *cis*-aconitate, glutarate, L-malate, L-aspartate, and 4-hydroxybenzoate	–	+
Assimilation of L-ornithine and L-serine	+	–

DNA is 62.9–63.9 mol %. The type species is *Pseudaminobacter salicylatoxidans*.

One additional species was described, *Pseudaminobacter defluvii*. Both species produce acid weakly from glucose, but not from lactose, sucrose, salicin, inositol, sorbitol, L-arabinose, raffinose, maltose, D-xylose, trehalose, cellobiose, D-arabitol, mannose, adonitol, rhamnose, methyl D-glucoside and erythritol. Both species hydrolyze bis-para-nitrophenyl (pNP)-phosphate, pNP-phenyl-phosphonate, L-alanine-para-nitroanilide (pNA), and L-proline-pNA, but not pNP-α-D-glucopyranoside, pNP-β-D-glucopyranoside, pNP-phosphorylcholine, esculin, pNP-β-D-galactopyranoside, pNP-β-D-glucuronide, 2-deoxythymidine-5′-pNP-phosphate, and L-glutamate-γ-3-carboxy-pNA. They do not assimilate p-arbutin, D-melibiose, salicin, maltitol, putrescine, trans-aconitate, adipate, azelate, fumarate, itaconate, mesaconate, suberate, L-tryptophan, 3-hydroxybenzoate, and phenylacetate. Additional characteristics of the *Psedaminobacter* species are given in *Table 18.10*.

Thermovum Yabe et al. 2012, 2994^{VP}

Ther.mo'vum. Gr. n. *thermê*, heat; L. neut. n. *ovum*, egg, oval; N.L. neut. n. *Thermovum*, a heat(-loving) oval-shaped organism.

Thermovum comprises Gram-positive ovoid cells that do not form spores. Thermophilic. Major fatty acids (>10 %) are C18:1 ω7c, C19:0 ω8c, and C18:0. Polar lipids comprise phosphatidylcholine, phosphatidylglycerol, phosphatidylethanolamine, hydroxyphosphatidylethanolamine, phosphatidylinositol, phosphatidylmonomethylethanolamine, an unknown glycolipid, and a ninhydrin-positive phospholipid. The main quinone is ubiquinone Q10. The type species is *Thermovum composti*.

Thermovum composti cells are nonmotile, ovoid shaped, and 0.9 μm × 1.4 μm (after 2 days at 50 °C). Catalase and oxidase positive. Growth occurs at 23–57 °C, with optimal growth at 50 °C, at pH 5.9–8.8 (optimum, pH 7.0) and in the presence of 0–4 % (w/v) NaCl. In addition to the major fatty acids listed above in the genus description, C16:0 is a further important fatty acid (5–10 %) in *Thermovum composti*, while no hydroxy fatty acids were reported. Negative for gelatinase, urease, and indole production. Positive for nitrate reduction and for the utilization of D-arabinose, L-arabinose, D-ribose, D-xylose, D-galactose, D-glucose, cellobiose, lactose, melibiose, gentiobiose, D-fucose, and potassium 5-ketogluconate; negative for the utilization of glycerol, erythritol, L-xylose, D-adonitol, methyl β-D-xylopyranoside, D-fructose, D-mannose, L-sorbose, L-rhamnose, dulcitol, inositol, D-mannitol, D-sorbitol, methyl α-D-mannopyranoside, methyl α-D-glucopyranoside, N-acetylglucosamine, amygdalin, arbutin, esculin ferric citrate, salicin, maltose, sucrose, trehalose, inulin, melezitose, raffinose, starch, glycogen, xylitol, turanose, D-lyxose, D-tagatose, L-fucose, DL-arabitol, potassium gluconate, and potassium 2-ketogluconate. The following enzyme activities were present (API ZYM): esterase C4, esterase C8, leucine arylamidase, α-chymotrypsin, naphthol-AS-BI-phosphohydrolase, trypsin, and valine arylamidase; the following were absent: alkaline phosphatase, lipase C14, cystine arylamidase, acid phosphatase, α-galactosidase, β-galactosidase, α-glucosidase, β-glucosidase, β-glucuronidase, N-acetyl-β-glucosaminidase, mannosidase, and α-fucosidase. The type strain JCM 17863^T was isolated from compost. The G+C content of its DNA is 63.4 mol %.

If appropriate, the description of metabolic pathways and/or physiology may deserve an individual heading.

Isolation, Enrichment, and Maintenance Procedures

The genera and species of the family have an aerobic respiratory metabolism and originate from a wide range of habitats. No single isolation or enrichment procedure is available to selectively obtain all or most members of the family, and therefore the genera are discussed separately below.

The only species of the genus *Ahrensia*, *Ahrensia kielensis*, was isolated from the Baltic Sea during studies of star-shaped-aggregate-forming bacteria and was originally named *Agrobacterium kielense* (Ahrens 1968). Because Dr. Renata Ahrens later withdrew the proposal, these species were not documented elsewhere in the following years, and no details on specific isolation conditions are available in recent literature (Rüger and Höfle 1992). With the recent sequencing of the genome of this organism, it may become possible in future to propose suitable isolation or enrichment strategies. The organism can be cultivated on regular marine media (e.g., Difco Marine Broth) at 26 °C and can be freeze-dried for long-term preservation.

Aliihoeflea was isolated from tidal flat sediment samples by plating on marine agar 2216 (Difco). Circular colonies—convex with entire margin, shiny, and cream colored—were 0.5–1.0 mm in diameter after 2 days incubation at 30 °C. Growth also occurs on trypticase soy agar (TSA, Difco), Luria agar (Difco), and yeast extract mannitol agar (YMA, per liter, 10 g D-mannitol, 0.5 g KH_2PO_4, 0.2 g $MgSO_4 \cdot 7H_2O$, 0.1 g NaCl, 4 g $CaCO_3$, 0.4 g yeast extract, 15 g agar; pH 6.8–7.0) (Roh et al. 2008).

All *Aminobacter* species were isolated from the soil using various enrichment or trapping methods. *Aminobacter anthyllidis* was isolated from the nodules of *Anthyllis vulneraria* that was used as a trapping plant and was grown in soil from a zinc and lead mining site (Maynaud et al. 2012). The surface-sterilized nodules were crushed in sterile water, and the bacteria were isolated by streaking the suspension on YMA (Vincent 1970; recipe as listed above) and incubating at 28 °C.

Aminobacter aganoensis, *Aminobacter aminovorans*, and *Aminobacter niigatensis* were isolated from soil by enrichment using methylamine compounds (mono-, di-, tri-, or tetramethylamine, trimethylamine-*N*-oxide, or tetramethylammonium hydroxide) or methylformamide compounds (*N*-methylformamide or *N,N*-dimethylformamide) (Urakami 2005). For routine growth of PYG medium, pH 7.0 can be used at 30 °C (Urakami et al. 1992).

Aminobacter ciceronei and *Aminobacter lissarensis* are methylotrophic species. *Aminobacter ciceronei* was isolated from CH_3Br-fumigated soil in the USA by enrichment on a mineral salt medium under a modified atmosphere of air plus CH_3Br (Miller et al. 1997). *Aminobacter lissarensis* strain CC495 was isolated from the top 5 cm of soil in a beech wood in County Down, Northern Ireland, by enrichment with CH_3Cl as the sole carbon and energy source. One gram of soil was added to 100 ml of minimal medium in 500-ml flasks containing 0.125 g of CH_3Cl. The minimal medium had the following composition (in grams per liter): KH_2PO_4 (4.5), K_2HPO_4 (10.5), $MgSO_4 \cdot 7H_2O$ (0.15), and NH_4NO_3 (1.5), pH adjusted to 7.2 with 6 M NaOH; a trace element solution was added (10 ml. l^{-1}) containing (in mg.l^{-1}) H_3BO_3(500), $CuSO_4 \cdot 5H_2O$ (40), KI (100), $FeSO_4 \cdot 7H_2O$ (200), $MnSO_4 \cdot 7H_2O$ (400), $(NH_4)6Mo_7O_{24} \cdot 4H_2O$ (200), and $ZnSO_4$ (400). In the pure cultures, the medium was additionally supplemented with a vitamin solution (5 ml.l^{-1}) containing (in milligrams per liter) folic acid (4), p-aminobenzoic acid (200), and cyanocobalamin (200). CH_3Cl (0.15 g) was added as an aqueous solution to give a concentration in the culture medium, after equilibration of the gaseous and aqueous phases, of 11.8 mM (30 mM if partitioning is neglected and the total CH_3Cl present is expressed as a concentration in the aqueous phase) (Coulter et al. 1999).

All *Aminobacter* species can be stored in broth medium plus 20 % glycerol at −80 °C or can be lyophilized and stored at 4 °C.

Two *Aquamicrobium* species were isolated from activated sludge, *Aquamicrobium defluvii* and *Aquamicrobium lusatiense* (Bambauer et al. 1998; Fritsche et al. 1999; Kämpfer et al. 2009). The former species originated from a municipal wastewater plant and was obtained on a mineral medium with thiophene-2-carboxylate as the sole source of carbon and nitrate as the electron acceptor. The mineral salt medium (Bambauer et al. 1998), also used for cultivation, contained per l 3.56 g $Na_2HPO_4 \cdot 2H_2O$, 0.4 g NH_4Cl, and 0.07 g K_2SO_4. After autoclaving, 1 l of medium was supplemented with 2 ml of a sterile solution containing per l 100 g MgCl2, 25 g CaCl2, 10 ml vitamin solution (Balch et al. 1979), and 1 ml trace element solution (Widdel et al. 1983). Thiophene-2-carboxylate (2–30 mM final concentration) was added from a sterile, tenfold concentrated stock solution. For anaerobic growth, the medium was supplemented with 5–20 mM KNO_3 (Bambauer et al. 1998).

Three other species were isolated from air or waste gas in a duck shed and an animal rendering plant: *Aquamicrobium aerolatum*, *Aquamicrobium ahrensii*, and *Aquamicrobium segne* (Kämpfer et al. 2009; Lipski and Kämpfer 2012). The latter two species were isolated on Antibiotic Sulfonamide Sensitivity-test agar (Merck 1.05392) (Ahrens et al. 1997). *Aquamicrobium aerolatum* was isolated collecting bioaerosol samples by filtration over gelatin filters and isolation on trypticase soy agar incubated at 26 °C. The organism can also be grown on nutrient agar (Kämpfer et al. 2009). *Aquamicrobium aestuarii* was isolated from crude oil-contaminated sediments of a tidal flat (Jin et al. 2013) by incubating approximately 10 g of sediment with 100 ml of 0.2 µm filtered seawater containing 3 ml crude oil in 500-ml Erlenmeyer flask at 25 °C. The enrichment was aerated (180 rpm) and was transferred (1:20) four times every 2 weeks. For isolation, the enrichment was plated on marine agar 2216 (BD) plates and incubated under aerobic conditions at 25 °C for 5 days. In addition, the species grows well on R2A agar (BD), Luria-Bertani agar, trypticase soy agar, and marine agar (Jin et al. 2013).

Chelativorans strains were obtained from sludge samples. *Chelativorans multitrophicus* was isolated from a mixed microbial culture enriched in a column packed with activated carbon that was continuously fed with a mineral medium containing EDTA as sole source of carbon, nitrogen, and energy. The original inoculum of the column was activated sludge from various industrial wastewater treatment plants and soil extracts. For the isolation, further aerobic enrichment in continuous culture on a column packed with glass beads and fed with mineral medium (per liter, 1.0 g MgSO4 · $7H_2O$, 0.2 g $CaCl_2$ · $2H_2O$, 0.13 g KH_2PO_4, and 0.615 g Na_2HPO_4, 2 ml of Widdel trace element solution (Pfennig et al. 1981) and 1 ml of a vitamin solution (Egli et al. 1988)) containing 200–300 mg.l^{-1} EDTA as well as batch cultures to establish optimal growth conditions were used (Weilenmann et al. 2004). The best conditions for growth were 30 °C, initial EDTA concentration in the range of 1–1.5 g.l^{-1}, $CaCl_2$ · $2H_2O$ concentration in the mineral medium of 0.4 g.l^{-1} and an initial pH of 7.0. Pure cultures were obtained by successive plating on Plate Count Agar and liquid culture in the mineral medium (Weilenmann et al. 2004). *Chelativorans multitrophicus* was obtained by enrichment from municipal sludge samples: 10 g of sample was suspended in 100 ml of medium (per liter, 1.0 g EDTA, 1.0 g MgSO4 · $7H_2O$, 0.4 g $CaCl_2$ · $2H_2O$, 0.26 g KH_2PO_4, and 0.83 g Na_2HPO_4 · $12H_2O$ and trace elements and vitamins (Egli et al. 1988), pH 7.0). The medium was incubated in a 750-ml flask on a shaker (150–200 rpm) at 28 °C for 2 weeks. Five milliliters of this enrichment then inoculated into a 750-ml flask with 100 ml of fresh medium and cultivated for 2 weeks. After five such transfers, pure colonies were picked from plates of the same medium plus agar (Chistyakova et al. 2005).

Hoeflea species have been isolated from different aquatic environments. *Hoeflea marina* comprises one strain, LMG 128^T, that was originally classified as *Agrobacterium ferrugineum* (other strains of this species have been renamed as *Pseudorhodobacter ferrugineus*, a member of the *Rhodobacteraceae*). *Hoeflea marina* was isolated from water from the Baltic Sea, off the coast of Germany, during a study of star-forming bacteria (Ahrens 1968; Peix et al. 2005). *Hoeflea phototrophica* was isolated from cultures of the marine dinoflagellates *Alexandrium lusitanicum* and *Prorocentrum lima*. Wine red colonies were obtained by plating washed single dinoflagellate cells onto 1/10-strength Difco marine agar. Pigmentation was found to depend on the salt concentration with cultures with 3, 6, or 9 g.l^{-1} sea salts being very pink, while at 35 g.l^{-1} cultures were colorless (Biebl et al. 2006). *Hoeflea alexandrii* was purified from cultures of another marine dinoflagellate, *Alexandrium minutum*. In this case, the washed dinoflagellate cells were sonicated prior to plating on full- and half-strength Difco marine agar and incubation during 7 days at 15 °C. Brown-pigmented colonies were obtained. Marine agar or broth was used for routine cultivation at 30 °C (Palacios et al. 2006). *Hoeflea anabaenae* was isolated from a culture of the cyanobacterium *Anabaena* under heterotrophic conditions in the brackish marine purity liquid medium (per liter, 20 g NaCl, 17 g AC broth (Difco), 8 g $MgSO_4$ · $7H_20$, 1.5 g $CaCl_2$ · $2H_20$ (Stevenson and Waterbury 2006)) from a culture in which it was attached almost exclusively to *Anabaena* heterocysts. It is also able to grow aerobically at 30 °C in full- and half-strength marine broth (Difco) and marine agar and liquid or solid PY medium (20 g sea salts, 3 g peptone, and 0.5 g yeast extract per liter (Biebl et al. 2005)). *Hoeflea suaedae* was isolated from the root surface of the halophyte *Suaeda maritima*. Surface-sterilized and dried root pieces (1 g) were ground in 9 ml of autoclaved filtered seawater (AFS) with a sterile mortar and pestle. Dilution series were plated in triplicate on one-tenth-strength R2A (1/10 R2A) medium in filtered seawater and supplemented with 50 μg/ml cycloheximide. Plates were incubated at 28 °C for 2–3 weeks. Routine maintenance is on 1/10 R2A medium in filtered seawater, and the organism can be stored with 15 % glycerol at −70 °C (Bibi et al. 2012).

Hoeflea siderophila was isolated from fresh ochreous sediments collected near the outlet of an iron-rich brackish spring using dilution plating on the following medium (g per liter): NaCl, 20; NH_4Cl, 0.3; $CaCl_2{\cdot}6H_2O$, 0.3; $MgCl_2{\cdot}7H_2O$, 3; $NaHCO_3$, 0.5; 10 % phosphate buffer (pH 7.0), 0.1; Hepes buffer (pH 7.2), 3.0; KNO_3, 0.3; CH_3COONa, 0.15; vitamins and trace elements (Pfennig and Lippert 1966); Difco agar, 5.0; and pH 7.0. Before inoculation, the medium was supplemented with fresh sterile FeS suspension (Hanert 1981) (0.2 mL per 10 mL of medium). Inoculated media were incubated for 2–3 weeks at 28 °C. Growth consisted of dense spherical colonies, orange-colored due to the formation of iron oxides. In liquid medium, iron oxidation results in an ochreous precipitate (Sorokina et al. 2012).

Hoeflea hydrophila was isolated from marine sediments by serial dilution in filter-sterilized natural seawater containing 0.1 % yeast extract. After aerobic incubation at 25 °C for 2 weeks, a sample from the lowest dilution showing growth was plated on the same medium, and after incubation at 25 °C for 2 weeks, single colonies that were beige, circular, and convex with regular edges were purified on marine agar 2216 (Difco). This species can be routinely grown on marine broth or marine agar. Marine broth cultures plus 20 % glycerol can be stored at −80 °C (Jung et al. 2013).

Lentilitoribacter was isolated from coastal seawater by dilution plating on marine agar 2216 (Becton–Dickinson) at 25 °C. These conditions were also used for routine cultivation. For short-term preservation, marine agar cultures can be stored at 4 °C, while for long-term preservation, glycerol suspensions (20 %) can be stored at −80 °C (Park et al. 2013).

Mesorhizobium comprises soil bacteria that can live endosymbiotically in root nodules on various legume plants where they can fix atmospheric nitrogen contributing to plant nutrition. A widely used approach to isolate rhizobia is through the use of legume plants to trap the bacteria from a particular soil. Surface-sterilized seeds are allowed to germinate in the soil, and after the plants develop, nodules are harvested for isolation of the bacteria (Vincent 1970). A similar approach is also used to verify the nodulation capacity of a strain with a particular host species. Isolation from surface-sterilized and crushed nodules is performed using yeast mannitol agar (YMA, per liter, 10 g

D-mannitol, 0.5 g KH_2PO_4, 0.2 g $MgSO_4 \cdot 7H_2O$, 0.1 g NaCl, 4 g $CaCO_3$, 0.4 g yeast extract, 15 g agar, pH 6.8–7.0). Incubation at 28 °C will result in the formation of creamy, entire, and convex mucoid colonies after 3–4 days. This procedure can result in growth of not only *Mesorhizobium* strains but also other rhizobia. Phenotypic distinctions are not straightforward: *Mesorhizobium* members can in some cases be distinguished in that they have a moderately fast growth rate (generation time 4–15 h) compared to *Rhizobium* (<6 h) and *Bradyrhizobium* (>6 h). Also they produce acid on YMA (as do *Rhizobium* strains), while *Bradyrhizobium* strains produce alkali (Chen et al. 2005). More certain genus assignment, however, requires verification of the partial 16S rRNA gene sequence.

All *Mesorhizobium* species have been isolated using the trap legume method except for one species, *Mesorhizobium thiogangeticum*, which was obtained from soil adjacent to the root of the legume *Clitoria ternatea* through enrichment using reduced sulfur compounds as sole carbon and energy source. Soil was supplemented with $Na_2S_2O_3 \cdot 5H_2O$ (5 %), Na_2S (1 %), and elemental sulfur powder (5 %) and incubated at 30°C for 2 weeks with intermittent sprinkling of sterile water. After this enrichment, soil samples (1 %, w/v) were incubated on a rotary shaker at 30 °C in mineral salt thiosulfate yeast extract liquid medium (20 mM $Na_2S_2O_3 \cdot 5H_2O$ supplemented with 5 g yeast extract per liter, pH 7.0–7.5) in mineral salt solution that contained (per liter of distilled water) 1 g NH_4Cl, 4 g K_2HPO_4, 1.5 g KH_2PO_4, 0.5 g $MgSO_4 \cdot 7H_2O$, and 5.0 ml trace metal solution (Vishniac and Santer 1957). When the color of the phenol red indicator had changed to yellow, serial dilutions were plated on the same agar medium for the isolation of pure cultures (Ghosh and Roy 2006).

Nitratireductor strains have been isolated from diverse marine sources, often by standard dilution plating techniques. *Nitratireductor aquibiodomus* was isolated from a marine aquarium denitrification system fitted with cellulose carriers. For the isolation, cellulose carriers were homogenized, and a dilution series was plated onto trypticase soy agar and R2A and incubated at room temperature for 3 weeks. *Nitratireductor aquibiodomus* was one of the several organisms that were picked up (Labbé et al. 2003); its colonies were white, smooth, circular, and convex (Labbé et al. 2004). *Nitratireductor basaltis* was isolated from black sand from Soesoggak beach, Jeju Island, Korea, by dilution plating onto marine agar 2216 (Difco) and incubating at 30–37 °C. It is not reported whether other organisms were able to grow in these conditions; the colonies of *Nitratireductor basaltis* were creamy, circular, convex, and smooth (Kim et al. 2009). *Nitratireductor kimnyeongensis* was isolated from a dried seaweed sample from Kimnyeong beach in Jeju, Republic of Korea (Kang et al. 2009), by transferring a piece of dried seaweed directly transferred onto isolation medium (WAT-SW agar) consisted of 0.05 % $MgSO_4.7H_2O$, 0.05 % $CaCl_2.2H_2O$, and 1.5 % agar in 60 % natural seawater and 40 % distilled water (pH 7.3) (Lee 2006). The organism can also be conveniently grown on trypticase soy agar where, after 5 days of incubation, colonies are small (0.5–1 mm in diameter), light yellow, circular, convex, smooth, and entire (Kang et al. 2009). *Nitratireductor aquimarinus* was isolated from exponential cultures of the marine diatom *Skeletonema costatum* by plating a 10-μl sample on marine agar 2216 (Difco) and incubating aerobically for 1 week. Colonies are creamy, smooth, circular, and convex. Growth is also good on trypticase soy agar at 35 °C. Strains can be preserved in trypticase soy broth supplemented with 30 % glycerol and −80 °C (Jang et al. 2011). *Nitratireductor indicus* was isolated from a deep-sea water sample taken at a depth of 2,488 m taken with Niskin bottles attached to a CTD (conductivity, temperature, and depth) sampler at 25.3217°S 70.0405°E in the southwestern part of the Indian Ridge. The seawater was enriched with 1 % sterilized crude oil, and after two months, bacteria were isolated by using the plating on 216L medium (per liter seawater: 1.0 g CH_3COONa, 10.0 g tryptone, 2.0 g yeast extract, 0.5 g sodium citrate, and 0.2 g NH_4NO_3; pH 7.5) (Lai et al. 2009; Lai et al. 2011b). On marine agar, colonies are unpigmented, smooth gray, and slightly raised in the center and have a regular margin (Lai et al. 2011a). *Nitratireductor pacificus* was also isolated from deep-sea water samples, this time from a pyrene-degrading enrichment (described in Wang et al. 2008) by using phthalate as sole carbon source in mineral medium (MM, comprising per liter: 3.5 g $MgSO_4 \cdot 7H_2O$, 0.05 g $CaCl_2$, 24 g NaCl, 0.35 g KCl, 1.0 g NH_4NO_3, 1.0 KH_2PO_4, 1.0 g K_2HPO_4, 0.01 g $FeCl_3$, 0.0001 g $ZnSO_4 \cdot 7H_2O$, 24 mg $SrCl_2 \cdot 6H_2O$, and 0.08 g KBr, adjusted to pH 7.4) (Wang et al. 2008; Lai et al. 2011a). On marine agar, colonies are smooth gray, nonpigmented with a regular margin, and slightly raised in the center (Lai et al. 2011a).

Most recently, a new species, *Nitratireductor lucknowense*, was published, though not yet validated. It was isolated from pesticide-contaminated soil from a γHCH (lindane) manufacturing site in India. Five-gram soil samples collected from three different locations were mixed together in 50 ml of sterile mineral medium (Senoo and Wada 1989). After the slurry had settled, the liquid phase was used to enrich for bacteria on 0.34 M lindane. On trypticase soy agar, the new species produces colonies that are straw yellow, smooth, circular, glistening, opaque, and convex with an entire margin (Manickam et al. 2012). NaCl is tolerated up to 2 % (Manickam et al. 2012), considerably less than most other *Nitratireductor* species which can tolerate up to 7 or 8 % (➋ *Table 18.8*).

Most *Phyllobacterium* species are plant associated, and while the first species were isolated from tropical ornamental plants, these bacteria have since also been isolated from other plants elsewhere and from non-plant sources such as volcanic rock used for construction. Different isolation procedures have been used and are summarized in the following overview. The selectivity in most cases is not documented.

Phyllobacterium myrsinacearum and its junior subjective synonym *Phyllobacterium rubiacearum* (Mergaert et al. 2002) have been isolated from leaf nodules of members of the plant families *Rubiaceae* (*Pavetta zimmermanniana*) and *Myrsinaceae* (*Ardisia crispa*, *Ardisia crenata*). Washed leaf pieces carrying nodules were macerated by rubbing and placed in saline. After shaking, dilutions were plated onto carrot juice agar containing yeast extract (fresh carrot juice, 500 ml; water, 500 ml;

$FeSO_4 \cdot 7H_2O$, 0.1 g; $MnSO_4 \cdot H_2O$, 0.1 g; agar, 15 g; pH 7.2; the medium is sterilized by fractional sterilization). After incubation at 28 °C, typical nonpigmented to beige, slimy, and circular colonies that are translucent to opaque in the center are transferred into liquid carrot juice medium. After 24- to 48-h phase, contrast microscopy can be used to verify the formation of star-shaped clusters. Stock cultures can be kept on trypticase soy agar at 5 °C for 1–2 months, and cultures can be lyophilized for long-term preservation (Knösel 1984). Isolates of this species have also been obtained from the root surface of sugar beet by using trypticase soy broth agar as a nonselective medium (Lambert et al. 1990; Mergaert et al. 2002).

Phyllobacterium trifolii was isolated from the nodules of *Trifolium pratense* as described above for *Mesorhizobium* species. Colonies on YMA are white, mucoid, translucent, and convex. The growth rate of this *Phyllobacterium* species (generation time 2 h) is faster than most mesorhizobia. Growth is also possible on nutrient agar (Valverde et al. 2005).

A further five species were also obtained using the same procedure, this time from roots of *Brassica napus* cv. Eurol (*Phyllobacterium bourgognense*, *Phyllobacterium brassicaearum*), root nodules of *Lathyrus numidicus* and *Astragalus algerianus* (*Phyllobacterium ifriqiyense*), root nodules of *Astragalus algerianus* and *Argyrolobium uniflorum* (*Phyllobacterium leguminum*) (Mantelin et al. 2006b), and root nodules of *Phaseolus vulgaris* (Flores-Felix et al. 2013). Colonies are circular, white or cream colored with regular margins, and in most strains highly mucoid (Mantelin et al. 2006b).

Phyllobacterium catacumbae does not originate from a plant-associated source. It was isolated from tuff, volcanic rock used in the walls of the Roman catacombs of Saint Callixtus, Rome, Italy. The B-4 medium used for isolation contained (per liter) 2.5 g calcium acetate, 4 g yeast extract and 15 g agar, pH 8, and incubation was at 28 °C. Colonies are circular, smooth, and beige. Growth is also good on trypticase soy agar (Jurado et al. 2005).

Phyllobacterium species can be stored at −80 °C in broth medium plus 20 % glycerol or at 4 °C lyophilized.

Pseudahrensia was isolated from seawater from the Yellow Sea, Korea, by the standard dilution plating on marine agar 2216 (Difco) and incubating at 25 °C. Colonies are circular, convex, smooth, glistening, and cream colored. This organism can be routinely cultivated on marine agar at 30 °C (Jung et al. 2012).

Although no precise isolation media have been published, *Pseudaminobacter* strains have been isolated by exploiting specific degradation capacities. The *Pseudaminobacter salicylatoxidans* type strain was isolated as a degrader 6-aminonaphthalene-2-sulfonate from a microbial consortium degrading this substrate and originating from the river Elbe, Germany (Nortemann et al. 1986; Kämpfer et al. 1999). The type strain of *Pseudaminobacter defluvii* was isolated from activated sludge which was enriched with thiocyanate (Katayama-Fujimura et al. 1983; Kämpfer et al. 1999). Growth is possible on several media including nutrient agar, trypticase soy agar, trypticase soy broth plus 1.5 % agar, and R2A (Oxoid) (Kämpfer 2005).

Thermovum composti was isolated from mature compost produced by a field-scale composter used for the treatment of livestock excreta. Dilution series of 1 g of compost in saline solution were plated onto isolation medium composed of (per liter distilled water) 1 g yeast extract, 2 g tryptone, 1 g NaCl, 1 g $MgSO_4 \cdot 7H_2O$, 20 g agar, 20 mg trimethoprim, 10 mg nalidixic acid, and 20 mg kanamycin, pH 7.0. After incubation at 50 °C for 7 days, colonies were picked and repeatedly transferred for purification. Colonies on nutrient agar are cream colored. Stock cultures in trypticase soy broth, grown for 2 days at 50 °C, can be supplemented with 20 % glycerol and stored at −80 °C (Yabe et al. 2012).

Ecology

Members of the *Phyllobacteriaceae* are versatile environmental bacteria that occur in diverse habitats that often are polluted or nutritionally rather rich. These habitats can be marine (*Aliihoeflea*, *Ahrensia*, *Aquamicrobium*, *Hoeflea*, *Lentilitoribacter*, *Nitratireductor*, *Pseudahrensia*) or polluted freshwater (*Pseudaminobacter*, *Aquamicrobium*, *Chelativorans*) systems, soil (*Aminobacter*, *Chelativorans*, *Mesorhizobium*, *Nitratireductor*, *Phyllobacterium*, *Thermovum*), or air (*Aquamicrobium*). Several genera are plant associated or associated with dinoflagellates or cyanobacteria (*Hoeflea*, *Mesorhizobium*, *Phyllobacterium*).

Aquamicrobium species have been isolated from diverse polluted environments (activated sludge, oil-polluted sediments, air/waste gas from poultry/animal rearing) and have degradative capabilities that may significantly contribute to the breakdown of pollutants: *Aquamicrobium defluvii* is able to degrade thiopene-2-carboxylate (Bambauer et al. 1998), *Aquamicrobium lusatiense* can utilize phenol and chlorophenols such as 4-chloro-2-methylphenol, 2,4-dichlorophenol, and 4-chlorophenol (Fritsche et al. 1999), and *Aquamicrobium aestuarii* was enriched from marine sediments using crude oil (Jin et al. 2013).

Chelativorans species have been found in municipal and industrial sludge samples and are able to degrade EDTA, a chelating agent with many applications that is generally recalcitrant to biodegradation. *Chelativorans multitrophicus and Chelativorans oligotrophicus* are able to use EDTA as sole carbon, nitrogen, and energy source, facultatively and obligately, respectively. They may have a significant role in the clearing of EDTA pollution in surface waters (Doronina et al. 2010).

Hoeflea phototrophica contains bacteriochlorophyll at reduced salt concentrations, but not at the concentration seawater (3.5 %); it also contains a carotenoid pigment thought to be spheroidenone and was found to contain *pufL* and *pufM* genes coding for proteins of the photosynthetic reaction center. However, *Hoeflea phototrophica* does not grow anaerobically in light or dark conditions, and conditions under which it may

live phototrophically have not been described in detail (Biebl et al. 2006).

Hoeflea siderophila is able to grow mixotrophically and organoheterotrophically. It is the only species of the genus that is capable of fac. chemolithotrophic growth through iron oxidation at neutral pH, in anaerobic conditions with nitrate or N_2O as terminal electron acceptor, and microaerobically with oxygen. It is one of the rare species that is capable of neutrophilic lithotrophic iron oxidation (Sorokina et al. 2012).

Mesorhizobium strains are soil bacteria that can, in the vicinity of a compatible legume host species, enter into a molecular dialogue with the plant, resulting in the formation of root nodules on the plant that can be occupied by the bacteria. The bacteria receive a safe habitat and food, while they in turn can fix atmospheric nitrogen and thus contribute to plant nutrition. Most *Mesorhizobium* species (29 of 30) have been described as symbiotic with various legume species (➋ *Table 18.11*). The only species that was not obtained from nodules, *Mesorhizobium thiogangeticum* obtained through enrichment from the soil adjacent to the legume *Clitoria ternatea*, was not able to nodulate this host nor *Pisum sativum* or *Cicer arietinum* (Ghosh and Roy 2006). *Mesorhizobium* has occasionally also been reported from marine systems (Sfanos et al. 2005; Krick et al. 2007) and from aquatic microbial mats in Antarctica (Peeters et al. 2012).

Several *Phyllobacterium* species have been isolated from leaf or root nodules of plants and contribute to plant growth promotion (➋ *Table 18.12*). For *Phyllobacterium myrsinacearum*, there is no direct evidence that it actively induces nodule formation in leaves. Nodulation has been confirmed for *Phyllobacterium trifolii* (Valverde et al. 2005),

Unspecified *Phyllobacterium* strains have also been reported from the rhizosphere of *Lotus* spp. (Oger et al. 2004), associated with roots in *Brassica napus* (Bertrand et al. 2001), as endophytes in *Ipomea batatas* (Khan and Doty 2009), and in root nodules of many legumes including *Dalbergia louvelii* (Rasolomampianina et al. 2005), *Lathyrus gmelinii* (Baymiev et al. 2011), *Acacia* sp. (Hoque et al. 2011), *Sophora alopecuroides* (Zhao et al. 2010), *Vicia* sp. (Lei et al. 2008), and *Ononis tridentata* (Rincon et al. 2008). They have also been found as free-living bacteria in water (Mergaert et al. 2001) and associated with unicellular organisms (Gonzalez-Bashan et al. 2000).

The possible symbiotic function of phyllobacteria is reported to be the production of plant growth hormones, protective antibacterial and antifungal activity (Lambert et al. 1990), phosphate solubilization (Chen et al. 2006), root hair elongation (Galland et al. 2012), and nitrogen fixation (Valverde et al. 2005).

Both *Pseudaminobacter* species have been isolated from polluted aquatic environments (Kämpfer et al. 1999). *Pseudaminobacter salicylatoxidans* can degrade substituted naphthalenesulfonates and substituted salicylates. One strain has also shown to be a facultative sulfur chemolithotroph that can oxidize $S_2O_3^{2-}$, $S_4O_6^{2-}$, SO_3^{2-}, S_2^{2-}, and S^0 directly to SO_4^{2-} without any intermediate formation (Ghosh and Dam 2009). In polluted oligotrophic aquatic systems, these bacteria may play an important role in biodegradation.

Thermovum is the only genus of the family that is thermophilic (maximum growth temperature 60 °C). It was isolated from mature compost; its role in the compost ecosystem is not documented (Yabe et al. 2012).

Pathogenicity, Clinical Relevance

Mesorhizobium amorphae has been reported as an amoeba-associated bacterium that may be involved in nosocomial pneumonia through contaminated water supplies (La Scola et al. 2003; Berger et al. 2006). As no recent reports confirming these observations were found, the significance of *Mesorhizobium amorphae* as a nosocomial pathogen is not clear. No other animal or human pathogens are among the current members of the *Phyllobacteriaceae.*

Many species, particularly of *Mesorhizobium* and *Phyllobacterium*, are plant endophytes, rhizoplane or rhizosphere bacteria that have plant beneficial effects (see next section below).

No plant pathogenic effects have been reported for most members of the family *Phyllobacteriaceae. Candidatus Liberibacter* is, however, a serious plant pathogen. It is included here, although the membership of this group is currently uncertain (see above under ➋ Sect. 1.2, "Phylogenetic Structure of the Family and Its Genera"). The trivial name "liberobacter" (*sic*) (from the Latin liber [bark] and bacter [bacteria]) was proposed in 1994 for a phloem-limited bacterium-like organism associated with citrus greening disease, also known as huanglongbing disease or yellow dragon disease, a severe and widespread citrus disease that is transmitted by the Asian citrus psyllid (*Diaphorina citri*) and the African citrus psyllid (*Trioza erytreae*) (Jagoueix et al. 1994). The disease causes yellowing and blotchy mottling of the leaves, production of bitter, small and misshapen fruits, and ultimately death of the tree (http://www.aphis.usda.gov/plant_health/plant_pest_info/). Two species, *Candidatus Liberibacter asiaticus* (originally Liberobacter asiaticum) and *Candidatus Liberibacter africanus* (originally Liberobacter africanum), were proposed for the Indian and South African liberibacters, respectively, which can be distinguished based on temperature sensitivity (in Africa symptoms occur only in cooler regions), serology, and genomic properties (Jagoueix et al. 1994). Garnier et al. (2000) corrected the spelling of the genus name and proposed a separate subspecies, *Candidatus Liberibacter africanus* subsp. capensis, for a South African liberibacter in the ornamental rutaceous tree, *Calodendrum capense.* The citrus disease was later also reported from Brazil, and the pathogen recognized as a new species, *Candidatus Liberibacter americanus*, spread by the vector *Diaphorina citri* (Texeira et al. 2005). Although the species epithet originally referred to the geographic occurrence of the group, *Candidatus Liberibacter asiaticus* has also been found in the Americas (Raddadi et al. 2011). In the USA, the Asian citrus psyllid,

Table 18.11
Host plants nodulated by *Mesorhizobium* species

Species	Host plants nodulated	References
Mesorhizobium abyssinicae	*Acacia abyssinica, Acacia tortilis, Acacia tortilis*	Degefu et al. 2013; Wolde-meskel et al. 2005
Mesorhizobium albiziae	*Albizia kalkora, Albizia julibrissin, Glycine max, Leucaena leucocephala, Phaseolus vulgaris*	Wang et al. 2007
Mesorhizobium alhagi	*Alhagi sparsifolia, Sophora alopecuroides, Glycyrrhiza inflata, Medicago sativa, Indigofera endecaphylla, Vicia cracca, Sophora flavescens*	Chen et al. 2010
Mesorhizobium amorphae	*Amorpha fruticosa, Cicer arietinum*	Rivas et al. 2007; Wang et al. 1999
Mesorhizobium australicum	*Biserrula pelecinus, Astragalus membranaceus, Macroptilium atropurpureum*	Nandasena et al. 2009
Mesorhizobium camelthorni	*Alhagi sparsifolia, Sophora alopecuroides, Glycyrrhiza inflata, Medicago sativa*	Chen et al. 2011
Mesorhizobium caraganae	*Caragana microphylla, Caragana intermedia*	Guan et al. 2008
Mesorhizobium chacoense	*Prosopis alba*	Velazquez et al. 2001
Mesorhizobium ciceri	*Cicer arietinum*	Nour et al. 1994
Mesorhizobium gobiense	*Astragalus filicaulis, Lotus frondosus, Lotus tenuis, Oxytropis glabra*	Han et al. 2008
Mesorhizobium hawassense	*Sesbania sesban*	Degefu et al. 2013
Mesorhizobium huakuii	*Astragalus sinicus, Robinia pseudoacacia*	Chen et al. 1991; Ulrich and Zaspel 2000
Mesorhizobium loti	*Lotus* spp., *Anthyllis vulneraria, Lupinus densiflorus, Robinia pseudoacacia*	Jarvis et al. 1982; Ulrich and Zaspel 2000
Mesorhizobium mediterraneum	*Cicer arietinum*	Nour et al. 1995
Mesorhizobium metallidurans	*Anthyllis vulneraria*	Vidal et al. 2009
Mesorhizobium muleiense	*Cicer arietinum*	Zhang et al. 2012
Mesorhizobium opportunistum	*Biserrula pelecinus, Astragalus adsurgens, Astragalus membranaceus, Lotus peregrinus, Macroptilium atropurpureum*	Nandasena et al. 2009
Mesorhizobium plurifarium	*Acacia* spp., *Leucaena* spp., *Prosopis juliflora, Chamaecrista ensiformis*	de Lajudie et al. 1998
Mesorhizobium qingshengii	*Astragalus sinicus*	Zheng et al. 2013
Mesorhizobium robiniae	*Robinia pseudoacacia*	Zhou et al. 2010
Mesorhizobium sangaii	*Astragalus luteolus*	Zhou et al. 2013
Mesorhizobium septentrionale	*Astragalus adsurgens, Phaseolus vulgaris, Glycine max, Leucaena leucocephala, Macroptilium atropurpureum, Lotus corniculatus, Robinia pseudoacacia*	Gao et al. 2004; Han et al. 2008
Mesorhizobium shangrilense	*Caragana* spp., *Glycyrrhiza uralensis, Astragalus adsurgens, Vigna unguiculata, Vigna radiata, Phaseolus vulgaris*	Lu et al. 2009
Mesorhizobium shonense	*Acacia abyssinica*	Degefu et al. 2013
Mesorhizobium silamurunense	*Astragalus membranaceus, Astragalus adsurgens, Caragana intermedia*	Zhao et al. 2012
Mesorhizobium tamadayense	*Anagyris latifolia, Lotus berthelotii*	Ramirez-Bahena et al. 2012
Mesorhizobium tarimense	*Lotus frondosus, Lotus tenuis*	Han et al. 2008
Mesorhizobium temperatum	*Astragalus adsurgens, Phaseolus vulgaris, Vigna unguiculata, Glycine max, Leucaena leucocephala, Medicago sativa, Lotus corniculatus*	Gao et al. 2004
Mesorhizobium thiogangeticum	None reported. Isolated from the rhizosphere of *Clitoria ternatea* although it did not nodulate this host	Ghosh and Roy 2006
Mesorhizobium tianshanense	*Glycyrrhiza, Sophora, Caragana, Halimodendron, Swainsonia, Glycine, Cicer arietinum*	Chen et al. 1995; Rivas et al. 2007

Table 18.12
Sources of isolation and nodulation capacity reported for the different *Phyllobacterium* species

Species	Source	Nodulation capacity	References
Phyllobacterium bourgognense	Root surface of *Brassica napus* vc. Eurol	No nodulation data	Mantelin et al. 2006b
Phyllobacterium brassicacearum	Root surface of *Brassica napus* vc. Eurol; root nodules of *Caragana microphylla*	No nodulation data	Mantelin et al. 2006b; Dai et al. 2012
Phyllobacterium catacumbae	Volcanic tuff stone used in the Roman catacombs of Saint Callixtus, Rome, Italy	No nodulation data	Jurado et al. 2005
Phyllobacterium endophyticum	Root nodules of *Phaseolus vulgaris*	Unable to nodulate *Phaseolus vulgaris*	Flores-Felix et al. 2013
Phyllobacterium ifriqiyense	Isolated from root nodules of *Lathyrus numidicus* and *Astragalus algerianus*	No nodulation data	Mantelin et al. 2006b
Phyllobacterium leguminum	Isolated from root nodules of *Astragalus algerianus* and *Argyrolobium uniflorum*	No nodulation data	Mantelin et al. 2006b
Phyllobacterium myrsinacearum	Leaf nodules of *Pavetta zimmermannia*, *Ardisia crispa*, and *Ardisia crenata;* root surface of sugar beet	No nodulation data	Knösel 1984; Lambert et al. 1990; Mergaert et al. 2002
Phyllobacterium trifolii	*Trifolium pratense, Trifolium repens, Lupinus albus*	Nodulates *Trifolium pratense, Trifolium repens*, and *Lupinus albus*; nodD gene present	Valverde et al. 2005

Diaphorina citri, has been present in Florida since 1998, and *Candidatus Liberibacter asiaticus* was found in Florida in early September 2005. In 2010, the USDA imposed a plant quarantine in several states and territories in the USA to stop the spread of citrus greening (http://www.aphis.usda.gov/plant_health/plant_pest_info/). The disease was reported in South California in 2012 (www.californiacitrusthreat.com). The European and Mediterranean Plant Protection Organization (EPPO) has placed *Liberibacter africanus*, *Liberibacter asiaticus*, and *Liberibacter americanus* and the vector *Diaphorina citri* on its A1 list of pests recommended for regulation as quarantine pests. This list comprises pests regarded as absent from the EPPO region. The vector *Trioza erytreae* was included on the A2 List of pests recommended for regulation as quarantine pests that are locally present in the EPPO region.

Citrus huanglongbing disease is regarded as a pest of urgent phytosanitary concern for southern parts of the EPPO region where citrus is grown. Several PCR and real-time PCR tests have been developed for the detection of these *Candidatus Liberibacter* sp. in plants and in the psyllid vectors (Morgan et al. 2012 and references therein). To eliminate or suppress *Candidatus Liberibacter asiaticus*, a combination of penicillin and streptomycin administered by trunk injection or root soaking was shown to be effective in citrus plants (Zhang et al. 2011).

Several additional species have more recently been reported to affect *Solanaceae* plants. *Candidatus Liberibacter psyllaurous* is associated with psyllid yellows disease of potato (*Solanum tuberosum* L.) and tomato (*Solanum lycopersicum* L.) in North America and is transmitted by *Bactericera cockerelli* (Hansen et al. 2008). *Candidatus Liberibacter solanacearum* was reported from tomato, capsicum (*Capsicum annuum*), potato, tamarillo (*Solanum betaceum*), cape gooseberry (*Physalis peruviana*), and chilli (*Capsicum* sp.) from New Zealand; it is transmitted by the psyllid *Bactericera cockerelli.* It has also been detected in the USA in potatoes affected by zebra chip disease (Liefting et al. 2009). *Candidatus Liberibacter solanacearum* and its vector *Bactericera cockerelli* have been placed on the EPPO A1 and A2 lists, respectively, and are considered of particular concern for southern and central parts of the EPPO region and for areas with mild winters in the northern part (http://www.eppo.int/QUARANTINE/quarantine.htm).

Candidatus Liberibacter europaeus, the most recently described species, is the only one presently considered to be an endophyte rather than a plant pathogen. It was reported from Italy and is found in the midgut lumen, salivary glands, and Malpighian tubules of the pear psyllid pest *Cacopsylla pyri* and has been detected in pear plant tissue, both in laboratory-inoculated plants and in field-collected samples. However, the plants remained free of disease symptoms (Raddadi et al. 2011).

As the family *Phyllobacteriaceae* comprises many soil bacteria and other free-living bacteria, it is not surprising that many species show diverse resistance patterns to a number of antibiotics which they can be expected to encounter in their natural habitat. These characters can often be used for phenotypic differentiation and have therefore been included above in the ➲ Sect 3, "Phenotypic Analyses".

Application

Most strains of the genus *Mesorhizobium* are capable of nitrogen-fixing symbiosis in root nodules of legume plants, allowing the host plant to grow in soils with lower nitrogen content than other plants. Several agricultural crops, including chickpea

(*Cicer arietinum*), alfalfa or lucerne (*Medicago sativa*), and several *Lotus* species (Table 18.11), are nodulated by mesorhizobia, and these bacteria thus make an important contribution to the success of these crops. Interest to introduce new *Lotus* forage species in Australia has stimulated research into compatible *Mesorhizobium* strains (Howieson et al. 2011). *Mesorhizobium* strains are also important as symbionts of legume trees such as *Acacia* and *Prosopis* spp. used in tropical agroforestry systems (de Lajudie et al. 1998; Bala et al. 2003; Degefu et al. 2013).

In addition to symbiotic nitrogen fixation, several strains of *Mesorhizobium* and *Phyllobacterium* are recognized for other plant growth-promoting effects. Mesorhizobia can exert these effects by producing the plant hormone indole acetic acid or ammonia (Ahmad et al. 2008). *Mesorhizobium mediterraneum* PECA21 was shown to solubilize phosphorus from tricalcium phosphate and improve growth and phosphorus content in chickpea (Peix et al. 2001). *Mesorhizobium loti* MP6 was shown to increase yield and resistance to white rot (*Sclerotinia sclerotiorum*) in *Brassica campestris* in India (Chandra et al. 2007). Other strains are resistant to heavy metals (Maynaud et al. 2013). *Phyllobacterium brassicacearum* STM 196 was shown to promote the growth of oilseed rape and *Arabidopsis* and to stimulate root hair elongation possibly through activation of the ethylene signalling pathway (Mantelin et al. 2006a; Galland et al. 2012).

A strategy for the regeneration of disused mining site is through revegetation to allow sustainable plant cover to stabilize the site and limit wider environmental impact. In France, *Anthyllis vulneraria* is one of the legume species tolerant of these contaminated sites (Mahieu et al. 2011). It is nodulated by two members of the *Phyllobacteriaceae*: *Aminobacter anthyllidis* and *Mesorhizobium metallidurans.* Both species are tolerant to high concentrations of heavy metals and contribute through this symbiosis to the success of the legume species in the process of revegetation of contaminated sites (Vidal et al. 2009; Maynaud et al. 2012). The combined inoculation of legumes with plant growth-promoting rhizobacteria and *Mesorhizobium loti* strains that have the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase which hydrolyzes the precursor to the plant hormone ethylene was shown to have a synergistic positive effect on plant growth, nutrition, and adaptation to metal-polluted soils. The ACC-hydrolyzing bacteria eliminate the plant growth inhibition caused by increased ethylene production and can thus be valuable participants in the phytostabilization of contaminated mining sites (Safronova et al. 2012). In an application of the same mechanism, a strain of *Mesorhizobium ciceri* transformed to express exogenous ACC deaminase was shown to improve yields of chickpea and reduce susceptibility to root rot disease (Nascimento et al. 2012). One highly chromium-tolerant *Mesorhizobium* strain was shown to improve the yield and decrease chromium uptake in chickpea (Wani et al. 2008).

Aminobacter strains were reported to be responsible for the degradation of 2,6-dichlorobenzamide, a frequent groundwater pollutant that is a degradation product of the herbicide 2,6-dichlorobenzonitrile (dichlobenil). A specific PCR test targeting the 16S rRNA genes was designed to monitor the distribution of *Aminobacter* strains (Sjoholm et al. 2010). *Aminobacter aminovorans* strains previously classified as *Chelatobacter heintzii* are able to degrade nitrilotriacetate and EDTA (Auling et al. 1993; Nortemann 1999). *Chelativorans* species are also able to degrade EDTA and particularly *Chelativorans oligotrophicus* has been applied in biofilters to remove EDTA and EDTA-metal complexes (Kuvichkina et al. 2012; Kaparullina et al. 2012).

Pseudaminobacter strains have been investigated for use in bioremediation of soil contaminated with atrazine and one strain was reported to use as sole carbon and nitrogen source (Topp 2001). They have also been implicated in the degradation of methyl parathion (Zhang et al. 2005).

The salicylate 1,2-dioxygenase from *Pseudaminobacter salicylatoxidans* BN12T has been characterized extensively (Hintner et al. 2004; Matera et al. 2008; Ferraroni et al. 2012). A soil isolate very similar to *Pseudaminobacter salicylatoxidans* was shown to be a sulfur chemolithotroph (Bagchi et al. 2005; Mandal et al. 2007).

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