20 The Family *Rhodobacteraceae*

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Abstract

The family *Rhodobacteraceae* can be considered a paradigm of modern taxonomy of prokaryotes. Taking into account the number of species and genera that conforms the family, together with the knowledge about their abundance and vast global distribution, it surprises that most of them have been described relatively recent to our days. Two notable exceptions are *Rhodonostoc capsulatum* (Molisch, Die purpurbakterien nach neuen untersuchungen, vols i–vii. G. Fischer, Jena, pp 1–95, 1907) and *Micrococcus denitrificans* Beijerinck and Minkman (Zentbl Bakteriol, Parasitenkd, Infektionskr Hyg. Abt II 25:30–63, 1910), early basonyms of *Rhodobacter capsulatus* and *Paracoccus denitrificans*, respectively. The fact that so many descriptions within this family are recent means that some studies have been concomitant and pose a challenge not only for pure taxonomic studies but also for interpreting other studies in which a rapidly evolving nomenclature had to be used anyway. The metabolic and ecological diversity of the group adds further complexity. In spite of all these difficulties, the picture is far from being a chaos and it can be considered an exciting and important bacterial group to study.

Rhodobacteraceae are, fundamentally, aquatic bacteria that frequently thrive in marine environments. They comprise mainly aerobic photo- and chemoheterotrophs but also purple non-sulfur bacteria which perform photosynthesis in anaerobic environments. They are deeply involved in sulfur and carbon biogeochemical cycling and symbiosis with aquatic micro- and macroorganisms.

One hundred genera are currently recognized as members of the family although the *Stappia* group, *Ahrensia*, *Agaricicola*, and *Rhodothalassium* do not belong, phylogenetically, to the family. The 90 other genera are distributed in 5 phylogenetic groups (the *Rhodobacter*, the *Paracoccus*, the *Rhodovulum*, the *Amaricoccus*, and the *Roseobacter* clades) that might be considered a family on its own.

Taxonomy, Historical and Current

Rho.do.bac.ter.a'ce.ae. M.L. masc. n. *Rhodobacter*, type genus of the family; -aceae ending to denote family; M.L. fem. pl. n. *Rhodobacteraceae*, the *Rhodobacter* family.

The family *Rhodobacteraceae* was first established by Garrity et al. (2005) as the sole member of the order *Rhodobacterales* (class *Alphaproteobacteria*, phylum Proteobacteria) in the 2nd edition of *Bergey's Manual of Systematic Bacteriology*. Both names were validated in Validation List 107 (Euzéby 2006). The circumscription of the taxon was based on the phylogenetic analysis of 16S rRNA gene sequences of their members, which, at that time, comprised 31 genera (*Rhodobacter*, the type genus, plus *Ahrensia*, *Albidovulum*, *Amaricoccus*, *Antarctobacter*, *Gemmobacter*, *Hirshia*, *Hyphomonas*, *Jannaschia*, *Ketogulonicigenium*, *Leisingera*, *Maricaulis*, *Methylarcula*, *Octadecabacter*, *Pannonibacter*, *Paracoccus*, *Pseudorhodobacter*, *Rhodobaca*, *Rhodothalassium*, *Rhodovulum*, *Roseibium*, *Roseinatronobacter*, *Roseivivax*, *Roseobacter*, *Roseovarius*, *Rubrimonas*, *Ruegeria*, *Sagittula*, *Staleya*, *Stappia*, and *Sulfitobacter*). In the same year, Lee et al. described the family *Hyphomonadaceae*, removing the prosthecate genera *Hirshia*, *Hyphomonas*, and *Maricaulis* from *Rhodobacteraceae* (Lee et al. 2005) among other proposals for the subdivision of *Alphaproteobacteria* that were also based on 16S rRNA gene analysis. These authors did not recognize *Rhodobacterales* as an order, but included both the families *Rhodobacteraceae* and *Hyphomonadaceae* in the order *Caulobacterales*, along with *Caulobacteraceae*. Whatever the hierarchy considered, *Hyphomonadaceae* is a neighboring family to *Rhodobacteraceae* (*sensu stricto*) (see *Fig. 20.1*, General tree of the family *sensu lato*). The family *Hyphomonadaceae* contains a dozen of genera of prosthecate marine bacteria. The next closer neighbor is represented by the family *Kordiimonadaceae* that includes only the genus *Kordiimonas*, with two marine and one terrestrial species. However, phylogenetic analysis using different data sets and methods, as the concatenated alignments for 104 well-behaved protein families (Williams et al. 2007), splits *Hyphomonadaceae* apart from the order *Rhodobacterales*, forming an expanded group with *Caulobacterales* that also includes *Parvularcula*.

According to Rule 51b (1) of the *Bacteriological Code*, the family name *Rhodobacteraceae* (Garrity et al. 2005) is illegitimate because the family contains the genus *Hyphomonas* (ex Pongratz 1957, Moore et al. 1984) which is the type of the family *Hyphomonadaceae* (Lee et al. 2005; Euzéby 2006).

Since the publication of these studies, and following an increase of taxonomic attention to the marine microbiota, dozens of new genera have been described into the family *Rhodobacteraceae*. To date it comprises 99 genera and 288 species, being one of the most "populated" families of the Domain Bacteria (*Table 20.1*).

As already stated at the time of its establishment, the family is phenotypically, metabolically, and ecologically diverse, including photoheterotrophs able to grow photoautotrophically or chemotrophically, aerobic and facultative anaerobic chemoorganoheterotrophs, and facultative methylotrophs. Several members are aerobic anoxygenic phototrophs (AAP) while others, as the type genus of the family, are classical purple non-sulfur photosynthetic bacteria, whose phototrophic ability is restricted to anaerobic conditions. The vast majority of the species contained in the family are aquatic, and many of them require sodium ion or combined salts for growth. Their cells are Gram negative and multiply by binary fission or by budding, following monopolar growth. When motile, they exhibit flagella, usually

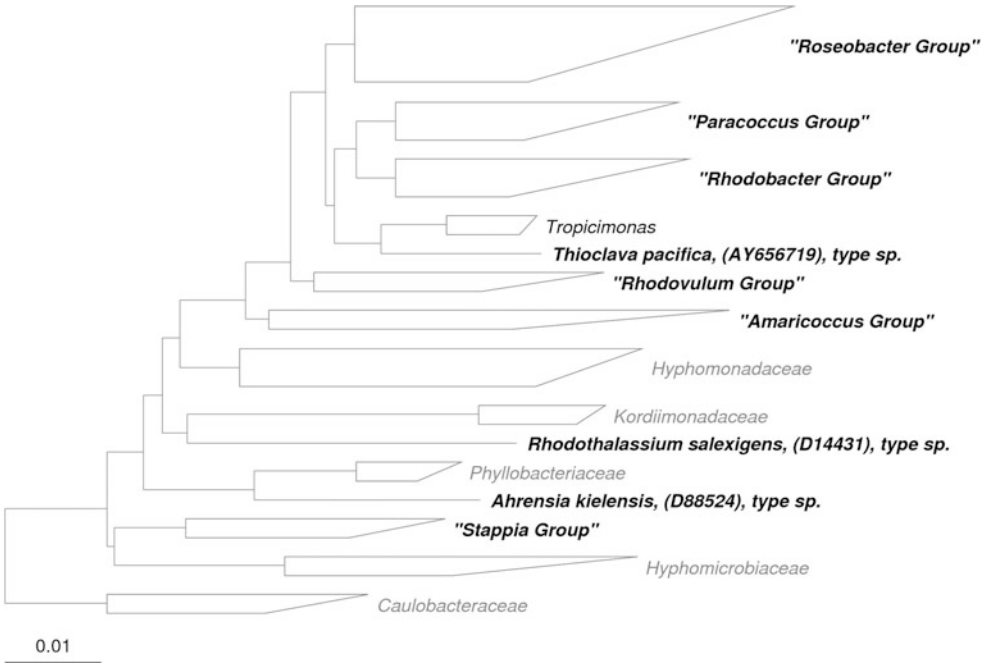

Fig. 20.1

Phylogenetic reconstruction of the family *Rhodobacteraceae* based on 16S rRNA and created using the neighbor-joining algorithm with the Jukes-Cantor correction. The sequence data sets 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

polar. Most species are positive for oxidase. Pigmentation does occur, not only in photosynthetic members (that present Bchl *a* and carotenoids of spheroidene class) but also in non-phototrophic members. Carbon reserve material is formed by some members as polyhydroxyalkanoates (PHA), commonly polyhydroxybutyrate (PHB). The major or only respiratory quinone is ubiquinone 10 (as occurs almost universally in the Class *Alphaproteobacteria*), and their cellular fatty acids are usually dominated by C18:1 ω7c, which very often constitutes more than 50 % of the total. Polar lipids may include phosphatidyl glycerol, diphosphatidyl glycerol, phosphatidyl ethanolamine, phosphatidyl choline, and several amino-, phospho-, and glycolipids in different combinations. The mol% G+C content of their DNA is above 50 %, with only one exception known (*Pelagicola*, 47 mol%), and being the most common range 55–70 mol% and the total range 47–76 mol%. A summary of the chemotaxonomic features of the genera is included as *Table 20.2*.

After introducing the common traits of the family, it should be stressed that its internal heterogeneity is not just a matter of metabolic or physiological diversity and/or versatility but also a matter of lack of phylogenetic homogeneity: as can be observed in *Fig. 20.1*, a bunch of genera formally included in the family lay far away from the large clade that comprises the true rhodobacters (family *Rhodobacteraceae sensu stricto*). These outsider genera fall in three groups: a well-defined clade comprising seven genera and sixteen species, labeled as "*Stappia* group," the genus *Ahrensia* (related to *Phyllobacteriaceae*), the genus *Agaricicola* (not shown), and the purple non-sulfur genus *Rhodothalassium*, which forms a distinct lineage in this part of the alphaproteobacterial tree. The separate position of this genus was already underlined in a Bergey's Editorial Note and by placing it as incertae sedis in the manual (Imhoff 2005). In fact, it was stated that *Rhodothalassium* could constitute a family on its own, but the scarcity of sequence data available prevented the proposal at that time.

Thus, the family *Rhodobacteraceae* formally contains, up to date, these ten genera (http://www.bacterio.cict.fr/classifgenerafamilies.html#Rhodobacteraceae) although they could certainly constitute two additional families, "*Stappiaceae*" (with *Labrenzia*, *Nesiotobacter*, *Pannonibacter*, *Polymorphum*, *Pseudovibrio*, *Roseibium*, and *Stappia*) and *Rhodothalassiaceae* (monogeneric) [Note: During the writing of the chapter, the proposal of *Rhodothalassiaceae* fam. nov. and *Rhodothalassiales* ord. nov. was published by Venkata Ramana et al. (2013), with an emended description of the genus *Rhodothalassium*]. On the other hand, *Ahrensia* could be transferred to the family *Phyllobacteriaceae*, where it is placed with *Hoeflea* species in more detailed trees (see the last release of the Living Tree Project 16S rRNA gene tree, LTP111, Yarza et al. 2010), and *Agaricicola*,

Table 20.1

List of genera in the family *Rhodobacteraceae sensu lato* (=order *Rhodobacterales*: 99 genera, 288 species), distributed by groups (tentative new families) by phylogenetic assignment

***Rhodobacter* group = *Rhodobacteraceae* (*sensu stricto*): 11 genera, 35 species**			
Catellibacterium[a]	*Defluviimonas*	*Gemmobacter*	*Haematobacter*
Pararhodobacter	*Pseudorhodobacter*	*Rhodobaca*	***Rhodobacter***
Roseibaca	*Roseicitreum*	*Roseinatronobacter*	*Thioclava*
***Rhodovulum* group = *Rhodovulaceae*: 3 genera, 18 species**			
Albidovulum	*Jhaorihella*	***Rhodovulum***	
***Amaricoccus* group = *Amaricoccaceae*: 5 genera, 9 species**			
Albimonas	***Amaricoccus***	*Oceanicella*	*Rubribacterium*
Rubrimonas			
***Paracoccus* group = *Paracoccaceae*: 2 genera, 42 species**			
Methylarcula	***Paracoccus***	*Thiosphaera*[a]	
***Roseobacter* group = *Roseobacteraceae*: 68 genera, 164 species**			
Actibacterium	*Antarctobacter*	*Celeribacter*	*Citreicella*
Citreimonas	*Dinoroseobacter*	*Donghicola*	*Epibacterium*
Gaetbulicola[a]	*Hasllibacter*	*Huaishuia*	*Hwanghaeicola*
Jannaschia	*Ketogulonicigenium*	*Leisingera*	*Lentibacter*
Litoreibacter	*Litorimicrobium*	*Loktanella*	*Lutimaribacter*
Mameliella	*Maribius*	*Marinovum*	*Maritimibacter*
Marivita	*Nautella*	*Nereida*	*Oceanibulbus*
Oceanicola	*Oceaniovalibus*	*Octadecabacter*	*Pacificibacter*
Palleronia	*Pelagibaca*	*Pelagicola*	*Pelagimonas*
Phaeobacter	*Planktotalea*	*Pontibaca*	*Ponticoccus*
Poseidonocella	*Primorskyibacter*	*Profundibacterium*	*Pseudoruegeria*
Roseibacterium	*Roseicyclus*	*Roseisalinus*	*Roseivivax*
Roseobacter	*Roseovarius*	*Rubellimicrobium*	*Ruegeria*
Sagittula	*Salinihabitans*	*Salipiger*	*Sediminimonas*
Seohaeicola	*Shimia*	*Silicibacter*[a]	*Staleya*[a]
Sulfitobacter	*Tateyamaria*	*Thalassobacter*	*Thalassobius*
Thalassococcus	*Tranquillimonas*	*Tropicibacter*	*Tropicimonas*
Vadicella	*Wenxinia*	*Yangia*	
***Stappia* group = *Stappiaceae*: 7 genera, 17 species**			
Labrenzia	*Nesiotobacter*	*Pannonibacter*	*Polymorphum*
Pseudovibrio	*Roseibium*	***Stappia***	
Unaffiliated: 3 genera, 3 species			
Agaricicola	*Ahrensia*	*Rhodothalassium*	

[a]Empty genera, all their species have been reclassified into other genera

which is related to *Prosthecomicrobium pneumaticum* (LTP111), should be also excluded from the family *Rhodobacteraceae*.

The remaining 89 genera (268 species) form a monophyletic clade that may be considered the true *Rhodobacteraceae* family, from a strictly phylogenetic point of view. Phylogenetic analysis, based on 16S rRNA gene sequences, allows the recognition of five well-defined groups among these 89 genera. Lee et al. (2005) already recognized these five main groups, although their work included less than 20 % (46 out of 268) of the currently established species. In *Figs. 20.1*, *20.2*, *20.3*, *20.4*, *20.5*, and *20.6* and *Table 20.1*, each of these groups is named after the senior genus contained. *Table 20.1* also reflects a suggestion for the nomenclature to be used if these groups are finally recognized as new families, a proposal that, in our opinion, merits consideration but is outside of the aim of this chapter. As it can be observed, the distribution of genera

Table 20.2

Chemotaxonomic traits of the genera in the family *Rhodobacteraceae sensu lato*, distributed by groups (tentative new families). Empty cells indicate that no information could be retrieved for that particular genus and trait. +, positive; −, negative; *v*, variable

Genus	Quinone	Polar lipids	Pigments	PHB/PHA	GC mol%	Other
***Rhodobacter* group**						
Rhodobacter	Q10	PG, PE, PC, AL, PL, L	Bchl *a* +, carotenoids[a]		62–73	
Defluviimonas	Q10		None		65	
Gemmobacter	Q10	PG, PE, PC, AL, DPG[b]	None	v	61–69.5	*m*-DAP[c]
Haematobacter			None		65	
Pararhodobacter	Q10		None		68	
Pseudorhodobacter	Q10	PC, PG, ALs, APLs	Bchl *a* −, *pufLM* -		57–62	
Rhodobaca			Bchl *a* +, demethylspheroidene and demethylspheroidenone	yes	58–60	
Roseibaca	Q10	DPG, PE, PG, PC	Bchl *a* +	yes	61	
Roseicitreum	Q10	PG, PE, PC, AL	Bchl *a* +	yes	63	
Roseinatronobacter			Bchl *a* +, spheroidene	yes	59–62	
Thioclava	Q10		Bchl *a* −		63	
***Rhodovulum* group**						
Rhodovulum	Q10	PE, PG, L, 2SL[d], SQD[e], DPG[e], APL[e]	Bchl *a* +, spheroidene		58–69	
Albidovulum	Q10	PG, PE, PC[f]	Bchl *a* −		63–71	
Jhaorihella	Q10	PC, PG, PE, DPG, PLs, ALs		yes	65	
***Amaricoccus* group**						
Amaricoccus[g]	Q10	PE, PC, PG, 2AL, GL		yes	51–63	
Albimonas	Q10	PG, DPG, PE, PC	Bchl *a* −		72	
Oceanicella	Q10	PC, PG, AL, DPG				
Rubribacterium			Bchl *a* +, spheroidene 60 % and spirilloxanthin 38 %	yes	70	
Rubrimonas	Q10	PG, PC, ALs, Ls, PL[h]	Bchl *a* +, *pufLM* +, carotenoid			
***Paracoccus* group**						
Paracoccus	Q10[i]	PG, PC, DPG (common), PE (rare), ALs, PLs	carotenoids when pigmented	most spp.	58–71	
Methylarcula	Q10	PE, PC, PG, DPG	carotenoids −	yes	57–61	Ectoine (main compatible solute)
***Roseobacter* group**						
Roseobacter	Q10	PG, DPG, PC, AL, PL, [PE absent]	Bchl *a* +, spheroidenone		56–60	
Actibacterium	Q10	PG, 2AL, 3L, 2PL, GL	Bchl *a* −	no	61.3	
Antarctobacter	Q10	PG, PC, AL, PL	Bchl *a* −	yes	62–63	*m*-DAP
Celeribacter	Q10	PG, AL, L, PE[j], PC[j], LPE[j]	Bchl *a* −	no	59–62	
Citreicella	Q10		Bchl *a* −		67–69	
Citreimonas			Bchl *a* −		67	
Dinoroseobacter	Q10	PG, DPG, AL, 8L	Bchl *a* +, spheroidene	yes	65	
Donghicola	Q10		Bchl *a* −		59–62	
Epibacterium	Q10	PG, PC, 2AL, 4PL	Bchl *a* −		52–53	
Hasllibacter	Q10				71.6	
Huaishuia	Q10	PG, PLs, AL, L		no	60	

Table 20.2 (continued)

Genus	Quinone	Polar lipids	Pigments	PHB/PHA	GC mol%	Other
Hwanghaeicola	Q10				61	
Jannaschia	Q10	PG, PC, PE, AL, DPG[k]	Bchl *a* −[l]	v	63–68	
Ketogulonicigenium					53–54	
Leisingera	Q10	PG, PE, PL, AL, L, [PC absent]	Bchl *a* −	v	60–62	
Lentibacter	Q10	PG, PE, PC, L, AL	Bchl *a* −	yes	55	
Litoreibacter	Q10	PC, PG, PE, L, AL, DPG[m]	Bchl *a* −	v	56–60	
Litorimicrobium	Q10	PG, DPG, PC, AL, PL, L			62	
Loktanella	Q10	PG, PC, PE[n], DPG[o]	Bchl *a* +[p], *pufLM* +[q]		55–69	
Lutimaribacter	Q10	PC, PG, PE, AL, 2PL	Bchl *a* −		63.5	
Mameliella	Q10			yes	63–64	
Maribius	Q10		Bchl *a* −	yes	66–70	
Marinovum	Q10	PG, PE, PC, DPG, AL, PL, L	Bchl *a* −	yes		
Maritimibacter	Q10	PE, PG, PC, [DPG absent]	Bchl *a* −	no	61–64	
Marivita	Q10	PC, PG, PE, DPG, AL, L	Bchl *a* v, *pufLM* +	v	58–65	
Nautella				yes	61	
Nereida				no	56	
Oceanibulbus	Q10	PG, PC, PE, DPG, AL	Bchl *a* −	yes	60	
Oceanicola	Q10	PC, PG, PE, AL, L	Bchl *a* −	yes	64–73	
Oceaniovalibus	Q10	PG, DPG	Bchl *a* −	no	62	
Octadecabacter			Bchl *a* −	no	56–57	
Pacificibacter	Q10	PC, PG, DPG, 2L	Bchl *a* −		52.6	
Palleronia	Q10		Bchl *a* −	yes	64	
Pelagibaca	Q10		Bchl *a* −	no	65	
Pelagicola	Q10	PC, PG, PE, AL, 3L	Bchl *a* −	no	47	
Pelagimonas	Q10	PC, PG, PE, DPG, PMME, AL, PL, L	Bchl *a* −, *pufLM* −		55	
Phaeobacter	Q10	PG, PE, PC, AL, L, PL[r]	Bchl *a* −	no[s]	56–65	
Planktotalea	Q10	PC, PG, AL, PL	Bchl *a* −, *pufLM* +		53–54	
Pontibaca	Q10	PC, PG, AL, PL, 3L	Bchl *a* −		65	
Ponticoccus	Q10	PC, PG, PE, 2AL, GL, L	Bchl *a* −, pufLM −	yes	68	
Poseidonocella	Q10	PC, PG, DPG, PA, AL, Ls	Bchl *a* −		60–65	
Primorskybacter	Q10	PC, PE, PG, DPG, L	Bchl *a* −		60–62	
Profundibacterium	Q10	PG, PE 2PL		no	64	
Pseudoruegeria	Q10	PG, PE, GL, DPG[t], PL[t], PC[u], AL[u], L[u]			67–73	
Roseibacterium	Q10		Bchl *a* +	v	68–76	
Roseicyclus			Bchl *a* +		66	
Roseisalinus	Q10	DPG, PG, PC	Bchl *a* +	yes	67	*m*-DAP
Roseivivax	Q10	PG, PE, PC, DPG, SQDG, 2-3PL, AL, L	Bchl *a* v	v	59–69	
Roseovarius	Q10	PG, PC, PE, DPG[v], AL, 1-2PL	Bchl *a* v		55–64	*m*-DAP
Rubellimicrobium	Q10	DPG, PC, AL, PG, PE[w]	Bchl *a* −, carotenoid +	yes	69–72	Polyamine pattern: putrescine, spermidine and *sym*-homospermidine
Ruegeria	Q10	PC, PG, Ls, AL[x], DPG[y], PL[z], PE[aa]	Bchl *a* −	v	55–68	

Table 20.2 (continued)

Genus	Quinone	Polar lipids	Pigments	PHB/PHA	GC mol%	Other
Sagittula			Bchl *a* −	yes	65	
Salinihabitans	Q10		Bchl *a* −		63.5	
Salipiger	Q10		Bchl *a* −	yes	64.5	
Sediminimonas	Q10	DPG, PG, PC, 4PL	Bchl *a* −	no	63–64	
Seohaeicola	Q10	PC, PG, PE, L			63.4	
Shimia	Q10		Bchl *a* −	no	55–57	
Sulfitobacter	Q10	PC, PG, PE, DPG[ab], AL[ac], PL[ad]	Bchl *a* −	v	55–62	
Tateyamaria	Q10	PG, PE, PC, L	Bchl *a* v		56–62	
Thalassobacter		PG, DPG, PC, 2PL, AL, PE[ae]	Bchl *a* +	yes	59	
Thalassobius	Q10	PC, PG, PE, L	*pufLM* −[af]	yes	57–61	
Thalassococcus	Q10	PG, PC, Ls, AL[ag], PE[ah]		v	57.8–58	
Tranquillimonas	Q10		Bchl *a* −	yes	69	
Tropicibacter	Q10	PE, PG, PC, AL, 4PL	Bchl *a* −	yes	58–65	
Tropicimonas	Q10 and Q9	PC, PG, DPG, AL, Ls, PL[ai]	Bchl *a* −	yes	66.5–69.6	
Vadicella	Q10	PC, PG, PA, AL, L, PE	Bchl *a* −		56–60	
Wenxinia	Q10	PG, PC, GL, PE, PL	Bchl *a* −	yes	69.4	
Yangia	Q10		Bchl *a* −	yes	63	
***Stappia* group**						
Stappia	Q10	DPG, PC, PG, PE, PMME[aj], AL[ak], PL[al]	Bchl *a* v		59–65.9	Major polyamines: spermidine and spermine
Labrenzia	Q10	DPG, PC, PG, PE, PMME, ALs, SQDG	Bchl *a* v		56–60	
Nesiotobacter			Bchl *a* −		61	
Pannonibacter	Q10	DPG, PG, PE, PC[am], PMME[am], 2AL[am], PS[an], PL[an]	Bchl *a* −		63–64.6	*m*-DAP
Polymorphum	Q10	DPG, PMME, PG, PC, AL, PLs, SQDG	Bchl *a* −		65.6	
Pseudovibrio			Bchl *a* −		50–52	
Roseibium	Q10	PG, DPG, PE, PC, SQDG, PMME, AL	Bchl *a* +		57.6–63.4	
Unaffiliated						
Ahrensia	Q10		Bchl *a* −	no	48	
Agaricicola	Q10	DPG, PC, PG, PE	Bchl *a* −	yes	62.7	
Rhodothalassium	Q10, MK10	DPG, PG, OL, PL, AL, L	Bchl *a* +, carotenoids: spirilloxanthine series		60–62.8	Contains aminopropylhomospermidine

Quinone systems: MK10, menaquinone 10; Q9, ubiquinone 9; Q10, ubiquinone 10

Polar lipids: *AL* aminolipid, *APL* aminophospholipid, *DPG* diphosphatidylglycerol, *GL* glycolipid, *L* lipid, *LPE* lysophosphatidylethanolamine, *OL* ornithine lipid, *PA* phosphatidic acid, *PC* phosphatidylcholine, *PE* phosphatidylethanolamine, *PG* phosphatidylglycerol, *PL* phospholipid, *PMME* phosphatidylmonomethylethanolamine, *PS* phosphatidylserine, *SL* sulfonolipid, *SQD* sulphoquinovosyldiglyceride, *SQDG* sulphoquinovosyldiacylglycerol

Other: *m*-DAP, meso-diamino pimelic acid in peptidoglycan

[a]spheroidene and spheroidenone/neurosporene in *R. viridis*; [b]DPG only in *G. caeni* and *G. nanjingensis*; [c]in *G. aquatilis*; [d]2SL *in R. bhavnagarense*; [e]SQD, DPG (cardiolipin) and APL in *R. euryhalinum* and *R. tesquicola*; [f]PC only in *A. xiamenensis*; [g]chemotaxonomic information, except for G+C mol%, only investigated in *A. kaplicensis*; [h]PL only in *R. shengliensis*; [i]ubiquinone 8 in *P. yeei*; [j]only in *C. neptunius*; [k]except in *J. seosinensis* and *J. donghaensis*; [l]except for *J. seohaensis*; [m]DPG in *L. janthinus*; [n]in *L. atrilutea*, *L. maricola*, and *L. tamlensis*; [o]DPG only in some species of *Loktanella*; [p]Bchl *a* + in *L. maricola*; [q]*pufLM* + in *L. vestfoldensis*; [r]PL in *P. gallaeciensis*, *P. inhibens*, *P. daeponensis*; [s]PHA/PHB in *P. caeruleus*; [t]DPG and PL in *P. aquimaris*; [u]PC, AL, and L in *P. lutimaris*; [v]DPG absent in *R. litoreus*; [w]PE in *R. aerolatum*; [x]AL absent in *R. marina*; [y]DPG in *R. conchae*, *R. faecimaris*, *R. halocynthiae*, and *R. atlantica*; [z]PL in *R. conchae* and *R. marina*; [aa]PE in *R. marina*; [ab]DPG absent in *S. guttiformis*; [ac]AL in *S. brevis* and *S. guttiformis*; [ad]PL in *S. brevis* and *S. donghicola*; [ae]PE in *T. arenae*; [af]*pufLM* in *T. aestuarii*; [ag]AL in *T. lentus*; [ah]PE in *T. halodurans*; [ai]PL absent in *T. sediminicola*; [aj]PMME in *S. indica* and *S. stellulata*; [ak]AL in *S. indica*; [al]PL in *S. taiwanensis*; [am]PC, PMME, and 2AL in *P. indica*; [an]PS and PL in *P. phragmitetus*

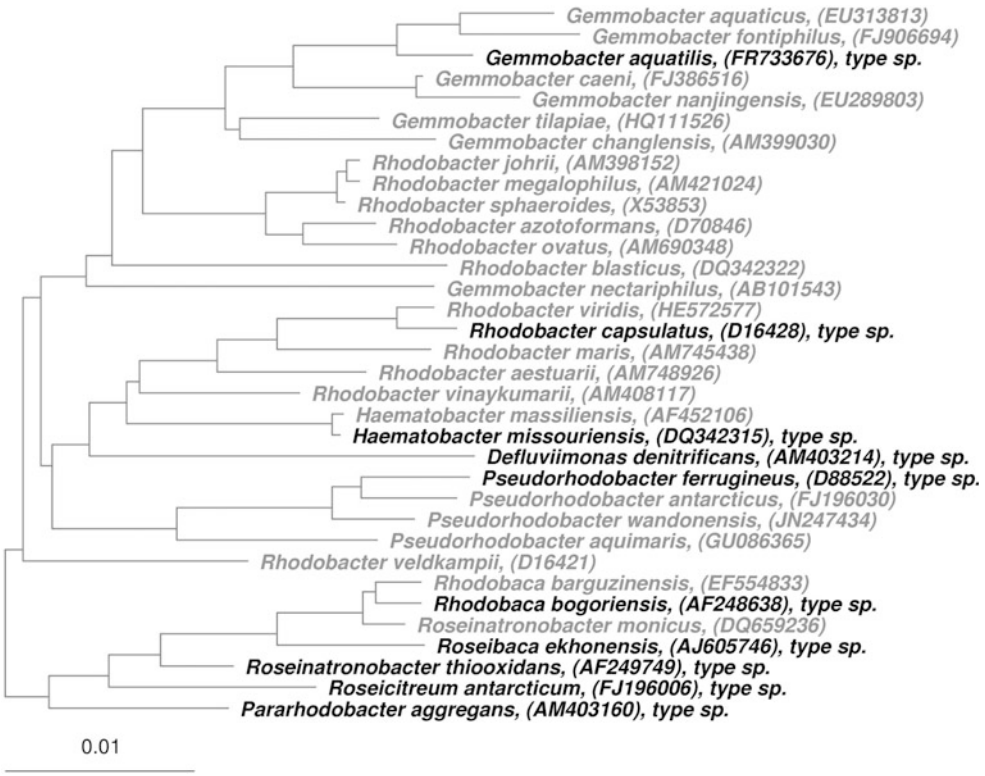

Fig. 20.2

Phylogenetic reconstruction of the *Rhodobacter* group based on 16S rRNA and created using the neighbor-joining algorithm with the Jukes-Cantor correction. The sequence data sets 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

among these groups is not even, but heavily biased to the *Roseobacter* group, that contains nearly 70 genera and more than 160 species. Metabolic, physiological, and ecological traits may differ between groups, giving a base for their suggested recognition as new families. For example, the *Rhodobacter* group contains mainly species from freshwater and terrestrial habitats, with few showing salt requirements, while *Rhodovulum* group is dominated by halophilic, marine species. On the other hand, the *Roseobacter* group contains mostly aerobic chemoorganoheterotrophs, occasionally AAP, isolated from marine habitats, but no purple non-sulfur photosynthetic genera, which are dominant in *Rhodobacter* and *Rhodovulum* groups. The *Paracoccus* group is composed almost exclusively by species of this genus, which thrives commonly in aquatic environments, including sewage and sewage treatment plants and is widely known for the denitrification activity displayed by some of its members.

Strains of the *Rhodobacteraceae* are successfully preserved in 20 % (w/v) glycerol suspension at −80 °C. Long-term preservation by freeze-drying gives good results. In our experience at CECT, the best protecting agent for lyophilization is 5 % (w/v) inositol. Some strains need the addition of salts for maintaining the ionic stability in the suspension. This could be achieved by adding the recommended culture broth to the cryoprotectant solution in a proportion of 1 to 1. Some strains could not be lyophilized successfully. Preservation and storage of these strains in liquid nitrogen is possible with 5 % (v/v) DMSO as cryoprotectant.

The *Rhodobacter* Group

This group comprises the following genera: *Defluviimonas*, *Gemmobacter*, *Haematobacter*, *Pararhodobacter*, *Pseudorhodobacter*, *Rhodobaca*, *Rhodobacter*, *Roseibaca*, *Roseicitreum*, *Roseinatronobacter*, and *Thioclava*.

The group contains a diverse collection of metabolic lifestyles, as purple non-sulfur photosynthetic bacteria (*Rhodobacter*, the type genus of the family, plus *Rhodobaca*), aerobic anoxygenic photoheterotrophs (*Roseibaca*, *Roseicitreum*, and *Roseinatronobacter*), chemoorganoheterotrophs (most *Gemmobacter* species, *Defluviimonas*, *Haematobacter*, *Pararhodobacter*, and *Pseudorhodobacter*), and facultative sulfur chemolithotrophs (*Thioclava*).

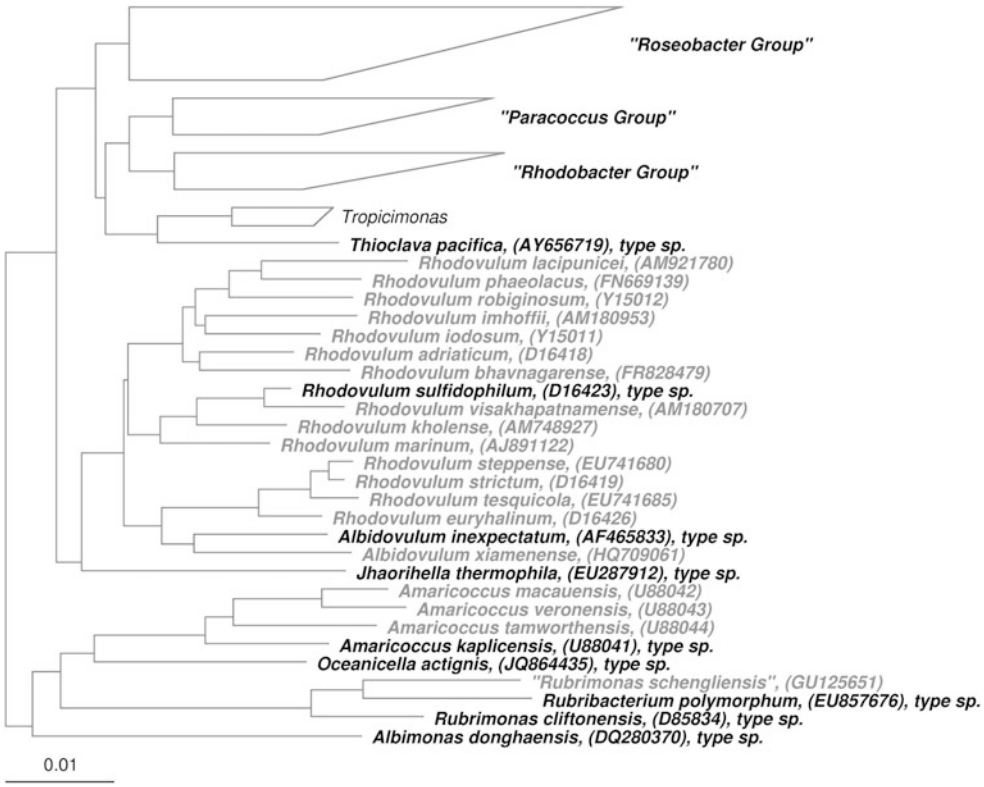

Fig. 20.3

Phylogenetic reconstruction of the *Rhodovulum* and *Amaricoccus* groups based on 16S rRNA and created using the neighbor-joining algorithm with the Jukes-Cantor correction. The sequence data sets 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

All of them, except for *Thioclava*, are grouped in a well-defined clade, whose nearest neighbor is the *Paracoccus* group (*Fig. 20.2*). *Thioclava* does not merge with the clade in the NJ analysis, but is clearly included when ML is used (not shown), having *Defluviimonas* as closest relative. The internal phylogenetic structure of the group does not reflect a separation of lifestyles or habitats, as a close relationship is found, for example, between the clinical chemoorganotrophic *Haematobacter* species and a subset of *Rhodobacter* species that include the three isolated from marine samples. An exception is the grouping of all AAPs together with the two *Rhodobaca* species, as most of them share hypersaline soda lake water as a common habitat (*Table 20.3*).

Rhodobacter

The type genus of the family, *Rhodobacter*, has been thoroughly treated by Imhoff (2005, 2006). The reader is addressed to those chapters for more detailed information on this genus (as well as *Rhodobaca* and *Rhodovulum*). A summary of its general characteristics is given here together with information on those species described after the reference work of Imhoff cited above.

Rhodobacter is defined, among all the phototrophic alphaproteobacteria, by a set of characters that include cellular morphology and division mode, intracytoplasmic membrane type, pigment composition, optimal phototrophic conditions, polar lipid content, saline preferences, and major products of sulfide oxidation. *Rhodobacter* cells are ovoid or short rods, with polar flagella (when motile) that divide by binary fission (sometimes forming chains) and exhibit vesicular intracytoplasmic membrane systems when grown phototrophically (an exception is *R. blasticus*, formerly *Rhodopseudomonas blastica*, which forms peripheral lamellae and divide by budding).

They present Q-10 as predominant quinone and have C18:1 ω7c as dominant cellular fatty acid, accompanied by C18:0 and C16:0 (Girija et al. 2010). Polar lipids may include PE and sulfolipids in addition to PC and PG. The DNA G+C content is 62–73 mol%.

Their preferred metabolism is photoorganoheterotrophy, with light and organic carbon and electron sources in anaerobic

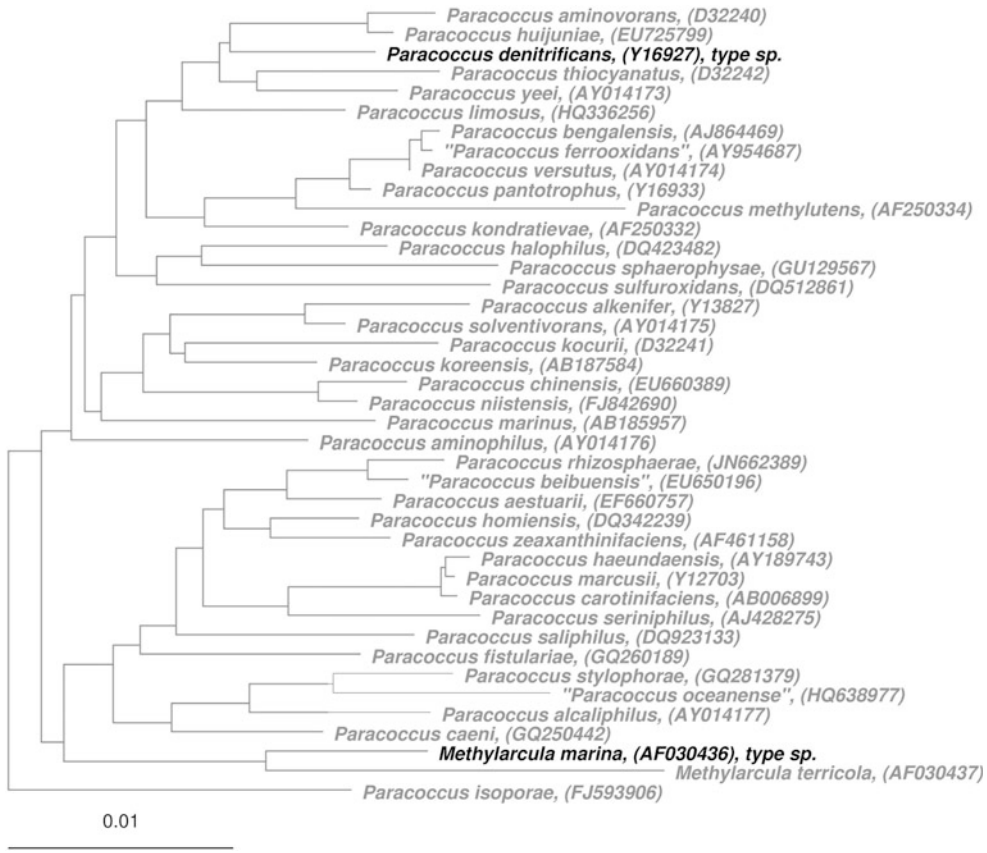

Fig. 20.4

Phylogenetic reconstruction of the *Paracoccus* group based on 16S rRNA and created using the neighbor-joining algorithm with the Jukes-Cantor correction. The sequence data sets 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

conditions. Phototrophically grown cultures are yellow brown to yellow green, but turn pink or red when exposed to oxygen. Main photosynthetic pigments are Bhcl *a* and carotenoids of the spheroidene series, with spheroidene and spheroidenone as the major components, except for *R. viridis* (Shalem Raj et al. 2013) which presents neurosporene as major carotenoid. In addition to the photoheterotrophic growth, some rhodobacters are able to thrive as photolithoautotrophs, using reduced sulfur compounds (sulfide, thiosulfate) or hydrogen as electron donors and bicarbonate/CO_2 as carbon source (fixed through Calvin cycle). Elemental sulfur is the common end product of sulfide oxidation, although some species can oxidize it to sulfate (*R. veldkampii*). Chemoheterotrophic growth in the dark by aerobic respiration is also common, being pyruvate, succinate, lactate, and other organic acids and sugars usually used. In anaerobic conditions, denitrification, other anaerobic respiration processes (with TMAO or DMSO), or fermentation (on pyruvate or sugars) could support chemoheterotrophic growth of some species. Chemolithoautotrophic growth is also possible with hydrogen being used by some species. Metabolic versatility, is, thus, considered a prominent character of this genus. Nevertheless, ability for photolithoautotrophic growth is restricted to only two out of the seven species described since 2007 and chemolithoautotrophy is even rarer. Thus, the current balance is that most *Rhodobacter* species are unable to growth autotrophically.

All *Rhodobacter* species have vitamin requirements (vitamin B12, biotin, niacin, thiamin, and/or *p*-aminobenzoic acid). Ammonium salts are the best nitrogen source, but they are also able to fix molecular nitrogen, both in phototrophic and in chemotrophic regimes (in this later case, with microoxic conditions). Sulfate is used as sulfur source by most species but some require reduced sulfur compounds.

Species of *Rhodobacter* are inhabitants of freshwater environments and are mesophilic and non-halophilic, being this later trait one that distinguish *Rhodobacter* from the members of *Rhodovulum*. While this assertion is true for the older members of the genus, however, three of the newest species come from marine samples and one of them displays saline requirements, as it needs NaCl for growth (*R. vinaykumarii*, Srinivas et al. 2007a).

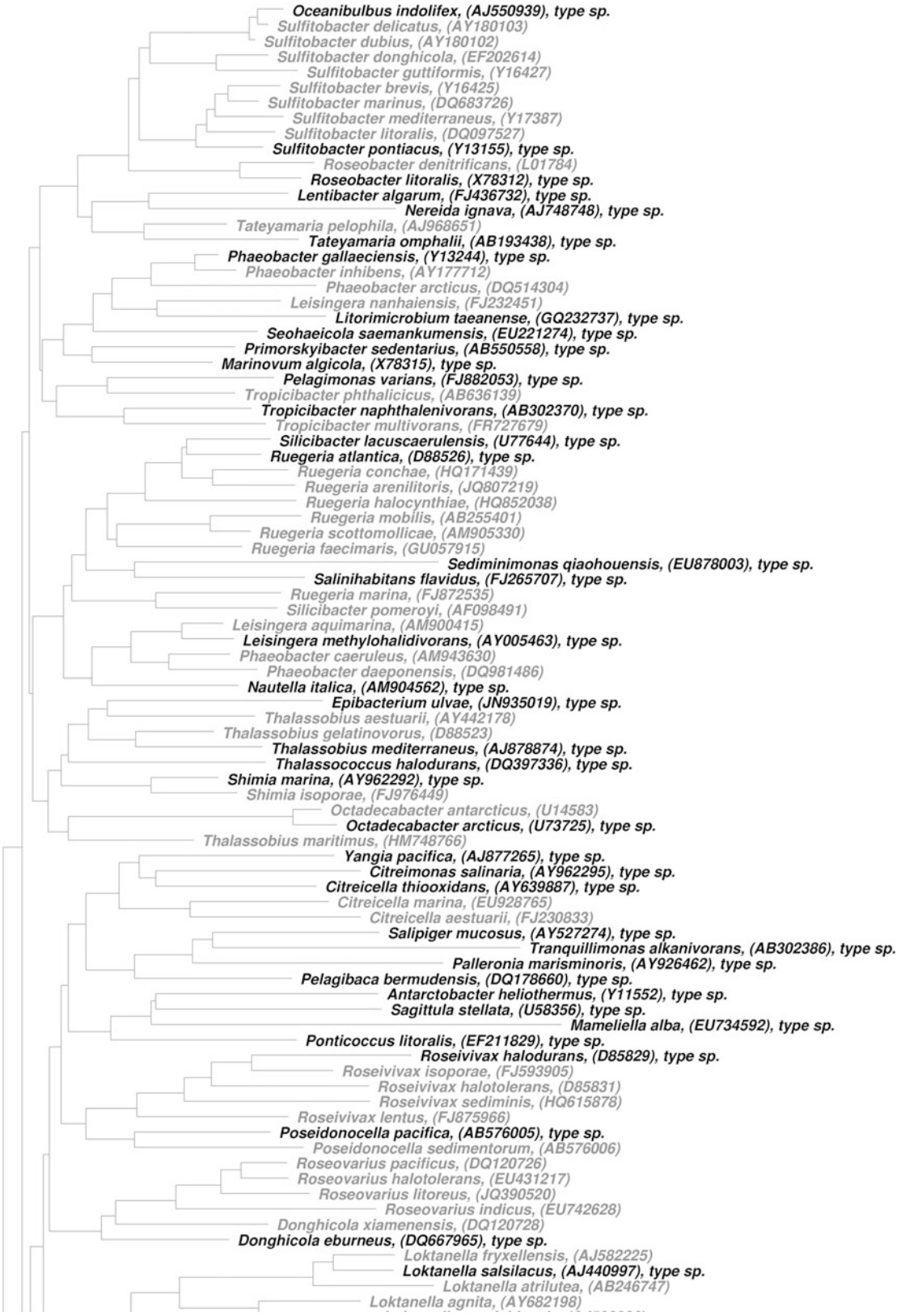

Fig. 20.5 (Continued)

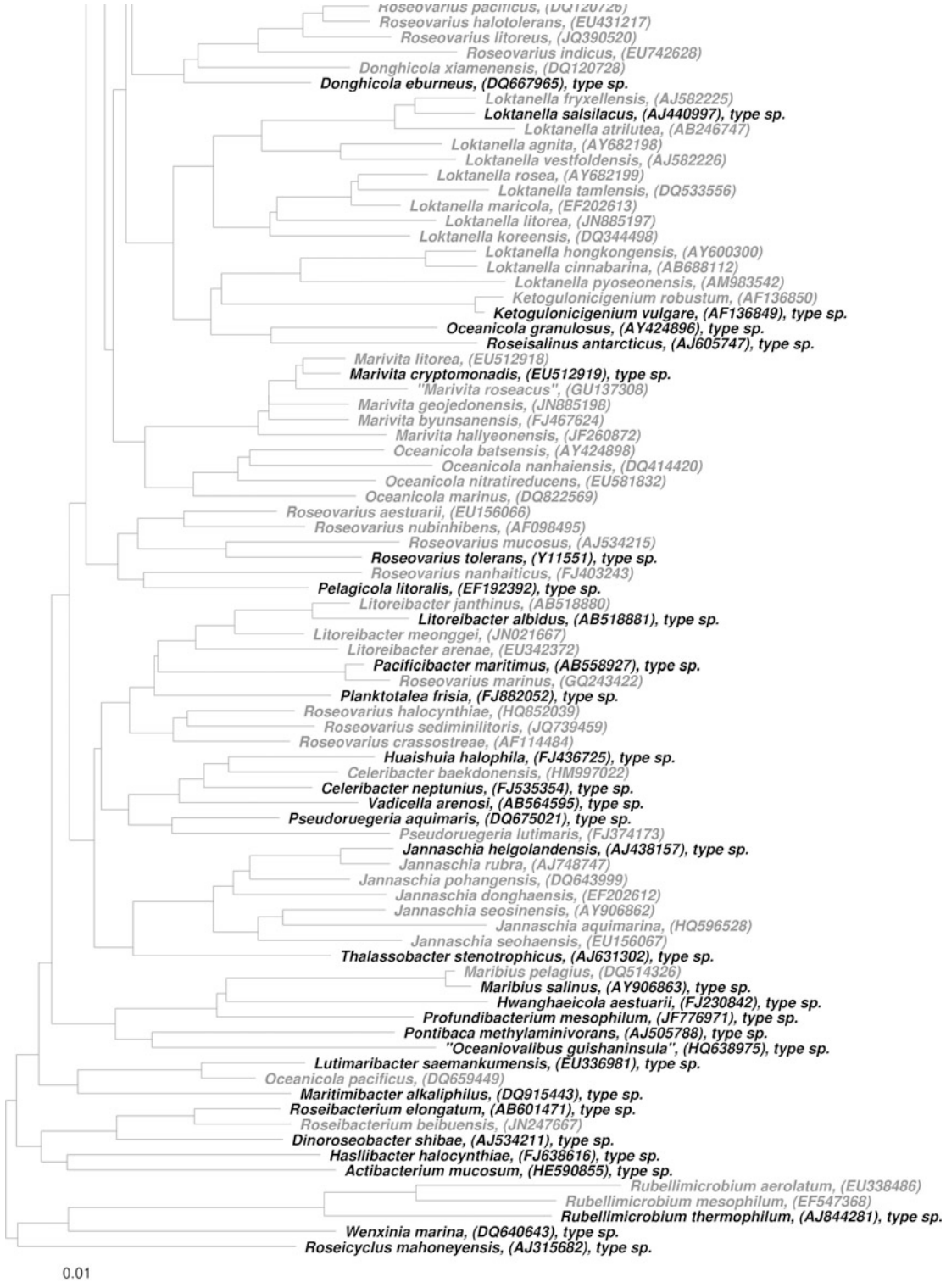

Fig. 20.5

Phylogenetic reconstruction of the *Roseobacter* group, based on 16S rRNA and created using the neighbor-joining algorithm with the Jukes-Cantor correction. The sequence data sets 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

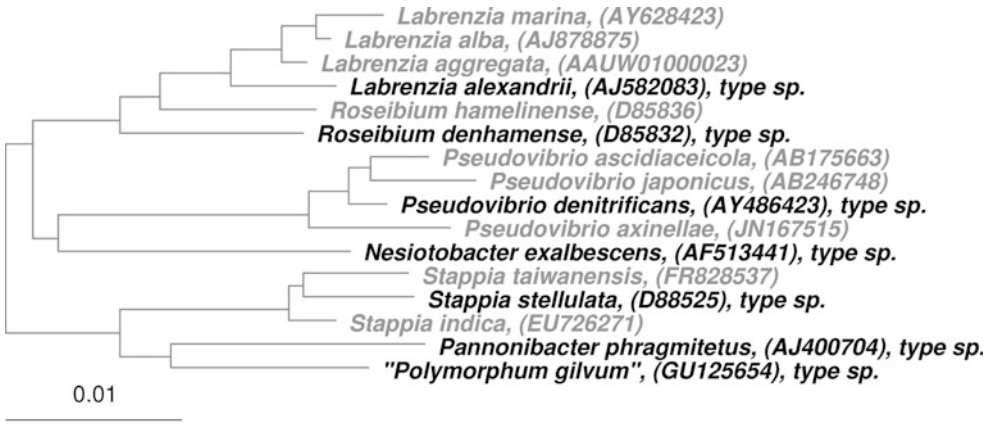

Fig. 20.6

Phylogenetic reconstruction of the *Stappia* group based on 16S rRNA and created using the neighbor-joining algorithm with the Jukes-Cantor correction. The sequence data sets 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

Other rhodobacters of marine origin are *R. maris* and *R. aestuarii* (Venkata Ramana et al. 2008, 2009), although they do not require NaCl for growth. The remaining recently recognized species have been isolated from soil (*R. megalophilus*, Arunasri et al. 2008; *R. jhorii*, Girija et al. 2010) or freshwater environments (*R. ovatus*, Srinivas et al. 2008; *R. viridis*, Shalem Raj et al. 2013).

A remarkable finding in one of the newly described species, *R. johrii*, is the ability to form endospores (Girija et al. 2010). This species was isolated from pasteurized rhizosphere soil and, after careful assessment of purity both by cultural and molecular methods, the presence and characteristic features of endospores were confirmed: dipicolinic acid content, staining behavior, induction upon stress, thermoresistance, thermal activation, ultrastructural appearance (not typical). To the best of our knowledge, genes encoding this complex ability have not been investigated; thus the ability is pending confirmation as in the case of other alleged endospore-formers outside *Firmicutes* (e.g., *Mycobacterium marinum*, Ghosh et al. 2009; Traag et al. 2010).

The complete genome sequence of *R. capsulatus* SB 1003 has been reported (Strnad et al. 2010). It consists of a 3.7 Mb chromosome and a 133 kb plasmid. The genome encodes genes for photosynthesis, nitrogen fixation, utilization of xenobiotic organic substrates, and synthesis of polyhydroxyalkanoates. In the case of *R. sphaeroides*, four strains have been fully sequenced (strains 2.4.1^T, ATCC 17019, ATCC 17025, and KD131) having two chromosomes, except strain ATCC 17019 with only one, one to five plasmids, and 4.5–4.7 Mb total size (Choudhary et al. 2007; Lim et al. 2009). In a recent comprehensive analysis of genomic islands in 70 selected marine bacterial genomes, Fernández-Gómez et al. found that *R. sphaeroides* ATCC 17025 had the highest ratio (0.12, genomic islands size/genomic size) of all.

Species of *Rhodobacter* separate in two clades (◉ *Fig. 20.2*), both in NJ and ML trees (ML not shown) suggesting a polyphyletic nature for the genus. In one hand, *R. capsulatus* joins *R. aestuarii*, *R. maris*, *R. vinaykumarii*, and *R. viridis* in a group that is more closely related to *Haematobacter* spp. than to the rest of *Rhodobacter* spp. On the other hand, the species *R. azotoformans*, *R. johrii*, *R. megalophilus*, *R. ovatus*, and *R. sphaeroides* form another clade that is closer to *Gemmobacter* species. *R. blasticus* is marginally related to this group and *R. veldkampii* occupies an isolated position among the main lineages.

Defluviimonas

Defluviimonas is a recently described monospecific genus, whose only species; *D. denitrificans* was isolated from a fluidized bed reactor from a recirculating marine aquaculture system (Foesel et al. 2011). *Defluviimonas* presents as Gram-negative rods that may be motile by polar flagella and divide by binary fission. They are chemoorganotrophic and facultatively anaerobic, with a strictly respiratory metabolism. Oxidase and catalase are positive. It is nonpigmented and non-phototrophic. *D. denitrificans* is able to grow anaerobically by denitrification, with N_2 as end product of the process. NaCl is not needed for growth, but it is tolerated up to 5 %. Q10 is the predominant quinone and C18:1 ω7c the major cellular fatty acid. DNA G+C content is 65 mol%.

Gemmobacter

The genus *Gemmobacter*, as currently defined, contains *G. aquatilis*, the type species (Rothe et al. 1987), *G. fontiphilus*

Table 20.3
Species in the *Rhodobacter* group

Species (synonym)	Isolation/habitat	Metabolism[a]	Na^+ requirement, others	References
Rhodobacter capsulatus (*Rhodopseudomonas*)	Stagnant freshwater exposed to the light with reduced oxygen, USA and Cuba	PNS	No	Imhoff et al. 1984
R. aestuarii	Microbial mat at mangrove forest, India	PNS	No	Venkata Ramana et al. 2009
R. azotoformans	Photosynthetic sludge from wastewater treatment, Japan	PNS	No	Hiraishi et al. 1997
R. blasticus (*Rhodopseudomonas*)	Stagnant freshwater exposed to the light with reduced oxygen, UK	PNS	No	Kawasaki et al. 1993
R. johrii	Pasteurized rhizosphere soil, India	PNS	No	Girija et al. 2010
R. maris	Coastal marine sediment, India	PNS	No	Venkata Ramana et al. 2008
R. megalophilus	Soil, Himalayas, India	PNS	No	Arunasri et al. 2008
R. ovatus	Sediment of industrially polluted pond, India	PNS	No	Srinivas et al. 2008
R. sphaeroides	Stagnant freshwater exposed to the light with reduced oxygen, the Netherlands and USA	PNS	No	Imhoff et al. 1984
R. veldkampii	Stagnant freshwater exposed to the light with reduced oxygen, Netherlands	PNS	No	Hansen and Imhoff 1985
R. vinaykumarii	Tidal seawater, India	PNS	Yes	Srinivas et al. 2007a
R. viridis	Stream water and mud, India	PNS	No	Shalem Raj et al. 2013
Defluviimonas denitrificans	Biofilter, marine aquaculture recirculating system, Israel	COH	No	Foesel et al. 2011
Gemmobacter aquatilis	Forest pond, USA	COH fac an	No	Rothe et al. 1987
G. aquaticus (*Catellibacterium*)	Water reservoir, China	COH	No	Chen et al. 2013a; Liu et al. 2010
G. caeni (*Catellibacterium*)	Activated sludge, China	COH	No	Chen et al. 2013a; Zheng et al. 2011a
G. changlensis (*Rhodobacter*)	Snow, Himalayas, India	PH	No	Chen et al. 2013a; Anil Kumar et al. 2007
G. fontiphilus	Freshwater spring, Taiwan	COH	No	Chen et al. 2013a
G. nanjingensis (*Catellibacterium*)	Activated sludge, China	COH	No	Chen et al. 2013a; Zhang et al. 2012a
G. nectariphilus (*Catellibacterium*)	Activated sludge, Japan	COH	No	Chen et al. 2013a; Tanaka et al. 2004
G. tilapiae	Freshwater fish culture pond, Taiwan	COH	No	Sheu et al. 2013a
Haematobacter missouriensis	Clinical samples (blood, wounds), USA	COH a	No	Helsel et al. 2007
H. massiliensis (*Rhodobacter*)	Amoebal coculture from nasal swab, France	COH a	No	Helsel et al. 2007; Greub and Raoult 2003
Pararhodobacter aggregans	Biofilter, marine aquaculture recirculating system, Israel	COH a	No	Foesel et al. 2011
Pseudorhodobacter ferrugineus (*Agrobacterium*)	Seawater, Baltic Sea, Germany	COH a	No	Lee et al. 2013a; Chen et al. 2013b; Jung et al. 2012a; Uchino et al. 2002
P. antarcticus	Intertidal sandy sediment, Antarctica	COH a	No	Chen et al. 2013b
P. aquimaris	Seawater, S. Korea	COH a	Yes (+ Mg^{2+})	Jung et al. 2012a
P. wandonensis	Wood falls at South sea, S. Korea	COH a	No	Lee et al. 2013a
Rhodobaca bogoriensis	Water and sediment of alkaline soda lakes, Rift Valley, Kenya	PNS	No, alkaliphilic	Milford et al. 2000

Table 20.3 (continued)

Species (synonym)	Isolation/habitat	Metabolism[a]	Na^+ requirement, others	References
R. barguzinensis	Sediment of alkaline soda lake, Russia	PNS	Yes, alkaliphilic	Boldareva et al. 2008
Roseibaca ekhonensis	Hypersaline Ehko Lake, Antarctica	AAP	Yes, alkalitolerant	Labrenz et al. 2009
Roseicitreum antarcticum	Intertidal sandy sediment, Antarctica	AAP	No	Yu et al. 2011
Roseinatronobacter thiooxidans	Siberian steppe soda lakes, Russia	AAP	Yes, alkaliphilic	Sorokin et al. 2000
R. monicus	Hypersaline soda lake, Mono Lake, USA	AAP	No, alkaliphilic	Boldareva et al. 2007
Thioclava pacifica	Coastal sulfidic seep, Papua New Guinea	fac CLA	Yes	Sorokin et al. 2005a

[a]*AAP* aerobic anoxygenic photoheterotroph, *COH* chemoorganoheterotroph, *COH a* chemoorganoheterotroph aerobic, *COH fac an* chemoorganoheterotroph facultative anaerobic, *fac CLA* facultatively chemolithoautotroph, *PH* photoheterotroph, *PNS* purple non-sulfur anoxygenic photoheterotroph

(Chen et al. 2013a), and *G. tilapiae* (Sheu et al. 2013a), and five species transferred from the genus *Catellibacterium* as new combinations (Chen et al. 2013a): *G. aquaticus*, *G. caeni*, *G. changlensis*, *G. nectariphilus*, and *G. nanjingensis*. As it can be observed in *Fig. 20.2*, the phylogenetic relationship within this group supports the combination of all species in one genus, with only some concern about the doubtful position of *G. nectariphilus*. *Gemmobacter* stands as a close relative of the "sphaeroides" clade of *Rhodobacter*.

After several emended descriptions of both *Catellibacterium* and *Gemmobacter* genera, the recent reclassification of Chen et al. (2013a) leaves the following general properties as characteristic of the newly defined *Gemmobacter*: Gram-negative rod-shaped cells that sometimes reproduce by budding and do not form endospores. Most species are nonmotile (except for *G. aquaticus*, with one polar flagellum). Chemoheterotrophs (*G. changlensis* is photoheterotroph able to live as chemoheterotroph in aerobic, dark conditions) use mainly carbohydrates aerobically (*G. aquatilis*, *G. nanjingense*, and *G. fontiphilus*, also anaerobically) as carbon and energy sources. Oxidase and catalase are positive. Main cellular fatty acid is C18:1 ω7c. Common polar lipids are PG, PE, PC, and one unidentified aminolipid. Q10 is the dominant ubiquinone. G+C content of DNA is 61–69.5 mol%. All species of *Gemmobacter* have been isolated from freshwater environments, including activated sludge and aquaculture facilities. They are non-halophilic and some have a low tolerance to NaCl (e.g., the maximum salinity tolerated by *G. fontiphilus* is 0.5 %, while *G. aquaticus* and *G. tilapiae* only tolerate 1 %). They are mesophilic and neutrophilic. One species isolated from snow at the Himalayas, *G. changlensis*, is able to grow at low temperatures (5 °C), but optimum is 25–30 °C.

DNA-DNA hybridization (DDH) experiments have been used to define the position of several close species of the group: type strains of *G. nanjingensis* and *G. caeni* show low levels of DDH (14–19 %, Zhang et al. 2012a); *G. tilapiae* and *G. aquatilis* are related by values of 45–48 % (Sheu et al. 2013a), *G. fontiphilus* and *G. aquatilis* show 46–52 %, *G. fontiphilus* and *G. aquaticus* 52–57 %, and *G. fontiphilus* and *G. caeni* 40–53 % DDH (Chen et al. 2013a).

The draft genome of *G. nectariphilus* DSM 15620^T has 4.52 Mb.

Haematobacter

Haematobacter was described in 2007 from a context atypical for members of *Rhodobacteraceae*, the clinical environment. In fact, it is the only genus being involved to some extension in pathogenicity, as it has been related to opportunistic infections. The genus name is taken from the most common source of isolates, human blood samples, although one species has been obtained from a nasal swab. The genus is defined as Gram negative, nonmotile, nonspore-forming, non-fermentative, and pleomorphic. Cultural properties have been determined as usual for clinical isolates, assuming chemoorganotrophy as the sole metabolic lifestyle; thus no information about other potential metabolisms is available. They are aerobic, oxidase and catalase positive, and not pigmented. DNA G+C content is around 65 mol% and main cellular fatty acids are C18:1 ω7c (50–90 %), C10:0 3OH, C16:1 ω7c, C16:0, C18:0, C18:1 ω9c, and C19:0 cyclo ω8c. There are two named species, *H. missouriensis* and *H. massiliensis*, related by interspecies DDH values of 40–55 % and one unnamed genospecies that shows 63–64 % DDH with *H. massiliensis* and *H. missouriensis* strains (Helsel et al. 2007). Buscher et al. (2010) have isolated a *Haematobacter*-like monoculture from blood of a patient with endocarditis which is only 96.7 % similar in its 16S rRNA gene sequence to the closer *Haematobacter* species. *H. massiliensis* was formerly described as a *Rhodobacter* species

(Greub and Raoult 2003) and was isolated through amoebal coculture; it was lately confirmed as able to resist amoeba grazing.

Aminoglycosides, fluoroquinolones, carbapenems, tetracycline, and chloramphenicol have good activity against *Haematobacter* isolates, while aztreonam and piperacillin have higher MIC values (Helsel et al. 2007).

Pararhodobacter

Pararhodobacter was described for accommodating one isolate obtained from the same environment that rendered *Defluviimonas denitrificans* (Foesel et al. 2011; see above). It was defined by its proximity to *Rhodobacter*, although its position in the complete *Rhodobacteraceae* tree seems closer to the *Rhodobaca* clade (Fig. 20.2). *Pararhodobacter* comprises Gram-negative, nonmotile, nonspore-forming rods that divide by binary fission and are chemoorganotrophic and strictly aerobic. Non-phototrophic. Catalase is positive but oxidase is negative. Similarly to *Defluviimonas denitrificans*, *Pararhodobacter aggregans*, the only species described so far, does not need NaCl for growth but tolerates up to 5 %. It grows with several organic acids and a few amino acids and sugars. It does not reduce nitrates or nitrites. DNA G+C content is 68 mol%. Q10 is the predominant quinone and C18:1 ω7c the main fatty acid.

Pseudorhodobacter

Pseudorhodobacter currently contains four species of chemoorganotrophs, unable to synthetize Bchl *a* and with a strictly respiratory type of metabolism. The type species *P. ferrugineus*, formerly one of the so-called marine *Agrobacterium* species (Rüger and Höfle 1992; Uchino et al. 1997), was reclassified to this new genus after an extensive study of the features common and differential from *Rhodobacter*, its closer neighbor (Uchino et al. 2002). The later descriptions of a second (*P. aquimaris*, Jung et al. 2012a) and a third species (*P. antarcticus*, Chen et al. 2013b) both including emended genus descriptions had modified slightly the original profile of the genus, which currently encompasses Gram-negative rods that may be motile or nonmotile, oxidase and catalase positive, with optimal growth at temperatures from 15 °C to 30 °C and with 1–3 % of NaCl. They contain Q10 as major quinone, C18:1 ω7c as predominant fatty acid, and C10:0 3OH as major hydroxylated fatty acid. Polar lipids include PG, PC, two unidentified aminophospholipids, and one unidentified aminolipid. G+C content is 57–62 mol%. *P. aquimaris* requires NaCl and Mg ions for growth, while the other species of the genus grow optimally in the presence of 1–3 % NaCl and do not have an absolute requirement of marine cations. The draft genome of *P. ferrugineus* DSM 5888^T contains 3.43 Mb. DNA-DNA relationship among *Pseudorhodobacter* species has been determined for *P. ferrugineus* to *P. antarcticus* (56 %; Chen et al. 2013b) and to *P. wandonensis* (12 %; Lee et al. 2013a). The four species form a well-defined clade in the vicinity of *Rhodobacter*, to which they associate, but not as closely as *Gemmobacter* or *Haematobacter* (Fig. 20.2).

Rhodobaca

The genus *Rhodobaca* comprises two species of alkaliphilic purple non-sulfur bacteria that have been isolated from distant soda lakes. The type species *R. bogoriensis* was described upon the study of several strains isolated from water and sediment samples from two African soda lakes located in the Rift Valley, Kenya (Milford et al. 2000), while *R. barguzinensis* corresponds to isolates obtained from a shallow, small soda lake in Siberia, Russia (Boldareva et al. 2008). Both species share a common metabolic profile that includes the ability for photoorganotrophic growth in anaerobic, light conditions, using several organic acids and some sugars, and also as chemoorganotrophs, in aerobiosis with almost the same carbon sources. None of them are able, apparently, of autotrophic growth, as they lack RubisCo gene nor are they able to fix N_2. They do not use nitrate as N source, but ammonium salts, urea, serine, or glutamate. Sulfide is oxidized to sulfur under photoheterotrophic growth conditions. Interestingly, both species are able to reduce tellurite and selenite to Te and Se, respectively, which are accumulated outside the cells. They synthetize Bchl *a* and carotenoids of the spheroidene series, being the major carotenoid demethylspheroidenone in the case of *R. bogoriensis* and demethyl spheroidene for *R. barguzinensis*. Cells of *Rhodobaca* species are motile, coccoid to short rods, and accumulate PHB-resembling granules. Under phototrophic conditions, they present vesicular intracytoplasmic membranes that are scarce and located in the peripheral zone of the cell. *R. barguzinensis* produces abundant slime and, unlike *R. bogoriensis*, divides by unequal fission. Biomass produced in anaerobic, light conditions is yellow brown (*R. bogoriensis*) or beige (*R. barguzinensis*), turning pink in both cases after exposure to oxygen or when cultured in aerobiosis.

Rhodobaca species behave as alkaliphiles: they do not grow at pH 7.0; their range starts at 7.5 and extends up to 10. The optimal pH of the type species is 9.0 while for *R. barguzinensis* is 8.2. They are mesophilic but *R. bogoriensis* has optimal and minimal temperatures for growth notoriously higher than the Siberian species (minimum 30, optimum 39 °C). Both are stimulated by NaCl but only *R. barguzinensis* has an absolute need of Na ion for growth.

Their major cellular fatty acids are C18:1 ω7c accompanied by C16:0, 11-methyl C18:1 ω7c, C16:1 ω7c, and C14:1 ω7c. The DNA G+C content is 58.8–59.8 mol%.

Rhodobaca-like isolates have been identified among the dominant bacteria obtained during the late-flooded phase of ephemeral hypereutrophic playa lakes in the Mojave Desert (Navarro et al. 2009).

Rhodobaca species form a coherent clade that also includes the following three genera, all of them aerobic, bacteriochlorophyll-containing heterotrophs isolated from soda lakes or

hypersaline lakes around the world (Table 20.3). The *Rhodobaca* clade lays at the edge of the *Rhodobacter* group (Fig. 20.2).

Roseibaca

Roseibaca contains a single species, *R. ekhonensis*, isolated from Ehko Lake, a hypersaline, meromictic, heliothermal lake in Antarctica (Labrenz et al. 2009). This species is similar to *Roseinatronobacter*, but alkalitolerant instead of alkaliphilic. It has been characterized more deeply in its chemotaxonomic features: it contains Q10 as predominant quinone, presents DPG, PE, PG, and PC as main polar lipids, meso-diaminopimelic acid in its peptidoglycan, and has a G+C content of 61 mol% in its DNA. The main fatty acids are C18:1 ω7c, C14:1 3OH, C16:1 ω9c, and C18:1 ω9c. *R. ekhonensis* is a strict aerobe and heterotroph, which synthetizes Bchl *a* and carotenoids, producing red to pink colonies. Cells are rod shaped, with a narrower end that suggests budding division, produce fimbria, and sometimes stemlike structures. The cells are often associated forming rosettes. They are nonmotile and accumulate PHB. It has an optimum temperature of 16 °C but grows from 10 °C to 30 °C and has a wide range of pH for growth (from as low as 5.5, in contrast with *Roseinatronobacter* and *Rhodobaca* species) with optimum between 7.0 and 9.0. It has an absolute requirement for Na ion and grows optimally at 2.5 % NaCl. It is positive for oxidase and gives a weak catalase reaction. Growth of *R. ekhonensis* requires thiamine and vitamin B12. Carbon sources used for growth include several organic acids and a large list of carbohydrates.

Roseicitreum

Roseicitreum is another AAP genus, currently containing a sole species, *R. antarcticum*, which was isolated from intertidal, sandy sediments in the coastal area of East Antarctica (Yu et al. 2011). Among its chemotaxonomic features, it contains the common quinone system of the family (Q10); its polar lipid composition includes PG, PE, PC, and one unidentified aminolipid; and its major fatty acids are C18:1 ω7c, C10:0 3OH, C16:0, C17:0 cyclo, and C19:0 cyclo ω8c. The DNA G+C content is 63 mol%. *R. antarcticum* cells are nonmotile, lemon shaped (hence the generic name), and accumulate PHB. They produce a small quantity of peripheral vesicles, similar to *Rhodobaca* cells. Colonies are pink to red. Bchl *a* is produced but *Roseicitreum* is unable to growth as photoautotroph or as anaerobic photoheterotroph. It is positive for oxidase and catalase tests. It uses carbohydrates and some organic acids as carbon and energy sources for growth. Preferred temperatures are in the mesophilic range (25–27 °C), but it is able to grow from 0 °C to 33 °C. Although Na ions are not required, growth is optimum at 7–8 % and occurs up to 15 % NaCl. The pH range is 5–9.5, with an optimum at 7.0. Thus, it is psychrotolerant and non-alkaliphilic.

Roseinatronobacter

Roseinatronobacter is the eldest of these *Rhodobaca*-associated soda lake AAPs. It was described by Sorokin et al. (2000) after the study of one pink pigmented, alkaliphilic strain isolated from a microbial mat sample obtained in a steppe soda lake in Siberia. The strain was able not only to synthetize Bchl *a* but also to oxidize thiosulfate to sulfate, using it as additional electron donor during heterotrophic growth. The species *R. thiooxidans* is also able to oxidize other sulfur compounds (sulfide, elemental sulfur, sulfite) producing sulfate. A second species was described in 2007, *R. monicus*, based on two strains isolated from Mono Lake, California (Boldareva et al. 2007). The cells of *R. thiooxidans* are elongated while *R. monicus* has oval cells, but both are nonmotile, divide by binary fission, and accumulate PHB. They are strictly aerobic and heterotrophic and able to oxidize thiosulfate, sulfide, polysulfide, and elemental sulfur. They synthetize Bchl *a* and carotenoids of the spheroidene series. Light inhibits synthesis of bacteriochlorophyll, and in the case of *R. thiooxidans*, full oxygen tension also inhibits bacteriochlorophyll and pigmentation. The highest pigment content is obtained in media rich in organic nitrogen compounds, micro-oxic, and in the dark. Both species are mesophilic, slightly halophilic (but do not have a strict Na ion requirement), and obligately alkaliphilic, with a pH range of 8.5 to 10.4 and optima at 9.0–10.0. They contain C18:1 ω7c as major cellular fatty acid, accompanied by C18:2 ω6,9c, 11-methyl C18:1 ω7c, C16:0, C14:1 ω7c, and C16:1 ω7c. G+C content is 59–61.5 mol% (Boldareva et al. 2007). The two species described so far are related by levels of DDH of 22–25 %. It is noteworthy that, based on 16S rRNA gene comparison, *R. monicus* is closer to *Rhodobaca* species than to *R. thiooxidans* (Fig. 20.2).

Roseinatronobacter-like isolates and phylotypes have been detected in soda lakes of other Russian regions (Gorlenko et al. 2010) and European countries (Borsodi et al. 2013).

Thioclava

The genus *Thioclava* does not show a definite affiliation to the *Rhodobacter* group when 16S rRNA gene sequences are analyzed through NJ method (Figs. 20.1 and 20.2) but relates to *Tropicimonas* species. However, its link to the *Rhodobacter* group is clear in ML analysis (not shown). Former phylogenetic analysis showed *Thioclava* grouped with two *Rhodobacter* species, *R. maris* and *R. aestuarii* (LTP111). Thus, *Thioclava* has been included in the *Rhodobacter* group. The genus is monospecific (A second species of the genus *Thioclava*, *T. dalianensis*, has been recently proposed for an isolate unable to grow chemolithoautotrophically on inorganic sulfur compounds. Its description is accompanied by an emended description of the genus *Thioclava* (Zhang et al. 2013)) since its description (Sorokin et al. 2005a) and contains *T. pacifica*, a species of facultative autotrophic, sulfur-oxidizing marine bacteria that was isolated from a coastal sulfidic hydrothermal area in Papua New Guinea. *T. pacifica* forms cells with widely different

Table 20.4
Species in the *Rhodovulum* group

Species (synonym)	Isolation/habitat	Metabolism[a]	Na^+ requirement, others	References
Rhodovulum sulfidophilum	Mud from intertidal flats, the Netherlands	PNS	No	Hiraishi and Ueda 1994; Hansen and Veldkamp 1973
R. adriaticum	Coastal lake, Eastern Adriatic Sea	PNS	Yes	Hiraishi and Ueda 1994
R. bhavnagarense	Sediment of pink pond, India	PNS	Yes	Srinivas et al. 2012
R. euryhalinum	Shallow saline waters, Russia	PNS	Yes	Hiraishi and Ueda 1994; Kompantseva 1985
R. imhoffii	Aquaculture pond water, India	PNS	Yes (low)	Srinivas et al. 2007b
R. iodosum	Coastal sediment, North Sea, Germany	PNS	Yes	Straub et al. 1999
R. kholense	Mangrove mud, India	PNS	Yes	Anil Kumar et al. 2008
R. lacipunicei	Saline purple pond water, India	PNS	No	Chakravarthy et al. 2009
R. marinum	Seawater, India	PNS	Yes (low)	Srinivas et al. 2006
R. phaeolacus	Sediment of brown pond, India	PNS	No	Lakshmi et al. 2011
R. robiginosum	Coastal sediment, North Sea, Germany	PNS	Yes	Straub et al. 1999
R. steppense	Steppe soda lakes, Siberia, Russia	PNS	Yes	Kompantseva et al. 2010
R. strictum	Tidal and seawater pools, coast of Japan	PNS	Yes	Hiraishi and Ueda 1995
R. tesquicola	Steppe soda lakes, Siberia, Russia	PNS	Yes	Kompantseva et al. 2012
R. visakhapatnamense	Tidal water, Bay of Bengal, India	PNS	No	Srinivas et al. 2007c
Albidovulum inexpectatum	Marine hot spring, Azores	COH	Yes, slightly thermophilic	Albuquerque et al. 2002
A. xiamenense	Terrestrial hot spring, Fujian, China	COH	Yes, slightly thermophilic	Yin et al. 2012
Jhaorihella thermophila	Coastal hot spring, Taiwan	COH	Yes	Rekha et al. 2011

[a]*COH* chemoorganoheterotroph, *PNS* purple non-sulfur anoxygenic photoheterotroph

morphologies depending of the media and growth conditions, from long filaments with swollen ends to short rods. This later morphology may exhibit motility by a polar flagellum. Oxidase and catalase are positive. *Thioclava* is mesophilic, neutrophilic, and requires NaCl for growth (1–8 %, optimum 3–4 %). It does not synthetize Bchl or carotenoids and is a strictly aerobic chemotroph, able to grow chemoautotrophically by thiosulfate (or sulfide) oxidation (CO_2 is then fixed through Calvin cycle) or chemoheterotrophically, using organic acids, carbohydrates, or amino acids as carbon and energy sources. It requires thiamine and biotin. It is also able to oxidize thiosulfate in mixotrophic conditions (acetate + thiosulfate), producing sulfate as terminal by-product. It does not ferment glucose and does not denitrify. The RubisCo produced by *Thioclava* is the green form of type I and its gene sequence (cbbL gene) relates specifically (but not very closely) to the corresponding genes of *Rhodobacter* spp., *Rhodovulum* spp., and *Hydrogenophilus thermoluteus* (a betaproteobacterium).

T. pacifica presents Q10 as sole quinone. The G+C content of its DNA is 63 mol%.

The *Rhodovulum* Group

Members of this group include the marine purple non-sulfur photosynthetic genus *Rhodovulum* that currently contains 15 species, along with the chemoorganotrophic, unpigmented, and slightly thermophilic species of *Albidovulum* and *Jhaorihella* (*Table 20.4*). *Albidovulum* is closely related to one of the subclades of *Rhodovulum* (*R. euryhalinum*, *R. steppense*, *R. strictum*, *R. tesquicola*), while *Jhaorihella* is marginal to the whole group (*Fig. 20.3*). Altogether, they form a clade that relates with the combined *Roseobacter* plus *Paracoccus* plus *Rhodobacter* groups, as can be seen in *Figs. 20.1* and *20.3*.

Rhodovulum

Rhodovulum is the largest genus in this group and the only one behaving as purple non-sulfur photosynthetic bacteria. The genus was created to accommodate three former *Rhodobacter* species of marine origin, with salt requirements for optimal

growth. Not only salt requirement but also sulfide tolerance, final product from sulfide oxidation, and polar lipid composition allow the differentiation of the species *R. sulfidophilum*, *R. adriaticum*, and *R. euryhalinum* from the freshwater, true *Rhodobacter* species (Hiraishi and Ueda 1994). Only 1 year later, the same authors described a fourth species, *R. strictum* (Hiraishi and Ueda 1995), which was followed by the recognition of *R. iodosum* and *R. robiginosum*, two ferrous iron-oxidizing new species (Straub et al. 1999). These six species were included in the excellent chapter on phototrophic Alphaproteobacteria (Imhoff 2006), where a full account for taxonomy, phylogeny, habitats, methods of isolation, culture and preservation, physiology, and metabolism of the whole group is given. The reader is addressed to this chapter for wider treatment of genus *Rhodovulum*, in all these aspects. Its general properties are summarized here, after including the nine *Rhodovulum* species described later, with special emphasis in those features that differed from the commonly accepted for the genus.

Rhodovulum includes purple non-sulfur anoxygenic photoheterotrophs that inhabit marine or saline shallow water masses or their sediments and form oval- to rod-shaped cells that are mainly nonmotile (when motile, they exhibit polar flagella). Cellular size is 0.5–0.9 × 0.9–3.8 μm. They are typical Gram-negative cells and display intracytoplasmic membrane invaginations of the vesicular type when grown in phototrophic regime. Division takes place by binary fission. They synthetize Bchl *a* and carotenoids of the spheroidene series (spheroidene, spheroidenone, demethylspheroidene, hydroxyspheroidene, neurosporene) in different proportions. They are mesophilic, with optimum temperatures between 25 °C and 35 °C, and slightly halophilic, growing best at salinities 1–7.5 %. Most of them require NaCl for growth. Two species *R. steppense* and *R. tesquicola*, isolated from shallow soda lakes, are alkaliphilic, with optimum growth at pH 8.5–9.0, and unable to grow at pH 7.0. They are closely related to *R. strictum*, also slightly alkaliphilic, to which they show moderate DDH values (40–53 %) (Kompantseva et al. 2010, 2012).

Preferred metabolism is photoorgano- or photolitho-heterotrophic, in anaerobiosis with light, (sulfide/thiosulfate) and organic carbon sources, but most can also thrive as chemoorganoheterotrophs, with oxygen and organic carbon in the dark (*R. euryhalinum*, *R. adriaticum*, *R. phaeolacus*, and *R. bhavnagarense* are exceptions, as they require sulfide or thiosulfate in addition to the organic compound). Some can also develop as photo- or chemo-lithoautotrophs, using reduced sulfur compounds (sulfide, thiosulfate, and sulfur), hydrogen, or ferrous iron as electron donors and bicarbonate as carbon source. Sulfur compounds are oxidized to sulfate (with a transitory deposition of extracellular elemental sulfur during sulfide oxidation in *R. steppense* and *R. tesquicola*, Kompantseva et al. 2010, 2012). Several species are unable to grow autotrophically: *R. marinum*, *R. lacipunicei*, *R. phaeolacus*, *and R. bhavnagarense*. None of the species described so far is able to grow fermentatively.

The preferred organic carbon sources for growth are organic acids such as pyruvate, lactate, Krebs cycle intermediates, and short-chain fatty acids. Some amino acids and sugars, as well as formate, may be used by some species. Vitamin requirement is a general rule for all species, which are variable for the given combination they need.

Species of *Rhodovulum* have C18:1 ω7c as major cellular fatty acids, with minor amount of C18:0, C16:0, 11-methyl C18:1 ω7c, and C10:0 3OH. The polar lipid composition includes PE, PG, several sulfolipids (including sulfoquinovosil diglyceride, SQD), and other lipids, but excludes PC. Although not regularly investigated, the two species that have been analyzed for this trait, *R. bhavnagarense* (Srinivas et al. 2012) and *R. tesquicola* (Kompantseva et al. 2012), confirm this general behavior. The major ubiquinone is Q10. The DNA G+C content, reported to be 62–69 mol% in the genus description (Hiraishi and Ueda 1994), has to be lowered, as *R. imhoffii* shows 58 mol% (Srinivas et al. 2007a) and *R. visakhapatnamensis* has 61.2 mol% (Srinivas et al. 2007b).

Recently, Khatri et al. (2012) have reported the 4.8 Mb draft genome of *Rhodovulum* sp. strain PH10 isolated from a mangrove soil sample. It contains 3 copies of the rRNA genes, 47 aminoacyl tRNA synthetase genes, and a DNA G+C content of 69.7 mol%.

Rhodovulum species (*R. sulfidophilum* in particular) have been investigated for the interest of some of its activities: hydrogen production (Cai and Wang 2013), PHB production (Cai et al. 2012), or anti-viral RNA aptamer secretion for aquaculture improvement (Hwang et al. 2012; Suzuki et al. 2010).

Albidovulum

The genus *Albidovulum* was described by Albuquerque et al. (2002) as a non-photosynthetic, thermophilic relative of *Rhodovulum*, with a single species, *A. inexpectatum*. Recently, a second species *A. xiamenense* (Yin et al. 2012) has been described and corresponds also to an inhabitant of a coastal hot spring. Similarity in 16S rRNA gene sequence between both species is around 96 %. Main characteristics of the genus include the absence of Bchl *a* and carotenoid production, the chemoorganotrophic, strict aerobic nature of its metabolism, and the slightly thermophilic character, with temperature optimum for growth at 50–58 °C (ranges: 28–65 °C for *A. xiamenense*, 35–60 °C for *A. inexpectatum*). Their cells are rod shaped and only *A. xiamenense* shows polar flagella and motility, while *A. inexpectatum* is nonmotile. They are positive for oxidase and catalase tests, reduce nitrates to nitrites (but are unable to grow with nitrate in anaerobiosis), do not ferment carbohydrates, and use a variety of organic compounds as carbon sources (sugars, polyols, amino acids, and organic acids) but are unable to fix CO_2. *A. inexpectatum* is facultatively chemolithoorganotrophic on reduced sulfur compounds, as it is able to oxidize thiosulfate to sulfate, deriving energy for increased growth, in the presence of organic carbon sources. Thiosulfate oxidation was not tested on *A. xiamenense*.

Table 20.5
Species in the *Amaricoccus* group

Species (synonym)	Isolation/habitat	Metabolism[a]	Na^+ requirement, others	References
Amaricoccus kaplicensis	Laboratory-scale sequence batch reactor, Czech Republic	COH a	No	Maszenan et al. 1997
A. macauensis	Activated sludge plant domestic waste, Macau	COH a	No	Maszenan et al. 1997
A. tamworthensis	Industrial plant treating malting waste, Australia	COH a	No	Maszenan et al. 1997
A. veronensis	Activated sludge plant, domestic waste, Italy	COH a	No	Maszenan et al. 1997
Albimonas donghaensis	Sea water, East Sea, S. Korea	COH a	No	Lim et al. 2008
Oceanicella actignis	Shallow marine hot spring, Azores, Portugal	COH	Yes, slightly thermophilic	Albuquerque et al. 2012
Rubribacterium polymorphum	Soda lake sediment, Siberia, Russia	PNS	Yes, alkaliphilic	Boldareva et al. 2009
Rubrimonas cliftonensis	Saline lake, Australia	AAP	yes	Suzuki et al. 1999a
R. shengliensis	Oil-polluted saline soil, China	AAP	No	Cai et al. 2011

[a]*AAP* aerobic anoxygenic photoheterotroph, *COH* chemoorganoheterotroph, *COH a* chemoorganoheterotroph aerobic, *PNS* purple non-sulfur anoxygenic photoheterotroph

Jhaoriella

Jhaoriella thermophila is the only recognized species of the genus *Jhaoriella* (Rekha et al. 2011). In spite of the specific name and isolation source, it is not a true thermophile, as it grows optimally at 37–45 °C and is able to grow from 25 °C up to 55 °C. The genus was defined on the basis of its deep lineage within the *Rhodobacteraceae*. It was found distantly related to some members of the *Roseobacter* clade and was compared to them in the description. It is a rod-shaped, unpigmented, nonmotile bacterium which shows Q10 as major respiratory quinone; PC, PG, and PE as major identified polar lipids; and cellular fatty acids dominated, as usual, by C18:1 ω7c. It requires seawater or combined sea salts for growth (2–6 %, with optimum at 3–4 %) and is obligately aerobic, unable to grow with nitrate in anaerobic conditions. It is positive for oxidase and catalase tests and PHB accumulation. The only known strain was isolated from a coastal hot spring and has a DNA G+C content of 65 mol%.

The *Amaricoccus* Group

In this group, five genera are recovered as part of a clade that always represents the deepest rooted and more distantly related clade to the rest of the family (*sensu stricto*) (*Fig. 20.3*). It includes *Amaricoccus* (with four species), *Albimonas* (one species), *Oceanicella* (one species), *Rubribacterium* (one species), and *Rubrimonas* (two species). Again, the group contains a purple non-sulfur photosynthetic member (*Rubribacterium*) and also aerobic anoxygenic phototrophs (*Rubrimonas* sp.), along with chemoorganotrophic, non-phototrophic members (*Table 20.5*).

Amaricoccus

The four species that constitute the genus *Amaricoccus* (Maszenan et al. 1997) were isolated after micromanipulation from activate sludge biomass obtained in geographically distant wastewater treatment plants. The aim of the study by Maszenan and coworkers was the isolation and characterization of the so-called G-bacteria, a morphotype common to the sludge and particularly difficult to cultivate. This morphotype corresponded to Gram-negative cocci arranged in tetrads and sheets. After trying a wide range of media, the isolates could be grown only in medium GS (Williams and Unz 1985) that contains (per liter) 0.15 g glucose, 0.50 g $(NH_4)_2SO_4$, 0.10 g $CaCO_3$, 0.10 g $Ca(NO_3)_2$, 0.05 g KCl, 0.05 g K_2HPO_4, 0.05 g $MgSO_4{\cdot}7H_2O$, 0.187 g $Na_2S{\cdot}9H_2O$, 15 g bacteriological agar (Difco), and 1.0 ml of a 10x vitamin stock solution. The new genus was described as large, Gram-negative, nonspore-forming cocci (mean cell diameter, 1.3–1.8 μm), usually arranged in tetrads. The cells were not motile and did not accumulate polyphosphate granules, either when growing in the sludge or in axenic lab cultures. They are aerobic chemoheterotrophs that use a large variety of carbohydrates and organic acids as substrates. They are oxidase positive, mesophilic (20–37 °C), and grow at pH between 5.5 and 9.0. The DNA G+C content is 51–63 mol%. According to Falvo et al. (2001), *A. kaplicensis* is able to store acetate as PHB at high rates. In a recent study, Albuquerque et al. (2012) report that this species is able to grow without NaCl addition and contains PE, PC, PG, and two unidentified aminolipids and one phospholipid as major polar lipids. These authors also report ubiquinone 10 as dominant quinone system, although its detection was difficult.

The four species can be distinguished by the differential use of several carbon sources, ability to reduce nitrate to nitrite,

some enzymatic activities (as determined in API ZYM strips), and the G+C content. *Amaricoccus kaplicensis* type species was isolated in Czech Republic, while *A. tamworthensis*, *A. veronensis*, and *A. macauensis* were isolated from Australian, Italian, and Macau wastewater samples, respectively. Up to date, activated sludge seems to be the only habitat of species of this genus that have been studied in different wastewater treatment systems by using in situ detection with FISH (Maszenan et al. 2000). They occur in large numbers not only in enhanced biological phosphate removal (EPBR) treatment plants (in which their abundance was suspicious of a detrimental role by competing phosphate removing bacteria) but also in conventional plants. They were particularly abundant in aerobic-anaerobic systems, although no evidence of that detrimental role has been found (Seviour et al. 2000). The effect of periodic acetate feeding in sequencing batch reactor on substrate uptake and storage rates by a pure culture of *A. kaplicensis* was investigated by Aulenta et al. (2003), who found that different cycle lengths resulted in different lengths of famine periods and different specific PHB contents at the end of each cycle. Moreover, as cycle length increased, flocculation and settleability of the culture significantly worsened, whereas the observed yield increased, showing that substrate removal was mainly due to oxidation and storage, whereas the growth played a minor role. Thus, a longer famine period caused a higher capacity of cells to answer quickly to sudden change of substrate availability.

Albimonas

Albimonas is a genus marginally related to the *Amaricoccus* group, from which it separates in some of the phylogenetic analysis performed. It is the deepest branch in the NJ analysis (◉ *Fig. 20.3*) but relates closely with the *Rubribacterium-Rubrimonas* subclade when ML is used for tree reconstruction. *Albimonas* contains one species, *A. donghaensis* (Lim et al. 2008), isolated in Marine Agar from seawater of the East Sea. It is an aerobic chemoorganotroph that does not synthetizes Bchl *a* and is not pigmented. Cells are short, nonmotile rods. It is positive for oxidase and catalase and negative for nitrate reduction to nitrite. Q10 is the major isoprenoid quinone, C18:1 ω7c and its 11-methyl derivative are the major cellular fatty acids, and PG, DPG, PE, and PC the major polar lipids. The DNA G+C molar content of the type strain is 72.0.

A. donghaensis grows as a mesophile, between 10 °C and 38 °C, with an optimum at 28–30 °C and pH 6.0–9.5 (optimum 7–8). It does not require sodium ions for growth, which is possible at salinities of 0–14 % (optimum 2–5 %).

Oceanicella

The genus *Oceanicella* (Albuquerque et al. 2012) has been recently described as the closer relative to *Amaricoccus*, with which it shares little resemblance in metabolic or ecological features. The pairwise similarities between *Amaricoccus* and *Oceanicella* 16S rRNA gene sequences are 93–95 %, and the relationship is supported by a bootstrap value of 96 % in the original phylogenetic analysis reported in *Oceanicella* description. *Oceanicella actignis*, the only species of the genus, is a slightly thermophilic and halophilic bacterium that forms pleomorphic, nonmotile cells. It was isolated from a shallow marine hot spring on a beach of Azores Islands. The genus is defined as organotrophic, strict aerobic, and oxidase and catalase positive. The major cellular fatty acids are C18:1 ω7c and 11-methyl C18:1 ω7c, while the major polar lipids are PC, PG, and one aminolipid. Q10 is the major respiratory quinone and the DNA G+C content of the type species is 71.2 mol%.

The temperature range for growth of *O. actignis* is 25–57.5 °C, with an optimum at 50 °C. Optimum pH is 7.5–8.0 and optimal salinity is 2–5 % (range, 1–9 %). The species does not grow without added NaCl. It reduces nitrate to nitrite, degrades gelatin and DNA, but not casein or starch. A few carbohydrates (glycerol, mannitol), several organic acids (2-oxoglutarate, lactate, acetate, pyruvate, succinate, malate, and fumarate), and several amino acids (aspartate, glutamate, alanine, asparagine, serine, leucine, proline, glutamine, phenylalanine, and isoleucine) are assimilated. *O. actignis* grows as unpigmented colonies in Degryse medium 162 (Degryse et al. 1978), containing 0.25 % yeast extract, 0.25 % tryptone, and 2 % NaCl.

Rubribacterium

In contrast to the previous genera, *Rubribacterium* and *Rubrimonas*, the remaining members of *Amaricoccus* group are phototrophic. Namely, *Rubribacterium* was described as purple non-sulfur anoxygenic photosynthetic bacterium, while *Rubrimonas* is an aerobic anoxygenic photoheterotroph (AAP) that contains two species of pink pigmented bacteria. The genus *Rubribacterium* (Boldareva et al. 2009) was established to account for a new alkaliphilic, phototrophic isolate from a soda lake in Siberia, described as a purple non-sulfur bacterium that lacks RuBisCo and grows better in aerobic than anaerobic conditions under illumination. The key difference between *Rubribacterium* and *Rubrimonas* is the ability of the former to grow photo-heterotrophically and form vesicular type of photosynthetic membranes in anaerobic conditions. *Rubribacterium polymorphum* cells are oval in young cultures, but become polymorphic with age and the accumulation of large storage granules interpreted as PHB. They may be motile by polar flagella. Carotenoids of both spheroidene and spirilloxanthin groups are formed. C18:1 ω7c is the major cellular fatty acid, accompanied by its 11-methyl derivative, C18:0, and C16:0. DNA G+C base content is 70 mol%, in the same range that of *Rubrimonas*.

Rubribacterium is a facultative anaerobe, able to grow (poorly) in anaerobiosis as photoheterotroph, with glucose, fructose, sucrose, pyruvate, malate, casein hydrolysate, yeast extract, and soyotone. These substrates also support good chemoheterotrophic growth in aerobic conditions in the dark. Nitrate is reduced to nitrite, but this activity does not support

growth. Ammonium salts are used as nitrogen source. *Nif* genes and RuBisCo activity are absent.

Rubribacterium polymorphum is a moderate alkaliphile, unable to grow at neutral pH, and shows optimal growth at 8.5–9.5. NaCl is required (0.5–4.0 %, optimum 1.0 %). Good growth occurs between temperatures of 20 °C and 35 °C.

Rubrimonas

Rubrimonas cliftonensis, the type species of the genus *Rubrimonas*, was isolated from a saline lake in Australia (Suzuki et al. 1999a). The genus was defined as aerobic and chemoheterotrophic, with the ability to synthesize Bchl *a* under aerobic conditions. Carotenoid pigments are also produced. Chemotaxonomic features include the presence of Q10 as ubiquinone system, C18:1 ω7c as dominant cellular fatty acid, and a 74–75 mol% G+C content of DNA. This later value has to be extended to a lower limit of 68 mol% with the recent recognition of a second species *R. shengliensis* (Cai et al. 2011), isolated from oil-contaminated saline soil. These authors reported data on the polar lipid composition of both species, which include PG, PC, and unidentified lipids and aminolipids. They are mesophilic (optimum 27–30 °C, but *R. shengliensis* has a wide temperature range for growth, 4–50 °C), neutrophilic (optimum pH 7–8), and slightly halophilic, with *R. cliftonensis* requiring NaCl for growth (range 0.5–7.5 %) and *R. shengliensis* being able to grow without NaCl, but growing optimally at 1 % (range 0–10 %). The cells of *R. cliftonensis* are polarly flagellated rods while *R. shengliensis* presents oval, nonmotile cells. Both form pink colonies, are positive for catalase, but differ in oxidase, nitrate reduction (see Cai et al., ❯ *Table 20.1*), gelatinase and amylase production, and ability to produce acid from several carbohydrates. Species of *Rubrimonas* show 95.7 % similarity on their 16S rRNA gene sequences, but also display a moderate similarity to *Rubribacterium polymorphum* sequence, the third member of the subgroup.

The *Paracoccus* Group

The clade that contains the forty species of the genus *Paracoccus* also groups the facultative methylotroph genus *Methylarcula*, with two species (❯ *Table 20.6*). They have the *Rhodobacter* group as closest relative (❯ *Fig. 20.4*). The close phylogenetic relationship between *Rhodobacter* and *Paracoccus* groups is also revealed by phylogenomic analysis of signature proteins, as reported by Gupta and Mok (2007) who suggest that both *Rhodobacter* and *Paracoccus* form a distinct clade that appears as the outgroup of other *Rhodobacterales* species.

In contrast with the previous groups in this chapter, *Paracoccus* encompasses strictly chemotrophic species, with no example of phototrophic activity, either aerobic or anaerobic.

Paracoccus

The genus *Paracoccus* was the subject of a thorough chapter by Kelly and colleagues (Kelly et al. 2006a) in the 3rd edition of The Prokaryotes, and the interested reader is addressed to this chapter for information on all the general aspects of this genus and the summary of the fourteen species included at that time. By then, a publication note came out (Kelly et al. 2006b) to clarify the taxonomic status of the culture collection strains of two key species of *Paracoccus*, the type species *P. denitrificans* and *P. pantotrophus*, which had been used for many years in fundamental biochemical studies and as reference species in the identification of new isolates of *Paracoccus*. Here, the complementary information on the 26 species described thereafter is developed, along with the emendation of the genus (Liu et al. 2008), underlying those aspects that complement, extend, or modify the previous information.

Paracocci have Gram-negative cells described as coccoid, coccobacilli, or short rods, usually nonmotile. When motile, they may present polar flagella (*P. homiensis*, *P. oceanense*, and *P. versutus*) or peritrichous (*P. carotinifaciens*). *P. chinensis* and *P. rhizosphaerae* are described as motile without reference to the flagellar arrangement. The remaining 34 species are nonmotile. They divide by binary fission and occur as single cells, pairs, short chains, or irregular clusters. They commonly contain PHB as carbon reserve material. Several species display pigmented colonies, most commonly orange to red, due to the production of carotenoids.

They are catalase and oxidase positive and contain ubiquinone 10 (Q10) as sole or dominant quinone, sometimes accompanied by small amounts (<5 %) of Q9 and Q11. Only one species differs from this pattern, *P. yeei*, as it has been reported to contain Q8 as major quinone (Daneshvar et al. 2003).

Major cellular fatty acids (FAs) are C18:1 ω7c, C18:0, 19:0 cyclo ω7c, and 16:0, and among the hydroxylated, C10:0 3OH is commonly present. C18:1 ω7c represents usually more than 70 % of the total FAs detected. Exceptions to this behavior are *P. caeni* (54 %, Lee et al. 2011a), *P. halophilus* (60 %, Liu et al. 2008), and *P. oceanense* with no C18:1 ω7c detectable (instead, it contains 39 % of C18:1 ω6c, Fu et al. 2011). C10:0 3OH is undetectable in *P. fistulariae* and *P. sulfuroxidans*, both containing other hydroxylated FAs (Kim et al. 2010a; Liu et al. 2006), and in *P. oceanense*, with no hydroxylated FAs reported (Fu et al. 2011).

Information on polar lipid (PL) composition is scarcer than other chemotaxonomic features. Kelly et al. (2006a) do not report PL composition of the fourteen *Paracoccus* species available, and the pattern is included only in part of the more recent descriptions. The information briefed here comes from the analysis of less than a half of the currently recognized species. Major PL recorded in all species reported are phosphatidyl glycerol (PG) and phosphatidyl choline (PC), while diphosphatidyl glycerol (DPG) is detected in most, but not all, the species tested. Phosphatidyl ethanolamine (PE) is present in *P. huijuniae*, *P. kondratievae*, and *P. rhizosphaerae*, out of the 15 species compositions known. One sphingoglycolipid is detected

Table 20.6
Species in the *Paracoccus* group

Species (synonym)	Isolation/habitat	Metabolism[a]	Na^+ requirement, others	References
Paracoccus denitrificans	Soil, sewage, manure, mud	fac CLA	No	Rainey et al. 1999; Ludwig et al. 1993; Nokhal and Schlegel 1983
P. aestuarii	Tidal flat sediment, S. Korea	COH	No	Roh et al. 2009
P. alcaliphilus	Soil	COH	No	Urakami et al. 1989
P. alkenifer	Biofilters treating waste gas from animal rendering plant	COH	No	Lipski et al. 1998
P. aminophilus	Soil, Japan	COH	No	Urakami et al. 1990
P. aminovorans	Soil, Japan	COH	No	Urakami et al. 1990
P. beibuensis	Seawater, S. Korea	COH	No	Zheng et al. 2011b
P. bengalensis	Rhizosphere of leguminose (*Clitoria*), India	fac CLA	No	Ghosh et al. 2006
P. caeni	Sludge from disposal plant, S. Korea	COH	No	Lee et al. 2011a
P. carotinifaciens	Soil, Japan	COH	No	Tsubokura et al. 1999
P. chinensis	Sediment from eutrophic water reservoir, China	COH	No	Li et al. 2009
P. ferrooxidans	Denitrifying fluidized bed bioreactor, the Netherlands	fac CLA	No	Kumaraswamy et al. 2006
P. fistulariae	Intestine of marine fish (*Fistularia*), S. Korea	COH	Yes (or Mg^{2+} at 0 % NaCl)	Kim et al. 2010a
P. haeundaensis	Seawater, S. Korea	COH	No	Lee et al. 2004
P. halophilus	Marine sediment, South China Sea, China	COH	Yes	Liu et al. 2008
P. homiensis	Sea sand, S. Korea	COH	No	Kim et al. 2006a
P. huijuniae	Activated sludge of a wastewater biotreatment facility, China	COH	No	Sun et al. 2013
P. isoporae	Reef-building coral (*Isopora*), Taiwan	COH	No	Chen et al. 2011a
P. kocurii	Activated sludge system for wastewater of semiconductor manufacturing process, Japan	COH	No	Ohara et al. 1990
P. kondratievae	Maize rhizosphere, Russia	COH	No	Doronina et al. 2002; Doronina and Trotsenko 2000
P. koreensis	Anaerobic sludge blanket reactor, S. Korea	COH	No	La et al. 2005
P. limosus	Activated sludge, sewage treatment plant, S. Korea	COH	No	Lee and Lee 2013
P. marcusii	Contaminant of agar plate	COH	No	Harker et al. 1998
P. marinus	Coastal seawater, Japan	COH	Yes	Khan et al. 2008
P. methylutens	Ground water contaminated with dichloromethane, Switzerland	COH	No	Doronina et al. 1998
P. niistensis	Forest soil, India	COH	No	Dastager et al. 2011
P. oceanense	Seawater, West Pacific Ocean	COH	Yes	Fu et al. 2011
P. pantotrophus (*Thiosphaera*)	Denitrifying, desulfurizer effluent treatment system, the Netherlands; soil (GB)	fac CLA	No	Rainey et al. 1999; Robertson and Kuenen 1983
P. rhizosphaerae	Rhizosphere of plant (*Crossostephium*), Taiwan	COH	Yes	Kämpfer et al. 2012
P. saliphilus	Saline soil near Ebinur Lake, China	COH	Yes (optimum 8 % NaCl)	Wang et al. 2009a
P. seriniphilus	Bryozoan (*Bugula*), North Sea, Germany	COH	Yes	Pukall et al. 2003
P. solventivorans	Soil at natural gas company site, Germany	COH	No	Lipski et al. 1998; Siller et al. 1996
P. sphaerophysae	Root nodules of leguminose (*Sphaerophysa*), China	COH	No	Deng et al. 2011

Table 20.6 (continued)

Species (synonym)	Isolation/habitat	Metabolism[a]	Na^+ requirement, others	References
P. stylophorae	Reef-building coral (*Stylophora*), Taiwan	COH	No	Sheu et al. 2011
P. sulfuroxidans	Activated sludge of a wastewater treatment bioreactor, China	fac CLA	No	Liu et al. 2006
P. thiocyanatus	Activated sludge with thiocyanate, Japan	fac CLA	No	Katayama et al. 1995
P. tibetensis	Permafrost, Tibet plateau, China	COH	No, alkaliphilic	Zhu et al. 2013
P. versutus	Soil, USA	fac CLA	No	Katayama et al. 1995; Harrison 1983
P. yeei	Clinical samples (wounds, bile, blood, eye), USA, Canada	COH	No	Daneshvar et al. 2003
P. zeaxanthinifaciens	Seaweed, Red Sea	COH	No	Berry et al. 2003
Methylarcula marina	Estuary seawater, Azov Sea, Russia	fac M	Yes	Doronina et al. 2000
M. terricola	Coastal salty soil, Black Sea, Russia	fac M	Yes	Doronina et al. 2000

[a]*COH* chemoorganoheterotroph, *fac CLA* facultatively chemolithoautotroph, *fac M* facultatively methylotroph

in *P. oceanense* (Fu et al. 2011) and several unidentified amino-phospho- and glycolipids are present in some species.

The molar % C+G content is 63–71 in Kelly et al. (2006) and Spanning et al. (2005), but several species with lower values have been described afterwards: *P. caeni*, 58.7 (Lee et al. 2011a); *P. oceanense*, 59.5 (Fu et al. 2011); *P. saliphilus*, 60.3 (Wang et al. 2009a); *P. sulfuroxidans*, 61.3 (Liu et al. 2006); *P. yeei*, 62 (Daneshvar et al. 2003); and *P. aestuarii*, 62.0 (Roh et al. 2009). Thus, the range of molar % G+C extends now from 58 to 71.

Other chemotaxonomic features, such as diamino acid on peptidoglycan or polyamine pattern, have been determined only for few species. *P. rhizosphaerae* (Kämpfer et al. 2012) contains *m*-diaminopimelic acid as diagnostic diamino acid and spermidine (SPE) and putrescine (PUT) as major polyamines, with cadaverine (CAD) and diaminopropane (Dap) as minor components. Hamana and Matsuzaki (1992) had previously determined the presence of PUT and SPE as the dominant polyamines in five species analyzed (*P. denitrificans*, *P. alcaliphilus*, *P. aminophilus*, *P. aminovorans*, and *P. kocurii*).

Species in the genus *Paracoccus* are chemoorganoheterotrophic, with a respiratory metabolism which uses oxygen as terminal electron acceptor. Some species can use, alternatively, nitrate which is reduced to nitrite or to molecular nitrogen. Nitrous oxide is also used by some species. Denitrification is not limited, when present, to chemoorganotrophic growth, but is also performed under chemolithoautotrophic conditions by some species (Kumaraswamy et al. 2006). None of the species is able to grow anaerobically by fermenting carbohydrates, although acid is produced aerobically from some of them. None of the species has been found to contain bacteriochlorophyll a, but carotenoids are common (astaxanthin, zeaxanthin, β-carotene). The range of organic substrates oxidized and used as carbon sources by paracocci is wide, including carbohydrates, organic acids, amino acids, and alcohols. In addition to this general mode of metabolism, several species in the genus, including the type species *P. denitrificans*, are able to grow as facultative chemolithoautotrophs, using reduced sulfur compounds as substrates (thiosulfate, tetrathionate, sulfur, or sulfide), and some are also able to oxidize hydrogen or ferrous iron. Finally, some species are able to live as facultative methylotrophs, using methylamines or methanol as substrate. During autotrophic growth, the Calvin-Benson cycle is used to fix CO_2. The chemoautotrophic ability is not always investigated when describing new species, so there is incomplete information about this trait in several of the 26 species not included in Kelly et al. (2006). In any case, at least two (*P. bengalensis* and *P. sulfuroxidans*) are able to thrive by oxidizing reduced sulfur compounds (Ghosh et al. 2006; Liu et al. 2006; Ghosh and Roy 2007) and one oxidizes Fe^{2+} (*P. ferrooxidans*, Kumaraswamy et al. 2006).

Some species have a requirement for growth factors when grown in minimal media (thiamine, biotin, B12, or unknown factors that may be covered with yeast extract).

Paracoccus species are mesophilic, growing optimally at 25–37 °C. The upper limit was established in 42 °C, but among the species recently described, *P. saliphilus* is able to grow up to 55 °C and *P. sphaerophysae* up to 60 °C. The optimal pH for most species is between 6.5 and 8.5, but there are moderate alkaliphilic species, as *P. alcalophilus*, that grows up to 9.5 (with optimum at 8–9) and a truly obligate alkaliphile, *P. tibetense*, which grows in the range 8.5–13.0 (optimum 9.5).

Paracocci are ubiquitous and ecologically diverse. While the earlier 14 species of *Paracoccus* were isolated from terrestrial or continental aquatic habitats (see *Table 20.6*), and none of

them displayed saline requirements for growth (Kelly et al. (2006)), most of the newly described species come from marine environments (seawater, tidal flat sediment, sand, and different marine organisms), and some are strictly halophilic (*P. halophilus*, *P. marinus*, *P. oceanense*, *P. rhizosphaerae*, *P. saliphilus*, and *P. seriniphilus* do not growth without NaCl). Others, although able to grow without added NaCl, have optimal growth at salinities ≥2 %. This motivated the emended description of the genus (Liu et al. 2008), aimed to account for the existence of halophilic and halotolerant species.

Three main environments have been the source of almost all the new descriptions of *Paracoccus* spp.: first, the already mentioned marine habitats; second, activated sludge from bioreactors in wastewater treatment plants; and finally, the rhizosphere and other plant-related sources. Interestingly, one species has been isolated from clinical sources (*P. yeei*), and since its description, it has been found in relation to opportunistic infections in the USA and Canada (Daneshvar et al. 2003; Funke et al. 2004; Schweiger et al. 2011).

The new species have been delineated with the aid of 16S rRNA gene sequence analysis and DNA-DNA hybridization (DDH) experiments. Thus, DDH values around 36 % relate *P. aminovorans* and *P. huijiniae* DNAs, *P. bengalensis* and *P. versutus* show values around 45 %, *P. chinensis* and *P. niistensis* have 44 % relatedness, *P. haeundaensis* and *P. marcusii* present 47 %, and *P. ferrooxidans* relates to *P. versutus*, *P. denitrificans*, and *P. pantotrophus* by 32–43 %. The former pairs are the closest in the tree, as can be seen in Fig. 20.4. However, some critical values are still missing, as the ones relating *P. carotinifaciens* with *P. marcusii* and *P. haeundaensis*. But being the type and only strain of *P. carotinifaciens* (IFO 16121^T) a patented strain, deposited only in one culture collection, it has not been possible to assess their DDH values. This fact also puts in question the status of the species *P. carotinifaciens*, according with rule 30 of the International Code of Nomenclature of Bacteria (http://www.bacterio.cict.fr/code.html). Other pairs of close species for which there are no DDH figures are *P. oceanense-P. stylophorae* (97.1 % similarity in 16S rRNA gene sequences) and *P. beibuensis-P. aestuarii* (97.2 %).

The genus *Paracoccus* is one of the most diverse carriers of insertion sequences within the *Alphaproteobacteria*. Dziewit et al. (2012) used trap plasmids (enabling positive selection of transposition events) to identify transposable elements residing in 25 strains representing 20 species of the genus *Paracoccus*. As a result, 41 elements were captured representing (i) insertion sequences, (ii) an IS-driven composite transposon, and (iii) non-composite transposons of the Tn3 family. By analyzing the functional transposable part of the mobilome, not only the dynamics of the process of transposition is better understood, but also its role in the dissemination of diverse genetic information (possibly of adaptative value) by HGT.

The genome of strain PD1222, a genetically modified version of strain *P. denitrificans* DSM 413^T, consists of two chromosomes and one plasmid totaling 5.24 Mb. The partial genome (contig assembly level) of *P. denitrificans* SD1 sourced from coal mine tailings in India and capable of *N*,*N*-dimethylformamide degradation has also been reported (Siddavattam et al. 2011). Yet, another draft genome sequence has been reported from a strain interesting for xenobiotic biodegradation and metabolism, *Paracoccus* sp. strain TRP isolated from activated sludge, that could completely biodegrade chlorpyrifos and 3,5,6-trichloro-2-pyridinol (Li et al. 2011a).

Paracoccus aminophilus JCM 7686^T has one chromosome and eight plasmids (total size 4.87 Mb) whereas the genome sequence of *P. zeaxanthinifaciens* ATCC 21588^T is only available as draft (3.05 Mb).

Methylarcula

The genus *Methylarcula*, the second component of the *Paracoccus* group, includes two species of facultative methylotrophs isolated from coastal saline environments (Doronina et al. 2000). Its separation by 16S rRNA sequence analysis from the genus *Paracoccus* is not as evident now as it was at the time of its description, although it occupies a marginal position in the clade, with only *P. isoporae* being more external to the main group (Fig. 20.4). The main characteristics of the genus are Gram-negative, nonmotile rods (0.5–0.8 × 1.0–2.0 μm in size), asporogenous, not pigmented; they divide by binary fission and accumulate PHB (up to 10–40 % of their total dry cell weight). Common cellular fatty acids are C18:1 ω7c (73–74 %), C18:0 (14–15 %), C19:0 cyclo (5–6 %), and C17:0 (2–3 %). Major PLs are PE and PC, with minor amounts of PG and DPG. The quinone system is Q10. Major compatible solute is ectoine. Molar % G+C is 57–61.

Both species require NaCl for growth, which is optimal at 3–8 % NaCl. Salinities over 12 % (*M. marina*) and 14 % (*M. terricola*) inhibit growth. Temperature range for growth is 10–42 °C with optimum at 30–35 °C and pH 7.5–8.5. They are oxidase positive, aerobic chemoorganotrophs, and facultatively methylotrophic, using methylamine, fructose, glucose, maltose, lactose, mannose, ribose, trehalose, galactose, xylose, sucrose, succinate, pyruvate, and acetate as carbon and energy sources. No growth is observed with $CO_2/H_2/O_2$ or CH_4/O_2. Growth factors are not required. Gelatin and starch are not hydrolyzed. Nitrate is not used as nitrogen source (ammonia and methylamine are) nor is it reduced to nitrite or further. Doronina et al. (2000) confirmed the presence of the (isocitrate lyase-negative) serine pathway for formaldehyde assimilation in methylamine-grown cells. The DDH values relating both species of this genus are 25–32 %.

The *Roseobacter* Group

It is the largest group in the family and the one that keeps enlarging at a fastest rate. At the moment of writing this chapter, 69 genera (comprising one hundred sixty species) have been described that join the phylogenetic group around the genus *Roseobacter*, the first described aerobic anoxygenic phototroph on this family (Fig. 20.5).

The clade is dominated by species of marine origin, chemoorganoheterotrophic, non-fermentative, most of them requiring Na ion (or sometimes combined marine salts) for growth. Thirteen of the genera contain at least one species that synthetize Bchl *a* (*Dinoroseobacter*, *Jannaschia*, *Loktanella*, *Marivita*, *Roseibacterium*, *Roseicyclus*, *Roseisalinus*, *Roseivivax*, *Roseobacter*, *Roseovarius*, *Sulfitobacter*, *Tateyamaria*, and *Thalassobacter*), and one more has been described as possessing *pufLM* genes, although Bchl *a* is not detected in the isolates grown at the lab (*Planktotalea*). No classical purple non-sulfur photosynthetic bacteria (anaerobic photoheterotrophs such as *Rhodovulum*) are included in this group, which also lacks any known autotrophic member. Some of them are able to oxidize sulfur compounds (sulfite, thiosulfate) with energy gain; thus, they may be defined as chemolithoheterotrophs. Carbon monoxide oxidation is a common ability of members of this group as well as the ability to degrade dimethylsulfoniopropionate (DMSP), either by the cleavage pathway or by the demethylation/dethionation pathway (Wagner-Döbler and Biebl 2006). González et al. (2000) reported that estimated abundance of *Roseobacter*-related bacteria was positively correlated with the concentration of DMSP in samples from a DMSP-producing algal bloom in the North Atlantic.

As already noted, the habitat of most of its members is the marine environment, including seawater, sea ice, estuarine, coastal and deep marine sediments, phytoplankton, algal surfaces, and marine invertebrates (sponges, ascidians, corals, mollusks, echinoderms), sometimes as biofilms attached to inert or living surfaces. A smaller group has been isolated from hypersaline environments (solar saltern water and sediments, salt lakes, salt mine sediment), and a minority comes from terrestrial (natural or man-made) environments: *Ketogulonicigenium* from soil samples and *Rubellimicrobium* from air, soil, and paper industry samples (❯ *Table 20.7*).

The so-called *Roseobacter* group/clade/lineage is usually one of the outstanding groups of marine bacteria detected in culture-independent studies, accounting for as much as 20 % of the total bacterial signal (Buchan et al. 2005; Wagner-Döbler and Biebl 2006; Brinkhoff et al. 2008; Giebel et al. 2011; Lenk et al. 2012). Its role on carbon and sulfur cycles in the marine environment as well as their contribution to other key activities (AAP, symbiotic relationships and pathogenesis, production of secondary metabolites) in the marine environment have been summarized and revised by Wagner-Döbler and Biebl (2006), and an excellent condensed overview on diversity, ecology, and genomics of the group was published by Brinkhoff et al. (2008). Recently, a comparative genomic approach (Chen 2012) revealed that many marine *Roseobacter* clade bacteria have the genetic potential to utilize methylated amines as alternative nitrogen sources since about half of the genomes available contained the key genes involved in this metabolism. Representative species bearing such potential were tested to confirm their abilities to use methylated amines. Moreover, trimethylamine monooxygenase (*tmm*) and gammaglutamylmethylamide synthetase (*gmaS*), two of the key enzymes, were chosen and successfully used as functional markers for detecting methylated amines-utilizing marine *Roseobacter* clade bacteria in the environment. These results suggest that methylated amines may serve as important nitrogen sources for *Roseobacter* clade bacteria in the marine environment and help to explain their numerical prevalence in the oceans.

The relative abundance of *Roseobacter* clade sequences among the alphaproteobacteria was quite different between two similarly hypersaline coastal lagoons as revealed through a metagenomic approach. At Mar Menor (Spain), they represented 30 % of all alphaproteobacterial reads, whereas at Punta Cormoran in Galapagos Islands (Ecuador), they were the most abundant representatives (Ghai et al. 2011, 2012). The study of coastal bacterioplankton community dynamics over an 8-month period, which encompassed a large storm event, revealed that during the natural perturbance, common bacterioplankton community members such as marine *Synechococcus* sp. and members of the SAR11 clade of *Alphaproteobacteria* decreased in relative abundance in the affected coastal zone, whereas several lineages of *Gammaproteobacteria*, *Betaproteobacteria*, and members of the *Roseobacter* clade increased (Yeo et al. 2013).

The nearly 70 genera that currently constitute the *Roseobacter* group have been defined (mainly) on a phylogenetic basis using 16S rRNA gene sequence analysis, and genomic relatedness based on DDH is commonly applied for species delimitation at high 16S rRNA sequence similarity (>97.0 %). A few descriptions also include an additional gene (*gyrB*) for inferring phylogeny but Multilocus Sequence Analysis (MLSA) as taxonomic tool is uncommon. Determination of alternative genomic parameters, as ANI values, is seen in the most recent species descriptions (Lucena et al. 2013). The accelerated pace of the new genera and species descriptions in the last few years is causing misclassifications, particularly affecting members of polyphyletic genera, as *Roseovarius* or *Oceanicola*.

Phylogenomics using protein signatures or other inference tools has been applied on data from complete genomes (Gupta and Mok 2007; Tang et al. 2010; Newton et al. 2010), with interesting results about the internal structure of the clade, but the limited number of representative taxa leave wide areas of shadow. These studies revealed five to six subclades within the group and are helpful to elucidate ecological strategies and evolutionary events.

Genome sequences and features of members of the *Roseobacter* group are reported and updated at the site Roseobase-Genomic Resource for Marine Roseobacters (http://www.roseobase.org/index.html).

Roseobacter

Roseobacter contains two species, *R. litoralis* and *R. denitrificans*. In spite of being the oldest named genus of the group, no other species has been added since the genus description (Shiba 1991). This description was based on the study of one strain, formerly identified as *Erythrobacter* sp., plus seven additional isolates from surface of seaweeds. In contrast with the orange pigmented

Table 20.7
Species in the *Roseobacter* group

Species (synonym)	Isolation/habitat	Metabolism[a]	Na^+ requirement, others	References
Roseobacter litoralis	Surface of marine algae, Japan	AAP	Yes	Shiba 1991
R. denitrificans	Surface of marine alga (*Enteromorpha*), Japan	AAP	Yes	Shiba 1991
Actibacterium mucosum	Seawater, Western Mediterranean Sea, Spain	COH	Yes	Lucena et al. 2012a
Antarctobacter heliothermus	Water, hypersaline Ekho Lake, Antarctica	COH	Yes	Labrenz et al. 1998
Celeribacter neptunius	Seawater, Australia	COH	Yes	Lee et al. 2012a; Ivanova et al. 2010
C. baekdonensis	Seawater, East Sea, S. Korea	COH	Yes	Lee et al. 2012a
Citreicella thiooxidans	O_2/H_2S interface Black Sea, Russia	COH/CLH ($S_2O_3^{2-}$ ox.)	Yes	Sorokin et al. 2005b
C. aestuarii	Tidal flat, S. Korea	COH/CLH	Yes	Park et al. 2011
C. marina	Deep sea sediment, Indian Ocean Ridge	CLH ($S_2O_3^{2-}$ ox.)	Yes	Lai et al. 2011a
Citreimonas salinaria	Solar saltern water, S. Korea	COH	Yes	Choi and Cho 2006a
Dinoroseobacter shibae	Cultured marine dinoflagellate (*Prorocentrum*), Germany	AAP	Yes	Biebl et al. 2005a
Donghicola eburneus	Seawater, East Sea, S. Korea	COH	Yes	Yoon et al. 2007a
D. xiamenensis	Seawater, Taiwan		Yes	Tan et al. 2009
Epibacterium ulvae	Marine algae (*Ulva*) surface, Australia	COH	Yes	Penesyan et al. 2013
Hasllibacter halocynthiae	Ascidian (*Halocynthia*), S. Korea	COH	Yes (+ Mg ion)	Kim et al. 2012a
Huaishuia halophila	Seawater during algal bloom, China	COH	Yes	Wang et al. 2012
Hwanghaeicola aestuarii	Tidal flat sediment, S. Korea	COH	Yes (+ Mg ion)	Kim et al. 2010b
Jannaschia helgolandensis	Seawater, North Sea, Germany	COH	Yes (complex)	Wagner-Döbler et al. 2003
J. aquimarina	Seawater, S. Korea	COH	Mg	Park and Yoon 2012a
J. donghaensis	Seawater, East Sea, S. Korea	COH	Yes	Yoon et al. 2007b
J. pohangensis	Seashore sand, S. Korea	COH	Yes (complex)	Kim et al. 2008a
J. rubra	Seawater, Mediterranean coast, Spain	COH	Yes (+ Mg ion)	Macián et al. 2005a
J. seohaensis	Tidal flat sediment, Yellow Sea, S. Korea	AAP	Yes	Yoon et al. 2010a
J. seosinensis	Hypersaline water, solar saltern, S. Korea	COH	Yes (complex)	Choi et al. 2006
Ketogulonicigenium vulgare	Soil samples, USA	COH fac an	No	Urbance et al. 2001
K. robustum	Cotton field soil, USA	COH fac an	No	Urbance et al. 2001
Leisingera methylohalidivorans	Tide pool seawater, California, USA	COH/fac M	Yes	Vandecandelaere et al. 2008a; Martens et al. 2006; Schaefer et al. 2002
L. aquimarina	Marine electroactive biofilm, Genoa Port, Italy	COH	Yes	Vandecandelaere et al. 2008a
L. nanhaiensis	Marine sandy sediment, South China Sea, China	COH	Yes	Sun et al. 2010
Lentibacter algarum	Seawater during algal bloom, China	COH a	Yes	Li et al. 2012
Litoreibacter albidus	Marine snail (*Umbonium*), sediment of Sea of Japan, Russia	COH a	Yes	Kim et al. 2012b; Romanenko et al. 2011a

Table 20.7 (continued)

Species (synonym)	Isolation/habitat	Metabolism[a]	Na^+ requirement, others	References
L. arenae (*Thalassobacter*)	Sea sand, S. Korea	COH a	Yes	Kim et al. 2012b; Kim et al. 2009
L. janthinus	Sediment, Sea of Japan, Russia	COH a	Yes	Romanenko et al. 2011a
L. meonggei	Ascidian (*Halocynthia*), South Sea, S. Korea	COH a	Yes (+ Mg ion)	Kim et al. 2012b
Litorimicrobium taeanense	Sandy beach, S. Korea	COH a	Yes	Jin et al. 2011
Loktanella salsilacus	Microbial mats in Antarctic lakes	COH	No	Tsubouchi et al. 2013; Lee 2012; Moon et al. 2010; Van Trappen et al. 2004
L. agnita	Seawater, Sea of Japan, Russia	COH	Yes	Ivanova et al. 2005
L. atrilutea	Seawater, Japan	COH	No	Hosoya and Yokota 2007a
L. cinnabarina	Deep sea floor sediment, Japan	COH	Yes	Tsubouchi et al. 2013
L. fryxellensis	Microbial mats in Antarctic lakes	COH	No	Van Trappen et al. 2004
L. hongkongensis	Marine biofilms, Hong Kong	COH	Yes	Lau et al. 2004
L. koreensis	Sea sand, S. Korea	COH	Yes	Weon et al. 2006
L. litorea	Seawater, South Sea, S. Korea	COH	Yes	Yoon et al. 2013a
L. maricola	Seawater, East Sea, S. Korea	AAP	Yes	Yoon et al. 2007c
L. pyoseonensis	Beach sand, S. Korea	COH	Yes	Moon et al. 2010
L. rosea	Marine sediment, Sea of Japan, Russia	COH	Yes	Ivanova et al. 2005
L. tamlensis	Seawater, S. Korea	COH	Yes	Lee 2012
L. vestfoldensis	Microbial mats in Antarctic lakes	COH	No	Van Trappen et al. 2004
Lutimaribacter saemankumensis	Tidal flat sediment, Yellow Sea, S. Korea	COH fac an	Yes	Yoon et al. 2009a
Mameliella alba	Seawater, South China Sea, China	COH	Yes	Zheng et al. 2010a
Maribius salinus	Hypersaline water, solar saltern, S. Korea	COH	Yes (+ Mg ion)	Choi et al. 2007
M. pelagius	Seawater, Sargasso Sea	COH	Yes (+ Mg ion)	Choi et al. 2007
Marinovum algicola (*Roseobacter*, *Ruegeria*)	Cultured dinoflagellate (*Prorocentrum*), Atlantic Ocean, Spain	COH a	Yes	Martens et al. 2006; Uchino et al. 1998; Lafay et al. 1995
Maritimibacter alkaliphilus	Seawater, Sargasso Sea	COH a	Yes, alkalitolerant	Lee et al. 2007a
Marivita cryptomonadis	Cryptomonas culture, S. Korea	AAP	Yes (complex)	Yoon et al. 2012; Hwang et al. 2009
M. byunsanensis (*Gaetbulicola*)	Tidal flat sediment, S. Korea	COH a	Yes	Yoon et al. 2012; Yoon et al. 2010b
M. geojedonensis	Coastal seawater, S. Korea	COH a	Yes	Yoon et al. 2013b
M. hallyeonensis	Seawater, S. Korea	COH a	Yes (+ Mg ion)	Yoon et al. 2012
M. litorea	Coastal seawater, S. Korea	AAP	Yes (complex)	Hwang et al. 2009
M. roseacus	Estuarine water, Chesapeake Bay, USA	AAP	Yes	Budinoff et al. 2011
Nautella italica	Marine electroactive biofilm, Italy	COH a	Yes	Vandecandelaere et al. 2009a
Nereida ignava	Seawater, Mediterranean Sea, Spain	COH a	Yes (complex)	Pujalte et al. 2005a
Oceanibulbus indolifex	Seawater, North Sea, Germany	COH a	Yes (complex)	Wagner-Döbler et al. 2004
Oceanicola granulosus	Seawater, BATS station, Sargasso Sea	COH a	Yes	Cho and Giovannoni 2004
O. batsensis	Seawater, BATS station, Sargasso Sea	COH a	Yes	Cho and Giovannoni 2004

Table 20.7 (continued)

Species (synonym)	Isolation/habitat	Metabolism[a]	Na^+ requirement, others	References
O. marinus	Coastal seawater, Taiwan	COH fac an	Yes	Lin et al. 2007
O. nanhaiensis	Marine sediment, South China Sea, China	COH a	No	Gu et al. 2007
O. nitratireducens	Surface seawater, South China Sea, China	COH a	Yes	Zheng et al. 2010b
O. pacificus	Pyrene-degrading consortium from marine sediment, Western Pacific Ocean	COH a	Yes	Yuan et al. 2009
O. litoreus	Seashore sediment, S. Korea	COH fac an	Yes (+ Mg ion)	Park et al. 2013a
Oceaniovalibus guishaninsula	Seawater, Taiwan	COH	Yes	Liu et al. 2012
Octadecabacter arcticus	Polar marine ice, Alaska, USA	COH a	Yes, psychrophilic	Gosink et al. 1997
O. antarcticus	Polar marine ice, Antarctica	COH a	Yes, psychrophilic	Gosink et al. 1997
Pacificibacter maritimus	Sandy marine sediment, Sea of Japan, Russia	COH a	Yes	Romanenko et al. 2011b
Palleronia marisminoris	Hypersaline soil near saltern, Spain	COH a	Yes (complex)	Martínez-Checa et al. 2005
Pelagibaca bermudensis	Seawater, BATS station, Sargasso Sea	COH fac an	Yes	Cho and Giovannoni 2006
Pelagicola litoralis	Coastal seawater, S. Korea	COH a	Yes	Kim et al. 2008b
Pelagimonas varians	Seawater during phytoplankton bloom, North Sea, Germany	COH a	Yes	Hahnke et al. 2013a
Phaeobacter gallaeciensis (*Roseobacter*)	Seawater of *Pecten* larvae culture, Atlantic Ocean, Spain	COH a	Yes	Yoon et al. 2007d; Martens et al. 2006; Ruiz-Ponte et al. 1998
P. arcticus	Marine sediment, Arctic Sea	COH a	Yes	Zhang et al. 2008
P. caeruleus	Marine electroactive biofilm, Genoa Port, Italy	COH a	Yes	Vandecandelaere et al. 2009b
P. daeponensis	Tidal flat, Yellow Sea, S. Korea	COH a	Yes	Vandecandelaere et al. 2008a; Yoon et al. 2007d
P. inhibens	Surface water, tidal flat, North Sea, Germany	COH a	Yes	Vandecandelaere et al. 2008a; Martens et al. 2006
Planktotalea frisia	Seawater during phytoplankton bloom, North Sea, Germany	COH a	Yes	Hahnke et al. 2012
Pontibaca methylaminovorans	Coastal sediment, enrichment with TMA, East Sea, S. Korea	COH fac an	Yes	Kim et al. 2010c
Ponticoccus litoralis	Coastal seawater, S. Korea	COH a	Yes (complex)	Hwang and Cho 2008
Poseidonocella pacifica	Shallow marine sediment, Sea of Japan, Russia	COH a	Yes	Romanenko et al. 2012
P. sedimentorum	Shallow marine sediment, Sea of Japan, Russia	COH a	Yes	Romanenko et al. 2012
Primorskyibacter sedentarius	Shallow marine sediment, Sea of Japan, Russia	COH a	Yes	Romanenko et al. 2011c
Profundibacterium mesophilum	Sea floor sediment, Discovery Deep, Red Sea	COH a	Yes	Lai et al. 2013
Pseudoruegeria aquimaris	Seawater, East Sea, S. Korea	COH a	Yes	Jung et al. 2010a; Yoon et al. 2007e
P. lutimaris	Tidal flat sediment, S. Korea	COH fac an	Yes (+ Mg ion)	Jung et al. 2010a

Table 20.7 (continued)

Species (synonym)	Isolation/habitat	Metabolism[a]	Na^+ requirement, others	References
Roseibacterium elongatum	Coastal sand, west coast of Australia	APP	Variable	Suzuki et al. 2006
R. beibuensis	Surface seawater, South China Sea, China.	AAP	No	Mao et al. 2012
Roseicyclus mahoneyensis	Saline meromictic lake, Canada	APP	Yes	Rathgeber et al. 2005
Roseisalinus antarcticus	Hipersaline, meromictic Ekho lake, Antarctica	APP	Yes (complex)	Labrenz et al. 2005
Roseivivax halodurans	Charophytes, saline lake, Australia	AAP	No	Chen et al. 2012a; Park et al. 2010; Suzuki et al. 1999b
R. halotolerans	Epiphytes on stromatolite, saline lake, Australia	AAP	Yes	Suzuki et al. 1999b
R. isoporae	Ree-building coral (*Isopora*), Taiwan	AAP	No	Chen et al. 2012a
R. lentus	Tidal flat, S. Korea	COH a	Yes	Park et al. 2010
R. sediminis	Sediment of crystallizer pond, salt mine, China	COH a	Yes	Xiao et al. 2012
Roseovarius tolerans	Hipersaline, meromictic Ekho lake, Antarctica	AAP	Yes	Labrenz et al. 1999
R. aestuarii	Tidal flat, Yellow Sea, S. Korea	COH a	Yes	Yoon et al. 2008
R. crassostreae	Juvenile oysters, NE coast USA	COH a	Yes	Boettcher et al. 2005
R. halocynthiae	Ascidian (*Halocynthia*), S. Korea	COH a	Only Mg ion	Kim et al. 2012c
R. halotolerans	Deep seawater, East Sea, S. Korea	COH a	Yes	Oh et al. 2009
R. indicus	Deep seawater, Indian Ocean	AAP	Yes	Lai et al. 2011b
R. litoreus	Seawater, S. Korea	COH a	Yes	Jung et al. 2012b
R. marinus	Seawater, Yellow Sea, S. Korea	COH a	Yes (+ Mg ion)	Jung et al. 2011
R. mucosus	Cultured dinoflagellate (*Alexandrium*), Germany	AAP	Yes	Biebl et al. 2005b
R. nanhaiticus	Sandy sediment, South China Sea	COH a	Yes	Wang et al. 2010
R. nubinhibens	Surface seawater, Caribbean Sea	COH a	Yes	González et al. 2003
R. pacificus	Deep sea sediment, W Pacific	COH a	Yes	Wang et al. 2009b
R. sediminilitoris	Seashore sediment, South Sea, S. Korea	COH a	Yes (+ Mg ion)	Park and Yoon 2013
Rubellimicrobium thermophilum	Slime on paper machines, Finland	COH a	No, thermophilic	Denner et al. 2006
R. aerolatum	Air sample, S. Korea	COH a	No	Weon et al. 2009
R. mesophilum	Soil, S Korea	COH a	No (sensitive to salinity)	Dastager et al. 2008
R. roseum	Forest soil, China	COH a	No (sensitive to salinity)	Cao et al. 2010
Ruegeria atlantica (*Agrobacterium*)	Marine sediment, NW Atlantic Sea	COH a	Yes	Uchino et al. 1998; Rüger and Höfle 1992
R. arenilitoris	Seashore sand, S. Korea	COH a	Yes	Park and Yoon 2012b
R. conchae	Ark clam (*Scapharca*), S. Korea	COH a	Yes	Lee et al. 2012b
R. faecimaris	Tidal flat, Yellow Sea, S. Korea	COH a	Yes	Oh et al. 2011a
R. halocynthiae	Ascidian (*Halocynthia*), S. Korea	COH a	Yes	Kim et al. 2012d
R. lacuscaerulensis (*Silicibacter*)	Geothermal lake, Iceland	COH a	Yes	Yi et al. 2007; Petursdottir and Kristjansson 1999

Table 20.7 (continued)

Species (synonym)	Isolation/habitat	Metabolism[a]	Na^+ requirement, others	References
R. marina	Marine sediment, East China Sea, China	COH a	No	Huo et al. 2011
R. mobilis (*R. pelagia*)	Biofilm, surface seawater, coelenterate (*Hexacorallia*), Sargasso Sea	COH a	No	Vandecandelaere et al. 2008b; Muramatsu et al. 2007
R. pomeroyi (*Silicibacter*)	Seawater, Georgia, USA	COH a	Yes	Yi et al. 2007; González et al. 2003
R. scottomollicae	Marine electroactive biofilm, Italy	COH a	Yes	Vandecandelaere et al. 2008b
Sagittula stellata	Seawater from salt marsh, Georgia, USA	COH a	Yes	Lee et al. 2013b; González et al. 1997
S. marina	Seawater, S. Korea	COH a	Yes	Lee et al. 2013b
Salinihabitans flavidus	Marine solar saltern, S. Korea	COH a	Yes	Yoon et al. 2009b
Salipiger mucosus	Hypersaline soil, Spain	COH a	Yes	Martínez-Cánovas et al. 2004
Sediminimonas qiaohouensis	Salt mine sediment, China	COH a	Yes	Wang et al. 2009c
Seohaeicola saemankumensis	Tidal flat, Yellow Sea, S. Korea	COH a	Yes	Yoon et al. 2009c
Shimia marina	Biofilm, coastal fish farm, S. Korea	COH a	Yes	Choi and Cho 2006b
S. isoporae	Coral (*Isopora*), Taiwan	COH a	Yes	Chen et al. 2011b
Sulfitobacter pontiacus	O_2/H_2S interface, Black Sea	COH/CLH ($S_2O_3^{2-}$, SO_3^- ox.)	Yes	Yoon et al. 2007f; Sorokin 1995
S. brevis	Hypersaline heliothermal Ekho lake, Antarctica	COH/CLH ($S_2O_3^{2-}$, SO_3^- ox.)	Yes	Labrenz et al. 2000
S. delicatus	Starfish (*Stellaster*), S. China Sea	COH/CLH ($S_2O_3^{2-}$, SO_3^- ox.)	Yes	Ivanova et al. 2004
S. donghicola	Seawater, East Sea, S. Korea	COH	Yes	Yoon et al. 2007f
S. dubius	Sea grass (*Zostera*), Sea of Japan	COH/CLH ($S_2O_3^{2-}$, SO_3^- ox.)	Yes	Ivanova et al. 2004
S. guttiformis (*Staleya*)	Hypersaline heliothermal Ekho lake, Antarctica	COH	Yes	Yoon et al. 2007f; Labrenz et al. 2000
S. litoralis	Seawater, East Sea, S. Korea	COH/CLH ($S_2O_3^{2-}$, SO_3^- ox.)	Yes	Park et al. 2007
S. marinus	Seawater, East Sea, S. Korea	COH	Yes	Yoon et al. 2007g
S. mediterraneus	Seawater, Mediterranean Sea, France	COH/CLH ($S_2O_3^{2-}$, SO_3^- ox.)	Yes	Pukall et al. 1999
Tateyamaria omphali	Molluscan (*Omphalius*), Japan	AAP, COH fac an, CLH ($S_2O_3^{2-}$, SO_3^- ox.)	Yes	Sass et al. 2010; Kurahashi and Yokota 2007
T. pelophila	Tidal flat sediment, North Sea, Germany	COH	Yes	Sass et al. 2010
Thalassobacter stenotrophicus (*Jannaschia cystaugens*)	Seawater, W Mediterranean Sea, Spain	AAP	Yes (complex)	Pujalte et al. 2005b; Macián et al. 2005b
Thalassobius mediterraneus	Seawater, Mediterranean Sea, Spain	COH a	Yes (complex)	Arahal et al. 2005
T. aestuarii	Tidal flat sediment, S. Korea	COH a	Yes	Yi and Chun 2006
T. gelatinovorus (*Ruegeria*)	Seawater, Baltic Sea, Germany	COH a	Yes	Arahal et al. 2005; Uchino et al. 1998
T. maritimus	Seawater, South Sea, S. Korea	COH a	Only Mg ion	Park et al. 2012

Table 20.7 (continued)

Species (synonym)	Isolation/habitat	Metabolism[a]	Na^+ requirement, others	References
Thalassococcus halodurans	Marina sponge (Halichondria), WA, USA	COH a	Yes	Lee et al. 2007b
T. lentus	Seawater, seaweed farm, S. Korea	COH a	Yes (+ Mg ion)	Park et al. 2013b
Tranquillimonas alkanivorans	Seawater, Semarang Port, Indonesia	COH a	Yes	Harwati et al. 2008
Tropicibacter naphthalenivorans	Seawater, Semarang Port, Indonesia	COH a	Yes	Harwati et al. 2009a
T. multivorans	Seawater, Mediterranean Sea, Spain	COH a	Yes (+ Mg or Ca ions)	Lucena et al. 2012b
T. phathalicicus	Seawater, Japan	COH a	Yes	Iwaki et al. 2012a
T. litoreus	Seawater, Mediterranean Sea, Spain	COH a	Yes	Lucena et al. 2013
T. mediterraneus	Seawater, Mediterranean Sea, Spain	COH a	Yes (+ Mg ion)	Lucena et al. 2013
Tropicimonas isoalkanivorans	Seawater, Semarang Port, Indonesia	COH a	Yes	Harwati et al. 2009b
T. aquimaris	Seawater, South Sea, S. Korea	COH a	Yes	Oh et al. 2012
T. sediminicola	Marine sediment of a cage-cultured ark clam farm, S. Korea	COH a	No	Shin et al. 2012
Vadicella arenosi	Sandy sediment, Sea of Japan, Russia	COH a	Yes	Romanenko et al. 2011d
Wenxinia marina	Sediment at oilfield, South China Sea, China	COH a	Yes	Ying et al. 2007
Yangia pacifica	Coastal sediment, East China Sea, China	COH a	Yes	Dai et al. 2006

[a]*AAP* aerobic anoxygenic photoheterotroph, *CLH* chemolithoheterotroph, *COH* chemoorganoheterotroph, *COH a* chemoorganoheterotroph aerobic, *COH fac an* chemoorganoheterotroph facultative anaerobic, *fac M* facultatively methylotroph

Erythrobacter, these strains were pink pigmented, contained a particular bacteriochlorophyll-protein complex and carotenoids not found in *Erythrobacter*, and showed unappreciable levels of DDH to the type strain of *E. longus* (3–5 %). The pink strains formed two genospecies, according to DDH values, one including seven isolates with 74–98 % intragroup relatedness and a second with only one strain, which showed 41–59 % DDH to the various strains in the former group. Thus, the new genus was described as containing two species, with the following general properties (Shiba 1991; Shiba and Imhoff 2005): cells are Gram negative, ovoid to rod shaped, motile by subpolar flagella, and divide by binary fission. They synthetize Bchl *a* (only in aerobic conditions) and spheroidenone as major carotenoid pigments. The major quinone is Q10 (menaquinones are absent), polar lipids include PG and DPG, and the dominant cellular fatty acid is C18:1 ω7c. DNA G+C content is 56–60 mol%. *Roseobacter* species are aerobic chemoheterotrophs that require biotin, thiamine, and nicotinic acid, as well as sodium ions, for growth. Preferred carbon sources are organic acids (acetate, pyruvate, succinate, malate, and citrate), some sugars (glucose) and amino acids (glutamate), but not methanol. They are proteolytic on gelatin, hydrolyze Tween 80, and are positive for both oxidase and catalase. Light inhibits respiration, decreasing O_2 consumption but not growth. The stronger suppression of respiration by light is observed when organic substrates are scarce (Shiba and Imhoff 2005). Bacteriochlorophyll synthesis is suppressed by anaerobiosis and by continuous light.

They are mesophilic (optimum 20–30 °C), neutrophilic (optimum pH 7–8), and slightly halophilic (optimum 2.5 %). The two named species differ, basically, in the denitrification activity, which gives name to *R. denitrificans* and confers to it the ability to thrive anaerobically, a lifestyle that is not possible for the type species *R. litoralis*. In addition to denitrification, *R. denitrificans* can also develop in anaerobiosis by using TMAO as electron acceptor.

A lytic siphovirus, designated RDJLΦ1, infecting *R. denitrificans* OCh 114^T has been characterized (Zhang and Jiao 2009), its genome fully sequenced (Huang et al. 2011), and the response to the infection of the host has been analyzed through real-time atomic force microscopy and proteomics (Zhang et al. 2012b).

The type strains of *R. litoralis* and *R. denitrificans* have their genomes fully sequenced (Swingley et al. 2007; Kalhoefer et al. 2011). A comparison indicates that major differences between them are due to lateral gene transfers and genome rearrangements. *R. litoralis* Och 149^T contains one chromosome (4.5 Mbp) and three plasmids (63.5–93.5 Kbp) with 4,537 protein-coding genes predicted. *R. denitrificans* OCh 114^T

genome is composed of one chromosome of 4.1 Mbp and four plasmids ranging from 5.8 to 106.5 Kbp, with a total of 4,129 predicted protein-coding genes. Genes shared by both type strains account for 3,415, a 75 % of *R. litoralis*' total genes. Photosynthetic genes are plasmid encoded in *R. litoralis*, but chromosomic in *R. denitrificans* (Kalhoefer et al. 2011; Pradella et al. 2004). The plasmid location of *pufML* genes also occurs in *Sulfitobacter* (*Staleya*) *guttiformis* (Pradella et al. 2004). Scaffolds or contigs of five additional *Roseobacter* sp. strains (AzwK-3b, CCS2, GAI101, MED193, and SK209-2-6) are also available at public repertories.

Roseobacter species form a compact grouping with members of the genus *Sulfitobacter* and *Oceanibulbus* in all assayed phylogenetic trees, and these three genera represent one of the few stable clades within this branch of the *Rhodobacteraceae*.

Actibacterium

Actibacterium is a recently described genus containing one species, *A. mucosum* (Lucena et al. 2012a), isolated from coastal seawater. *Actibacterium* is a strictly aerobic chemoorganotroph with complex ionic requirements. Cells do not accumulate PHB and contain PG, an unidentified aminolipid and a lipid as major polar lipids. Q10 is the predominant quinone and C18:1 ω7c the major fatty acid. It is oxidase and catalase positive and its DNA G+C content is around 61 mol%. *A. mucosum* is not pigmented and its cells are ovoid to rod shaped and nonmotile. It is mesophilic (15–37 °C) and halophilic (1.7–5 % total salinity) and requires a mixture of marine salts that include Na, K, Ca, Mg, and sulfate ions for optimal growth or the addition of seawater to the medium. It does not reduce nitrates and does not have growth factor requirements, as it is able to grow on defined medium with several carbohydrates, organic acids, and amino acids as sole carbon and energy sources. Its cellular fatty acids include, in addition to the dominant C18:1 ω7c, C16:0, C10:0 3-OH, and C12:0 3OH. *Actibacterium* was found to constitute an independent lineage, with no close relatives, in 16S rRNA gene-based trees and also in *gyrB* gene trees (Lucena et al. 2012a). In the complete tree of ❯ *Fig. 20.5*, *Actibacterium mucosum* relates distantly (but stably) to the newly described *Hasllibacter halocynthiae*, both lying near the edge of the *Roseobacter* group.

Antarctobacter

Antarctobacter and its sole species *A. heliothermum* described in the 1990s were one of the first members of the *Roseobacter* clade (Labrenz et al. 1998) from water samples of the hypersaline Antarctic Ehko Lake. It is a Gram-negative, budding bacterium that forms rosettes and accumulates PHB. Cells may be motile (one to three polar flagella). Colonies are brownish yellow or brownish red, depending upon the medium, and have a wide range of growth temperatures (from less than 3 °C to 43 °C) and pHs (5.3 to 9). NaCl is required for growth (optimum 2–6 %). Not phototrophic, Bchl *a* is not synthetized. Oxidase and catalase are positive. Peptidoglycan contains *m*-diaminopimelic acid and is direct cross-linked (A1γ). It contains Q10 as respiratory quinone; its main polar lipids are PG, PC, and unknown phospho- and aminolipids. C18:1 ω7c is the dominant fatty acid and C12:1 3OH is a diagnostic one. The DNA G+C content is 63 mol%. The species, *A. heliothermus*, has the following additional characteristics: requires thiamin and nicotinic acid; reduces nitrate, at least to nitrite; hydrolyzes gelatin and DNA; and grows with small organic acids (acetate, pyruvate, butyrate, malate, and succinate) and with glucose or glutamate.

Celeribacter

Celeribacter was described by Ivanova et al. (2010) as a new genus containing the species *C. neptunius*. Lee et al. (2012a) described a second species *C. baekdonensis* and emended the genus description. Currently, *Celeribacter* contains ovoid- to rod-shaped Gram-negative cells that may be motile by a single polar or subpolar flagellum or nonmotile. Q10 is the predominant quinone; C18:1 ω7c is the major fatty acid, accompanied by 11-methyl C18:1 ω7c, C18:0, C16:0, and C10:0 3OH. The polar lipid profile was somewhat under dispute, but Lee et al. (2012a) determined for both species that common polar lipids were PG, one unidentified aminolipid and one lipid. The G+C content was 59–61 mol%. *Celeribacter* species are chemoorganotrophic, do not produce Bchl *a* nor other pigments, do not accumulate PHB, and are able to grow anaerobically on Marine Agar. Although *C. neptunius* was described as oxidase negative, Lee et al. (2012a) found a positive response for this test in both species that differ in Na ion requirement and in the ability for nitrate reduction, proteolytic activity, and production of acid from a large number of carbohydrates. They show low levels of DDH (17 %). Both species are mesophilic (5–35 °C, optimum 25–30 °C), neutrophilic (with optimum at pH 7–8), and slightly halophilic, with *C. baekdonensis* having a range from 0 % to 13 % NaCl (optimum: 2 %) and requiring Mg ion and *C. neptunius* growing between 1 % and 8 % and requiring Na ion. *Celeribacter* species are phylogenetically close to *Huaishuia halophila*, *Vadicella arenosi*, and both species of *Pseudoruegeria* in the *Roseobacter* detailed tree (❯ *Fig. 20.5*). The draft genome of *C. baekdonensis* B30 has 4.33 Mb.

Four strains (YSCB1, YSCB2, YSCB3, and YSCB4) were found to produce unique intracellular chromium-rich aggregates. This remarkable capacity makes them model bacteria for studies of chromium metabolism and its biological function and suitable candidates for chromium decontamination and environmental remediation (Gao et al. 2006). These strains exhibit yet another interesting feature, since they produce spinae that are built from proteolysis-resistant filaments winding into a tubular architecture by a mechanism different from those of other bacterial appendages. An excellent study, including many striking micrographs, was published recently (Bernadac et al. 2012). Although reported as *Roseobacter* sp., they can be now

identified as members of the genus *Celeribacter*, probably *C. baekdonensis*, according to 16S rRNA data.

One of the few known roseophages is a *Celeribacter* phage, P12053L. Its complete genome has been sequenced recently (Kang et al. 2012).

Citreicella

The study of strains isolated from the oxygen-sulfide interface of the Black Sea served Sorokin and colleagues to describe a new genus of lithoheterotrophic sulfur-oxidizing bacteria *Citreicella* that presently contains three species: *C. thiooxidans* (Sorokin et al. 2005b), *C. marina* (Lai et al. 2011a), and *C. aestuarii* (Park et al. 2011). The genus is defined as Gram-negative, nonmotile (or sometimes motile by lateral flagella, as in *C. aestuarii*) cells with lemon-shaped morphology, obligately heterotrophic, and aerobic. Carbon sources used for chemoheterotrophic growth are short-chain organic acids, hexoses, and amino acids. Catalase and oxidase are positive. Citreicellas do not synthetize Bchl *a* or other pigments; they form PHB granules and oxidize, at least, thiosulfate to sulfate (*C. thiooxidans* also oxidizes sulfide and sulfur), gaining energy from this activity during its heterotrophic growth. Its predominant quinone is Q10, C18:1 ω7c is the major fatty acid (with C16:0 and C19:0 cyclo ω8c also abundant), and the DNA G+C content is between 67 and 69 mol%. They prefer neutrophilic and mesophilic conditions (25–30 °C is the optimal range) but could grow from 4 °C (*C. marina*) to 40 °C (*C. thiooxidans*). They require sodium ion (at least 0.5–1 % NaCl) and grow optimally with 2–7 % NaCl, with a maximum of up to 12 % in *C. marina*, the more halotolerant and 6 % in *C. thiooxidans*, the less halotolerant. *C. marina* and *C. thiooxidans*, the closest species, are related by DDH values of 48 % (Lai et al. 2011a). Recently, a draft genome sequence of a strain (not the type strain) of *C. aestuarii* isolated from a petroleum contaminated beach has been reported (Suarez-Suarez et al. 2012): it contains, among the genes for major metabolic pathways, sox genes (sulfite oxidation) and cox genes (carbon monoxide oxidation), and some 120 protein-coding genes were found that may be involved in the metabolism of aromatic compounds.

All three species of *Citreicella* form a well-defined clade whose nearest neighbors are *Yangia pacifica* and *Citreimonas salinaria*.

Citreimonas

Citreimonas and its sole currently recognized species *C. salinaria* were isolated and described from samples of solar saltern water (Choi and Cho 2006a). Although it is next to *Citreicella* spp. in the 16S rRNA-based tree, they do not show the thiosulfate-oxidizing ability that characterizes *Citreicella* species. *Citreimonas salinaria* is, as *Citreicella*, obligately heterotrophic, aerobic, positive for catalase (but it is negative for oxidase), and unable to synthetize Bchl *a* or carotenoids. Cells are ovoid to rod shaped and nonmotile. They do not accumulate PHB. The two major fatty acids are C18:1 ω7c and C19:0 cyclo ω8c and the DNA G+C content is in the same range than *Citreicella* (67.3 % mol%). The ranges for temperature and salinity are also similar (15–40 °C and 1–10 % total salts, with optima at 30–35 °C and 5–6 %, respectively). It grows with a large variety of sugars and some organic acids and amino acids as carbon and energy sources in a basal medium supplemented with low levels of yeast extract. It reduces nitrate and is proteolytic on gelatin.

Dinoroseobacter

The genus *Dinoroseobacter* (Biebl et al. 2005a) contains a single species, *D. shibae*, isolated from the marine dinoflagellate *Prorocentrum lima*. Members of the genus are Gram-negative cocci or ovoid rods, motile by a single polar to subpolar flagellum. Pigmentation of cultures is pink to wine red, provided that the incubation is performed in the dark or with intermittent illumination. They are strict aerobes, non-fermentative heterotrophs, which synthetize Bchl *a* and carotenoids (spheroidene). They require at least 1 % sea salts for growth and have Q10 as predominant quinone. The species *D. shibae* requires biotin, nicotinic acid, and 4-aminobenzoic acid for growth and uses acetate, succinate, fumarate, malate, lactate, citrate, pyruvate, and some simple carbohydrates (glucose, fructose, glycerol) and glutamate as carbon and energy sources (but no butyrate, ethanol, or methanol). Nitrate is reduced to N_2 and gelatin and Tween 80 are degraded. Cells of *D. shibae* contain PG, DPG, one unidentified aminolipid, and other lipids as principal polar lipids. As usual in the family, C18:1 ω7c is the dominant fatty acid, with minor amounts of C18:0, C12:1 ω5c, C10:0 3OH, C14:1 3OH, and C19:0 cyclo ω8c. DNA G+C content is 65 mol%. *Dinoroseobacter* is consistently located next to *Roseibacterium* species in the *Roseobacter* phylogenetic tree, either using NJ (*Fig. 20.5*) or ML (LTP108) methods.

D. shibae is an algal symbiont that lives attached to the surface of different algal partners (*Prorocentrum*, *Alexandrium*, *Isochrysis*), some of them toxic and responsible of diarrheic shellfish poisoning (Wagner-Döbler et al. 2010). A symbiotic relationship in which the bacterium provides the algae with growth-limiting vitamins (B12) and the bacterium thrives on the organic matter synthetized by the alga has been suggested, based in physiological and field data and also in the information provided by the study of the complete genome of *D. shibae* type strain (Wagner-Döbler et al. 2010). Moreover, research in metabolic pathways of *D. shibae* has served as a model for the understanding of the whole *Roseobacter* group in terms of the general pattern of carbon fluxes (Fürch et al. 2009). *D. shibae* DFL12^T has a genome composed of one chromosome and five plasmids (total 4.4 Mbp), containing around 4,200 protein-encoding genes. In common with known *Roseobacter* spp. genomes, it harbors information for important biogeochemical metabolic abilities, such as anoxygenic photosynthesis

(*pufLM* genes), oxidation of CO (*cox* genes), degradation of aromatic compounds (*pcaGH* and *boxC* genes), sulfur oxidation (*soxB*), dimethylsulfoniopropionate use (*dmdA*), denitrification (*nirS*/*K*), and also several families of transposases/integrases and site-specific recombinases/resolvases, which indicates a large potential for DNA exchange. Through functional analysis, Fürch et al. (2009) demonstrated that *D. shibae* metabolizes glucose exclusively through the Entner-Doudoroff pathway, has an active cyclic respiratory TCA cycle, and incorporates CO_2 through a mechanism that does not involve PEP synthesis from pyruvate, as previously thought. Tomasch et al. (2011) suggest that *D. shibae* might use the 3-hydroxypropionate cycle for CO_2 fixation, in addition to showing the changes in photoheterotrophic behavior in response to light regime and organic carbon availability.

Donghicola

Donghicola is an inconspicuous genus of chemoheterotrophic, aerobic, nonpigmented, nonmotile bacteria which was described on an isolate from seawater (Yoon et al. 2007a). Cells are coccoid to rod shaped and do not synthetize Bchl *a* or carotenoids. Basic chemotaxonomic features (quinone system, major fatty acids) are the common in the group and the DNA G+C content is 59–62 mol%. Two species have been recognized, *D. eburneus* (Yoon et al. 2007a), the type species, and *D. xiamenensis* (Tan et al. 2009), that differ mainly in the pattern of carbon source utilization. Both species are catalase and oxidase positive, slightly halophilic, requiring NaCl for growth (optimum 1–3 %, tolerance up to 11 %), mesophilic, and neutrophilic. Their closest phylogenetic relatives are a group of four *Roseovarius* species that do not include the type species of *Roseovarius*, but the relationship is not maintained in other methodological conditions. The draft genomes of *D. xiamenensis* DSM 18339^T and *Donghicola* sp. S598 have 4.73 and 3.22 Mb, respectively.

Epibacterium

Epibacterium ulvae, the type and sole species of *Epibacterium* (Penesyan et al. 2013), is rod shaped and motile by a polar flagellum. Generic features include, in addition to cell morphology, presence of catalase and oxidase activities and requirement of aerobic conditions and sodium for growth. Polar lipids are PG and PC plus two unidentified aminolipids and four unidentified phospholipids. Cellular fatty acids include C18:1 ω7c, C16:0, C18:2, C10:0 3OH, C12:0, C20:1 2OH, C16:0 2OH, C12:0 3OH (amide linked), and C18:0. Q10 is the sole respiratory quinone. The type strain of *E. ulvae* has a DNA G+C content of 52.6 mol %. Strains of this species, isolated from the surface of the marine alga *Ulva australis*, are brown-black pigmented but do not produce Bchl *a* or possess *pufLM* genes. Its optimal growth conditions are 25 °C, neutral pH, and 2–3 % NaCl. Growth is produced on a variety of carbon sources that include hexoses, disaccharides, and organic acids. *E. ulvae* strains are able to inhibit the growth of other marine bacteria through production of antibacterial compounds of unknown chemical nature. The species is related to the *Thalasobium-Thalassococcus* subclade within the *Roseobacter* group.

Hasllibacter

Hasllibacter is another recently described genus, interesting because of its ability to produce cholic acid derivatives (Kim et al. 2012a, e), including nutriacholic acid. Strains of the only described species *H. halocynthiae* are Gram negative, ovoid, or rod shaped, with a single polar flagellum, that may reproduce by budding. They have Q10 as predominant quinone and C18:1 ω7c as major fatty acid (plus C18:0, C10:0 3OH, C19:0 cyclo ω8c, and C20:1 ω7c). They are strict aerobes and have an absolute requirement for Na and Mg ions (optimal growth: 1–5 % NaCl). Their colonies are light-red pigmented (but no data on Bchl *a* or carotenoid synthesis is given in the description). The G+C content is 71.6 mol%. On 16S rRNA trees, it forms a deep lineage distantly related to *Actibacterium mucosum*.

Huaishuia

Huaishuia contains a single species, *H. halophila*, isolated from seawater during a massive green algal bloom (dominated by *Enteromorpha prolifera*) (Wang et al. 2012). It is Gram negative, nonmotile, strictly aerobic, and slightly halophilic. PHB accumulation is not observed. Catalase and oxidase are positive. Nitrate is not reduced. Major fatty acids are C18:1 ω7c, C18:1 ω6c, and 11-methyl C18:1 ω7c. It presents PG, one unidentified aminolipid, and two unidentified phospholipids as major polar lipids and a DNA G+C content of 60 mol%. Requires sodium ion and grows between 0.5 % and 11 % NaCl and between 4 °C and 45 °C. *H. halophila* appears among the members of the *Celeribacter* subclade (which groups the two *Celeribacter* species, plus *Vadicella arenosi* and *Huaishuia halophila*, and is close to *Pseudoruegeria* spp.).

Hwanghaeicola

Kim et al. (2010b) described *Hwanghaeicola aestuarii* as a new genus and species from an isolate obtained from a tidal flat. It is entirely typical in its chemotaxonomic and biochemical features: contains Q10 (major quinone), C18:1 ω7c, plus C16:0 and C10:0 3OH (major fatty acid), is a strict aerobe with oxidase and catalase activities, not able to reduce nitrate and with a DNA G+C content of 61 mol%. The strain requires Na and Mg ions for growth, which is optimal at 2–3 % NaCl (range: 1.5–6 %) and 25–30 °C (range: 15–35 °C) and neutral pH (6.0–8.0). Colonies of *H. aestuarii* are pale pink, but no information on Bchl *a* synthesis is given in the description. It shows a distant relationship with *Maribius* species.

Jannaschia

Jannaschia is a well-defined, coherent genus that currently contains seven species isolated from seawater of distant geographic areas, seashore sand, tidal flat sediment, and solar saltern water. The type species *J. helgolandensis* (Wagner-Döbler et al. 2003) and the remaining six species *J. rubra*, *J. seosinensis*, *J. donghaensis*, *J. pohangensis*, *J. seohaensis*, and *J. aquimarina* constitute a stable clade in all analyses performed on 16S rRNA gene sequences so far, an unusual case among the multispecies genera of the *Roseobacter* group. The genus, as originally defined (Wagner-Döbler et al. 2003), contains Gram-negative, irregular rods, with a tendency to form chains, that grow optimally at 30 °C, at pH of 7.0–8.0, and have an absolute requirement of sea salts, not fulfilled by the sole addition of NaCl to the medium (salinity range: 1–7 % sea salts). They are heterotrophic, strict aerobes, non-fermentative, not able to reduce nitrates, and give a weak response to the oxidase test. Main fatty acids are C18:1 ω7c, C18:0, C19:0 cyclo, C17:0, C10:0 3OH, C14:0, C14:0 3OH/C14:1 3OH, and C12:1. They contain Q10 as predominant respiratory quinone and PG, DPG, PC, PE and one aminolipid as major polar lipids. DNA G+C content of the type species is 63 mol%. The remaining six species generally fulfill this description with only a few exceptions: nitrate reduction to nitrite is performed by some species; the salinity range may be slightly wider, 11-methyl C18:1 ω7c is a major part of the fatty acid profile of most species. The polar lipid profile does not include DPG or AL in some species (*J. donghaensis*, *J. seosinensis*). In addition, the G+C of the genus expands up to 68 mol%. Most species are pigmented in various shades of orange, yellow, or red but only one of them has been confirmed as synthetizing Bchl *a* (*J. seohaensis*). Reports on oxidase activity are sometimes contradictory: *J. seosinensis* is described as negative (Choi et al. 2006) but reported as positive in a later study (Yoon et al. 2010a). Motility is variable among species, but when present it is due to flagella (usually several) located polarly. Levels of DDH between different species are low: *J. pohagensis* shows 21 % against *J. helgolandensis*, a 38 % against *J. rubra*, and 24 % against *J. seosinensis* (Kim et al. 2008a), *J. rubra* is related to *J. helgolandensis* by a value of 42 % DDH (Macián et al. 2005a), and *J. seosinensis* and *J. seohaensis* show only 17 % relatedness (Yoon et al. 2010a). The genus is phylogenetically close to *Thalassobacter stenotrophicus*, which currently contains the former *Jannaschia cystaugens* (Adachi et al. 2004). *J. cystaugens* was found to be a heterotypic synonym of *T. stenotrophicus* (Pujalte et al. 2005b).

Despite the fact that only one of the seven species of *Jannaschia* is able to produce Bchl *a*, *Jannaschia*-related clones are a substantial part of the AAP bacteria in some extensively studied environments, as the Central Baltic Sea (Salka et al. 2008), where they account for 25–30 % of the total AAP clones obtained and occur in all locations investigated. *Jannaschia* sp. and *Sulfitobacter brevis* are two of the prominent members of experimental microcosms that show an increase after exposition to crude oil contamination (Jung et al. 2010b).

The first complete *Jannaschia* genome obtained corresponds to strain CCS1, a *Jannaschia* sp. isolated from Pacific coastal seawater and Bchl *a* producer: it consist of one chromosome (4.3 Mbp) and one plasmid (86 Kbp). Among others, it contains information for phototrophy, CO oxidation, aromatic compound degradation, nitrate assimilation, and DMSP demethylation. *Jannaschia* sp. CCS1 possesses six distinct ring-cleaving pathways, all of them chromosomally encoded (Moran et al. 2007). An enzyme produced by this strain, a D-hydantoinase is of interest, due to the application of these enzymes to the industrial production of pure amino acids (Cai et al. 2009).

Ketogulonicigenium

The genus *Ketogulonicigenium* is atypical within the *Roseobacter* group because its natural habitat is not the marine environment but continental and soil related. The two species included in the genus were obtained after a search for strains able to efficiently convert L-sorbose to 2 keto L-gulonic acid (2-KLG) from soils of different locations in the USA. This conversion is of great interest for the industrial production of L-ascorbic acid (vitamin C), and in fact strains of the type species *K. vulgare* are used for this purpose in coculture with *Bacillus megaterium* (Zhang et al. 2011a).

The genus is defined as containing Gram-negative, facultatively anaerobic cells, ovoid to rod shaped, that may form flagella and fimbriae. They produce a tan pigmentation that is diffusible in agar cultures of 48 h or more. Catalase and oxidase are positive. Best growth is observed at 27–31 °C, pH 7.2–8.5, and 117–459 mM Na^+, although this ion is not required for growth. They are chemoheterotrophs which use a wide range of carbohydrates for growth (inositol, mannitol, glycerol, sorbitol, lactose, and arabinose are preferred). All strains produce 2-KLG from L-sorbose. Major cellular fatty acids are C18:1 ω7c and C16:0. DNA G+C content is 52–54 mol%, according to the genus description, but complete genome sequencing of various strains gives somewhat higher figures (≈61–62 mol%). Both species, *K. vulgare* and *K. robustum*, could be distinguished by motility, intensity of pigmentation, and DDH values of 37–40 % (reciprocal values are much lower, 11–18 %). The type strains *K. vulgare* DSM 4025^T and *K. robustum* X6L^T are patented strains (Urbance et al. 2001); thus, according to Rules 27(3) and 30 of the Bacteriological Code, these names are not validly published (see notes for the genus at Euzéby's site, now http://www.bacterio.net/).

Complete genome sequences of two industrial *K. vulgare* strains (Y25 and WSH-001) reveal that they are composed of a circular chromosome and two plasmids (sizes: ≈2.77 Mbp, 267–268 Kbp, and 242–243 Kbp for the plasmids). Genes encoding sorbose dehydrogenase are chromosomic and are in multiple (four) copies, hence the highly efficient conversion of sorbose exhibited by these strains (Xiong et al. 2011; Liu et al. 2011).

Leisingera

Leisingera is a genus described in 2002 by Schaefer and col., which currently contains three species: *L. methylohalidivorans*, *L. aquimarina* (Vandecandelaere et al. 2008a), and *L. nanhaiensis* (Sun et al. 2010). The most outstanding activity of *Leisingera* species is their ability to oxidize methyl halides (methyl chloride, methyl bromide) with the concomitant liberation of halide atoms into the atmosphere (where they contribute to ozone destruction). At the time of the description of *L. methylohalidivorans*, the type species of the genus, the knowledge of marine methyl halide-oxidizing strains was scarce. Strain MB2^T was obtained from enrichment cultures inoculated with tide pool seawater after more than 3 years of maintenance with MeBr as sole carbon and energy source. The strain grows as regular straight rods with methyl halides, methionine, or DMS on mineral medium but forms elongated rods and filaments when grown on yeast extract or glycine betaine. It is Gram negative, motile, and not pigmented. Additional genus features are as follows: obligate aerobic, moderately halophilic, and growing by oxidation of methyl halides or selected methylated substrates, such as methionine. The DNA G+C content of the type strain is 60 mol%. The emendation to the genus description by Martens et al. (2006) added the following information: Q10 is the predominant quinone; PG, PE, one phospholipid, one aminolipid, and two other lipids are produced; but PC is absent in the polar lipid profile; major fatty acids are C18:1 ω7c, C16:0 2OH, C16:0, 11-methyl C18:1 ω7c, C18:1 ω9c, C14:1, C10:0 3OH, and C12:0 3OH (amide linked). In addition, the type species is defined as having temperature and pH optima of 27 °C and 7.7, respectively, and requiring Na^+ for growth that occurs only with more than 1 % NaCl. It is catalase and oxidase positive, not able to respire with nitrate as alternative electron acceptor, and shows a narrow number of carbon sources, which include methyl halides, DMS, methionine, and glycine betaine as methylotrophic substrates, and excludes carbohydrates, amino acids (other than methionine), and small organic acids. Growth is possible on yeast extract and Casamino acids-based media and in Marine Broth.

L. aquimarina is closely related to the type species, to which it shows a 56 % value of DDH. In contrast to *L. methylohalidivorans*, it is unable to grow on methionine and it is pigmented (dark beige pink).

A third species was described recently, *L. nanhaiensis* (Sun et al. 2010), which uses both methionine and betaine and shows a profile of polar lipids, fatty acids, and DNA G+C content compatible with the genus description. However, it is not unambiguously linked to the other two species and shows a closer relationship with *Litorimicrobium taeanense*, another recently described member of the *Phaeobacter* subclade.

Leisingera-like isolates have been obtained as a part of the culturable microbiota of Chinese sea anemones (Du et al. 2010).

Lentibacter

The genus *Lentibacter* was recently described (Li et al. 2012) as containing the species *L. algarum*. The strains were isolated from a seawater sample obtained during a massive algal bloom dominated by *Enteromorpha prolifera* in China. The genus is defined as Gram negative, aerobic, not flagellated, and lacking Bchl *a*. Additional features included in the genus description are a narrow range of growth temperatures (22–28 °C) and slow growth; a salinity range of 3–9 %; oxidase, catalase, and PHB production; and ability to reduce nitrate to nitrite. Major fatty acids are C18:1 ω7c, C18:0, and C16:0. Major polar lipids are PG, PE, PC, one amino lipid, and one lipid. Q10 is the predominant respiratory quinone. The DNA G+C content is between 54 and 57 mol%. The species is notable for its wide pH range (from 2.0 to 9.0) enabling growth—the lowest pH registered in the whole *Roseobacter* group.

In addition to its original isolation, *Lentibacter* sp. has been simultaneously isolated and detected as a dominant band in DGGE from seawater samples obtained during algal blooms in the North Sea (Hahnke et al. 2013b).

Lentibacter algae forms a moderately deep lineage in the *Roseobacter* group, with *Nereida ignava* as relative.

Litoreibacter

Litoreibacter (Kim et al. 2012b; Romanenko et al. 2011a) contains four species: *L. albidus*, *L. janthinus*, *L. meonggei*, and *L. arenae* (formerly, *Thalassobacter arenae*). They have been isolated from marine invertebrates and sediments and they are defined by the following traits: Gram negative, strictly aerobic, oxidase and catalase positive, and rod-shaped bacteria which divide by budding. Chemoorganoheterotrophic. Sodium ion is essential for growth. The predominant isoprenoid quinone is Q10. Common polar lipids are PC, PG, PE, an unidentified lipid, and an aminolipid. The predominant fatty acid is C18:1 ω7c. The G+C content is 56–60.4 mol%. In addition to these characters, species of the genus lack Bchl *a*, do not reduce nitrate to nitrite, and are psychrotolerant (temperature minimum is 4–5 °C, optimum being 25–30 °C). Some species produce PHB granules (*L. meonggei* and *L. arenae*) and most are pigmented (*L. janthinus*, grayish violet; *L. arenae*, brown; and *L. meonggei*, yellow) and nonmotile (exception is *L. arenae*, which forms polar flagella).

DDH levels between *Litoreibacter* species are low: Romanenko et al. (2011a) reported levels of 15 % between type strains of *L. albidus* and *L. janthinus*. Kim et al. (2012b) found values of 12 %, 14 %, and 9 % when testing *L. meonggei* type strain against *L. albidus*, *L. janthinus*, and *L. arenae* type strains, respectively. The four species form a well-defined clade, with *Pacificibacter marinus* and *Roseovarius marinus* (that might be considered a misclassified species) as nearest neighbors. The draft genome of *L. arenae* DSM 19593^T has 3.69 Mb.

Litorimicrobium

The genus *Litorimicrobium* (Jin et al. 2011) currently contains the single species *L. taeanense*. It contains Gram-negative, nonmotile, ovoid rods, which are oxidase and catalase positive and reduce nitrates to nitrites. They present Q10 as predominant quinone and C18:1 ω7c as major fatty acid, followed by its 11-methyl derivative, C12:1 3OH, C16:0 2OH, and C16:0. Its most abundant polar lipids are PG, DPG, PC, an unidentified aminolipid, a phospholipid, and a lipid. DNA G+C content is 62.4 mol%.

The closest relative to *L. taeanense* in the 16S rRNA gene trees is *Leisingera nanhaiensis*, followed by several *Phaeobacter* species and *Seohaeicola saemankumensis*.

Loktanella

Loktanella is the most populated genus in the *Roseobacter* group, with a total of 13 species described so far (*Roseovarius* equals this figure but the taxonomic status of some of its species deserves a reevaluation). The genus was proposed by Van Trappen et al. (2004) after studying isolates from microbial mats of Antarctic lakes (Fryxell Lake, Ace Lake, Organic Lake, Pendant Lake) and has been further enlarged to encompass species isolated from diverse marine samples (seawater, sediments, and beach sand) around the world. Emended descriptions of the genus accompanied the descriptions of *L. pyoseonensis* (Moon et al. 2010), *L. tamlensis* (Lee 2012), and *L. cinnabarina* (Tsubouchi et al. 2013). The following are currently considered the basic properties of the genus: cells are Gram negative, rod shaped, nonspore-forming, strictly aerobic, chemoorganotrophic, and moderately halotolerant. Oxidase and catalase are positive. Motility is variable among species. Colony color is also variable (white, pink, beige, light orange). Optimal temperature is around 25 °C. The most abundant fatty acid is C18:1 ω7c, Q10 is the predominant quinone, and major polar lipids are DPG, PC, and PG. DNA G+C content is 55–69 mol%.

The genomes of two strains of *L. vestfoldensis* (DSM 16212^T and SKA53) have been sequenced: the draft genomes are 3.7 and 3.1 Mbp in size and have 61.8 and 60.0 mol% G+C content, respectively. *L. cinnabarina* LL-001^T and *L. hongkongensis* DSM 17492^T have similar genome sizes (3.9 Mb and 3.2 Mb, respectively) but higher G+C content (66.7 and 68.4 mol%, respectively).

Data from DDH experiments give the following figures for the species that have been submitted to this determination: *L. vestfoldensis*, *L. fryxellensis*, and *L. salsilacus* type strains are interrelated by values from 10 % to 18 % (Van Trappen et al. 2004); *L. vestfoldensis* and *L. agnita* show a 35 % relatedness (Ivanova et al. 2005); Hosoya and Yokota (2007a) reported a 28–36 % relatedness between *L. atrilutea* and *L. salsilacus* and an 11–31 between *L. atrilutea* and *L. fryxellensis*; *L. tamlensis* (Lee 2012) is related to *L. rosea* by 11–15 % values and by just 8 % to *L. maricola* (Yoon et al. 2007c); finally, *L. cinnabarina* and *L. hongkongensis* show 41–44 % DDH values (Tsubouchi et al. 2013).

The thirteen *Loktanella* species recognized so far differ in several traits, in addition to motility (three species are motile, *L. atrilutea*, *L. pyoseonensis*, and *L. tamlensis*) and pigmentation: one of them is the requirement of Na^+ for growth, which occurs in all but four species (*L. salsilacus*, *L. fryxellensis*, *L. vestfoldensis*, and *L. atrilutea*), nitrate reduction (positive only for *L. agnita*, *L. koreensis*, and *L. pyoseonensis*), psychrotolerant character (all but *L. litorea* and *L. cinnabarina* are able to grow at 4–8 °C), use of carbohydrates (present only in *L. hongkongensis*, *L. maricola*, *L. atrilutea*, *L. pyoseonensis*, and *L. litorea*), and Bchl *a* synthesis, found in *L. maricola* (although *L. vestfoldensis* also contains photosynthetic genes).

All *Loktanella* species are included in a single clade (*Fig. 20.5*) except for three: *L. hongkongensis*, *L. pyoseonensis*, and *L. cinnabarina* (all with DNA G+C content in the upper limit of the genus) that merge with the genus *Ketogulonicigenium*.

In addition to the isolation sites of the type strains, Loktanellas have been isolated and/or detected among the microbiota of hypersaline, cold environments (Jiang et al. 2010; Niederberger et al. 2010) and have been found associated to some members of marine fauna: tentacles of cnidarians (Doepke et al. 2012) and sea anemones (Du et al. 2010). *Loktanella* AAP clones have also been found in high proportions as a part of the AAP bacteria in localized basis of Central Baltic Sea (Salka et al. 2008). They are also a major part of clone libraries obtained at the surface of tropical South Pacific Ocean, along with SAR86 and unclassified Flavobacteria (Stevens and Ulloa 2008), components of biofilms formed in marine coastal water, after the first 24–36 h colonization (Lee et al. 2008), and members of summer community of ephemeral desert playa lakes (Costa et al. 2008).

L. rosea has raised interest for its highly unusual LPS composition, which includes an atypical lipid A composed of a trisaccharide backbone lacking the phosphate groups (two β-glucosamines plus an α-galacturonic acid) and a core region with unusual composition (Ieranò et al. 2010) not seen in other Gram-negative marine bacteria studied so far (Nazarenko et al. 2011).

Lutimaribacter

Lutimaribacter saemankumensis is the type and only species of the genus *Lutimaribacter* (Yoon et al. 2009a). They are Gram-negative, non-flagellated rods, positive for oxidase and catalase, and facultatively anaerobic. Q10 is the predominant quinone and C18:1 ω7c plus its 11-methyl derivative are the major cellular fatty acids. The species shows the following traits: it is pigmented (pale yellow), grows in Marine Agar in anaerobic conditions, does not reduce nitrates, requires Na^+ for growth, tolerates up to 10 % NaCl, and does not synthetize Bchl *a*. Its major polar lipids are PC, PG, PE, an unidentified aminolipid, and two phospholipids. The DNA G+C content is 63.5 mol%. The closest neighbor of *L. saemankumensis* is *Oceanicola pacificus*, one of the *Oceanicola* species that appears to be misclassified.

Mameliella

Mameliella (Zheng et al. 2010a) contains a single species, *M. alba*, isolated from seawater. The genus is described as follows: Gram-negative, nonmotile rods that multiply by binary fission and accumulate PHB granules. The predominant respiratory quinone is Q10. It is oxidase and catalase positive but negative for urease, hydrolysis of starch and gelatin, and indole production. Forms white colonies in RO (Rich Organic) medium containing (in grams per liter) yeast extract, 1.0; Bacto Peptone, 1.0; sodium acetate, 1.0; KCl, 0.3; $MgSO_4 \cdot 7H_2O$, 0.5; $CaCl_2 \cdot 2H_2O$, 0.05; NH_4Cl, 0.3; K_2HPO_4, 0.3; and NaCl, 20.0; plus 20 μg of vitamin B12, 200 μg of nicotinic acid, 80 μg of biotin, 400 μg of thiamine, and 1.0 ml of a trace element solution. The species is described as mesophilic and neutrophilic and is able to grow with 1–10 % NaCl in the medium and able to reduce nitrates and to use several carbohydrates and some organic acids. Contains C18:1 ω7c, C18:0, C12:1 3OH, C16:0, and 11-methyl C18:1 ω7c as major fatty acids. Its DNA G+C content is 63.7 mol%. In spite of its general lack of phenotypic distinctiveness, *M. alba* forms a distinct lineage in the 16S rRNA tree, forming a long branch connected to the pair *Antarctobacter heliothermus-Sagittula stellata*.

Maribius

The genus *Maribius* (Choi et al. 2007) contains two species *M. salinus* and *M. pelagius* isolated from distant saline waters (a Chinese solar saltern and Sargasso Sea seawater). They form a tight group, related to *Hwanghaeicola aestuarii* and to the newly described *Profundibacterium mesophilum*. The main characteristics of the genus are: rod-shaped, nonmotile, Gram-negative cells. They are obligate aerobic heterotrophs, positive for oxidase and catalase, and require Na^+ and Mg^{2+} for growth. They accumulate PHB and have Q10 as predominant quinone and C18:1 ω7c plus C19:0 cyclo ω8c as major fatty acids. Colonies on Marine Agar are opaque and beige in color and do not contain Bchl *a*. The DNA G+C content is 66–70 mol%. None of the species reduces nitrate to nitrite or hydrolyzes gelatin, but both are amylolytic. Surprisingly, the species isolated from seawater tolerates higher salinities (up to 15 %) than the one isolated from solar saltern water, *M. salinus* (up to 10 %).

Marinovum

A long path took the former *Roseobacter algicola* (Lafay et al. 1995) and then *Ruegeria algicola* (Uchino et al. 1998) to be finally recognized in a separate genus *Marinovum* (Martens et al. 2006) as *M. algicola*. The strains that served to describe the species were isolated from cultured, toxin-producing dinoflagellate *Prorocentrum lima*. The phylogenetic position of *Marinovum algicola* as an independent branch, separated from true *Roseobacter* and *Ruegeria* species, is clear in all analyses.

The genus contains Gram-negative, ovoid cells, motile through flagella that are subpolarly inserted. Colonies develop a pinkish-beige pigmentation after a few days incubation. They do not accumulate PHB but Lafay et al. (1995) show electron micrographs in which refringent spherical bodies can be seen inside the cells. They are strict aerobes, non-fermentative, unable to denitrify, and oxidase, catalase, and gelatinase positive. Do not synthetize Bchl *a*. They are mesophilic (optimum temperature 25–30 °C) and require Na^+, thiamine, and biotin for growth. They use several carbohydrates (hexoses, disaccharides) and some organic acids (pyruvate, malate, and citrate) as carbon sources. The major quinone is Q10; dominant fatty acids are C18:1 ω7c, 11-methyl C18:1 ω7c, C18:0, C12:0 3OH, and C10:0 3OH (amide linked); and major polar lipids are PG, PE, PC, an unidentified phospholipid, one lipid, and one aminolipid. The G+C content is not included in any of the three papers that concern the taxonomy of the genus. Pradella et al. (2010) determined the structure of the genome in several strains of *M. algicola*, including the type strain: it is composed of one circular chromosome (3.60–3.74 Mbp) and 9–12 plasmids (7–477 Kbp), giving a total genome size of 5.0–5.35 Mbp.

Maritimibacter

Maritimibacter alkaliphilus, the single species of the genus *Maritimibacter*, was isolated by applying dilution-to-extinction, high-throughput culturing methods to Sargasso Sea seawater (Lee et al. 2007a). The strain that served to describe the new genus and species is a Gram-negative, nonmotile, rod-shaped bacterium that does not accumulate PHB and does not synthetize Bchl *a* or carotenoids. It is chemoheterotrophic, strict aerobe and requires sodium ion for growth. Its dominant fatty acids are C16:0 2OH, C16:0, C18:1 ω7c (in lower proportion than is usual in the family), 11-methyl C18:1 ω7c, and C18:1 2OH. Q10 is the predominant quinone. Major polar lipids are PC, PE, and PG. In addition to these generic characteristics, the species presents the following traits: mesophilic (16–37 °C, optimum 30 °C), slightly halophilic (0.5–7.5 % NaCl, optimum 2.5–3.0 %), and alkaliphilic (4–12, optimum pH 10). Catalase, oxidase, and urease are positive. Although no nitrate reduction is detected in the API strips, the draft genome of the strain has been obtained, and it contains a complete nitrate reduction pathway to N_2. Other specific genes include two putative Na^+/H^+ antiporters, considered essential for alkaliphilic behavior. Genome size of *M. alkaliphilus* HTCC2654^T is 4.53 Mbp and its G+C content is 64 mol%. It contains 49 tRNA genes and one each of 5S rRNA, 16S rRNA, and 23S rRNA genes (Thrash et al. 2010a).

The position of *M. alkaliphilus* in the *Roseobacter* group is isolated, with no close relative and by the edge of the clade.

Marivita

The genus *Marivita* was proposed to accommodate two species, *M. cryptomonadis* and *M. litorea*, isolated from a culture of *Cryptomonas* sp. and a coastal seawater sample, respectively

(Hwang et al. 2009), and nowadays it contains six. Among the species added later, *M. byunsanensis* corresponds to a reclassification of the former *Gaetbulicola byunsanensis* (Yoon et al. 2010b) (so the genus *Gaetbulicola* is now "empty") and the remaining three have been isolated from seawater (*M. hallyeonensis*, *M. geojedonensis*) or estuarine water (*M. roseacus*). The genus has been emended twice (Budinoff et al. 2011; Yoon et al. 2012).

Marivita species form one of the few well-defined, tightly delimited, generic clades in the *Roseobacter* group, with all the six species closely located at the end of a rather long branch that joins to a clade of misplaced *Oceanicola* spp. (see below). Pairs of *Marivita* species for which DDH has been determined show low levels of relatedness: *M. cryptomonadis* and *M. litorea* show 13 % DDH value (Hwang et al. 2009); *M. hallyeonensis* shows 15, 17, and 11 % to *M. cryptomonadis*, *M. litorea*, and *M. byunsanensis*, respectively (Yoon et al. 2012); *M. roseacus* shows 30–33 % against *M. litorea* and 19–20 to *M. cryptomonadis* (Budinoff et al. 2011). Finally, *M. geojedonensis* presents values between 17 % and 22 % to *M. cryptomonadis*, *M. litorea*, *M. byunsanensis*, and *M. hallyeonensis* (Yoon et al. 2013b).

The genus, as presently recognized, contains Gram-negative, strictly aerobic, heterotrophic bacteria that contain genes for Bchl *a* synthesis (although some of them do not produce the pigment). Oxidase and catalase are positive. Cell morphology varies from short rods to long rods associated in chains or pleomorphic cells. May be motile by polar flagella or nonmotile. Major fatty acid is C18:1 ω7c. Q10 is the predominant quinone, while major polar lipids are PC, PG, PE, and an unidentified aminolipid. The DNA G+C content is 58–65 mol%.

Species of *Marivita* differ in motility (although there are contradictory data in different studies, see Budinoff et al. (2011) on motility and nitrate reduction activity of *M. cryptomonadis* and *M. litorea*), PHB production, nitrate reduction, pigmentation (from cream to pink or light yellow), and the use of different carbon sources (if any). All species require Na^+ for growth, some also Mg^{2+}, yet others combined sea salts. They are mesophilic, neutrophilic, and able to grow with 0.5–1.0 to a maximum of 6–10 % salinity, depending of the species. *M. cryptomonadis*, *M. litorea*, and *M. roseacus* have *puf* genes encoding phototrophic ability, but only *M. roseacus* synthetizes Bchl *a* in standard growth conditions. The rest of the species have not been tested for *puf* genes.

Nautella

The genus *Nautella* (Vandecandelaere et al. 2009a) contains one species, *N. italica*, isolated from a marine electroactive biofilm grown on a stainless steel cathode exposed to natural seawater. *Nautella* is defined as Gram-negative, motile, rod-shaped, strictly aerobic and moderately halophilic, with a positive response to catalase and oxidase tests and able to grow in the range of 4–45 °C.

The species is characterized by the following properties: cells are motile by a polar flagellum and accumulate PHB. Colonies are beige. They require Na^+ and grow from 1 % to 7 % NaCl (optimum 2–3 %). Temperature optimum is 20–28 °C and optimum pH is between 6.0 and 8.0. They are non-fermentative and do not reduce nitrate to nitrite or hydrolyze gelatin, casein, starch, chitin, or DNA. They contain C18:1 ω7c, C16:0 2OH, 11-methyl C18:1 ω7c, C10:0 3OH, C18:0 2OH, C12:0 3OH, C16:0, and C18:0 as major fatty acids. Their DNA G+C content is 61 mol% (Vandecandelaere et al. 2009a).

At the moment of its description, the closer relatives to *Nautella* were *Phaeobacter* species. Thus, in addition to the intraspecific level of DDH between the five isolates included in the species description, the relatedness with some *Phaeobacter* species (*P. daeponensis*, *P. inhibens*, and *P. gallaeciensis*) was also determined and found to be low (7–17 %).

Nautella-like isolate R11 (formerly *Ruegeria* sp. R11) has been characterized as an algal pathogen, causing bleaching disease in the marine red alga *Delisea pulchra* (Case et al. 2011). Sequencing and analysis of its genome has revealed clues for understanding the pathogenicity of the strain: adhesion mechanisms, transport of algal metabolites, oxidative stress protection, cytolysins, and other pathogen-related activities were found coded in the genome of *Nautella* sp. R11 (Fernandes et al. 2011). The genome of this strain is composed of a circular chromosome of 3.62 Mbp and a plasmid of 197 Kbp. Other closely related strains show detrimental activities in different marine organisms, as *Raphidophyceae* algae, sea urchins, and corals.

Nereida

Nereida was described as a genus containing Gram-negative, strictly aerobic, chemoorganotrophic, slightly halophilic bacteria (Pujalte et al. 2005a). They are positive for oxidase and catalase, mesophilic, require combined sea salts for growth and do not ferment carbohydrates or reduce nitrates. They do not form gas vesicles or PHB granules in the cells, which are nonmotile, coccoid, elongated, or tear-shaped rods that divide by budding. They contain C18:1 ω7c, C18:0, and C16:0 as main fatty acids and have a G+C content of 56 mol%.

The only species so far recognized in the genus is *N. ignava*, related to the sequences of uncultured symbiotic bacteria from the galls of the alga *Prionitis lanceolata* and neighbor to the recently described *Lentibacter algarum*. The species shows undetermined nutritional requirements and uses a narrow range of carbon sources, provided that the basal medium is supplemented with low amounts of yeast extract.

Oceanibulbus

Oceanibulbus indolifex is the sole species of the genus *Oceanibulbus* (Wagner-Döbler et al. 2004). This species is a member of the subclade containing *Roseobacter* and *Sulfitobacter* species. In fact, it is so closely related to the species *Sulfitobacter delicatus* and *S. dubius* (99.5 % 16S rRNA sequence

similarity, according to Ivanova et al. 2004) that they might well be members of a single genus, if only phylogenetic information were used to define the rank. *Oceanibulbus* is Gram-negative and nonmotile and the cells are irregular rods with swollen ends and inclusion bodies (PHB). They do not synthetize Bchl *a*. They are strictly aerobic, non-fermentative heterotrophs that require sea salts (NaCl alone does not support growth) and are able to develop in media with 1–7 % sea salts content. Optimum temperature and pH are 25–30 °C and 7.0–8.0, respectively. Oxidase reaction is weak. Do not reduce nitrates to nitrites. They contain Q10 as predominant quinone. PG, DPG, PC, PE, and an aminolipid are the main polar lipids and C18:1 ω7c, C18:0, C16:1 ω7c, C16:0, C10:0 3OH, and C12:1 3OH as major fatty acids. *O. indolifex* has a 60 mol% G+C content. It shows 21 % relatedness on DDH experiments to *Sulfitobacter mediterraneus* (Wagner-Döbler et al. 2004). To the best of our knowledge, the DDH levels between *O. indolifex* and *S. delicatus* and *S. dubius* have not been tested.

O. indolifex produces some interesting secondary metabolites, as indole and several indole derivatives, some cyclic dipeptides and tryptanthrin (Wagner-Döbler et al. 2004). It also produces sulfur volatiles during metabolism of S-containing compounds, as sulfides and thioesters, some of them were new natural compounds as 5-methyl phenylethanethioate and butyl methanesulfonate (Thiel et al. 2010). It was one of the species included in the development of genetic tools for investigation of regulatory and metabolic networks in the *Roseobacter* group (Piekarski et al. 2009). The genome of the type strain has an estimated size of 4.11 Mbp and contains 4,153 ORFs, with a G+C content of 59 mol%.

Oceanicola

The genus *Oceanicola* currently contains seven species: *O. granulosus*, the type species, and *O. batsensis*, both isolated by high-throughput culturing methods from seawater (Cho and Giovannoni 2004); *O. nanhaiensis*, obtained from deep (1,100 m) marine sediments (Gu et al. 2007); *O. marinus*, from seawater (Lin et al. 2007); *O. pacificus*, also from deep marine sediments (Yuan et al. 2009); *O. nitratireducens*, from seawater (Zheng et al. 2010b); and *O. litoreus* (Park et al. 2013a) from seashore sediment. The phylogenetic relationships among the members of the genus are, however, dubious, as the type species separates from the larger *Oceanicola* clade (*O. batsensis*, *O. nanhaiensis*, *O. nitratireducens*, *O. marinus*) and associates with *Roseisalinus antarcticus*, while *O. pacificus* groups very close to *Lutimaribacter saemankumensis* (both with NJ and ML). Given that the genus seems polyphyletic (as it was also recognized and reported by Thrash et al. (2010b) and Newton et al. (2010)), the generic assignment of all (but type) species is pending of a reevaluation taking into account all the neighboring new taxa recognized since the genus was first described. This situation is not uncommon; similar problems affect the genus *Roseovarius* and *Phaeobacter*. Despite the large separation in the 16S rRNA tree, the type strains of *O. granulosus* and *O. batsensis* displayed 48 % relatedness in DDH determinations (Wagner-Döbler et al. 2004). DDH values relate *O. marinus* to *O. granulosus* by 7 % and to *O. batsensis* by 26 % (Lin et al. 2007). *Oceanicola* comprises Gram-negative, nonmotile short rods that multiply by binary fission and accumulate PHB granules. They do not synthetize Bchl *a*. Their metabolism is chemoorganotrophic and aerobic to microaerotolerant (*O. marinus* and *O. litoreus* are described as facultative anaerobes due to their ability to grow on Marine Agar in anaerobic conditions, but they do not ferment glucose nor do they respire with nitrate). Oxidase test is positive but they are negative for denitrification, glucose acidification, arginine dihydrolase, indole production, and gelatinase. Main fatty acids are C18:1 ω7c, C16:0, and C 19:0 cyclo (except for *O. nitratireducens* and *O. nanhaiensis*). DNA G+C content is 64–73 mol%. Predominant quinone is reported to be Q10 for *O. nanhaiensis*, *O. nitratireducens*, and *O. litoreus*. Polar lipid composition is reported only for *O. litoreus* and *O. granulosus* (Park et al. 2013a) and consists of PC, PG, PE, an unidentified aminolipid, and a lipid for *O. litoreus*, while the type species lacks PE. Species of *Oceanicola* are neutrophilic and mesophilic but display a wide range of growth temperatures, with four of the species growing from 4 °C to 40 °C (*O. granulosus*, *O. batsensis*, *O. marinus*, and *O. litoreus*). All, except *O. nanhaiensis*, need Na^+ for growth (*O. litoreus*, also requires Mg^{2+}) and grow from 0.5 to 7–10 % salinity. They could be differentiated by the carbon sources used, presence of urease, minimum growth temperature, gelatin and esculin hydrolysis, and the percentage of the fatty acid C10:0 cyclo. As many other roseobacters, *Oceanicola* sp. participate in the transformation of DMSP in DMS, as documented by Curson et al. (2008) and Mou et al. (2005).

The genomes of *O. granulosus* and *O. batsensis* type strains have been sequenced (Thrash et al. 2010b). The genome of the type species comprises 4.04 Mbp, 3,855 ORFs and has a G+C content of 70.4 mol%. It contains genes for the Calvin cycle including the large (but not the small) RuBisCo subunit. The genome of *O. batsensis* comprises 4.44 Mbp, 4,261 ORFs and has a G+C content of 66 mol%. It does not contain *che* gene homologs, in contrast *to O. granulosus* genome. Both have putative genes for PHB synthesis. The draft genome of a third *Oceanicola* sp. strain able to degrade xylan has been reported (Kwon et al. 2012).

Oceaniovalibus

Oceaniovalibus and its single species *O. guishaninsula* (Liu et al. 2012) occupy a detached position, next to *Pontibaca methylaminivorans*, in the *Roseobacter* clade. It contains Gram-negative, ovoid to coccoid cells and is nonmotile and unable to produce PHB or synthetize Bchl *a*. Pigmentation of the colonies grown in Rich Organic medium or Marine Agar is pink. Catalase, oxidase, and nitrate reduction to nitrite are positive. They contain C18:1 ω7c, C19:0 cyclo, and C16:0 as major fatty acids and Q10 as predominant quinone.

O. guishaninsula was isolated from surface seawater. Its DNA G+C content is 62 mol%. It is neutrophilic (pH 4–10, optimum 6–9), mesophilic (16–40 °C, optimum 20–30 °C), and slightly halophilic (0.5–12 % NaCl, optimum 4–5 %). It is amylolytic but not gelatinolytic, uses as carbon sources some carbohydrates (L-arabinose, D-cellobiose, D-mannitol, and D-glucose), organic acids, and amino acids. Major polar lipids are PG and DPG. A draft genome (2.9 Mb) of the type strain JLT2003^T has been reported (Tang et al. 2012).

Octadecabacter

Octadecabacter is one of the oldest members of the *Roseobacter* group, described by Gosink et al. (1997) from sea ice samples obtained at the two polar regions. It contains heterotrophic, psychrophilic, gas vacuolated, nonpigmented bacteria distributed in two species: *O. arcticus* from Arctic ice samples and *O. antarcticus* from Antarctic sea ice. The two species maintain a moderate relatedness, a 42 % level of DDH (Gosink et al. 1997). Their distribution at the poles was the basis for discussion about biogeography of sea ice bacteria (Staley and Gosink 1999; Brinkmeyer et al. 2003).

Octadecabacter comprises Gram-negative, nonmotile rods with gas vesicles. They are aerobic to microaerophilic and do not reduce nitrates. Bacteriochlorophyll *a* is not synthetized. Catalase test is positive, but oxidase is negative (an uncommon trait in the *Roseobacter* group). True psychrophilic, they grow down to 4 °C (with maxima at 10–15 °C). No growth is observed without Na^+; the salinity growth range is 1.7 –7 %. They have nutritional requirements that may be covered by yeast extract, but even with the addition of this supplement, turbidity of the cultures is always low. Carbon sources used include L-glutamate, glycerol, and Casamino acids. The dominant fatty acid is C18:1 ω7c and the DNA G+C content is 56–57 mol%. *O. arcticus* requires thiamine, nicotinic acid, and pantothenic acid and grows up to 15 °C, while *O. antarcticus* grows only up to 10 °C. Both species contain, in addition to C18:1 ω7c, C16:1 ω7c, C16:0, and C10:0 3OH as major fatty acids.

The two species form a tight, isolated clade in the 16S rRNA tree.

Genomes of the types of both species have been finished and manually annotated (Vollmers et al. 2013). The genome size of *O. arcticus* 238^T is 5.20 Mbp (with 4,683 protein-coding genes) and 4.88 Mbp for *O. antarcticus* 307^T (4,492 protein-coding genes), both having the same DNA G+C content, 55 mol%, and exhibiting a high genome plasticity caused by an unusually high density and diversity of transposable elements. Interestingly, genes representing a new subgroup of xanthorhodopsins as an adaptation to icy environments were found in both *Octadecabacter* strains that differed from the previously characterized xanthorhodopsins of *Salinibacter ruber* and *Gloeobacter violaceus* in phylogeny, biogeography, and the potential to bind 4-keto-carotenoids. Biochemical characterization of the *Octadecabacter* xanthorhodopsins revealed that they function as light-driven proton pumps (Vollmers et al. 2013).

Pacificibacter

Pacificibacter (Romanenko et al. 2011b) accounts for marine bacteria which display the following properties: they are Gram-negative budding rods, strictly aerobic, chemoorganotrophic, and oxidase and catalase positive. They require sodium ions for growth. Q10 is the predominant quinone and their polar lipids contain PC, PG, DPG, and unidentified lipids as major components. The most abundant fatty acids are C18:1 ω7c, C16:0, C10:0 3OH, and C12:1 3OH. The only species of *Pacificibacter* currently recognized is *P. maritimus* (although the close position of *Roseovarius marinus* in the 16S rRNA tree suggests that it might be reclassified as a second species of *Pacificibacter*), which is nonmotile, unpigmented, does not synthetize Bchl *a*, and grows at 0.5–6 % salinity, at 2–36 °C (optimum 25–30 °C), and at pHs of 5.5–9.5 (6.5–8.5 optimum). It uses a few sugars (glucose, maltose, cellobiose, melibiose) and organic acids (acetate, lactate, and citrate) as carbon sources. *P. maritimus* is unable neither to reduce nitrates nor to hydrolyze gelatin, casein, or DNA. The DNA G+C content is 52.6 mol%.

Palleronia

Palleronia is one of the few genera in the *Roseobacter* clade that have been isolated from a non-marine habitat: its type species *P. marisminoris* was obtained from a saline soil sample in the surroundings of a solar saltern in Murcia, Spain (Martínez-Checa et al. 2005). *Palleronia* is defined as Gram negative, rod shaped, nonmotile, chemoheterotrophic, and aerobic. It does not synthetize Bchl *a* and it is unable to grow anaerobically either by fermentation, nitrate or fumarate reduction, or photoheterotrophy. Oxidase test is negative. They produce pink-pigmented colonies, are strictly halophilic, and require sodium, magnesium, and potassium ions for growth. They have a low nutritional versatility. Chemotaxonomic markers include Q10 as dominant quinone and C18:1 ω7c plus C19:0 cyclo ω8c as major fatty acids.

P. marisminoris is an exopolysaccharide-producing species that forms capsulated cells and mucoid colonies. Salinity growth range is 0.5–15 %, with an optimum at 5 %. Mesophilic, it grows from 20 °C to 37 °C and at pH from 5 to 10. It is negative for nitrate reduction to nitrite and for hydrolytic activities on gelatin, casein, lecithin, starch, Tween 80, or DNA. No growth was obtained in any of 35 carbon sources tested (Martínez-Checa et al. 2005). The cells accumulate polyhydroxyalkanoate granules. The DNA G+C content is 64 mol%.

The species is located next to *Tranquillimonas alkanivorans* and *Salipiger mucosus* (another taxon isolated from hypersaline soil).

Pelagibaca

Pelagibaca bermudensis is the only named species of the genus *Pelagibaca* (Cho and Giovannoni 2006). Isolated from Sargasso

Sea water by high-throughput culturing involving dilution to extinction, it is another new taxon recovered along with *Maritimibacter alkaliphilus*, *Oceanicola granulosus*, and *O. batsensis*. The genus is chemoheterotrophic and facultatively anaerobic. Cells are ovoid, nonmotile, divide by binary fission, and do not produce PHB or exopolysaccharides. Bchl *a* and carotenoids are absent. Able to reduce nitrate and nitrite. They require sodium ion for growth and are slightly halophilic. Glucose is acidified. They use a wide variety of sole carbon sources for growth. Their predominant fatty acid is C18:1 ω7c and its 11-methyl derivative. The only respiratory quinone is Q10 and the G+C content of DNA is 65.4 mol%.

P. bermudensis displays the following specific traits: grows between 10 °C and 40 °C (optimum 30–33 °C), at pH 5.5–10.5 (optimum 8.5) and from 0.25 % to 15 % salinity (optimum 3.0 %). It is oxidase and catalase positive; hydrolyzes gelatin, urea, and esculin; uses a large number of carbohydrates, organic acids, and amino acids as sole carbon and energy sources, including methanol. In addition to the fatty acids cited above, it contains more than 1 % of C16:0 and C12:0 3OH.

It is marginally related to the loose clade that contains *Saligipiger mucosus*, *Palleronia marisminoris*, and *Tranquillimonas alkanivorans*. At the time of its description, *Salipiger mucosus* was the nearest taxon, so the levels of DDH with its type strain were determined, resulting in a value of 26 % (Cho and Giovannoni 2006).

Pelagibaca sp. has been isolated, among other genera of the *Roseobacter* clade, as phthalate-degrading bacteria from seawater off the coast of Japan (Iwaki et al. 2012b).

A draft genome sequence of *P. bermudensis* HTCC2601^T has been obtained (Thrash et al. 2010a): it comprises 5.43 Mbp, 5,522 ORFs and has a G+C content of 66.4 mol%. It contains fifty-six tRNA genes, five 5S rRNA genes, four 16S rRNA genes, and five 23S rRNA genes. In addition to the general information for central metabolic pathways (complete glycolysis, Entner-Doudoroff pathway, TCA cycle), pathways for oxidation of C1 compounds are present, as well as a complete RubisCo complex, unique to the currently sequenced roseobacters. Other information includes biosynthesis of most essential amino acids and some vitamins, assimilatory nitrate reduction pathway, several type VI secretion genes, complete *sec* pathways, and a large number (362) of ABC transporters. These later gene groups are similarly present in other *Roseobacter* clade representatives sequenced so far.

Pelagicola

The genus *Pelagicola* and is type species *P. litoralis* (Kim et al. 2008b) are similar in most traits to other members of the group, except for a low G+C content, 47 mol%, which is the lowest recorded in the whole group and the only one below 50 mol%. Other traits are typical of roseobacters: they are Gram negative, nonmotile, strict aerobic and the cells are club shaped. Do not accumulate PHB. Catalase and oxidase are positive. Bchl *a* is absent. Q10 is the predominant quinone and C18:1 ω7c the major fatty acid. It contains PC, PG, PE, an unidentified aminolipid, and three lipids as major polar lipids. *Pelagicola litoralis*, which is close to the main *Roseovarius* clade, is not pigmented, grows with 2–6 % sea salt concentration (optimum 3–4 %), at 20–30 °C, and pH 6–8. Hydrolyzes starch and Tween 80 but not gelatin and does not reduce nitrate to nitrite. Sole carbon sources include acetate, betaine, glucose, L-lysine, L-proline, and L-serine. The type strain was isolated from costal seawater.

Pelagimonas

Pelagimonas is a recently described genus (Hahnke et al. 2013a) related to the *Sulfitobacter* subclade (in the paper) or to *Tropicibacter* genus (NJ tree, ❯ *Fig. 20.5*). The type strain of the type and only species *P. varians* was isolated from a seawater sample taken during an algal bloom at the North Sea. It is Gram negative, aerobic, chemoorganotrophic, catalase positive but oxidase negative. The cells are irregular rods. It does not synthetize Bchl *a* or other pigments, and *puf* genes for bacterial photosynthesis are absent. They require vitamins and sodium ion for growth. Major quinone is Q10. Dominant fatty acids are C18:1 ω7c and C18:2, accompanied by C10:0 3OH, C12:1, C14:1 3OH, C16:0, C18:0, and 11-methyl C18:1 ω7c. Major polar lipids are PC, PG, PE, DPG, PME, an unidentified aminolipid, one PL, and one lipid. The species is characterized by the presence of at least one flagellum, the ability to grow from 4 °C to 37 °C (optimum 28–32 °C), at pH 6.0–9.5 (optimum 7.0–8.5) and with salinities from 1.25 % to 8 % (optimum 1.25–5 %). It requires nicotinic acid amide. Does not reduce nitrate to nitrite. It grows with several amino acids, sugars, and organic acids as carbon sources. The G+C content of the DNA is 55 %.

Phaeobacter

The genus *Phaeobacter* currently contains five species: *P. gallaeciensis* (formerly *Roseobacter gallaeciensis*), the type species (Martens et al. 2006; Ruiz-Ponte et al. 1998), *P. inhibens* (Martens et al. 2006), *P. daeponensis* (Yoon et al. 2007d), *P. arcticus* (Zhang et al. 2008), and *P. caeruleus* (Vandecandelaere et al. 2009b). Phaeobacters are often regarded as efficient surface colonizes and as producers of inhibitory compounds that enable them to antagonize invertebrate settlement and algal or microbial growth.

General properties of the genus, as described by Martens et al. (2006) and emended by Yoon et al. (2007b) are as follows: cells are Gram negative, ovoid, and multiply by binary fission. They are motile by polar flagella and have a tendency to aggregate in liquid medium forming rosettes. Colonies are generally pigmented, brown/ochre, yellow, or blue. May produce a diffusible brownish pigment. Bchl *a* is absent. They do not grow photoheterotrophically or with methyl halides or DMS. Metabolism is chemoheterotrophic and obligately

aerobic. Oxidase and catalase are positive, but amylase, gelatinase, and tweenase are negative. The major respiratory lipoquinone is Q10. Polar lipids comprise PG, PE, PC, one aminolipid, and two phospholipids. Fatty acids comprise C18:1 ω7c, 11-methyl C18:1 ω7c, C16:0, C16:0 2OH, C18:0, C10:0 3OH, C14:1, C12:0 3OH (amide linked), and C14:1 3OH (amide linked).

The currently recognized species of *Phaeobacter* display a DNA G+C content of 55–65 mol%.

DDH experiments between different type strains of these species have been published in some of the original descriptions, for example, *P. gallaeciensis* and *P. inhibens* are related by figures of 16–20 % (while *P. gallaeciensis* showed less than 5 % against *Leisingera methylohalidivorans*, *Roseobacter* spp., and *Ruegeria*—now *Marinovum—algicola*). *P. daeponensis* was related to *P. gallaeciensis* and *P. inhibens* by values of 15 % and 18 %, respectively. *P. arcticus* showed 33 % relatedness to *P. inhibens*, the only species with more than 97 % 16S rRNA gene similarity at that time. Finally, *P. caeruleus* exhibits DDH levels of 25 % to *P. inhibens*, 28 % to *P. daeponensis*, and 40 % to *P. gallaeciensis*, well in the range for congeneric species. However, the values shown by this species towards type strains of closely related genera are, sometimes, even higher, and specially with two species of the genus *Leisingera*, the type species *L. methylohalidivorans* (55 %) and *L. aquimarina* (35 %). Also noticeable are the levels displayed with *Ruegeria atlantica* (23 %), *Silicibacter lacuscaerulensis* (29 %), and *Silicibacter pomeroyi* (18 %). These values are understandable in the light of the phylogenetic relationships revealed by comparative 16S rRNA analysis: as it can be observed in ❯ *Fig. 20.5*, the five *Phaeobacter* species are distributed in two subclades, one of them, that includes *P. gallaeciensis*, *P. inhibens*, and *P. arcticus*, relates with some recently described genera as *Seohaeicola* and *Litorimicrobium*, as well as to one misplaced *Leisingera* species, *L. nanhaiensis*, while the other two *Phaeobacter* spp., *P. daeponensis* and *P. caeruleus*, both merge with *Leisingera methylohalidivorans* and *L. aquimarina*, to which *P. caeruleus* showed the high DDH levels commented above. Clearly, a revision of the generic assignment of several species of the *Roseobacter* clade is pending, and among them *Phaeobacter* spp.

The draft genomes of three *P. gallaeciensis* and one *Phaeobacter* sp. strains are available: strain ANG1 (Collins and Nyholm 2011), strain DSM 17395^T, strain 2.10 (Thole et al. 2012) and strain Y4I (Roseobase). The estimated genome sizes are 4.16–4.59 Mbp, with 3,723–4,358 ORFs. G+C content is 59–62.6 mol% in *P. gallaeciensis* strains and 64 mol% in *Phaeobacter* sp. Y4I (an indigoidine producer).

An outstanding feature of some members of *Phaeobacter* is the ability to synthetize the antibiotic tropodithietic acid (TDA), which occurs also in members of the genera *Silicibacter* and *Ruegeria* (Brinkhoff et al. 2004). The antibiotic seems to have a key role in the interactions with algae and bacteria. TDA, a biologically active sulfur-containing tropolone compound, is synthetized in response to quorum sensing signals: *N*-acyl homoserine lactones (Berger et al. 2011) and TDA itself (Geng and Belas 2010) can act as autoinducers. Synthesis of the brown pigment is also controlled through the same regulatory mechanism and, consequently, they are enhanced in biofilms (and other aggregative growth forms, as rosettes or colonies).

Other bioactive compounds that have been studied among the secondary metabolites produced by phaeobacters are the roseobacticides (Seyedsayamdost et al. 2011a, b), compounds pertaining to the troponoid family, as TDA, which are produced and act as algaecides in response to algal senescence factors, changing the mutualistic behavior that maintain algal surface-colonizing phaeobacters to an opportunistic parasitic lifestyle. Another antimicrobial secondary metabolite indigoidine is produced by *Phaeobacter* sp. Y4I and has been demonstrated that contributes to competitive surface colonization and inhibition of *Vibrio* spp. (Cude et al. 2012). Indigoidine is synthetized via a nonribosomal peptide synthase (NRPS)-based biosynthetic pathway, one of the several identified in members of the *Roseobacter* clade (Martens et al. 2007).

As a consequence of its ability to efficiently adhere and grow on surfaces (Thole et al. 2012) and to secrete inhibitors active on other potentially harmful colonizers (pathogenic bacteria, fouling organisms), *Phaeobacter* spp. are candidates to be used as probiotics in marine aquaculture, where they have been studied as fish probiotics (Porsby et al. 2008; Prol et al. 2009; Pintado et al. 2010; D'Alvise et al. 2013) and bivalve probiotics (Prado et al. 2009; Kesarcodi-Watson et al. 2012).

In addition to the close link with algae and phytoplankton members, to which *Phaeobacter* cells associate (*Emiliania huxleyi*, e.g., Seyedsayamdost et al. 2011b), an intimate association has been documented between *P. gallaeciensis* and the accessory nidamental gland of the bobtail squid *Euprymna scolopes*, where its cells represent the dominant fraction of bacterial consortia (Collins and Nyholm 2011).

Planktotalea

Planktotalea (Hahnke et al. 2012) contains a single species, *P. frisia*, isolated from filtered seawater during a phytoplankton bloom in the North Sea. Although *Pelagicola litoralis* is cited as the nearest phylogenetic neighbor of *P. frisia* in its description, the analysis shown in ❯ *Fig. 20.5* presents *Planktotalea* as a distinct lineage in the subclade defined by *Litoreibacter* spp. and *Pacifibacter maritimus*.

Members of *Planktotalea* are Gram negative, irregular small rods. They are aerobic, oxidase and catalase positive, require vitamins and sodium ion for growth, and grow poorly on media with single (carbon) substrates. They possess *pufLM* genes. Major respiratory lipoquinone is Q10; polar lipids are PC, PG, an aminolipid, and a phospholipid, and the major fatty acids comprise C18:1 ω7c, C18:2, C16:0, C18:0, C12:1, C10:0 3OH, C12:1 3OH, and 11methyl C18:1 ω7c.

P. frisia forms small, unpigmented colonies on Saltwater Medium. Flagella are not observed and swimming motility was not clearly determined, although the cells exhibit wobbling. It grows in the ranges 4–32 °C (optimum 20–25 °C), pH 6.0–9.5 (optimum 7.5–9.0), and 1.25–8.0 % salinity (optimum 3.75 %).

It requires pantothenic acid and nicotinic acid amide. It is negative for denitrification, gelatin, and starch hydrolysis but positive for Tween-80 hydrolysis. It utilizes several amino acids, sugars, and organic acids as carbon and energy sources. Despite the presence of *pufLM* genes, Bchl *a* is not produced in laboratory cultures. The DNA G+C content is 53.8 mol%.

Pontibaca

Pontibaca methylaminovorans, the type species of the genus *Pontibaca* (Kim et al. 2010c), was isolated after an enrichment culture of a shallow marine sediment sample with trimethylamine in anaerobic conditions: as a result, two facultatively anaerobic strains were isolated which served to describe the new genus and species. Phylogenetically, *P. methylaminovorans* is loosely related to *Oceaniovalibus* and the subclade containing *Maribius* spp. (NJ) or to *Donghicola* (ML, not shown), but no close relative is evident in the trees.

Pontibaca is described as containing Gram-negative, nonmotile ovoid rods, which are slightly halophilic and facultatively anaerobic. They reduce nitrates and nitrites and do not synthetize Bchl *a*. Catalase and oxidase tests are positive. The major polar lipids are PC and PG. The dominant fatty acids include C18:1 ω7c, C16:0, and C19:0 cyclo ω8c. Q10 is the predominant respiratory quinone. The species is defined as unpigmented, mesophilic (15–37 °C, optimum 30 °C), neutrophilic (pH 6–10, optimum 7–8), and slightly halophilic (0.5–10 % NaCl, optimum 2–3 %). It presents urease activity and produces acid from several carbohydrates but does not hydrolyze gelatin, casein, or starch. Trimethylamine, dimethylamine, methyl amine, and tetramethylammonium are used as sole carbon sources both in aerobic and anaerobic conditions. It also uses acetate, 3-hydroxybutyrate, and L-serine. The DNA G+C content is 65 mol%.

Ponticoccus

Ponticoccus (Hwang and Cho 2008) contains a single species, *P. litoralis*, isolated from coastal seawater. The species joins to the base of the clade formed by *Antarctobacter heliothermus*, *Sagittula stellate*, and *Mameliella alba* but shows not close relatedness with them or the rest of the *Roseobacter* clade. The genus does not have a clear set of distinctive features and shows the same general profile of other roseobacters: Q10 as predominant quinone, C18:1 ω7c as major fatty acid (plus 11methyl C18:1 ω7c, C16:0, C18:0, and C12:1 3OH), and polar lipids that include PC, PG, PE one glycolipid, two aminolipids, and a lipid. The G+C content is 68 mol%. Cells are coccoid to rod shaped and nonmotile, strictly aerobic, and oxidase and catalase positive. No Bchl *a* is detected in the cultures. In addition, the species *P. litoralis* is characterized by the following traits: it is positive for PHB accumulation, mesophilic (10–37 °C, optimum 20 °C), neutrophilic (pH 6–8, optimum 7), and slightly halophilic (1–15 %, optimum 3–5 %), with ionic requirements that are not fulfilled only by sodium ion. It is positive for gelatin and starch hydrolysis but negative for Tween-80 hydrolysis. It reduces nitrate to nitrite and uses several carbohydrates, organic acids, and amino acids as sole carbon and energy sources.

Poseidonocella

Poseidonocella, containing the species *P. pacifica* and *P. sedimentorum*, was isolated from sediment samples taken at the Sea of Japan (Romanenko et al. 2012). The pair has *Roseivivax* spp. clade as the closest neighbor (*Fig. 20.5*) but relates to *Loktanella* spp. in other analyses. Generic features include Gram-negative cells with enlarged poles that divide by budding. They are strict aerobes, oxidase and catalase positive, chemoorganoheterotrophic, and Na^+ requiring. They do not produce Bchl *a*. PC, PG, DPG, phosphatidic acid, one aminolipid, and other lipids are present. C18:1 ω7c and its 11-methyl derivative are the major fatty acids. Q10 is the predominant quinone. The two recognized species have ovoid, nonmotile cells and produce beige or yellowish beige colonies. Their temperature range is 5–42 °C (*P. pacifica*) and 7–41 °C (*P. sedimentorum*) with optimum above 20 °C. They grow at pH from 4 to 9.5 and optimally at 7–8. Salinity ranges are 0.5–8 % for *P. pacifica* and slightly lower (up to 6 %) for *P. sedimentorum*, with optima between 2 % and 4 % NaCl. They are negative for nitrate reduction to nitrite. Both species are able to use glucose, maltose, citrate, L-serine and L-treonine, among others, as sole carbon and energy sources.

The G+C content of their DNA is 60–65.4 mol%.

Primorskyibacter

Primorskyibacter was described by Romanenko et al. (2011c) as a new genus on isolates obtained from the same source than the previous *Poseidonocella* spp. shallow sediments of the Sea of Japan. From a phylogenetic point of view, *P. sedentarius*, the type and sole species currently recognized in the genus, is a relative of *Marinovum algicola*, to which it merges in different analyses. The genus is defined as Gram negative, strictly aerobic, oxidase and catalase positive, rod shaped, and budding. It is chemoorganoheterotrophic and requires sodium ion for growth. The polar lipid profile includes PC, PE, PG, DPG, and one unidentified lipid. C18:1 ω7c and 11-methyl C18:1 ω7c are the major fatty acids and Q10 is the predominant respiratory quinone. The G+C content of the single species, *P. sedentarius*, is 60–62 mol%. The species produces nonmotile cells, is Bchl *a* negative, and is able to grow with only NaCl added to the medium. Growth occurs at salinities from 0.5 % to 8 % (optimally at 3–5 %) and at temperatures of 4–39 °C (optimum 25–30 °C). The pH range is 6.5–9.5 with its optimum at 7.5–8.5. It is unable to reduce nitrates or hydrolyze gelatin or starch. It uses glucose, maltose, L-rhamnose, L-arabinose, sucrose, fructose, cellobiose, raffinose, D-mannitol, L-ornithine, L-tyrosine, L-asparagine, citrate, acetate, fumarate, and malate as carbon and energy sources.

Profundibacterium

Profundibacterium mesophilum, the type and sole species of this recently described genus, was isolated from a deep sea sediment sample (Lai et al. 2013). The genus is described as Gram negative, strictly aerobic, chemoheterotrophic, slightly halophilic, and halotolerant. The cells are non-flagellated cocci. Oxidase and catalase tests are positive, while nitrate reduction is negative. Among the chemotaxonomic features, *Profundibacterium* shows Q10 as predominant quinone; its major fatty acids are C18:1 ω7C/ω6c, 11-methyl C18:1 ω7c, and C16:1 ω7c/ω6c. The DNA G+C content of the type species is 64 mol%. *P. mesophilum* is a slow-growing bacterium with huge spherical cells (5.0–8.0 μm diameter) that do not accumulate PHB. They require NaCl (0.5 %) and tolerate up to 20 % (optimum 2–6 %). Mesophilic and neutrophilic, they are unable to hydrolyze gelatin, casein, DNA, or starch and grow on few carbohydrates (D-galactose, D-xylose, D-glucose, glycerol), organic acids (pyruvate, succinate, citrate, propionate), and amino acids (L-glutamate, L-arginine) as sole carbon sources. Major polar lipids are PG and PE.

P. mesophilum is distantly related to *Hwanghaeicola* and *Maribius* species.

Pseudoruegeria

The genus *Pseudoruegeria* was described by Yoon et al. (2007e) with *P. aquimaris* as type species and emended recently (Jung et al. 2010a) to incorporate a second species, *P. lutimaris*. In addition to the common features shared with the vast majority of members of the *Roseobacter* group (Gram-negative, nonmotile, aerobic rods with Q10 as major quinone and C18:1 ω7c as dominant fatty acid). The G+C content is 67–73.5 mol%. The emended description of the genus states that PG plus an unidentified lipid and one aminolipid are the common polar lipids but the polar lipid profile is quite different between the two species: *P. aquimaris* shows PG, DPG, an aminolipid, and a lipid as major components while *P. lutimaris* contains PC, PG, PE, an aminolipid, a glycolipid, and a lipid (Jung et al. 2010a). The fatty acid composition is also very different, as none of the components of their profiles (see *Table 20.2* in Jung et al. 2010a) is common to both strains, with the only exception of C18:1 ω7c. DDH levels relating *P. aquimaris* and *P. lutimaris* DNAs are only 5 % (which is at the borderline of "noise"). Altogether, considering the high similarity in 16S rRNA gene sequences (96.6 %) and in *gyrB* sequences (79.4 %), Jung and col. (2010b) considered them members of the same genus.

P. aquimaris forms grayish-yellow colonies on Marine Agar, grows between 15 °C and 49 °C, and with up to 8 % NaCl (but not in the absence of this salt). Anaerobic growth with nitrate does not occur. Acid is produced from several carbohydrates, and fructose and malate are used as carbon and energy sources. *P. lutimaris* has a lower maximum temperature for growth (37 °C), requires not only sodium but also magnesium ions, and is able to grow in the absence of O_2 on Marine Agar (alone or with nitrate). Both species are positive for catalase and oxidase tests and are unable to hydrolyze gelatin, casein, starch, or Tweens.

The two species of the genus relate marginally to the subclade containing *Celeribacter*, *Vadicella*, and *Huaishuia* species.

Roseibacterium

Roseibacterium includes two species: *R. elongatum* (Suzuki et al. 2006) and *R. beibuensis* (Mao et al. 2012). The genus comprises bacteriochlorophyll-producing aerobes with a consistent phylogenetic relationship to *Dinoroseobacter shibae*, another AAP (*Fig. 20.5*). Phylogenies based on *pufM* gene sequences reveal a relationship between the photosynthetic genes of both species that is closer to *Jannaschia* sp. CCS1 than to *D. shibae* (Mao et al. 2012).

Roseibacterium species have been isolated from coastal sand and from surface marine water. The two species form pigmented colonies, pink to red, and their cells are nonmotile rods with monopolar growth and budding division. They are aerobic chemoorganotrophs and synthetize bacteriochlorophyll *a* under aerobic conditions. Oxidase and catalase are positive. C18:1 ω7c is the major cellular fatty acid and Q10 is the predominant quinone. While the type species *R. elongatum* requires sodium ion for growth (range 0.5–7.5 % NaCl), *R. beibuensis* is able to grow without NaCl, although it has its optimum at 3–4 % NaCl. Growth is optimal at 28–30 °C and pH is 7.5–8.0 for both species. They are urease positive and able to accumulate PHA but differ in the ability to reduce nitrates to nitrites and in the minor components of the fatty acid profile. The G+C content is 68–76 mol%.

A close phylogenetic neighbor of *Roseibacterium* was described recently (Csotonyi et al. 2011) and given the generic name of *Charonomicrobium*, a name without standing in nomenclature to date and lacking public available deposition of the type strain. *Charonomicrobium ambiphototrophicum* shows a 98.3 % 16S rRNA gene similarity in to *R. elongatum*. This level might be compatible with generic identity, but the species is described as unique and separated from other taxa in the vicinity due to its ability to grow as photoorganoheterotroph both in aerobic and anaerobic conditions in the light, a behavior not found in any of the phototrophic members of the family. EG17, the proposed type strain, produces LHI complex (expressed aerobically and anaerobically) and LHII complex (mostly anaerobically). It was found to yield proportionally the greatest aerobic photosynthetic biomass under oligotrophic conditions. Other features of *C. ambiphototrophicum* are oxidase negative, brown pigmentation, the requirement of yeast extract as growth factor, a salinity range of 2–16 % NaCl, and a G+C content of 65.6 mol%. Clearly, more studies are needed to assess the taxonomic relationships between this strain and members of the genus *Roseibacterium*.

Roseicyclus

Roseicyclus mahoneyensis, isolated from a meromictic saline lake from Canada, is currently the only species of the genus *Roseicyclus* and another AAP of the *Roseobacter* group (Rathgeber et al. 2005). In contrast with the majority of members of the family, cells of *Roseicyclus* are ring shaped (although rods and ovoid cells are also observed). They are similar to other AAP bacteria in the pigmentation (pink to purple), strictly aerobic character, lack of motility, and ability to accumulate PHA. They synthetize Bchl *a* and carotenoids and produce LHI and LHII complexes. They do not denitrify or ferment carbohydrates. *R. mahoneyensis* strains are able to grow with yeast extract, but also with acetate, pyruvate, butyrate, citrate, malate, succinate, lactate, fructose, glucose, or glutamate. They are mesophilic (4–37 °C) and slightly halophilic (0.5–10 % NaCl, sodium ion is required) and have a G+C content of 66 mol%.

The photosynthetic apparatus and photoinduced electron transfer of *R. mahoneyensis* strain ML6 have been analyzed recently (Rathgeber et al. 2012).

The species occupies an isolated position among the members of the *Roseobacter* group, as an independent lineage in the edge of the clade, with a distant connection to *Wenxinia marina* and the rubellimicrobia.

Roseisalinus

The hypersaline, meromictic, Antarctic Ekho Lake has been the source of several genera and species of the *Roseobacter* group, including *Roseisalinus antarcticus*, the only recognized species of the genus *Roseisalinus* (Labrenz et al. 2005). It is, as the previous genus, an AAP which synthetizes Bchl *a* and carotenoids in aerobic conditions, producing red colonies. The genus contains Gram-negative, motile rods which accumulate PHB and have complex ionic requirements. Growth in aerobic to microaerophilic conditions is positive with various carboxylic acids and sugars as carbon and energy sources. They do not grow photoautotrophically with H_2/CO_2, photoorganotrophically with glutamate or acetate or fermentatively with glucose. Oxidase, catalase, and peroxidase activities are present. Temperature range for growth is <3–33 °C, pH range is 5.5–9.5, and salinities allowing growth are 1–13 % artificial seawater. The peptidoglycan contains *m*-diaminopimelic acid. Polar lipids present are DPG, PG, and PC, but PE and phosphatidyl-momomethylethanolamine are absent. Dominant fatty acids are C18:1 ω7c and C16:0, with minor amounts of C18:0, C10:0 3OH, and C16:1 ω7c. The quinone system is Q10.

In addition to this generic profile, the species *R. antarcticus* is characterized by a strong tendency to form rosettes, monopolar growth that suggests budding division, and a DNA G+C content of 67 mol%.

The position of the species in the 16S rRNA gene tree suggests a moderate relationship to the type species of the genus *Oceanicola*, *O. granulosus*.

Roseivivax

The genus *Roseivivax* includes five species: *R. halodurans* and *R. halotolerans* (Suzuki et al. 1999b), *R. lentus* (Park et al. 2010), *R. isoporae* (Chen et al. 2012a), and *R. sediminis* (Xiao et al. 2012). Three of them (*R. halodurans*, *R. halotolerans* and *R. isoporae*) isolated from biological material (charophytes and stromatolites from a saline lake, coral tissues) synthetize Bchl *a* and form pink pigmented colonies. They form the core of the clade containing the five *Roseivivax* species (Fig. 20.5), while the other two members of the genus, *R. lentus* and *R. sediminis*, isolated from sediments from a tide flat and a salt mine crystallizer pond, respectively, do not produce Bchl *a* and develop grayish-yellow or cream-yellow colonies. The genus, as defined by Suzuki et al. (1999b) and emended by Park et al. (2010) and Chen et al. (2012a), includes Gram-negative chemoheterotrophic rods that, when motile, have subpolar flagella. Catalase and oxidase tests are positive. It may be aerobic or facultatively anaerobic (some species grow on Marine Agar under anaerobic conditions) and may synthetize Bchl *a* in aerobiosis. The quinone system is Q10. The major cellular fatty acid is C18:1 ω7c and the dominant polar lipids are PG, PE, and an unidentified phospholipid. G+C content of the DNA is 59–69 mol%. The species in the genus are mesophilic, neutrophilic, and variable in their preferred salinities: all of them tolerate salinities over 12 % (some up to 20 %) and two, including the type species *R. halodurans*, are able to grow without salt addition to the media; hence they have to be regarded as halotolerant rather than halophilic. They are able to use several sugars, organic acids, and some amino acids as sole carbon sources. Acid is produced from some carbohydrates and nitrate reduction to nitrite is variable among species. *R. isoporae* produces PC, DPG, phosphatidyl-dimethylethanolamine, and sulfo-quinovosil diacylglycerol, in addition to unidentified phospholipids, among its major polar lipids, exhibiting a more complex profile than the other *Roseivivax* species. In addition to the dominant fatty acid, C18:1 ω7c, other major components are C19:0 cyclo ω8c, 11-methyl C18:1 ω7c, C18:0, C16:0, and C12:0 3OH.

Roseivivax halodurans DSM 15395^T contains two large linear plasmids of 264 and 368 kbp and its *pufLM* genes are located in the chromosome (Pradella et al. 2004).

Roseovarius

Roseovarius is, together with *Loktanella*, the largest genus in the *Roseobacter* group, containing 13 species at present, but almost all phylogenetic analyses show that the genus is not coherent and comprises four different lineages dispersed among other roseobacters (Fig. 20.5): the true *Roseovarius*, grouped along with the type species *R. tolerans* (Labrenz et al. 1999) are *R. aestuarii* (Yoon et al. 2008), *R. mucosus* (Biebl et al. 2005b), *R. nanhaiticus* (Wang et al. 2010), and *R. nubinhibens* (González et al. 2003). Another group includes *R. crassostreae*

(Boettcher et al. 2005), causative agent of the juvenile oyster disease (JOD) or *Roseovarius* oyster disease (ROD), *R. halocynthiae* (Kim et al. 2012c), and *R. sediminilitoris* (Park and Yoon 2013). A third group is formed by *R. pacificus* (Wang et al. 2009b), *R. halotolerans* (Oh et al. 2009), *R. indicus* (Lai et al. 2011b), and *R. litoreus* (Jung et al. 2012b). This group merges with the "tolerans" group in ML analysis and both have *Pelagicola litoralis* marginally related (not shown). Finally, the species *R. marinus* (Jung et al. 2011) is kept apart from other *Roseovarius* species and very close to *Pacifibacter maritimus* (99.2 % 16S rRNA similarity), being a candidate for reclassification in this genus or even into the species (synonymy).

The genus description, not emended since the original publication, states that *Roseovarius* members are Gram-negative rods with one or both poles pointed, multiplying by monopolar growth (budding process). Motility and PHB accumulation may be positive, as well as Bchl *a* production and colony pigmentation. Temperature range enabling growth is from <3 °C to 43 °C, salinity from <1 % to 10 % NaCl, and pH from 5.3 to >9. They are heterotrophic, strict aerobes, and have no fermentative ability. They do not grow in anaerobiosis with nitrate and not able to grow photoautotrophically with H_2/CO_2 or photoorganotrophically with acetate or glutamate. Catalase, peroxidase, and cytochrome oxidase activities are positive, although the latter is weak. Cells contain the following polar lipids: DPG, PG, PC, PE, an unknown phospholipid, and an unknown lipid. The dominant fatty acid is C18:1 ω7c, accompanied by C18:2, C12:0 2OH, C12:1 3OH, C16:1, C16:0, and C18:0. Q10 is the major respiratory quinone. The G+C content of the type species is 62–64 mol%. The range of G+C content within the currently named species goes from 55.4 to 66 mol%. Some species require vitamins. Despite the absence of emendation to this description, some species of *Roseovarius* have been described as denitrifiers (*R. crassostreae*) or have different polar lipid profiles (*R. litoreus* lacks DPG). As a general rule, *Roseovarius* spp. require sodium ion for growth and some require also magnesium (*R. halocynthiae*, *R. marinus*, and *R. sediminilitoris*). The salinity range of some species reaches 20 % (*R. halotolerans*). Bchl *a* production is detected in strains of *R. tolerans* and *R. mucosus* (weakly in the later) and *pufLM* genes are present in the genome of *R. indicus* but absent for all other species except for *R. tolerans* and *R. mucosus* (Lai et al. 2011b). An outstanding activity of *R. nubinhibens* is its ability to demethylate dimethylsulfoniopropionate (DMSP), one of the key activities in the marine sulfur cycle.

DDH experiments between *Roseovarius* species have been performed for several pairs with the following results: González et al. (2003) reported 42 % between *R. nubinhibens* and *R. tolerans*; Boettcher et al. (2005) found 11 % relatedness between *R. crassostreae* and *R. tolerans* and 47 % between the former and *R. nubinhibens*; a 13 % DDH was found between *R. aestuarii* and *R. nubinhibens* by Yoon and coworkers (2008); *R. halotolerans* showed 1–5 % DDH relatedness to *R. tolerans*, *R. crassostreae*, and *R. nubinhibens* and 25 % to *R. mucosus*, according to Oh et al. (2009); the relationship between *R. indicus* and *R. halotolerans* and *R. pacificus* was 48 % and 44 %, respectively (Lai et al. 2011b); *R. halocynthiae* exhibited a 13 % relatedness to *R. crassostreae* (Kim et al. 2012c); and *R. litoreus* showed 33 % relatedness to *R. halotolerans* and 18 % to *R. pacificus* (Jung et al. 2012b). The recently described *R. sediminilitoris* was related to its neighbors *R. crassostreae* and *R. halocynthiae* by 16 and 22 % DDH, respectively (Park and Yoon 2013).

The genome of *R. nubinhibens* ISM^T has been sequenced and their general features are as follows: estimate genome size is 3.68 Mbp, estimated number of coding sequences is 3,547, and G+C content is 63.9 mol%. This strain has been the subject of several studies related to its activities on sulfur-containing organic molecules (González et al. 1999, 2003).

A "hidden" prophage has been reported in the genome of *R. nubinhibens* ISM^T (Zhao et al. 2010) that was unnoticed when employing methods aimed to classical prophage gene detection, but could be revealed through induction experiments.

Strains close to *R. tolerans* are able to produce free and organic iodine from iodide (Fuse et al. 2003), and iodide-oxidizing bacteria related to this species were isolated from iodide-rich natural gas brines and seawater (Amachi et al. 2005).

While members of the *Roseobacter* group are mostly non-pathogenic, a few exceptions could be found among *Roseovarius* species: *R. crassotreae* is involved in the juvenile oyster disease (JOD), also called *Roseovarius* oyster disease (ROD), a condition that causes seasonal mortalities among commercially produced eastern oysters (*Crassostrea virginica*) in the Northeastern coast of the USA. *R. crassotreae* is dominant among the bacterial consortia associated with the inner shell surface of JOD-affected animals. The polar attachment of the *R. crassostreae* cells to shell and conchiolin is believed to be related to polar fimbriae production and may protect the bacteria from hemocyte-mediated killing (Boardman et al. 2008). Culture-independent methods have revealed that strains similar to *R. crassostreae* are significantly associated to Australian Subtropical White Syndrome, an infectious, temperature-dependent disease of the coral *Turbinaria mesenterina*. The fact that this association is seen in a range of different types of disease lesions and on a range of different coral species suggests that these strains may be present simply as opportunists and are not directly responsible for causing the disease, but their possible role as pathogens cannot be ruled out (Godwin et al. 2012).

Rubellimicrobium

The genus *Rubellimicrobium* contains four species isolated from habitats other than the typical marine environments that inhabit most roseobacters. The first species described, *Rubellimicrobium thermophilum* (Denner et al. 2006), was isolated from colored biofilms formed in two fine-paper machines and a pulp dryer from the paper industry in Finland. The strains were slightly thermophilic, pigmented, and resistant to a common industrial biocide, 2,2-dibromo-3-nitrilopropionamide. Two other species, *R. mesophilum* (Dastager et al. 2008) and

R. roseum (Cao et al. 2010), were isolated from soil, while *R. aerolatum* was obtained from an air sample (Weon et al. 2009). In addition, field studies using culture-independent detection methods have revealed that *Rubellimicrobium* is a part of the characteristic soil communities of noncultivated soils, from which they disappear after agricultural use (Köberl et al. 2011). Along with *Acidobacteria*, they have been proposed as management indicator to discriminate between sustainable and non-sustainable agricultural practices (Figuerola et al. 2012). It has been also suggested that terrestrial hot springs might be a habitat for rubellimicrobia: isolate OSrt, enriched from Octopus Spring (Yellowstone Park, USA) and used as feed bacterium for the cultivation of the thermophilic amoeba *Echinamoeba thermarum*, is either a strain of *Rubellimicrobium thermophilum* or a closely related, unnamed species, based on 16S rRNA gene sequence similarity (>99 %) (Baumgartner et al. 2003; Denner et al. 2006).

Rubellimicrobium spp. form a well-defined subclade in the boundaries of the *Roseobacter* clade, to which *Roseicyclus mahoneyensis* and *Wenxinia marina* are loosely related (*Fig. 20.5*).

Defining features of the genus, as established by Denner et al. (2006), were as follows: Gram-negative, rod-shaped cells that produce carotenoids but not endospores, strict aerobes, positive for oxidase, and weakly positive for catalase. It is chemoorganoheterotrophic, using a large number of organic compounds for growth. Q10 is the major respiratory lipoquinone and DPG and PC are the major polar lipids, with minor amounts of PG. The predominant fatty acid is C19:0 cyclo ω8c, followed by C18:0 and C16:0. Main polyamines are spermidine, *sym*-homospermidine, and putrescine. DNA G+C content is 69–70 mol% for the type species, *R. thermophilum*, but the range for the four recognized species is 67–72 mol%. The type species differ from the rest by its moderate thermophily, having an optimum temperature for growth of 45–52 °C and a maximum of 56 °C, while the other three species are clearly mesophilic (28–30 °C optima, maxima 30–37 °C). Notable differences in polar lipid profile and cellular fatty acid composition are also found among species (probably as a consequence of the different growth conditions). In particular, the dominant fatty acids of the mesophilic rubellimicrobia are more similar to the typical major fatty acids of the rest of the roseobacters, with C18:1 ω7c as the most abundant one. Rubellimicrobia are non-halophilic, in consonance to their habitats; some of the species are sensitive to NaCl, which is not tolerated in the medium or only when lower than 1 %. All species form red colonies.

Draft genome of *R. thermophilum* DSM 16684^T, which is 3.16 Mb in size, contains 3,244 protein-coding genes.

Ruegeria

Ruegeria, one of the earliest described genera in the *Roseobacter* group, contains ten species. The history of this genus is an example of the taxonomic turmoil undergone at other parts of the group. The type species of the genus *R. atlantica* was formerly known as *Agrobacterium atlanticum*. Uchino and coworkers reclassified this and other species of the so-called marine agrobacteria (Rüger and Höfle 1992) in three new genera, *Stappia*, *Ahrensia*, and *Ruegeria* (Uchino et al. 1998). At that time, the genus comprised the species *Ruegeria atlantica* (resulting from the reclassification of *Agrobacterium atlanticum* and *Agrobacterium meteori*, both considered synonyms), *Ruegeria gelatinovora* (from *Agrobacterium gelatinovorum*), and *Ruegeria algicola* (from *Roseobacter algicola*). *R. gelatinovora* was later reclassified in the genus *Thalassobius* (Arahal et al. 2005) and *R. algicola* became *Marinovum algicola* (Martens et al. 2006), leaving the genus with only one species. Shortly after, Yi et al. (2007) proposed to transfer the two species of the genus *Silicibacter*, *S. lacuscaerulensis* (Petursdottir and Kristjansson 1999), and *S. pomeroyi* (González et al. 2003) to the genus *Ruegeria*, based on the close phylogenetic relationship between the three taxa (sequence similarities of 96.9–98.2 % on 16S rRNA gene, monophyletic clade), and emended the genus for a second time (a first emendation was proposed by Martens et al. 2006). The transfer has not been universally accepted, as some authors still support the maintenance of *Silicibacter* genus based on phenotypic differences (Muramatsu et al. 2007). Since, the following species have been described within the genus: *R. mobilis* (Muramatsu et al. 2007), *R. pelagia* (Lee et al. 2007c; found to be a later heterotypic synonym of *R. mobilis* by Lai et al. 2010a), *R. scottomollicae* (Vandecandelaere et al. 2008b), *R. marina* (Huo et al. 2011), *R. faecimaris* (Oh et al. 2011a), *R. halocynthiae* (Kim et al. 2012d), *R. arenilitoris* (Park and Yoon 2012b), and *R. conchae* (Lee et al. 2012b). All species have been isolated from marine samples, except for *R. lacuscaerulensis*, that were isolated from the water of the Blue Lagoon, a shallow geothermal lake in Iceland.

All *Ruegeria* species, including the two reclassified *Silicibacter*, merge in one clade that includes also *Sediminimonas* and *Salinihabitants* and have the clade *Phaeobacter caeruleus-Phaeobacter daeponensis-Leisingera sensu stricto-Nautella italica* as closest neighbor (*Fig. 20.5*).

After the last emendation, the genus is defined by the following traits: Gram-negative, chemoheterotrophic, strict aerobes, negative for Bchl *a* production and *puf* genes; they accumulate PHB and require sea salts for growth. Oxidase and catalase are positive. When motile, cells have polar flagella. Q10 is the dominant quinone, major fatty acids are C18:1 ω7c and 11-methyl C18:1 ω7c, and polar lipids include PC, PE, PG, and several phospholipids. The DNA G+C content is 55–68 mol%. Some exceptions to this profile can be found among currently recognized species; thus, *R. mobilis* and *R. marina* do not have a strict requirement of salt for growth, and PE is not detected among the polar lipids of several species (*R. faecimaris*, *R. halocynthiae*, *R. arenilitoris*, and *R. conchae*). Some species denitrify (*R. atlantica*, *R. lacuscaerulensis*); others are described as able to reduce nitrate or to grow with nitrate in anaerobic conditions, but denitrification ability is not confirmed (*R. faecimaris*, *R. arenilitoris*, *R. halocynthiae*). *R. lacuscaerulensis*

and *R. mobilis* produce tan or brown pigments, which may be related to antifouling/antimicrobial activities, in a way similar to that of *Phaeobacter* species (Porsby et al. 2008; Gram et al. 2010). Riclea et al. (2012) have identified five lactones in the volatile fraction of *R. pomeroyi* DSS-3. The structures of these lactones have been unambiguously assigned by comparison to synthetic standards that showed, in agar diffusion assays, specific activity against algae, but not against bacteria or fungi, suggesting that the lactones may have an ecological function in the interaction between the bacteria and the algae in fading algal blooms, similar to the recently described roseobacticides from *P. gallaeciensis*, which are active against *Emiliania huxleyi*.

Ruegeria species are relevant for the metabolism of DMSP in the marine environment, being *R. pomeroyi* one of the most studied contributors (González et al. 2003; Reisch et al. 2008, 2011; Todd et al. 2011, 2012).

The genomes of up to six *Ruegeria* strains have been sequenced (Roseobase), being *R. pomeroyi* type strain, DSS-3^T, the first of the *Roseobacter* clade that was completed and analyzed (Moran et al. 2004). It contains 4,283 coding sequences distributed between a chromosome of 4.11 Mbp and one megaplasmid of 491 Kbp. Three rRNA operons and 53 tRNA genes are present. Analysis of gene content revealed a metabolic strategy based on lithotrophic exploitation of carbon monoxide and sulfide, combined with heterotrophy. Abundant genes encoding for ABC-type transporters of peptides, amino acids, polyamines, and osmolytes (glycine betaine, DMSP) are also present, as well as multiple TRAP transporter systems. Other *Ruegeria* genomes also contain genes for carbon monoxide oxidation, namely, strain TM1040 (Moran et al. 2007) and TW15—now *R. conchae* (Lee et al. 2011b). Quorum-sensing related genes are also present in some *Ruegeria* genomes, including the one of *R. pomeroyi* DDS-3^T and *Ruegeria* sp. KLH11 (Zan et al. 2011).

An interesting approach by high-throughput proteogenomics has been conducted on *R. pomeroyi* DDS-3^T aiming at a better genomic annotation for the whole marine *Roseobacter* clade (Christie-Oleza et al. 2012). For this, a large dataset of peptides was obtained after searching over 1.1 million MS/MS spectra, from *R. pomeroyi* DDS-3^T cultivated under 30 different conditions against a six-frame translated genome database. The authors detected open reading frames that had not previously been annotated and genes that were wrongly annotated. By extending these re-annotations to the genomes of the other 36 *Roseobacter* isolates (20 different genera) available at that time, they proposed the correction of the assigned start codons of 1,082 homologous genes in the clade and reported the presence of novel genes within operons encoding determinants of the important tricarboxylic acid cycle, a feature characteristic of some *Roseobacter* genomes.

Bacteriophages infecting *R. pomeroyi* (Zhao et al. 2009) and *Ruegeria* sp. strain TM1040 (Chen et al. 2006) have been detected and characterized. The former were lytic phages isolated from seawater, while the later were obtained after induction with mitomycin C and were assumed to be attenuated phages representative of three of the five prophage-like elements detected in the genome of TM1040.

Sagittula

Sagittula stellata is the type species of the genus *Sagittula* (González et al. 1997), one of the oldest members of the *Roseobacter* group and distantly related to *Antarctobacter heliothermus*, *Ponticoccus litoralis*, and *Mameliella alba* (Fig. 20.5). The type strain E-37^T was isolated from a marine enrichment community obtained from salt marsh seawater in Georgia (USA) and grown on pulp mill effluent, rich in lignin.

The genus is defined by the following traits: cells are rod shaped and Gram negative, have a polar holdfast, and numerous vesicles on the surface, derived from the outer membrane. They form rosettes and aggregates. They are strict aerobes, oxidase and catalase positive, and grow on sugars, fatty acids, and amino acids. The type species also uses methanol and some aromatic compounds. They require sea salts for growth. In a recent emendation of the genus, Lee et al. (2013b) added to these generic properties the presence of Q10 as major respiratory quinone and a complex polar lipid profile: DPG, PC, PE, PG, and several unidentified (two ALs, one PL, and four Ls) polar lipids. These authors added a second species to the genus *S. marina*, which shows biochemical and physiological features similar to the ones of *S. stellata*: both species are mesophilic, neutrophilic, and grow up to 7 % NaCl; do not reduce nitrates; are able to use several carbohydrates, organic acids, and amino acids; and have C18:1 ω7c, C12:1 3OH, 11-methyl C18:1 ω7c, and C16:0 as major fatty acids. However, *S. marina* lacks the ability to degrade carboxymethylcellulose and to partially solubilize synthetic lignin in presence of glucose, defining properties of the genus according to González (2005), among other differences. The C+G content of the genus is 61–65 mol%.

The estimated genome size of E-37^T, type strain of *S. stellata*, is 5.26 Mbp and contains 5,067 coding sequences (Roseobase). *S. stellata* produces amphiphilic exopolymeric substances which induce self-assembly of marine dissolved organic matter and formation of microgels (Ding et al. 2008), and it is able to use dimethylsulfide oxidation as an anergy source, while growing on fructose or succinate (Boden et al. 2011).

Salinihabitans

Salinihabitans currently contains a single species, *S. flavidus* (Yoon et al. 2009b), represented by a single strain that shows optimal growth at 7 % NaCl and tolerates up to 17 % in the culture media. Thus, it is a true moderate halophile better adapted to the conditions of the isolation habitat, a marine solar saltern, than most other roseobacters. It forms pale yellow colonies on Marine Agar, is mesophilic, neutrophilic, and strictly aerobic. Chemotaxonomic features include Q10 as predominant quinone and a fatty acid composition that features C19:0 cyclo ω8c as the major fatty acid (46 % of the total), an atypical trait in the whole family (the usually dominant fatty acid is 18:1 ω7c, which represents only 18 % of the total in *S. flavidus* profile). This trait, being the only that clearly

differentiates this taxon from other related roseobacters, might be due to methodological bias (Yoon et al. 2009b).

Salinihabitans flavidus merges the *Ruegeria* clade in the complete analysis of the *Rhodobacteraceae*, along with *Sediminimonas qiaohouensis*.

Salipiger

The genus *Salipiger* was described based on an isolate from a saline soil bordering a saltern, at the Spanish Mediterranean coast (Martínez-Cánovas et al. 2004). To date, it contains a single species, *S. mucosus*, named after its ability to produce an exopolysaccharide. This polysaccharide incorporates notorious amounts of sulfates, an unusual trait in other bacterial counterparts, according to Llamas et al. (2010) who characterized its composition and properties.

The genus is related to *Tranquillimonas* and *Palleronia*, the later isolated from the same geographic area than *Salipiger mucosus* type strain.

Characters defining the genus are as follows: Gram-negative, nonmotile rods; strictly aerobic chemoorganotrophs; unable to grow in anaerobic conditions either by fermentation, nitrate or fumarate reduction, or photoheterotrophy; produce polyhydroxyalkanoates (PHA); and are oxidase and catalase positive. Strictly halophilic, they require Na ion for growth and display very low nutritional and biochemical versatility. Contain ubiquinone Q10 and present C18:1 ω7c and C16:0 as major cellular fatty acids.

The species *S. mucosus* forms encapsulated cells and mucoid colonies, growing optimally with 9–10 % sea salts added to the medium (total range 0.5–20 % NaCl), at 20–40 °C and at pH 6 to 10. Hydrolytic abilities are restricted to urea and Tween 20. It does not synthetize Bchl *a* and is unable to use any of the sole carbon and energy sources tested. The C+G molar content is 64.5 mol%. The draft genome of *S. mucosus* DSM 16094^T has 5.7 Mb.

Sediminimonas

Sediminimonas, described by Wang et al. (2009c), accommodates one species, *S. qiaohouensis*, a relative to the *Ruegeria* clade and to the genus *Salinihabitans*. The species was isolated from a salt mine sediment in China but has been also detected by DGGE in coastal seawater (South China Sea; Yang et al. 2012).

The genus contains Gram-negative, nonmotile rods that are aerobic and unable to synthetize Bchl *a*, do not produce PHB or exopolysaccharides, and are able to reduce nitrates to nitrites. It is chemoheterotrophic and strictly halophilic, require NaCl for growth, and are able to use a variety of carbon sources, including carbohydrates. Major fatty acids are C18:1 ω7c, C16:0, C18:1 ω9c, 11-methyl C18:1 ω7c, and C19:0 cyclo ω8c. Polar lipids include DPG, PG, PC, and four unknown PLs. Q10 is the only respiratory quinone and the G+C molar content of the type and only species is 63–64 mol%. The draft genome of *S. qiaohouensis* DSM 21189^T has 3.55 Mb.

S. qiaohouensis is able to grow between 0.25 % and 20 % NaCl content, having optimal growth between 1.5 % and 10 % NaCl. Colonies are faint brown to yellow colored. It is mesophilic and neutrophilic, positive for catalase and oxidase, able to use several sugars (D-glucose, D-fructose, D-galactose, maltose, D-mannose, sucrose, D-psicose, trehalose, turanose), sugar alcohols (glycerol, D-mannitol), and some amino acids (D- and L-alanine, L-glutamic acid, and L-serine).

Seohaeicola

Seohaeicola is another monospecific genus: *S. saemankumensis*, the only species recognized up to date, was described based on a single strain isolated from a tidal flat (Yoon et al. 2009c). It is close to the *Phaeobacter sensu stricto* clade. Main generic traits include the presence of Q10 as predominant quinone, C18:1 ω7c and 11-methyl C18:1 ω7c as major cellular fatty acids, and PC, PG, and PE plus an unidentified lipid as major polar lipids. The cells are Gram negative, ovoid to coccoid, and nonmotile. The species forms pale yellow colonies on Marine Agar and does not synthetize Bchl *a*. It is unable to growth without NaCl or with more than 7 %. Growth is possible between 4 °C and 40 °C. The strain grows anaerobically in Marine Agar with or without nitrate, which is reduced. Catalase and oxidase tests are positive. Acetate was used as sole carbon and energy source. The G+C molar content is 63.4 mol%.

Shimia

Shimia marina, the type species of the genus, was described by Choi and Cho (2006b) after the study of one isolate obtained from a fish farm biofilm. A second species, *S. isoporae*, was later described to accommodate novel isolates from the reef-building coral *Isopora palifera* (Chen et al. 2011b). The genus is related to the clade that contains all the *Thalassobius* species plus *Epibacterium ulvae*.

Traits defining the genus *Shimia* include presence of Q10 and C18:1 ω7c as dominant quinone and cellular fatty acid, respectively, absence of Bchl *a*, a positive response to oxidase and catalase tests, and a heterotrophic, strictly aerobic metabolism. Their cells are Gram negative, rod shaped, and do not contain cytoplasmic granules.

Shimia species are slightly halophilic (with salinity ranges of 1–5 %, *S. isoporae*, and 1–7 % NaCl, *S. marina*), neutrophilic (optimal growth at pH 7–8), and mesophilic (optimal growth at 30–35 °C, *S. marina*, or 25–30 °C, *S. isoporae*). They are motile by monopolar flagella. Both species of *Shimia* are related by DDH levels around 43 % (Chen et al. 2011b) and differ in their response to nitrate reduction, indole, arginine dihydrolase, lipase, lecithinase, and β-galactosidase activities, as well as in their ability to assimilate some sugars (glucose, maltose, and mannose).

Sulfitobacter

The genus *Sulfitobacter* is one of the oldest members of the *Roseobacter* group. It was described by Sorokin (1995) to encompass a new heterotrophic, marine species able to oxidize sulfite, *Sulfitobacter pontiacus*, isolated from the Black Sea. Currently, the genus contains nine species, including the former *Staleya guttiformis* that was reclassified as *Sulfitobacter guttiformis* (Yoon et al. 2007f). The nine species are grouped in a stable clade that also includes *Oceanibulbus indolifex* as a very close relative to the pair *S. delicatus* and *S. dubius*. Next to the clade two *Roseobacter* species appear as their closest neighbors. A deeply branching clade that contains *Sulfitobacter* (plus *Oceanibulbus*) and *Roseobacter* species is also recovered by analyzing 70 conserved, single-copy genes retrieved from 32 roseobacters genomes (Newton et al. 2010), confirming the solid nature of the *Sulfitobacter-Oceanibulbus-Roseobacter* grouping.

Members of the genus *Sulfitobacter* have rod-shaped cells, sometimes pointed for one pole and showing monopolar growth and budding division. Rosette formation is common. When motile, flagella are inserted subpolarly. Several species, including the type species, accumulate PHB granules. None of them synthetizes Bchl *a*, with the exception of some *S. guttiformis* strains, a trait that contributed to its former consideration as a different genus. Photosynthetic genes are plasmid located in *S. guttiformis* (Pradella et al. 2004), and the plasmid has an independent origin from the one in *Roseobacter denitrificans*, the other AAP with plasmid-encoded photosynthetic gene clusters (Petersen et al. 2012). Sulfite oxidation is displayed by five species, being *S. pontiacus* the one with higher tolerance to this compound (up to 60 mM). *S. pontiacus* derives energy from sulfite oxidation during growth on organic compounds as acetate. Thus, it can be considered a lithoheterotroph. It is also able to oxidize sulfur and thiosulfate. Ability to perform oxidation of sulfite to sulfate is dependent of an AMP-independent soluble sulfite dehydrogenase (Sorokin et al. 2005a). As obligate heterotrophs, sulfitobacters are able to assimilate a variety of organic acids and amino acids. They are strict aerobes and present oxidase and catalase activities. Peptidoglycan contains *m*-DAP in *S. guttiformis* and *S. brevis**. Common polar lipids of the genus are PC, PG, and PE (with low levels of DPG in some species and the occasional presence of one AL or one PL), and main cellular fatty acids correspond to C18:1 ω7c, C16:0, C10:0 3OH, and 11-methyl C18:1 ω7c. Predominant quinone is Q10 and the G+C content of their DNA is 55 to 64 mol%.

*[Gorshkova et al. (2007) reported a surprising finding in *Sulfitobacter brevis* KKM 6006: a teichoic acid containing glycerol, ribitol, and *N*-Acetyl-D-glucosamine. To the best of our knowledge, this is the first time a teichoic acid is found in Gram-negative bacteria].

The highest interspecific value of DDH between *Sulfitobacter* species relates the pair *S. pontiacus-S. mediterraneus* by 46 % (Pukall et al. 1999). Ivanova et al. (2004) determined the DDH values for the type strains of *S. dubius* and *S. delicatus* against *S. pontiacus*, *S. mediterraneus*, *S. brevis*, and *S. guttiformis*, with the higher figure relating *S. mediterraneus* and *S. dubius* (41 % DDH) and the lower *S. guttiformis* and *S. delicatus* (5 %). Yoon et al. (2007g) found values of 9–21 % DDH between *S. marinus* and the *Sulfitobacter* species previously described. *S. litoralis* and *S. pontiacus* are related by a 24 % DDH (Park et al. 2007) and *S. donghicola* and *S. guttiformis* show a 17 % DDH, according to Yoon et al. (2007f).

Sulfitobacter species are widespread in marine habitats: they have been detected/isolated from seawater, biofilms, sediments, marine animals, and algae and aquaculture environments. In addition to the original isolation from Black Sea waters (Sorokin 1995), they have been found as part of the bacterioplankton of polar seawater (Mergaert et al. 2001), deep layer oxycline at South Pacific waters (Stevens and Ulloa 2008), Adriatic seawater (Silović et al. 2012), near-shore mud in French Guiana (Madrid et al. 2001), biofilms formed in submersed glass (Kwon et al. 2002), and microbial mats in Antarctic lakes (Van Trappen et al. 2002), and they are enriched in oil-contaminated seawater (Brakstad and Lødeng 2005; Prabagaran et al. 2007; Jung et al. 2010b). As epiphytes, they have been found on diatoms (Shäfer et al. 2002; Hünken et al. 2008), marine brown and red algae (Beleneva and Zhukova 2006), or dinoflagellates—*Alexandrium fundyense* (Li et al. 2011b). Isolation from marine animals is also documented, both from wild and cultured fish and invertebrates: Griffiths et al. (2001) isolated *Sulfitobacter* strains from healthy haddock larvae; McIntosh et al. (2008) found them in cod larvae, and several invertebrates also show *Sulfitobacter* colonization—spiny lobster larvae (Payne et al. 2008), cultivated mollusks (Beleneva et al. 2007), sea anemones (Du et al. 2010), cnidarians (Schuett and Doepke 2010), and corals (Higuchi et al. 2012).

Sulfitobacter participates in the metabolism of diverse sulfur compounds in marine environments: they are among the bacteria that show elevated nucleic acid content when the water is amended with DMSP (Mou et al. 2005) and, in fact, are able to metabolize DMSP to DMS (Curson et al. 2008). Other interesting metabolic abilities of members of the genus are related to phthalate degradation (Iwaki et al. 2012b). *S. pontiacus* sulfite oxidase has been investigated with the aim of constructing a biosensor system for sulfite detection on food and beverages (Muffler and Ulber 2008).

The ethanol extract of strain P1-17B, an isolate close to *S. pontiacus* and collected from the interface of brine pools and sea water of the Red Sea, was among the most potent against tested cancer cell lines in a study of bioactive molecules with cytotoxic and apoptotic activity (Sagar et al. 2013).

Genomes of two *Sulfitobacter* strains have been sequenced: *Sulfitobacter* EE-36 has an estimated genome size of 3.55 Mbp with 3,474 coding sequences and a G+C molar content of 60.3 mol%. This strain is a host for a bacteriophage isolated from Baltimore Inner Harbor water (Zhao et al. 2009), similar to the one isolated from *Ruegeria pomeroyi* DSS-3 by the same authors. *Sulfitobacter* NAS-14.1, an isolate that was obtained

with DMSP as sole carbon source, has a genome of 4.0 Mbp in size that contains 3,962 coding sequences (Roseobase).

Tateyamaria

The genus *Tateyamaria* (Kurahashi and Yokota 2007) was raised to encompass a single species, *T. omphalii*, isolated from the shell of a molluskan collected in Japan coastal waters. Three years later, a second species was described, *T. pelophila*, on isolates obtained from tidal flat sediments from the German coast of the North Sea. The description of the second species was accompanied by an emendation of the genus (Sass et al. 2010). The pair of species is located nearby *Nereida*, *Lentibacter*, and the *Roseobacter-Sulfitobacter* clade, in the 16S rRNA-based tree (Fig. 20.5).

The emended description of the genus establishes that *Tateyamaria* members are Gram-negative coccoid or short rods that may be motile by polar flagella and require sodium chloride for growth. They are aerobic, mesophilic, and positive for oxidase, catalase, and phosphatase activities. They may produce Bchl *a*. Q10 is the predominant respiratory quinone. Cellular fatty acids comprise C18:1 ω7c, C16:0, 11-methyl C18:1 ω7c, C19:0 cyclo ω8c, C10:0 3 OH, and C12:0 3 OH. The G+C content of the two currently recognized species is 56.4–61.6 mol%.

T. omphalii and *T. pelophila* differ in several traits, as motility and the ability for Bchl *a* production, both positive in the second species. *T. pelophila* is also able to oxidize sulfite, thiosulfate, and hydrogen while growing lithoheterotrophically. Its salinity range is wider (0.3–10 % NaCl) than the one of *T. omphalii* (0.2–6 % NaCl), but the maximal temperature for growth is lower. Both species require biotin and pantothenate (plus thiamine in *T. pelophila*). Polar lipids have been determined only for *T. pelophila*, which shows PG and PE as major components and only trace amounts of PC and an unidentified lipid.

Tateyamaria is one of the genera recently isolated from soft corals and shown to display antimicrobial activities (Chen et al. 2012b).

Thalassobacter

The genus *Thalassobacter* (Macián et al. 2005b) is phylogenetically allocated in the vicinity of the genus *Jannaschia* (Fig. 20.5). It contains a single species, *T. stenotrophicus*, which includes the strain used for the genus description, along with the ones originally proposed as members of *Jannaschia cystaugens* (Adachi et al. 2004), later considered a synonym of *T. stenotrophicus* (Pujalte et al. 2005b).

The genus includes Gram-negative ovoid to irregular rods, motile by one polar flagellum. They are strict aerobes, chemoorganotrophic, and slightly halophilic, positive for catalase and oxidase. Cells show budding and binary division and accumulate PHB. Bchl *a* is produced. Seawater or a complex mixture of marine salts is required for growth. Mesophilic. No hydrolytic activities on polymeric substrates (proteins, polysaccharides, lipids, nucleic acids) are observed. Major polar lipids are PG, DPG, and PC. PE is absent. Major cellular fatty acids are C18:1 ω7c, 11-methyl C18:1 ω7c, C18:1 ω9c, and C20:1 ω7c. The G+C content of its DNA is around 59 mol%. The predominant respiratory quinone was determined by Adachi et al. (2004) to be Q10.

In 2009 a second species, *T. arenae*, was described by Kim et al., but it was later reclassified into the genus *Litoreibacter* as *L. arenae* (Kim et al. 2012b).

T. stenotrophicus grows on Marine Agar producing reddish to brown pigmentation and does not reduce nitrate to nitrite or gas. The type strain is able to use several organic acids and amino acids as sole carbon and energy source (pyruvate, acetate, 2-oxoglutarate, succinate, 3 hydroxybutyrate, L-glutamate, L-ornithine, L-citrulline, and putrescine) provided that the basal medium is supplemented with small amounts of yeast extract, a fact that suggests growth factor requirements. The preferred carbon sources of the species were confirmed in enrichment experiments by Gómez-Consarnau et al. (2012) who found that *Thalassobacter* sp. increased in relative abundance in seawater amended with pyruvate and amino acids.

The strains formerly known as *J. cystaugens* are able to inhibit cyst formation on toxic dinoflagellate *Alexandrium tamarense* (Adachi et al. 2002).

Thalassobius

The genus *Thalassobius* was established by Arahal et al. (2005) to account for two species, *T. mediterraneus* type species, isolated from seawater, and *T. gelatinovorus*, which corresponds to the reclassification of the former *Ruegeria gelatinovorans* (Uchino et al. 1998). Currently, two more species are included in the genus: *T. aestuarii* (Yi and Chun 2006) and *T. maritimus* (Park et al. 2012). The four species merge in a group that also includes *Epibacterium ulvae* (specifically related to *T. aestuarii*), both species of *Shimia*, *Thalassococcus* and *Octadecabacter* (Fig. 20.5), with *T. maritimus* being the more loosely related to the *Thalassobius* core species.

Thalassobius species present the following features: they are Gram-negative, strictly aerobic, chemoorganotrophic bacteria that divide by binary fission. Cells are coccoid to rod shaped and accumulate PHB. They require seawater or combined marine salts for growth and are slightly halophilic and mesophilic. They do not ferment carbohydrates and prefer organic acids and amino acids as carbon sources. Their G+C content ranges from 57–61 mol%. The predominant quinone is Q10. Major cellular fatty acid is C18:1 ω7c, with minor amounts of C16:0, C18:0, and 11-methyl C18:1 ω7c. Park et al. (2012) determined polar lipids for the four species, which include PE and PG and smaller amounts of PC plus an unidentified lipid.

T. aestuarii shows DDH values of 20 % and 43 % to *T. mediterraneus* and *T. gelatinovorus*, respectively (Yi and Chun 2006), while *T. maritimus* is related to *T. gelatinovorus* (its nearest species) by 17 % (Park et al. 2012). The four species could be differentiated by motility and nitrate reduction (both positive for *T. aestuarii* and *T. gelatinovorus*), a distinctive range of hydrolytic abilities on casein, gelatin, Tweens, and urea and differences on the carbon source pattern (Park et al. 2012).

Unidentified *Thalassobius* spp. have been related to epizootic shell disease (ESD) lesions on American lobster, *Homarus americanus*, and other crustacea. The lesions are colonized by a Bacteroidetes bacterium (*Aquimarina* sp.) altogether with *Thalassobius* sp. (Quinn et al. 2012; Chistoserdov et al. 2012). Algicidal activities have been also reported for strains tentatively identified as *Thalassobius* (Oh et al. 2011b; Wang et al. 2010b). A *Thalassobius* sp. strain able to utilize phthalate has been isolated from seawater (Iwaki et al. 2012b).

The genome draft of a strain of *Thalassobius* sp., R2A62, has been obtained (Roseobase) and reveals a genome size of 3.49 Mbp, 3,696 coding sequences, and a G+C content of 55 mol%, slightly below of the one of the species described so far.

Thalassococcus

Closely related to *Thalassobius* species, the genus *Thalassococcus* contained a single species *T. halodurans* (Lee et al. 2007b) until the recent proposal of *Thalassococcus lentus* (Park et al. 2013b). The type species was isolated from the surface of a marine sponge, *Halichondria panicea*, at the pacific coast of the USA.

Defining features of the genus are as follows: Gram-negative, ovoid-shaped, nonpigmented cells. They are nonmotile, oxidase and catalase positive, strictly aerobic, and halophilic. Q10 is the major respiratory quinone and C18:1 ω7c, C18:1 ω9c, C16:0, and C18:0 are the major cellular fatty acids. *T. halodurans* requires at least 2% NaCl for growth and is able to grow in the presence of up to 18 %. It is mesophilic and neutrophilic, lacks extracellular hydrolytic abilities, and reduces nitrates to nitrite, but not to N_2. It produces acid from some carbohydrates on API 50CH and is also able to use carbohydrates as carbon sources (glycerol, glucose, and galactose, among others). The G+C content of its DNA is 58.8 mol% (58 % for *T. lentus*, which is related by a 17 % DDH value to *T. halodurans*, according to Park et al. 2013b).

Tranquillimonas

This monospecific genus occupies an isolated position near *Salipiger mucosus* and *Palleronia marisminoris* in the 16S rRNA tree. Its type and single species, *Tranquillimonas alkanivorans* (Harwati et al. 2008), was isolated from seawater at the Semarang Port, Indonesia, during a search for hydrocarbon-degrading bacteria, and, as indicated by the species name, it is able to degrade alkanes ($C_{10–13}$). Its general characteristics fit the profile of the majority of roseobacters, with no other special trait: they are Gram negative, nonmotile, obligately halophilic, requiring Na ion for growth, oxidase and catalase positive, and pink pigmented on Marine Agar. Cells contain polyhydroxyalkanoates, Q10 as major respiratory quinone, and C18:1 ω7c, C19:0 cyclo ω8c, and C16:0 as major fatty acids. DNA G+C content is 69 mol%. *T. alkanivorans* is able to grow up to 13 % NaCl and from 10 °C to 50 °C, with an optimum at 43 °C. It uses a variety of carbon sources on Biolog plates, including carbohydrates, organic acids, and amino acids, and is able to reduce nitrate to nitrite.

Tropicibacter

In 2009, Harwati and colleagues proposed a new genus, *Tropicibacter*, to allocate a marine species able to degrade aromatic hydrocarbons. *Tropicibacter naphthalenivorans* (Harwati et al. 2009a) was isolated from Indonesian Semarang Port seawater and demonstrated to degrade hydrocarbons in crude oil (Harwati et al. 2007). The same study also originated the isolates later described as *Tropicimonas isoalkanivorans* (Harwati et al. 2009b). The type species of *Tropicibacter* was soon followed by new members of the genus, *T. multivorans* (Lucena et al. 2012b), *T. phthalicicus* (Iwaki et al. 2012a), *T. mediterraneus*, and *T. litoreus* (Lucena et al. 2013). *Tropicibacter* species are close to *Pelagimonas* and to the clade of *Phaeobacter sensu stricto* and relatives (*Fig. 20.5*).

The genus was described as containing Gram-negative, rod-shaped, peritrichously flagellated rods, but species described lately failed to show motility (*T. mediterraneus* and *T. litoreus*) or, when motile, displayed polarly flagellated cells (*T. multivorans*, *T. phthalicicus*). All species require sodium ion for growth and some of them also magnesium or calcium ions. The oxidase test is positive. Three of the species, including the type, are able to reduce nitrate to nitrite or to nitrogen gas. PHB accumulation is found only in *T. naphthalenivorans*. As it is usual among roseobacters, they contain Q10 as predominant quinone and their major cellular fatty acid is C18:1 ω7c, followed by C16:0 and 11-methyl C18:1 ω7c. Polar lipids have been determined in two species: they include PE, PG, PC, and AL and four PLs in *T. multivorans*, while *T. mediterraneus* contains PG, PE, and unidentified amino- and phospholipids, and lipids but lacks PC. The G+C content ranges from 58 to 64.6 mol%.

ANI values were used as alternative parameter to DDH for species delineation of *T. mediterraneus* and *T. litoreus*: the former species contains four strains that showed 97.5–99 % ANIb (98.9–99.7 ANIm) while interspecies values were 85–86 % ANIb (90 % ANIm) between both species (Lucena et al. 2013).

Tropicimonas

Harwati and coworkers described *Tropicimonas* after studying isolates obtained from the same location and samples that gave origin to the description of *Tropicibacter*, Semarang Port

seawater (Indonesia). The type species of their new genus, *Tropicimonas isoalkanivorans*, was able to degrade alkanes, branched alkanes, and alkylnaphthalenes (Harwati et al. 2009b). Two additional species have been recently added: *T. aquimaris*, which description was accompanied by an emended description of the genus (Oh et al. 2012), and *T. sediminicola* (Shin et al. 2012), both isolated from marine samples. Phylogenetic relatives of *Tropicimonas* species within the *Rhodobacteraceae sensu lato* are somewhat difficult to determine, as there is not always agreement between the trees obtained by different reconstruction methods. A relation with *Thioclava* was reported at the time of genus description and is recovered with NJ methods, but most parsimonious analyses fail to support this relation and locate the genus within *Roseobacter* group (this study, MP tree, not shown and LTP 111). In any case, all three species merge in a well-defined clade.

The genus contains members with the following features: cells are Gram negative, peritrichously flagellated (when motile), rod shaped, and oxidase positive. Catalase and PHA accumulation are variable. Halophilic, they require sodium ion for growth (but *T. sediminicola* is able to grow without NaCl). They grow optimally at 30–37 °C. Although Q10 is the most abundant respiratory quinone (57–60 %), it is accompanied by substantial amounts of others: 36 % of Q9 in *T. aquimaris* and two quinones of undetermined chain length in *T. isoalkanivorans*, accounting for 28 % and 14 % each. The major cellular fatty acids are C18:1 ω7c, C18:1 ω9c, and C16:0. Common major polar lipids are PC, PG, an unidentified aminolipid, and an unidentified lipid. G+C content of their DNA is 66.5–69.6 mol%.

All *Tropicimonas* species described so far are able to reduce nitrates to nitrites and *T. aquimaris* grows on Marine Agar incubated anaerobically, with and without nitrate supplementation. They grow at least up to 40 °C (*T. isoalkanivorans* up to 46 °C) and up to 6 % salinity. They produce acids from several carbohydrates and are able to assimilate a variety of carbon sources. *T. isoalkanivorans* is able to use decane, pristane, and methylnaphthalene for growth, but it is unable to grow on thiosulfate as energy source.

T. aquimaris shows a DNA-DNA relatedness of 12 % to the type species *T. isoalkanivorans* (Oh et al. 2012). On the other hand, *T. sediminicola* is related to *T. aquimaris* by DDH values of 46 %, while only a 6 % DDH could be found with *T. isoalkanivorans* (Shin et al. 2012).

Vadicella

The genus *Vadicella* contains a single species, *V. arenosi*, described after the study of several isolates obtained from a sandy sediment sample of the Sea of Japan (Romanenko et al. 2011d). The species has the genus *Celeribacter* as closest phylogenetic relative and belongs to the clade that also includes *Huaishuia* and *Pseudoruegeria* (Fig. 20.5). Basic properties defining the genus are as follows: they are rod shaped, Gram negative, strictly aerobic, oxidase and catalase positive, and chemoorganotrophic. They have an absolute requirement for sodium ion. They do not synthetize Bchl *a*. Their predominant quinone is Q10. Polar lipids include PC, PG, phosphatidic acid, an unknown aminolipid, and an unknown lipid; PE is present in minor amounts. Their major cellular fatty acids are C18:1 ω7c, 11-methyl C18:1 ω7c, C12:1, and C10:0 3OH. The only currently recognized species of *Vadicella* is nonmotile and nonpigmented, grows from 1 % to 7 % NaCl, from 4 °C to 37 °C, and from pH 5.5 to 9.5. It reduces nitrate and does not produces acid from carbohydrates. It uses a few sugars and organic acids as carbon and energy sources. The G+C content of its DNA is 56.7–60 mol%.

Wenxinia

Wenxinia marina represents the only recognized species so far in the genus *Wenxinia* (Ying et al. 2007). The type and single strain of this species was isolated from the sediment of an oil field (100 m depth) in the South China Sea. *Wenxinia* occupies a marginal position on the *Roseobacter* group, having a distant relationship to the genera *Rubellimicrobium* and *Roseicyclus*, at the edge of the clade.

The genus was described as containing Gram-negative, ovoid or short rods that are nonmotile, strictly aerobic, and heterotrophic. They require NaCl for growth and are slightly pigmented of pink, but do not produce Bchl *a*. Catalase and oxidase tests are positive. They reduce nitrates to nitrites. Their quinone system is Q10; they contain PG, PC, and an unidentified glycolipid as major polar lipids and have C18:1 ω7c and C16:0 as major cellular fatty acids.

W. marina is able to grow from 15 °C to 42 °C, from 0.5 % to 9 % NaCl, and at pH 6.5–8.5. It accumulates PHA and contains PE and an unidentified phospholipid as minor components of its polar lipid profile. It is able to produce acid from some carbohydrates and uses several sugars, organic acids, and amino acids. The C+G content of its DNA is 69.4 mol%. The draft genome of *W. marina* DSM 24838^T has 4.2 Mb.

Yangia

The genus *Yangia* belongs to the subclade that contains *Citreicella* and *Citreimonas* (Fig. 20.5). It was recognized as a new genus by Dai et al. (2006) and contains a single species, *Y. pacifica*, whose type and only characterized strain was isolated from a coastal sediment of the East China Sea. The genus is defined by the following properties: cells are Gram-negative, motile rods. They are aerobic, heterotrophic, and require NaCl for growth. They form slightly yellowish colonies on Marine Agar, which are positive for catalase and weakly positive for oxidase tests. Q10 is the predominant quinone, C18:1 ω7c and C16:0 are the major fatty acids, and C12:0 is also present.

Y. pacifica, the type species, does not produce Bchl *a*, accumulates PHB, is negative for nitrate reduction, and grows at 22–40 °C, with 1–10 % NaCl and with maltose, lactate,

malate, arginine, and glutamate as sole carbon sources. The DNA G+C content is 63.3 mol%.

In a survey about polyester production by halophilic and halotolerant bacterial strains obtained from mangrove soil samples located in Northern Vietnam, five strains (QN187, ND199, ND218, ND240, and QN271) phylogenetically close to *Y. pacifica* were found to accumulate PHAs in noticeable amounts. Strains QN187, ND240, and QN271 synthesized poly(3-hydroxybutyrate) (PHB) from glucose, whereas strains ND199 and ND218 synthesized poly(3-hydroxybutyrate-*co*-3-hydroxyvalerate) (PHBV) from this carbohydrate (Van-Thuoc et al. 2012).

Genera Not Belonging (Phylogenetically) to *Rhodobacteraceae Sensu Stricto*

The Stappia Group

The group formed by the genera *Stappia*, *Labrenzia*, *Nesiotobacter*, *Pannonibacter*, *Polymorphum*, *Pseudovibrio*, and *Roseibium* (Fig. 20.6) constitute the clearest candidate to the rank of new family in the currently heterogeneous *Rhodobacteraceae sensu lato*. These genera form a well-defined, stable, and neat clade, separated from *Rhodobacteraceae sensu stricto* by several other alphaproteobacterial branches that constitute families by themselves (*Hyphomonadaceae*, *Koordimonadaceae*, *Phyllobacterriaceae*, *Hyphomicrobiaceae*, etc., Fig. 20.1). The detachment of stappias from the rest of *Rhodobacteraceae* was already noted by Gupta and Mok (2007) in their phylogenomic study of the alphaproteobacteria, on the basis of signature proteins. These authors suggested the placement of *Labrenzia* (*Stappia*) *aggregata* among *Rhizobiaceae*, although more recent analysis based on 16S rRNA gene of the whole group indicates a separate position from this family (LTP111).

Stappias are aerobic or facultatively anaerobic and chemoorganotrophic but some species do contain *pufLM* genes (*Roseibium* spp., *Labrenzia alexandrii*, *Stappia stellulata*) and are able to synthetize Bchl *a*, although its amount may be very low in some species (Biebl et al. 2007). Members of the group display interesting activities related to the production of different bioactive compounds, carbon monoxide oxidation, aromatic ring cleavage, heavy metal detoxification, and oil degradation abilities. While several of the species are isolated from marine water and sediments, some were isolated from lake water, hot springs, or saline soil, as well as from marine invertebrates and surfaces of aquatic plants and algae. One species has been isolated from human blood samples and the other is related to an oyster disease affecting juveniles of *Crassostrea virginica* cultured in USA (Table 20.8).

Stappia

The genus *Stappia* has a history that parallels that of *Ruegeria*, in the *Roseobacter* group. As *Ruegeria*, *Stappia* was established as a new genus by Uchino et al. (1998) to accommodate species previously known as marine agrobacteria: *Agrobacterium stellulatum* and *Agrobacterium aggregatum* (Rüger and Höfle 1992). The new genus *Stappia* was phylogenetically distant to agrobacteria and was defined in terms of chemotaxonomic as well as physiological and biochemical properties (Uchino et al. 1998). After the description of two additional species, *S. alba* (Pujalte et al. 2005c) and *S. marina* (Kim et al. 2006b), Biebl and colleagues (2007) rebuilt the group by creating a new genus, *Labrenzia*, to which they transferred *S. alba* and *S. marina* as new combinations. Almost simultaneously, Weber and King (2007) proposed four new *Stappia* species which names have never been validated and thus have no standard in nomenclature (*S. meyerae*, *S. conradae*, *S. kahanamokuae*, and *S. carboxydovorans*). 16S rRNA genes of these species were analyzed by Lai et al. (2010b) who found they probably are more related to *Labrenzia* and *Pannonibacter* than to *Stappia*. The genus *Stappia* remained as monospecific until then with the description of *S. indica* (Lai et al. 2010b), and more recently *S. taiwanensis* (Kämpfer et al. 2013a) has also been proposed.

The emended description of *Stappia* by Biebl et al. (2007) defined the genus by the following properties: Gram-negative rods, motile by polar flagella, aerobic, and oxidase and catalase positive. They require seawater or Na ion for growth. Q10 is the predominant quinone. Polar lipid profile includes PG, DPG, PE, PMME, PC, and an aminolipid. The glycolipid SQDG is absent. Cellular fatty acids comprise C16:1 ω7c, C16:0, C18:1 ω7c, C18:0, 11-methyl C18:1 ω6t, C20:1 ω7c, C22:0, C22:1, and the hydroxy fatty acids C14:0 3OH (ester linked), C16:0 3OH, C18:1 3OH, C18:0 3OH, and C20:0 3OH (all amide linked). The G+C content of the type species is 59 mol% but extends up to 65.9 % in *S. indica*. *S. taiwanensis* contains spermidine and spermine as major polyamines. The draft genome of *S. stellulata* DSM 5886^T has 4.6 Mb.

DDH relatedness between *Stappia* species are reported by Lai et al. (2010b) for *S. indica* and *S. stellulata* (43 %) and Kämpfer et al. (2013a) for *S. taiwanensis* and *S. stellulata* (24–25 %) and *S. indica* (27 %).

Some *Stappia* contain *coxL* gene, being able to oxidize carbon monoxide (a common ability in members of the group) (Biebl et al. 2007), and some also present *pcaH* gene, encoding for a key ring-cleaving enzyme of the β-ketoadipate pathway (Buchan et al. 2001). *S. stellulata*-like strains have been related to a pathology of cultured oysters, JOD (juvenile oyster disease), that causes seasonal mortalities in *Crassotrea virginica* hatcheries, in the USA Northeast coast (Boettcher et al. 2000). *Stappia* spp. also participates in DMS production from DMSP, through a DMSP-lyase also present in several members of the *Roseobacter* group (Curson et al. 2008).

Labrenzia

Labrenzia was established as a new genus by Biebl et al. (2007), with the Bchl *a*-producing *L. alexandrii* as type species and the former *Stappia aggregata*, *S. marina*, and *S. alba* as new combinations. The four *Labrenzia* species were closely related according with the analysis of their 16S rRNA genes and only loosely related to *Stappia stellulata*, the type species of the genus *Stappia*, which joined to the clade only after *Roseibium spp.*,

Table 20.8
Species in the *Stappia* group and unaffiliated or isolated genera

Species (synonym)	Isolation/habitat	Metabolism[a]	Na^+ requirement, others	References
Stappia stellulata (*Agrobacterium*)	Marine sediment and water	AAP	Yes	Uchino et al. 1998
S. indica	Deep seawater, Indian Ocean	COH a	Yes	Lai et al. 2010b
S. taiwanensis	Coastal hot spring, Taiwan	COH a	Yes	Kämpfer et al. 2013a
Labrenzia alexandrii	Cultured dinoflagellate (*Alexandrium*), Germany	AAP	Yes	Biebl et al. 2007
L. aggregata (*Stappia*)	Sediment, Baltic Sea, Germany	COH a	Yes	Biebl et al. 2007; Uchino et al. 1998
L. alba (*Stappia*)	Oysters, Mediterranean coast, Spain	COH a	Yes	Biebl et al. 2007; Pujalte et al. 2005c
L. marina	Tidal flat, Yellow Sea, S. Korea	AAP	Yes	Biebl et al. 2007; Kim et al. 2006b
Nesiotobacter exalbescens	Hypersaline lake water, Hawaii, USA	COH	Yes	Donachie et al. 2006
Pannonibacter phragmitetus	Decomposing rhizomes of reed (Phragmites), from soda lake, Hungary	COH fac an	No, alkalitolerant	Biebl et al. 2007; Borsodi et al. 2003
P. indicus	Hot spring sediment, India	COH a	No	Bandyopadhyay et al. 2013
Polymorphum gilvum	Crude oil-contaminated, saline soil, China	COH fac an	No	Cai et al. 2011
Pseudovibrio denitrificans	Seawater, Taiwan	COH fac an	Yes	Shieh et al. 2004
P. ascidiaceicola	Ascidians (Polycitor and Botryllidae), Japan	COH fac an	Yes	Fukunaga et al. 2006
P. axinellae	Marine sponge, Axinella, Ireland	COH fac an	Yes	O'Halloran et al. 2013
P. japonicus	Coastal seawater, Japan	COH fac an	Yes	Hosoya and Yokota 2007b
Roseibium denhamense	Red algae (Botryocladia) surface, Australia	AAP	Yes	Biebl et al. 2007; Suzuki et al. 2000
R. hamelinense	Marine sand, Australia	AAP	No	Biebl et al. 2007; Suzuki et al. 2000
Unaffiliated				
Agaricicola taiwanensis	Mushroom (Agaricus), Taiwan	COH a	No	Chu et al. 2010
Ahrensia kielensis[b] (*Agrobacterium*)	Seawater, Baltic Sea, Germany	COH a	Yes	Uchino et al. 1998
Rhodothalassium salexigens[c] (*Rhodospirillum*)	Salterns, hypersaline lakes, Oregon, USA	PNS	Yes	Venkata Ramana et al. 2013a; Imhoff et al. 1998

[a] *AAP* aerobic anoxygenic photoheterotroph, *COH* chemoorganoheterotroph, *COH a* chemoorganoheterotroph aerobic, *COH fac an* chemoorganoheterotroph facultative anaerobic, *PNS* purple non-sulfur anoxygenic photoheterotroph
[b] *Phyllobacteriaceae*
[c] *Rhodothalassiaceae*

Pannonibacter phragmitetus, two *Pseudovibrio spp.*, and *Nesiotobacter exalbescens*. The current phylogenetic tree, including all newly described members of the *Stappia* group, maintains the same large separation between *Stappia* and *Labrenzia* species (*Fig. 20.6*).

Members of *Labrenzia* are defined as having Gram-negative, rod-shaped cells that are motile by one to several polar flagella. They may produce small amounts of Bchl *a* in the dark and a pink colony pigment in appropriate conditions. They require NaCl for growth, which occurs optimally in 1–10 % NaCl concentrations. Optimum pH is 7 to 8.5. Nitrate reduction activity (to nitrite or to N_2) is variable. They are chemoheterotrophic and non-fermentative under aerobic or anaerobic conditions. Indole production is negative. The major respiratory quinone is Q10. Polar lipids include PG, DPG, PE, PMME, PC, SQDG, and an amino lipid. Fatty acids comprise C16:0, C18:1 ω7c, C18:0, 11-methyl C18:1 ω6t, and C20:1 ω7c and the following hydroxy fatty acids: C14:0 3OH, C18:0 3OH, and C20:0 3OH (all amide linked). The G+C content ranges from 56 to 60 mol%.

The four species are mesophilic and neutrophilic and some are denitrifiers and accumulate PHB (*L. alba*). *L. marina* and

L. alexandrii produce Bchl *a*, while *L. alba* and *L. aggregata* lack this ability and the *pufLM* genes. All four species contain *coxL* genes and are capable of carbon monoxide oxidation (Biebl et al. 2007; Weber and King 2007).

Labrenzia strains have been isolated from the dinoflagellate *Alexandrium lusitanicum* (*L. alexandrii*), marine sediment (*L. aggregata*), oysters (*L. alba*), and tidal flat (*L. marina*), but isolates pertaining to the genus have also been found on estuarine microbial mats (Villanueva et al. 2010), as endophytes on siphonous green seaweeds (Hollants et al. 2011) and in soft corals (Chen et al. 2012b). A putative new *Labrenzia* species has been isolated and extensively investigated in suboxic waters of the Arabian Sea, where they contribute actively to the removal of N_2O through its N_2O-reductase activity, developing in colonies of *Trichodesmium* spp. (Wyman et al. 2013). Some *Labrenzia* spp. draw attention because of their polyhydroxyalcanoate accumulation (Koller et al. 2011; Xiao and Jiao 2011) or because of the production of particular enzymes, as a new nitrilase from *L. aggregata*, interesting to the drug manufacturing industry (Zhang et al. 2012c).

The genome of *L. alexandrii* type strain, DFL-11^T, has been sequenced, bringing attention, among other traits, in the ability to form R-bodies (Fiebig et al. 2013). The genome size is 5.46 Mbp and comprises one chromosome (5.3 Mbp) and two plasmids. It contains 3 rRNA operons and 52 tRNA genes, and its G+C content is 56.4 mol%. Homologues to the three *Caedibacter taeniospiralis* genes determining R-body production were found in the chromosome. The draft genome of *L. aggregata* IAM 12614^T has 6.56 Mb and a G+C content of 59.4 mol%.

Nesiotobacter

Nesiotobacter contains a single species, *N. exalbescens*, isolated from hypersaline lake water in Hawaii (Donachie et al. 2006). The species occupies a position next to *Pseudovibrio* in the *Stappia* clade (Fig. 20.6). Strains belonging to *Nesiotobacter* are Gram-negative, motile rods, positive for oxidase and catalase tests, which reduce nitrates to N_2. They do not synthetize Bchl *a*. Their major fatty acid is C18:1 ω7c. The DNA G+C content of the only strain is 61 mol%.

N. exalbescens grows on Tryptone Soya Agar with 0.5–13.5 % NaCl added (but not at 0 % NaCl) and in Marine Broth with 1–17.5 % NaCl added. It is able to grow up to 45 °C but not at 50º, a behavior that was described as moderately thermophilic in the species description, but corresponds probably to a mesophile with a high upper temperature limit. It produces acid from several carbohydrates and hydrolyzes gelatin. DNA of the type strain showed 14–15 % DDH levels with type strains of *Roseibium denhamense* and *Labrenzia aggregata*, their closest neighbors at the time of the description. The draft genome of *N. exalbescens* DSM 16456^T has 4.16 Mb.

Pannonibacter

The type species of the genus *Pannonibacter*, *P. phragmitetus*, was isolated from rhizomes of reed (*Phragmites australis*) in a Hungarian soda lake (Borsodi et al. 2003). A few years later, Holmes et al. (2006) reported that the new genus and species have been isolated and characterized previously (as *Achromobacter* groups B and E) from blood samples of human origin. This makes *P. phragmitetus* one of the very few *Rhodobacteraceae* bacteria isolated from human clinical specimens, along with *Paracoccus yeei* and *Haematobacter* spp. (see above). The human strains were related to a case of replacement valve endocarditis and two septicemia cases (Holmes et al. 2006).

The original genus description was emended by Biebl et al. (2007), by adding information on their chemotaxonomic traits. It includes strains with Gram-negative, rod-shaped cells, which are motile by polar flagella, contain PHA, and are chemoorganotrophic and facultative anaerobic. They ferment glucose without gas production, are positive for oxidase and catalase, and reduce nitrate to dinitrogen gas. Bchl *a* is not synthetized. The dominant quinone is Q10. Polar lipid profile includes PG, DPG, PMME, PC, an amino lipid, and an unidentified lipid. PE is not detected (although it is a precursor of PMME). Phosphatidylserine and SQDG are absent. Cellular fatty acid comprise C16:1 ω7c, C16:0, C18:1 ω7c, C18:0, 11-methyl C18:1 ω6t, C20:1 ω7c, C22:0, and the hydroxy fatty acids C14:0 3OH (ester linked), C16:0 3OH, C18:1 3OH, C18:0 3OH, and C20:1 3OH (all amide linked). The peptidoglycan contains *m*-DAP. The G+C content of the species described so far is 63–64.6 mol%. The draft genome of *P. phragmitetus* DSM 14782^T has a size of 4.8 Mb.

P. indicus, the second species in the genus, shows DDH values of 34–55 % against different strains of *P. phragmitetus* (Bandyopadhyay et al. 2013) and, unlike the type species, is unable to grow anaerobically, does not reduce nitrates, and is able to grow up to 45 °C. It resembles *P. phragmitetus* in its alkalitolerant character and in the absence of salt requirements for growth.

Pannonibacter strains isolated from wastewater treatment plants have shown remarkable abilities for degradation of some undesired compounds as tert-butyl alcohol (Reinauer et al. 2008) or 4-aminobenzene sulfonate (Wang et al. 2009d; Zhang et al. 2011b), but the bulk of the literature on applied uses of *Pannonibacter* is related to its activity as a chromium (IV) reducing agent, which makes *Pannonibacter phragmitetus* (strains BB and LSSE-09, among others) an effective resource for contaminated soil bioremediation (Chai et al. 2009; Xu et al. 2011a, b, 2012; Wang et al. 2013a). It is also remarkable the tolerance to arsenate of the newly described species *P. indicus* (Bandyopadhyay et al. 2013), which type strain is able to grow in the presence of up to 500 mM of sodium arsenate. The strain was isolated from hot spring sediment in India. Other hot spring environments also contain *Pannonibacter* strains, as recently reported by Coman et al. (2013).

Polymorphum

The genus *Polymorphum* was recently described to accommodate a new species, *P. gilvum*, isolated from crude oil-contaminated saline soils, in China (Cai et al. 2011), the same samples from which *Rubrimonas shengliensis* was isolated and described. *Polymorphum's* closest taxon corresponds to the pair

of *Pannonibacter* species (*P. phragmitetus* and *P. indicum*) (Fig. 20.6, LTP111), to which they reassemble in their facultatively anaerobic character.

Cells of *Polymorphum* exhibit different morphologies, as suggested by the generic name, as short rods or dumb-shaped cells with different branches that occasionally aggregate in star-shaped groups. They are Gram negative, facultatively anaerobic, and motile (one polar flagellum is present in the cells of the type species). The predominant quinone is Q10; major fatty acids correspond to C18:1 ω7c, 11-methyl C18:1 ω7c, C18:0, C16:0, and C20:1 ω7c. The polar lipid profile includes DPG, PMME, PG, PC, SQDG, and unidentified aminolipids and phospholipids. The type species has a DNA G+C content of 65.6 mol%.

P. gilvum is able to grow from 4 °C to 50 °C, at pH 5–9, and with 0–6 % NaCl. Optimum growth occurs at 37 °C, pH 6.0, and 1 % NaCl. The species is positive for catalase activity but negative for oxidase, an atypical behavior in the group. It does not reduce nitrates. Bchl *a* is not synthetized and *pufLM* genes are absent. Acid is produced from several carbohydrates (glycerol, L-arabinose, D-ribose, D-xylose, D-glucose, D-fructose, D-mannose, and D-cellobiose, among others). The type strain SL003B-26A1^T is able to grow on crude oil as sole carbon source, an ability that justifies the interest in its complete genome sequence: Li et al. (2011c) found that the genome of this strain consists of a circular chromosome 4.65 Mbp in size and a plasmid of 69.6 kbp with 67 and 61 mol% G+C content, respectively. The chromosome contains 50 tRNA and two rRNA encoding operons. The genes for membrane-bound alkane monooxygenase and for cytochrome P450 (related to oil degradative capabilities in other bacteria) are not found, but *ladA*, coding for long chain-alkane hydroxylation, is present. This gene codes for an extracellular enzyme that can hydroxylate C_{15} to C_{36} alkanes. The authors suggest it might have been acquired by horizontal gene transfer.

Pseudovibrio

Four species have been described in the genus *Pseudovibrio* since Shieh et al. (2004) named the new genus: *P. denitrificans*, the type species, *P. ascidiaceicola* (Fukunaga et al. 2006), *P. japonicus* (Hosoya and Yokota 2007b), and *P. axinellae* (O'Halloran et al. 2013). All four contain strains of Gram-negative, straight, or curved rods, which are motile by one to several lateral/subpolar flagella. *P. ascidiaceicola* forms conspicuous rosettes. They are able to grow in anaerobic conditions, either by carbohydrate fermentation (glucose and mannose are fermented by the four species) or through denitrification, as all of them reduce nitrates to nitrogen gas. They are oxidase and catalase positive, mesophilic and halophilic, requiring NaCl for growth. Their fatty acid profile includes C18:1 ω7c as major component, accompanied by varying amounts of C16:0, C18:0, C19:0 cyclo ω8c, and the hydroxylated C14:0 3OH (as SF 2), C16:0 3OH, and C18:0 3OH (O'Halloran et al. 2013). The G+C content of their DNA is 50–52 mol%. The species could be differentiated by their fermentative and assimilative patterns as well as for the relative amounts of minor fatty acids. DDH values between *P. ascidiaeceicola* and *P. denitrificans* are lower than 30 % (Fukunaga et al. 2006); *P. japonicus* shows values of 35 % against *P. denitrificans* and 14–32 % against *P. ascidiaceicola* strains (Hosoya and Yokota 2007b). Finally, *P. axinellae* shows DDH values of 26 % with *P. ascidiaceicola*, 18 % with *P. denitrificans*, and 16 % with *P. japonicus* (O'Halloran et al. 2013).

Pseudovibrio species form a well-defined, tight clade, which closest relative is *Nesiotobacter exalbescens* (Fig. 20.6).

Although two of the species were isolated from seawater, most of the reports on isolation of pseudovibrios are associated to microbiota of marine invertebrates, with a significative dominance of sponges of very different geographic sites. Several reports document the production of bioactive metabolites from these sponge-, tunicate-, ascidian-, coral- or polychaetide-associated bacteria (Radjasa et al. 2007; Muscholl-Silberhorn et al. 2008; Riesenfeld et al. 2008; Kennedy et al. 2009; Santos et al. 2010; O'Halloran et al. 2011; Penesyan et al. 2011; Flemer et al. 2012; Margassery et al. 2012; Chen et al. 2012b; Rizzo et al. 2013). The genomes of two *Pseudovibrio* strains, isolated from a coral and a sponge, revealed a number of ORFs and gene clusters that seem to be involved in symbiont-host interactions: attachment and interaction with eukaryotic cell machinery, production of secondary metabolites, and supply of the host with cofactors (Bondarev et al. 2013). The size of these genomes, 5.73 and 5.92 Mb, are among the largest reported within the *Rhodobacteraceae*.

Roseibium

The genus *Roseibium* was described by Suzuki et al. (2000) to accommodate two new species of APPs isolated from algal surfaces and sand from coastal areas of Australia. *R. denhamense* and *R. hamelinense* synthetized Bchl *a* in aerobiosis and produced pink colonies. Their cells are Gram-negative rods, motile by means of peritrichous flagella. They are aerobic, chemoorganotrophic, and positive for catalase, oxidase, phosphatase, and nitrate reductase. Q10 is the predominant quinone and C18:1 ω7c is the major fatty acid. The G+C molar content of their DNA expands from 57.6 to 63.4 mol%. Biebl et al. (2007) emended the genus description, adding the polar lipid profile, which comprises PG, DPG, PE, PMME, PC, SQDG, and an amino lipid. They also added a more detailed fatty acid profile that includes C16:0, C18:1 ω7c, C18:0, 11-methyl C18:1 ω6t, and C20:1 ω7c and the hydroxy fatty acids C14:0 3OH (ester linked), C18:0 3OH, C20:0 3OH, and C20:1 3OH (amide linked).

Roseibium species are mesophilic and neutrophilic (optimal growth at 27–30 °C and pH 7.5–8.0). *R. hamelinense* does not require NaCl for growth (range: 0–10 % NaCl), in contrast to *R. denhamense* (range: 0.5–7.5 % NaCl). They are chemoorganotrophic and aerobic and unable to grow phototrophically under anaerobic conditions in the light. Their carbon sources include butyrate, L-glutamate, L-aspartate, and pyruvate. Acid is produced from some carbohydrates: D-glucose, D-fructose, D-ribose, and maltose. They produce indole and hydrolyze gelatin. DDH determinations related both species by values of 12–17 % (Suzuki et al. 2000).

Roseibium species have *Labrenzia* spp. as their closest phylogenetic relatives (Fig. 20.6). The draft genome of strain *Roseibium* sp. TrichSKD4 has 5.7 Mb and a G+C content of 53.9 mol%.

Agaricicola

The description of the genus *Agaricicola* and its only species, *A. taiwanensis*, was based on the study of a single strain, CC-SBAB117^T, isolated from the stipe of the edible mushroom *Agaricus blazei* in Taiwan. After analysis of the 16S rRNA gene sequence, a distant relationship was found to some members of the *Stappia* clade (*Pannonibacter phragmitetus*, 92.5 % sequence similarity; *Nesiotobacter exalbescens*, 91.5 %) and to *Prosthecomicrobium pneumaticum* (92.3 %) (Chu et al. 2010). Although some early analysis might suggest *Agaricicola* being a peripheral member of the clade *Stappia*, the more recent version of LTP, LTP111, shows *Agaricicola* paired with *Prosthecomicrobium pneumaticum* and clearly unrelated to the stappias. Thus, *Agaricicola* should be removed from *Rhodobacteraceae sensu lato*, as currently considered.

The genus is defined by the following traits: Gram-negative, strictly aerobic, nonspore-forming, motile, club-shaped cells that accumulate PHB granules as polar inclusions. Oxidase test is positive but catalase is negative. It contains the following polar lipids: DPG, PG, PC, and PE. SQDG and PMME are not detected. The major respiratory quinone is Q10. The predominant fatty acids are C18:1 ω7c, C19:0 cyclo ω8c, C16:0, and C18:0 whereas C10:0 3OH is absent.

The type and only species of the genus, *A. taiwanensis*, grows in Nutrient Agar forming circular, shiny, beige pigmented colonies. Growth is optimal at 30–35 °C and occurs between 20 °C and 40 °C, at pH 6.0–9.0 and with 1–4 % NaCl. NaCl is not required for growth. Cells have polar flagella. Nitrate reduction to nitrite or N_2 is negative and no growth is observed with nitrate in anaerobic conditions. Bchl *a* is not synthetized. No acid is produced from carbohydrates. It uses a few sugars and several organic acids as carbon sources, including acetate, pyruvate, propionate, and β-hydroxybutyric acid. The G+C content of its DNA is 62.7 mol%.

Ahrensia

The type species of the genus *Ahrensia*, *A. kieliensis*, was formerly known as one of the "marine agrobacteria," but its relation to the main group was considered ungranted by Rüger and Höfle (1992). Years later, Uchino et al. (1997) revised the phylogenetic position of the whole group of marine agrobacteria, including the non-validated species names, based on 16S rRNA sequence analysis: they found that *Agrobacterium kieliense* IAM 12618 sequence was positioned in the α-2 branch of *Proteobacteria* and recognized it should be classified as a species in new genera. Shortly after that, the proposal of *Ahrensia kieliense* (corrected *kielensis*) gen. nov., sp. nov., nom. rev. was published (Uchino et al. 1998), and since then *Ahrensia* has remained as a monospecific genus, distantly related to the other reclassified marine agrobacteria (*Stappia stellulata*, *Labrenzia aggregata*, *Ruegeria atlantica*, *Thalassobius gelatinovorus*). On recent times, the affiliation of *Ahrensia* to the family *Phyllobacteriaceae* has become evident: *A. kieliensis* merges with species of the genus *Hoeflea*, in particular, with *H. phototrophica* (LTP 111), to which it shows a 95.7 % 16S rRNA gene sequence similarity (Kim et al. 2012f). It should be noted that the type species of the genus *Hoeflea*, *H. marina*, is itself a reclassified marine agrobacterium (*A. ferrugineum* LMG 128).

Ahrensia displays the following generic features: Gram-negative rods, motile by polar flagella, aerobic, and they have a strictly respiratory type of metabolism with oxygen as terminal electron acceptor. Catalase and oxidase are positive. Nitrate is not reduced; gelatin, starch, chitin, and alginate are not hydrolyzed; and indole is not produced. Sodium ion is required for growth. Optimal temperatures are 20–30 °C (range: 5 °C to less than 37 °C). The major fatty acid is C18:1 ω7c and hydroxyl fatty acid is C12:0 3OH, while 2OH fatty acids are absent. Major respiratory quinone is Q10. The G+C content is 48 mol% (Uchino et al. 1998; Krieg 2005). *A. kieliensis* was isolated from seawater from the Baltic Sea.

The draft genome of *A. kieliensis* DSM 5890^T has 3.36 Mb and a G+C content of 48.1 mol%, whereas *Ahrensia* sp. R2A130 has similar size (3.73 Mb) but a considerably higher G+C content (56.9 mol%).

Rhodothalassium

The position of *Rhodothalassium salexigens* (Imhoff et al. 1998; formerly, *Rhodospirillum salexigens*) as a separate phylogenetic branch amid alphaproteobacterial families in the vicinity of *Rhodobacteraceae* was already stressed in the second edition of *Bergey's Manual of Systematic Bacteriology*, where it is classified as Genus *Incertae Sedis*. This unique position in the 16S rRNA tree is accompanied by a combination of chemotaxonomic features unlike other purple non-sulfur phototrophs in *Rhodobacteraceae*: presence of menaquinones (MK10), ornithine lipids, or carotenoids of the spirilloxanthine series. Only the lack of additional strains had prevented an earlier reclassification of the genus, but after the study of several *R. salexigens*-like strains obtained from a solar saltern in India, Venkata Ramana et al. (2013) had emended the description of *Rhodothalassium* and proposed *Rhodothalassiaceae* fam. nov. and *Rhodothalassiales* ord. nov. At the time of writing of this chapter, these names have not been yet validated.

The closest relatives to *Rhodothalassium*, according to the more recent 16S rRNA phylogenetic analyses, are *Kordiimonas* species (fam. *Kordiimonadaceae*, order *Kordiimonadales*), as can be seen in *Fig. 20.1* and LTP111 tree.

According to the emended description, the genus *Rhodothalassium* is defined by the following traits: cells are Gram negative, vibrioid to spiral shaped, motile by polar flagella, and multiply by binary fission. The intracytoplasmic photosynthetic membranes are lamellar stacks. Bchl *a* and carotenoids of the spirilloxanthin series are the major photosynthetic pigments. The quinone system is composed of ubiquinone Q10 and menaquinone MK10. Halophilic, they require NaCl or sea salts for growth. Optimum salinity is above the seawater salt content and tolerate up to 20 % total salts. Growth occurs

preferably photo-organotrophically under anoxic conditions in the light, but is generally possible under microoxic to oxic conditions in the dark (except in some strains). They may require amino acids or niacin and thiamine. Major polar lipids are DPG, PG, ornithine lipid (OL), an unidentified phospholipid, and an amino lipid. Major fatty acids are C18:1 ω7c, 11-methyl C18:1 ω7c, and C16:0, with minor amounts of C14:0, C18:0, C18:1 ω5c, and C16:1 ω7c/C16:1 ω6c. The G+C content of the DNA is 60–62.8 mol%. Hamana et al. (2001) reported aminopropylhomospermidine as the major polyamine in *R. salexigens* cells.

The only species currently recognized is *R. salexigens*. This species is able to grow with N_2 as nitrogen source, requires glutamate, and is unable to grow photoautotrophically with H_2, sulfide, or thiosulfate as electron donors. The temperature range is 20–45 °C (optimum 40 °C) and the salinity range is 5–20 % NaCl (optimum: 4–8 %). Their habitats include anoxic zones of hypersaline environments, such as salterns and partially evaporated seawater pools.

Addendum

The following new genera and species have been effectively published after completion of the manuscript and are not included in the phylogenetic trees and the main text, but their names might be eventually included in validation lists.

Genera:

- *Albirhodobacter marinus* gen. nov., sp. nov. (Nupur et al. 2013), affiliated to the *Rhodobacter* group.
- *Falsirhodobacter halotolerans* gen. nov., sp. nov. (Subhash et al. 2013), affiliated to the *Rhodobacter* group.
- *Litorisediminicola beolgyonensis* gen. nov., sp. nov. (Yoon et al. 2013c), affiliated to the *Roseobacter* group.
- *Paenirhodobacter enshiensis* gen. nov., sp. nov. (Wang et al. 2013b), affiliated to the *Rhodobacter* group.
- *Planktomarina temperata* gen. nov., sp. nov. (Giebel et al. 2013), affiliated to the *Roseobacter* group.
- *Pleomorphobacterium xiamenensis* gen. nov., sp. nov. (Yin et al. 2013), affiliated to the *Amaricoccus* group.
- *Sinorhodobacter ferrireducens* gen. nov., sp. nov. (Yang et al. 2013), affiliated to the *Rhodobacter* group.

Species:

- *Albimonas pacifica* (Li et al. 2013).
- *Defluviimonas aestuarii* (Math et al. 2013).
- *Gemmobacter lanyuensis* (Sheu et al. 2013b).
- *Gemmobacter megaterium* (Liu et al. 2013)
- *Litoreibacter halocynthiae* (Kim et al. 2013).
- *Loktanella sediminilitoris* (Park et al. 2013c).
- *Loktanella soesokkakensis* (Park et al. 2013d).
- *Pelagicola litorisediminis* (Park et al. 2013e).
- *Phaeobacter leonis* (Gaboyer et al. 2013).
- *Roseivivax pacificus* (Wu et al. 2013).
- *Roseovarius lutimaris* (Choi et al. 2013).
- *Roseovarius marisflavi* (Li et al. 2013).
- *Ruegeria intermedia* (Kämpfer et al. 2013b).
- *Shimia biformata* (Hameed et al. 2013).
- *Shimia haliotis* (Hyun et al. 2013).
- *Sulfitobacter porphyrae* (Fukui et al. 2013).
- *Thioclava dalianensis* (Zhang et al. 2013), with emended description of the genus.

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