9 The Family *Erythrobacteraceae*

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Abstract
Erythrobacteraceae is one of the two families that belong to the order *Sphingomonadales*, and it is affiliated with the class *Alphaproteobacteria*. The family *Erythrobacteraceae* includes five genera – *Altererythrobacter*, *Croceicoccus*, *Erythrobacter*, *Erythromicrobium* and *Porphyrobacter* – for a total of 33 species, including 29 with validly published names and 4 new species. Members of the family are Gram-negative, aerobic, rod-shaped or pleomorphic coccoid bacteria; they are motile or nonmotile, chemo-organotrophic, produce pigments (yellow, orange, red or pink), and do not form spores. Some species require biotin. Most members contain bacteriochlorophyll a (*BChl a*), several types of carotenoids, and monosaccharide-type glycosphingolipid. Representatives of the clade have been isolated from diverse environments: wild rice, cold-seep sediment, desert sand, tepid water, seawater, tidal flats, marine sediment, and marine invertebrates. Whole-genome sequencing has been reported in only two genera of the *Erythrobacteraceae* family, including *Erythrobacter* (three strains) and *Porphyrobacter* (one strain). Family members offer a valuable source of information for further studies focused on aerobic anoxygenic phototrophic (AAP) metabolism, physiological nature, and high potential for biotechnological purposes by the presence of important hydrolases.

Taxonomy: Historical and Current

Erythrobacteraceae (E.ry.thro.bac.te.ra'ceae. N.L. masc. n. *Erythrobacter* type genus of the family; -aceae ending to denote a family; N.L. fem. pl. n. *Erythrobacteraceae* the *Erythrobacter* family) (Lee et al. 2005 emend. Xu et al. 2009).

Erythrobacteraceae DNA mol% G+C content varies between 54.5 and 71.5. The type genus is *Erythrobacter*. *Erythrobacteraceae* is phylogenetically closest related to the family *Sphingomonadaceae*. These two families integrate the order *Sphingomonadales*, and they are affiliated with the class *Alphaproteobacteria*.

Physiologically, the group is very similar. Members are Gram-negative, rod-shaped, or pleomorphic coccoid bacteria and aerobic chemoorganotrophs. Most species contain carotenoids and require NaCl for growth (although it is not essential in many cases), some species contain *BChl a*. Autotrophic growth has not been reported, but one genus may be facultative photoheterotrophs. Members of this taxon have been isolated

E. Rosenberg et al. (eds.), *The Prokaryotes – Alphaproteobacteria and Betaproteobacteria*, DOI 10.1007/978-3-642-30197-1_376,

mainly from aquatic environments, but there are also isolation reports from sediment, sand, and rice.

Erythrobacter, the type genus of the *Erythrobacteraceae* family, was originally described by Shiba and Simidu in 1982. Members of this genus are orange- and pink-pigmented Gram-negative bacteria. They are aerobic chemoorganotrophs that are motile by subpolar flagella. *Erythrobacter* are halophilic carotenoids that are able to use glucose, pyruvate, acetate, butyrate, and glutamate as sole organic carbon sources, but not methanol. Strains require biotin and are able to hydrolyze gelatin, tween 80, and alginate. Although these organisms do not grow phototrophically, the presence of bacteriochlorophyll *a* indicates that this taxon is most closely related to the *Rhodospirillaceae* family (*Rhodospirillales* order), so it was maintained as a new genus inside this family. Later, the nonphotosynthetic *Sphingomonas* group was included in the α-4 subclass of *Proteobacteria* (Yabuuchi et al. 1990), as well as the *Erythrobacter-Porphyrobacter-Erythromicrobium* cluster, which was defined to be most closely related to members of the genus *Sphingomonas* (Yurkov et al. 1994). A new order was proposed to accommodate this clade. The *Sphingomonadales* order was created based on 16S rRNA sequence comparisons, as well as phenotypic and morphological characteristics (Yabuuchi and Kosako 2005).

Strain representatives of the *Porphyrobacter* genus proposed by Fuerst et al. (1993) shared ultrastructural similarities with members of the *Planctomycetales*. However, 16S rRNA sequence data indicated that these bacteria shared a position within the Alfa subclass of the *Proteobacteria* with *Erythrobacter longus*, but they were distinguishable in their sequences and in other characteristics, such as their requirement of vitamins for growth; acetate, glutamate, and butyrate utilization; gelatin hydrolysis; and quantitative differences in detectable cellular fatty acids.

The photosynthetic apparatus, biochemical, morphological, and 16S rRNA sequence data for strain E5T (= DSM 8510^T) also supported the proposal that a new genus and a new species should be described. The *Erythromicrobium* genus was introduced by Yurkov et al. (1992) as a genus of freshwater, obligatory aerobic, facultative, photoheterotrophic bacteria that included five species tentatively identified on the basis of DNA–DNA hybridization and phenotypic data (Yurkov et al. 1991): *Erythromicrobium sibiricum*, *Erythromicrobium ursincola*, *Erythromicrobium ezovicum*, *Erythromicrobium hydrolyticum*, and *Erythromicrobium ramosum*. However, the genus was validly published in 1994 with *Erythromicrobium ramosum* as the type strain (Yurkov et al. 1994) and the unique valid named species in the genus. In 1997, the genus *Erythromicrobium* was taxonomically reorganized, resulting in the exclusion of *E. sibiricum* and *E. ursincola* from the genus, being transferred to new genera, *Sandaracinobacter* and *Erythromonas*, respectively (Yurkov et al. 1997). Subsequently, phylogenetic analysis of the class *Alphaproteobacteria* based on 16S rRNA sequence comparisons through phylogenetic tree led to the reclassification of the genera *Erythrobacter* (Shiba and Simidu 1982), *Porphyrobacter* (Fuerst et al. 1993), and *Erythromicrobium* (Yurkov et al. 1994) into a new family named *Erythrobacteraceae* by Lee and colleagues (2005).

Further, the *Altererythrobacter* genus was suggested by Kwon et al. (2007) to accommodate new species in the clade. *Altererythrobacter* showed high similarity to the genus *Erythrobacter* but did not share its phyletic line. Another taxonomic rearrangement was related to reclassification of *Erythrobacter luteolus* (Yoon et al. 2005a) as *Altererythrobacter luteolus* comb. nov. (Kwon et al. 2007).

The last genus introduced in *Erythrobacteraceae* family was *Croceicoccus* (Xu et al. 2009), represented by aerobic and chemoheterotrophic bacteria containing carotenoids but not *BChl a*. The emended description of the family *Erythrobacteraceae* was also included in the study of Xu et al. (2009).

At the time of writing (September 2012), the family *Erythrobacteraceae* consisted of five genera (*Table 9.1*) with 33 species (*Tables 9.2*, *9.3*, *9.4*, and *9.5*): *Erythrobacter* (type genus) (13 species, 2 of which were only effectively published), *Altererythrobacter* (12 species, 2 of which were only effectively published) *Croceicoccus* (1 species), *Erythromicrobium* (1 species), and *Porphyrobacter* (6 species).

Phylogenetic Structure of the Family and Its Genera

The phylogenetic reconstruction of the 33 type species of the family *Erythrobacteraceae* based on 16S rRNA gene sequence is represented in *Fig. 9.1*. *Erythrobacteraceae* is most closely related to *Sphingomonadaceae*. These families belong to the order *Sphingomonadales*, and it is affiliated with the class *Alphaproteobacteria*.

The five genera (*Erythrobacter*, *Altererythrobacter*, *Croceicoccus*, *Erythromicrobium* and *Porphyrobacter*) currently recognized within the *Erythrobacteraceae* family are separated in the tree based on the topology created using the randomized axelerated maximum likelihood algorithm (RAxML; Stamatakis 2006). Representative sequences from *Rhodospirillaceae* and *Rodobiaceae*, which are closely related taxa, were used as outgroups. In addition, a 10 % maximum frequency filter was applied in order to remove hypervariable positions and potentially misplaced bases from the alignment of the sequences. The scale bar in *Fig. 9.1* represents 0.02-bp substitutions per nucleotide position.

Molecular Analyses

DNA–DNA Hybridization

DNA-DNA hybridization (DDH) studies have been performed on several *Erythrobacteraceae* family members including *Altererythrobacter*, *Erythrobacter*, and *Porphyrobacter* genera, confirming the taxonomic positions of the species proposed in each taxon. *Tables 9.6*, *9.7*, and *9.8* summarize the DNA–DNA similarities among the type strains of the *Erythrobacteraceae* family.

Levels of DNA–DNA relatedness between *A. marensis* MSW-14^T and its closest relatives, *A. epoxidivorans* KCCM

Table 9.1

The genera classified within the family *Erythrobacteraceae*, as on September 2012

Genus	Number of species[a]	Type species	General properties
Erythrobacter (type genus)	13	*Erythrobacter longus*	Gram-negative aerobic chemoorganotrophs non-spore-forming containing ubiquinone-10 (Q-10) as the predominant respiratory lipoquinone, most species contain carotenoids, require NaCl for growth, utilize glucose, but do not hydrolyze starch, gelatin and do not reduce nitrate. Autotrophic growth has not been reported. Two species contain bacteriochlorophyll *a* (*BChl a*)
Altererythrobacter	12	*Altererythrobacter epoxidivorans*	The members share many phenotypic and chemotaxonomic characteristics such as the absence of motility, rod-shaped cells. C18:1 ω7*c* and ubiquinone-10 are the dominant fatty acid and respiratory quinone, respectively. Members can be characterized by the yellow to orange-red colony color on agar plates, lack of *BChl a*. DNA G+C content ranging between 54.5 and 67.2 mol%, and the temperature range for optimal growth occurs at 15–35 °C. All species can grow in the presence of NaCl, though not essential in many cases
Croceicoccus	1	*Croceicoccus marinus*	Gram-negative and non-spore-forming cocci. Divide by binary division. Capable of producing multifibrillar stalk-like fascicle structures on the cell surface. Contains carotenoids, but not *BChl a*. Aerobic and chemoheterotrophic. No growth occurs anaerobically in the light. Ubiquinone-10 is the major respiratory quinone. The polar lipid profiles comprise phosphatidylglycerol, two unidentified glycolipids, phosphatidylcholine and an unidentified phospholipid
Erythromicrobium	1	*Erythromicrobium ramosum*	Gram-negative, rod-shaped, and usually motile by means of flagella. Branching may occur. The cells are orange, contain *Bchl a* and carotenoids, and multiply by binary division. Aerobic chemoorganotrophs and facultative photoheterotrophs. No growth occurs anaerobically in the light. Ribulose diphosphate carboxylase is not detected. No fermentation and no denitrification activities occur
Porphyrobacter	6	*Porphyrobacter neustonensis*	Gram-negative, pleomorphic motile rods or cocci, non-sporulating, reproducing by polar growth or budding. Capable of producing multifibrillar stalk-like fascicle structures and crateriform structures on the cell surface. Aerobic. Chemoheterotrophic Synthesizes *BChl a* on low-nutrient media under aerobic and semiaerobic conditions. DNA base composition is 63.8–66.8 mol% G+C. Positive for calatase, presence of BChl a, and utilization of D-glucose, negative for utilization of citrate and L-Arabinose

[a]Including species whose names have been effectively but not yet validly published

42314^T and *A. luteolus* KCTC 12311^T were determined to be 26.0–27.3 % and 9.8–15.2 %, respectively (Seo and Lee 2010). The value between *A. xinjiangensis* S3-63^T and the type strain of the phylogenetically most closely related species *A. marinus* H32^T was 54.5 ± 2 % (Xue et al. 2012). DNA–DNA similarity between *A. troitsensis* KMM 6042^T and *A. dongtanensis* was 34.4 % ± 7.6 % (Nedashkovskaya et al. 2013).

DNA–DNA relatedness between *E. citreus* strains RE35F/1^T and RE10F/45 was (79 % ± 6 %). However, values between *E. citreus* strains and *E. litoralis* DSM 8509^T were 25 % ± 2 % and 34 % ± 2 %, respectively, and between *E. citreus* and *Erythromicrobium ramosum* DSM 8510^T were 20 % ± 3 % and 34 % ± 4 %, respectively (Denner et al. 2002). *E. flavus* strains SW-46^T and SW-52 exhibited DNA–DNA relatedness levels of 94.0 % and 94.7 % against each other, although *E. flavus* strains and the type strains of *E. longus* DSM 6997^T, *E. litoralis* DSM 8509^T, and *E. citreus* DSM 14432^T were 4.2 % and 3.6 %; 6.0 % and 7.4 %; and 13.1 % and 14.7 %, respectively (Yoon et al. 2003).

Levels of DNA relatedness observed between *E. aquimaris* strains SW-110^T, SW-116, and SW-140 were 88.5–102.1 %, but DNA relatedness of *E. aquimaris* strains against *E. longus*, *E. litoralis*, *E. citreus*, and *E. flavus* were between 5.3 % and 12.7 % (Yoon et al. 2004a). DNA similarity between *E. seohaensis* SW-135^T and *E. gaetbuli* SW-161^T was 12.3 %. Moreover, *E. seohaensis* SW-135^T and *E. gaetbuli* SW-161^T exhibited DNA similarity levels of 9.7–20.2 % and 8.5–18.9 % against *E. longus*, *E. litoralis*, *E. citreus*, *E. flavus*, and *E. aquimaris* (Yoon et al. 2005b).

DNA–DNA hybridization similarity among four *E. vulgaris* strains (i.e., 022-2-10^T, 022-2-9, 022-2-12 and 022-4-7) was 94–98 %. DNA relatedness between *E. vulgaris* and *E. flavus* KCCM 41642^T, *E. citreus* DSM 14432^T, *E. litoralis* DSM 8509^T, *E. aquimaris* KCCM 41818^T, and *E. longus* ATCC 33941^T were 39 %, 37 %, 33 %, 33 %, and 30 %, respectively (Ivanova et al. 2006). DNA–DNA relatedness values between *E. nanhaisediminis* T30^T and *E. aquimaris* JCM 12189^T, *E. seohaensis* JCM 21815^T, *E. citreus* JCM 21816^T, *E. vulgaris* DSM 17792^T, and *E. longus* JCM 6170^T were 56.9 %, 40.3 %, 19.7 %, 14.7 %, and 14.5 %, respectively (Xu et al. 2010). DNA–DNA relatedness between *E. pelagi* UST081027-248^T and *E. citreus* DSM14432^T,

Table 9.2
Comparison of selected characteristics of the members of the genus *Erythrobacter*

Character	*E. aquimaris*	*E. citreus*	*E. flavus*	*E. gaetbuli*	*E. gangjinensis*	*"E. jejuensis"*	*E. litoralis*
Type strain	KCCM 41818^T = JCM 12189^T	CIP 107092^T = DSM 14432^T	KCCM 41642^T = JCM 11808^T	DSM 16225^T = KCTC 12227^T	JCM 15420^T = KCTC 22330^T	KCTC 23090^T = JCM 16677^T	DSM 8509^T
Acession no 16S rRNA gene	AY461441	AF118020	AF500004	AY562220	EU428782	DQ453142	AF465836
Description year	2004	2002	2003	2005	2010	2012	1994
Number of strain in the clade	3	2	2	1	1	1	1
Colony color	Orange	Yellow	Yellow	Orange-yellow	Orange	Yellow	Red-orange
Cell size (μm)	0.6–0.9 × 2.0–4.0	0.3–0.7 × 1.0–1.5	0.7–0.9 × 1.5–2.5	0.6–0.8 × 2.0–4.0	0.3–0.4 × 0.6–0.8	0.2–0.3 × 0.6–0.9	0.2–0.3 × 1.0–1.3
Motility	−	−	+, polar flagellum	−	−	−	+
Optimal pH	6.5–7.5	NR	6.5–7.5	7.0–8.0	7.0–8.0	7.0–8.0	NR
Optimal temperature (°C)	30–37	25–30	30–37	30–37	30	30	25–30
Tolerance to NaCl (%)	10	10[a]	14	9	5	5	NR
Growth requirement	NaCl	−	NaCl	NaCl	NaCl	NR	−
Nitrate reduction	−	+	−	−	−	−	−
Utilization of:							
Glucose	+	(+)	−	+	−	−	+
Acetate	+	+	+	+	NR	NR	+
Pyruvate	+	−	+	+	NR	NR	+
Glutamate	−	+[b]	−	−	NR	NR	+
Butyrate	+	NR	+	+	NR	NR	+
Methanol	−	NR	−	−	NR	NR	−
Susceptibility to:							
Chloramphenicol	+ (100 pg)	+ (30 ug)	+ (100 ug)	− (100 pg)	+ (30 ug)	+ (30 ug)	+ (100 ug)
Penicillin	− (20 U)	− (10 U)	− (20 U)	− (20 U)	+ (10 U)	+ (10 U)	− (20 U)
Tetracycline	− (30 ug)[c]	− (30 ug)	− (30 ug)[c]	− (30 ug)[d]	+ (30 ug)	+ (30 ug)	+
Hydrolysis of:							
Gelatin	−	−	−	−	−	−	−
Starch	(+)	−	+	−	+	−	−
Tween 80	+	−[b]	+	+	+	+	+
Voges-Proskauer reaction	−[c]	−[c]	+[c]	NR	−	−	NR

H_2S production	–	NR	–	–	–	–	NR
Indole production	NR	NR	NR	NR	–	–	NR
Bacteriochlorophyll a	–	–	–	–	–	–	+
Major quinone	Q-10	Q-10	Q-10	Q-10	Q-10	Q-10	NR
G+C content of DNA (mol%)	62.2–62.9 (62.2)	62.0–62.4 (62)	64.0–64.1 (64.0)	64.5	61.6	58.9	67
Sample source and site	Seawater, Korea	Seawater, France	Seawater, Korea	Tidal flat, Korea	Seawater, Korea	Seawater, Korea	Cyanobacterial mat, The Netherlands

Character	*E. longus*	*"E. marinus"*	*E. nanhaisediminis*	*E. pelagi*	*E. seohaensis*	*E. vulgaris*
Type strain	IF0 14126^T	KCTC 23554^T = CCUG 43 60528^T	CGMCC 1.7715^T = JCM 16125^T	JCM 17468^T = NRRL 59511^T	KCTC 12228^T = DSM 16221^T	CIP 108956^T = KMM 3465^T
Acession no 16S rRNA gene	AF465835	HQ117934	FJ654473	HQ203045	AY562219	AY706935
Description year	1982	2011	2010	2012	2005	2006
Number of strain in the clade	11	1	1	1	1	4
Colony color	Orange	Yellowish-orange	Orange	NR	Orange-yellow	Yellow
Cell size (μm)	0.3–0.4 × 2.0–5.0	0.3–0.5 × 0.5–1.0	0.3–0.5 × 0.5–1.7	2.5–3.0 × 0.5–0.6	0.6–0.8 × 1.5–4.0	0.6–0.8 × 1.2–1.8
Motility	+, subpolar flagella	–	+	–	–	–
Optimal pH	7.0–8.0	7.0–8.0	7.0–7.5	8.0–9.0	7.0–8.0	7.5–8.5
Optimal temperature (°C)	25–30	25	30	28–36	30–35	20–30
Tolerance to NaCl (%)	7	5	10	8	9	8
Growth requirement	Biotin, NaCl	NaCl	NaCl	NaCl	NaCl	NaCl
Nitrate reduction	+	–	–	+	–	–
Utilization of:						
Glucose	+	+	+	+	+	–
Acetate	+	–	+	+	+	–[b]
Pyruvate	+	+	+	+	+	+[a]
Glutamate	+	+	+	+	–	–
Butyrate	+	NR	+	NR	+	NR
Methanol	–	NR	–	NR	–	NR
Susceptibility to:						
Chloramphenicol	+ (100 pg)	– (100 ug)	+ (30 ug)	+ (30 ug)	– (100 pg)	NR
Penicillin	+ (20 U)	+ (20 U)	– (10 U)	+ (20 U)	– (20 U)	– (10 U)[a]
Tetracycline	– (50 pg)	+ (30 ug)	– (30 ug)	+ (30 ug)	– (30 ug)[c]	– (30 ug)

Table 9.2 (continued)

Character	*E. longus*	*"E. marinus"*	*E. nanhaisediminis*	*E. pelagi*	*E. seohaensis*	*E. vulgaris*
Hydrolysis of:						
Gelatin	+	–	–	–	–	–
Starch	–	–	–	–	–	–
Tween 80	(+)	+	+	–	+	+
Voges-Proskauer reaction	–	NR	NR	NR	NR	–
H_2S production	–	–	–	–	–	–
Indole production	+	NR	NR	+	NR	–
Bacteriochlorophyll a	+	–	–	–	–	–
Major quinone	NR	Q-10	Q-10	Q-10	Q-10	NR
G+C content of DNA (mol%)	60–64 (60.7)	66.1	59.5	60.4	62.2	60–62 (60.5)
Sample source and site	Seaweeds, Japan	Seawater, Korea	Sea sediment, China	Seawater, Israel	Tidal flat, Korea	Marine invertebrate, China

Data taken from:
[a]Xu et al. (2010)
[b]Wu et al. (2012)
[c]Lee et al. (2010)
[d]Yoon et al. (2013)
NR not reported
Additional data on growth substrates are given in the original species descriptions

Table 9.3

Comparison of selected characteristics of the members of the genus *Altererythrobacter*

Character	*A. aestuarii*	*A. dongtanensis*	*A. epoxidivorans*	*"A. gangjinensis"*	*A. indicus*	*A. ishigakiensis*	*A. luteolus*
Earlier name							*"Erythrobacter luteolus"*
Type strain	KCTC 22735^T = JCM 16339^T	KCTC 22672^T = CCTCC AB 209199^T	KCCM 42314^T = JCM 13815^T	KACC 16190^T = JCM 17802^T	LMG 23789^T = DSM 18604^T	NITE-AP48T = ATCC BAA-2084^T	KCTC 12311^T = JCM 12599^T
Acession no 16S rRNA gene	FJ997597	GU166344	DQ304436	JF751048	DQ399262	AB363004	AY739662
Description year	2011	2011	2007	2012	2008	2011	2007
Number of strain in the clade	1	1	1	1	1	1	1
Colony color	Yellow	Yellow	Yellow	Ochre	Yellow	Orange-red	Yellow
Cell shape	Rod	Rod	Ovoid-rod	Rod	Rod	Rod	Rod
Motility	–	–	–	–	–	–	–
Optimal pH	6–8	7–9	6.5	6.5–7.0	7	7.5	7–8
Temperature range (°C)	10–40	10–37	20–40	7–35	4–42	25–40	4–36
NaCl concentration range (%)	0–6	0–1	0–6	0–9	0–12	1.5–2	0.5–9
Nitrate reduction	–	–	–	–	–	+	–
Indole production	–	–	–[a]	–	–	–	–[a]
H_2S production	–	–	–	–	–[b]	NR	–
Utilization of							
Glucose	–	+	–	–	+	–	+
Mannose	–	–	–[c]	–	–[c]	–	–
Malate	–	+	–	–	+	–	–
Acetate	–	+	–	NR	+	NR	–
Hydrolysis of							
Gelatin	–	–	–	–	–[b]	–	–
Aesculin	+	–	–	+	+	+	+
Urea	–		+[d]	–	–[d]	–	–
Enzyme activity of							
Esterase	–	+	+	–	+[d]	NR	+[a]
Trypsin	+	–	+	+	–[d]	NR	+[a]
B-galactosidase	–	+	+	+	+[d]	+	+
Bacteriochlorophyll a	–	NR	–	–	–	–	–
G+C content of DNA (mol%)	67.2	66.4	54.5	60.2	66.8	59.1	60.3
Sample source and site	Seawater, Korea	Tidal flat, China	Sediments, Japan	Tidal flat, Korea	Mangrove- rice, India	Sediment, Japan	Tidal flat, Korea

Table 9.3 (continued)

Character	*A. marensis*	*A. marinus*	*A. namhicola*	*"A. troitsensis"*	*A. xinjiangensis*
Earlier name					
Type strain	KCTC 22370^T = DSM 21428^T	CCTCC AB 208229^T = LMG 24629^T	KCTC 22736^T = JCM 16345^T	KCTC 12303^T = JCM 17037^T	CCTCC AB 207166^T = CIP 110125^T
Acession no 16S rRNA gene	FM177586	EU726272	FJ935793	AY676115	HM028673
Description year	2010	2009	2011	2012	2012
Number of strain in the clade	1	1	1	1	1
Colony color	Yellow	Yellow	Orange	Yellow	Yellow
Cell shape	Rod	Rod	Rod	Ovoid-rod	Rod
Motility	+	–	–	+	–
Optimal pH	7.1	7–8	6–7	7.2–7.6	8
Temperature range (°C)	4–42	10–42	15–37	4–39	20–37
NaCl concentration range (%)	0–9	0.5–5	1–2	0–4	0–3
Nitrate reduction	–	–	–	+	–
Indole production	–	–	–	–	–
H_2S production	NR	–	–	NR	NR
Utilization of					
Glucose	–	–	–	–	+
Mannose	–	–	–	–	–
Malate	+	–	+	–	+[e]
Acetate	NR	+	–	+	NR
Hydrolysis of					
Gelatin	–	–	–	–	–
Aesculin	+	+	+	+	+[e]
Urea	–	–	–	–	–
Enzyme activity of					
Esterase	w	w	–	w	+
Trypsin	–	+	+	–	+
B-galactosidase	–	–	–	–	+
Bacteriochlorophyll a	–	–	–	–	–
G+C content of DNA (mol%)	63.1	66.5	63.8	65	64.6
Sample source and site	Seawater, Korea	Seawater, Indian Ocean	Seawater, Korea	Sea urchin, East sea	Desert, China

Data taken from:

[a]Seo and Lee (2010)

[b]Lai et al. (2009)

[c]Matsumoto et al. (2011)

[d]Park et al. (2011)

[e]Nedashkovskaya et al. (2013)

NR not reported

Additional data on growth substrates are given in the original species descriptions

Table 9.4
Comparison of selected characteristics of the members of the genera *Croceicoccus* and *Erythromicrobium*

Character	*Croceicoccus marinus* (2009)	*Erythromicrobium ramosum* (1994)
Type strain	CGMCC 1.6776^T = JCM 14846^T	DSM 8510^T
Acession no 16S rRNA gene	EF623998	AF465837
Cell shape	Cocci	Rod
Color of colony	Yellow	Red-orange
Motility	+	+
Presence of BChl a	–	+
Growth in NaCl (%):	0–10 (0–1)	NR
Growth pH:	6.0–9.0 (7.0)	(7.0–8.5)
Growth temperature (°C):	4–42 (25)	(25–30)
H_2S production	–	NR
Hydrolysis of:		
Aesculin	+	NR
Casein	+	+
Gelatin	+	–
Starch	+	–
Tween 80	+	–
Acid production from:		
Glucose	+	NR
Maltose	+	NR
Sucrose	+	NR
Utilization of:		
Acetate	+	+
Cellobiose	–	NR
Citrate	–	+
Ethanol	+	+
Glutamate	+	+
Glycerol	+	–
Lactate	+	+
Malate	+	+
Maltose	+	+
Mannose	+	NR
Pyruvate	+	+
Succinate	+	+
Sucrose	+	+
Xylose	–	
Major cellular fatty acids	Anteiso-$C_{15:0}$	$C_{17:1}$ ω6*c*, $C_{18:1}$ ω7*c*
DNA G+C content (mol%)	71.5	64.2
Sample source	Deep-sea sediment, East Pacific Ocean	Freshwater cyanobacterial mat from alkaline spring

Data taken from Yurkov et al. (1994), Rainey et al. (2003), Xu et al. (2009). *NR* not reported
Additional data on growth substrates are given in the original species descriptions

E. seohaensis DSM 16221^T, *E. flavus* DSM16421^T, *E. vulgaris* DSM 17792^T, and *E. nanhaisediminis* DSM 16125^T were 62 %, 48 %, 24 %, 14 %, and 14 %, respectively (Wu et al. 2012).

P. sanguineus strains IAM 12620^T and ATCC 25661 showed DNA–DNA relatedness of 88 % against each other. In addition, the DNA relatedness between *P. sanguineus* IAM 12620^T and its phylogenetic neighbors *Erytromicrobium ramosum* DSM 8510^T, *P. tepidarius* DSM 10594^T, *P. neustonensis* DSM9434^T, *Erytrobacter litoralis* DSM8509^T, *Erytrobacter longus* IFO 14126^T, *Blastomonas natatoria* DSM 3183^T, and *Sphingomonas paucimobilis* IFO 13935^T were 38 %, 36 %, 31 %, 18 %, 14 %, 2 %, and <1 %, respectively (Hiraishi et al. 2002). DNA–DNA relatedness between *P. neustonensis* DSM 9434^T and *P. tepidarius* DSM 10594^T, *P. sanguineus* ATCC 25661 and IAM 12620^T, *Erytromicrobium ramosum* DSM 8510^T, *Erytrobacter litoralis* DSM8509^T, *Erytrobacter longus* IFO 14126^T, *Blastomonas natatoria* DSM 3183^T, and *Sphingomonas paucimobilis* IFO 13935^T were 38 %, 32 %, 29 %, 29 %, 14 %, 11 %, 4 %, and <1 %, respectively (Hiraishi et al. 2002).

DNA–DNA relatedness of *P. cryptus* ALC-2^T and ALC-3 strains against *P. neustonensis*, *P. tepidarius*, *Erythrobacter longus*, and *Erythromicrobium ramosum* were 25 %, 31 %, 35 %, 40 %, 19 %, 20 %, 22 %, and 21 %, respectively. DDH relatedness of *P. neustonensis* against *P. tepidarius*, *E. longus*, and *E. ramosum* were 24 %, 21 %, and 24 %, respectively. Values for *P. tepidarius* against *E. longus* and *E. ramosum* were 22 % and 24 %, respectively. DNA similarity between *E. longus* and *E. ramosum* was 25 % (Rainey et al. 2003). *P. donghaensis* strains SW-132^T and SW-158 exhibited a mean level of DNA–DNA relatedness of approximately 86 %. Values between *P. donghaensis* strains and the type strains of *Porphyrobacter* species (i.e., *P. neustonensis*, *P. tepidarius*, *P. sanguineus* and *P. cryptus*) were in the range of 9.4–20.3 % (Yoon et al. 2004b). Levels of DNA–DNA relatedness between *P. dokdonensis* DSW-74^T and the type strains *P. neustonensis*, *P. tepidarius*, *P. sanguineus*, *P. cryptus*, and *P. donghaensis* were in the range of 9–25 % (Yoon et al. 2006).

Genome Analysis

As of May 2013, no type strains genome sequence is available in the *Erythrobacteraceae* family. However, three genomes belonging to the *Erythrobacter* genus have been reported, but only one is completely closed. Moreover, a draft genome has also stated for the *Porphyrobacter* genus. The main features of these genomes are summarized in *Table 9.9*.

The *E. litoralis* genome, strain HTCC2594, was isolated from a depth of 10 m in the Sargasso Sea, Atlantic Ocean, and cultured in a low-nutrient heterotrophic medium. It contains one circular chromosome of 3,052,398 bp, 3.011 protein coding genes, one copy of 16S-23S-5S rRNA, 45 tRNA genes encoding 19 aminoacyl-tRNA sequences, and 63.07 % G+C content (Oh et al. 2009). No plasmids are present. Moreover, the HTCC2594 genome lacks reaction center genes for phototrophic metabolism, genes for CO_2 fixation such as ribulose-1,5-bisphosphate carboxylase/oxygenase, and components of the reverse trichloroacetic acid cycle.

Table 9.5

Comparison of selected characteristics of the members of the genus *Porphyrobacter*

Character	*P. cryptus*	*P. dokdonensis*	*P. donghaensis*	*P. neustonensis*	*P. sanguineus*	*P. tepidarius*
Type strain	DSM 12079^T = ATCC BAA-386^T	KCTC 12395^T = DSM 17193^T	KCTC 12229^T = DSM 16220^T	ACM 2844^T	ATCC 25659 ^{T} = IAM 12620^T	DSM 10595^T
Accession no 16S rRNA gene	AF465834	DQ011529	AY559428	AB033327	AB021493	AB033328
Description year	2003	2006	2004	1993	2002	1997
Strain number in the clade	2	1	2	4	2	1
Cell morphology	Short rods	Pleomorphic	Pleomorphic	Pleomorphic	Pleomorphic	Ovoid or short rods
Presence of BChl a	+	+	+	+	+	+
Oxidase	+	+	+	−	+	−
Growth in NaCl (%):	0 – NR	0–7 (2)	0–7 (2)	0 – NR	(1)	0–1.3
Growth pH:	6–9 (7.5–8)	5.5–8 (7–8)	5–8 (7–8)	(7.2)	(7–7.5)	NR
Growth temperature (°C):	<60 (50–55)	10–43 (35–37)	10–45 (30–37)	10–37 (30)	20–37 (30)	<52 (40–48)
Motility	+	−	−	+	+	−
Hydrolysis of:						
Aesculin	+	+	+	V (+)	+	+
Casein	−	−	−	V (−)	−	−
Gelatin	+	−	−	−	−	−
Starch	+	+	+	−	−	+
Tween 80	+	+	+	+	−	+
Utilization of:						
D-Fructose	−	−	−	V (−)	−	−
D-Galactose	−	−	−	+	−	−
D-Cellobiose	+	+	+	V (−)	+	+
D-Mannose	−	−	−	+	−	−
D-Trehalose	−	−	−	V (+)	+	−
D-Xylose	+	−	V (+)	+	−	−
L-Arabinose	−	−	−	−	−	−
Sucrose	+	−	V (−)	+	+	−
Acetate	−	−	V (−)	−	+	+
Succinate	−	+	+	V (+)	−	−
L-Malate	−	+	+	−	−	−
Pyruvate	+	+	+	V (+)	+	−
L-Glutamate	+	−	−	−	+	+
DNA G+C content (mol%)	66.2	65.8	65.9−66.8 (66.8)	65.7−66.4 (66.4)	63.8−64	65
Sample source and site	Hot spring, Portugal	Seawater, Korea	Seawater, Korea	Freshwater, Australian	Brackish and marine environments, Baltic sea	Brackish hot spring

Data taken from Fuerst et al. (1993), Hanada et al. (1997), Hiraishi et al. (2002), Rainey et al. (2003), Yoon et al. (2004b). *V* variable reaction; data in parentheses are for the type strain. Optimal growth conditions are in parentheses. *NR* not reported. Additional data on growth substrates are given in the original species descriptions

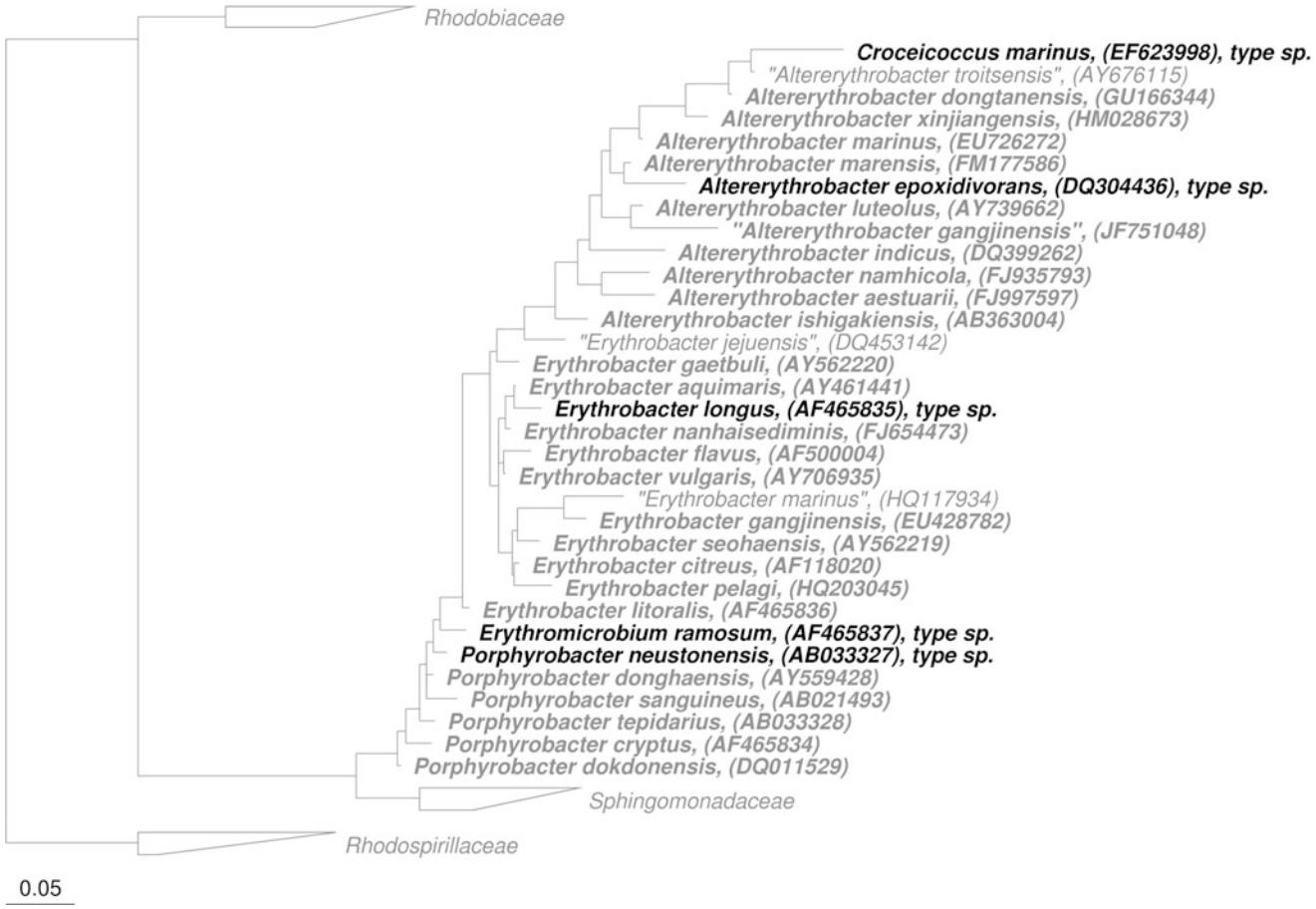

Fig. 9.1

Phylogenetic reconstruction of the family *Erythrobacteraceae* based on 16S rRNA and created using the maximum likelihood algorithm RAxML (Stamatakis 2006). The sequence datasets and alignments were used according to the All-Species Living Tree Project (LTP) database (Yarza et al. 2010; http://www.arb-silva.de/projects/living-tree). Representative sequences from closely related taxa were used as outgroups. In addition, a 10 % maximum frequency filter was applied in order to remove hypervariable positions and potentially misplaced bases from the alignment. Scale bar 2 % indicates estimated sequence divergence

The HTCC2594 strain encodes three distinct epoxide hydrolases with enantioselectivity towards styrene oxides, which may be exploited for biotechnological purposes (Woo et al. 2007; Oh et al. 2009).

So far, two other *Erythrobacter* draft genomes have been documented: *Erythrobacter* sp. strain NAP1, available as 2 scaffolds, and *Erythrobacter* sp. strain SD-21, available as 19 scaffolds. The NAP1 strain, which is an aerobic, anoxygenic, phototrophic bacterium, was isolated by plating on minimal medium from a water sample collected in the Northwest Atlantic in 2000 (Kolber et al. 2001; Koblízek et al. 2003). The genome of *Erythrobacter* sp. NAP1 consists of a single circular chromosome of 3,264,238 bp with 3.177 putative genes that cover 92 % of the genome, one copy of each of the rRNA genes, 45 genes for tRNAs, G+C content of 61 %, and a complete set of genes for bacteriochlorophyll biosynthesis and reaction center proteins (Koblízek et al. 2011). The continuous 38.9-kb-long photosynthetic gene cluster is organized as follows: *bchIDO-crtCDF-bchCXYZ-pufBALM-tspO-bch*PORF-*bchG-ppsR-ppaA-bchFNBHLM-lhaA-puhABC-acsF-puhEhemA-cycA*. Homologs of regulatory genes *ppaA* (cobalamin binding) and *ppsR* (*crtJ* homologue) are also present in the gene cluster, but most of the carotenoid biosynthesis genes are located outside the cluster (Koblízek et al. 2011). The NAP1 genome contains a full set of genes for heme biosynthesis; γ-aminolevulinic acid is synthesized through the Shemin (C4) pathway, besides a complete set of genes for the siroheme biosynthesis pathway, although final enzymes of cobalamin (vitamin B12) biosynthesis are missing.

Although the NAP1 strain lacks the genes of any autotrophic CO_2 fixation pathway (Koblízek et al. 2011), this strain may augment heterotrophic growth with light harvesting encoded by the *puf* operon and ribulose-1,5-bisphosphate carboxylase/oxygenase independent CO_2 fixation (Koblízek et al. 2003). Genes for nitrogenase or nitrate reductase are also absent in this genome, which is consistent with its inability to grow on nitrate. The NAP1 genome offers a valuable source of information for further studies focused on AAP metabolism and physiological nature (Koblízek et al. 2011).

Table 9.6
DNA–DNA hybridization similarities (%) of *Altererythrobacter* genus members

Taxon	Species name	1	2	3	4	5	6	7
1	*A. marensis* MSW-14^T	**100**						
2	*A. epoxidivorans* KCCM 42314^T	26.0–27.3[a]	**100**					
3	*A. luteolus* KCTC 12311^T	9.8–15.2[a]		**100**				
4	*A. xinjiangensis* S3-63^T				**100**			
5	*A. marinus* H32^T				54.5 ± 2[b]	**100**		
6	*A. troitsensis* KMM 6042^T						**100**	
7	*A. dongtanensis*						34.4 ± 7.6[c]	**100**

Original data:
[a]Seo and Lee (2010)
[b]Xue et al. (2012)
[c]Nedashkovskaya et al. (2013)

Table 9.7
DNA-DNA hybridization similarities (%) among type strains of the *Erythrobacter* genus

Taxon	Species name	1	2	3	4	5	6	7	8	9	10	11
1	*E. citreus* RE35F/1^T = DSM14432^T JCM 21816^T	**100**										
2	*E. litoralis* DSM 8509^T	25 ± 2[a]	**100**									
3	*E. flavus* SW-46^T = KCCM 41642^T = DSM16421^T	13.1[b]	6.0[b]	**100**								
4	*E. longus* DSM 6997^T = JCM 6170^T = ATCC 33941^T			4.2[b]	**100**							
5	*E. aquimaris* SW-110^T = KCCM 41818^T = JCM 12189^T	Range 5.3–12.7[c]				**100**						
6	*E. seohaensis* SW-135^T = JCM 21815^T = DSM 16221^T	Range 9.7–20.2[d]					**100**					
7	*E. gaetbuli* SW-161^T	Range 8.5–18.9[d]					12.3[d]	**100**				
8	***E. vulgaris*** 022-2-10^T = DSM 17792^T	37[e]	33[e]	39[e]	30[e]	33[e]			**100**			
9	*E. nanhaisediminis* T30^T = DSM 16125^T	19.7[f]			14.5[f]	56.9[f]	40.3[f]		14.7[f]	**100**		
10	*E. pelagi* UST081027-248^T	62[g]		24[g]			48[g]		14[g]	14[g]	**100**	
11	*Erythromicrobium ramosum* DSM 8510^T	20 ± 3[a]										**100**

Original data:
[a]Denner et al. (2002)
[b]Yoon et al. (2003)
[c]Yoon et al. (2004a)
[d]Yoon et al. (2005b)
[e]Ivanova et al. (2006)
[f]Xu et al. (2010)
[g]Wu et al. (2012)

Erythrobacter sp. strain SD-21 was isolated from surface sediment from the San Diego Bay, based on its ability to oxidize soluble Mn(II) to insoluble Mn(III, IV) oxides. The genome of SD-21 strain contains 2,970,874 bp, 2.941 protein coding genes that cover 85 % of the genome, one copy of the rRNA genes, 41 genes for tRNAs, and 62.9 % G+C content (http://www.ncbi.nlm.nih.gov/genome/browse/; https://moore.jcvi.org/moore/) (*Table 9.9*). The SD-21 strain was reported as the first bacterium within the alpha-4 Proteobacteria that is able to oxidize Mn(II) as well as the first marine Gram-negative bacterium containing Mn(II)-oxidizing proteins (Francis et al. 2001). In addition to being a robust Mn(II) oxidizer, SD-21 clusters with the aerobic anoxygenic phototrophs, which may comprise as much as 11 % of the microbial community in the upper ocean and exert a significant impact on global carbon cycling (Kolber et al. 2001). This nonphotosynthetic, manganese(II)-oxidizing bacterium (Francis et al. 2001; Oh et al. 2009) has a new type of manganese-oxidizing enzyme (Anderson et al. 2009) and may serve as a useful model for studying the mechanism of Mn(II) oxidation within the α-*Proteobacteria* and the biological function of bacterial Mn(II) oxidation.

Porphyrobacter sp. strain AAP82 was isolated from the Huguangyan Maar Lake in southern China. The genome of the AAP82 strain has a BioProject number in the Genebank

Table 9.8

DNA–DNA hybridization similarities (%) among type strains of the *Porphyrobacter* genus

Taxon	Species name	1	2	3	4	5	6	7	8	9	10	11
1	*P. sanguineus* IAM 12620^T = DSM11032^T	**100**		29[a]								
2	*P. tepidarius* DSM10594^T	36[a]	**100**	24[b]								
3	*P. neustonensis* DSM9434^T	31[a]	38[a]	**100**					21[b]			24[b]
4	*P. cryptus* ALC-2^T = DSM 12079^T		31[b]	25[b]	**100**							
5	*P. donghaensis* SW132^T	Range 9.4–20.3[c]				**100**						
6	*P. dokdonensis* DSW74^T	Range 9–25[d]					**100**					
7	*Erythrobacter litoralis* DSM8509^T	18[a]		14[a]				**100**				
8	*Erythrobacter longus* IFO14126^T = DSM6997^T	14[a]	22[b]	11[a]	35[b]				**100**			
9	*Blastomonas natatoria* DSM3183^T	2[a]		4[a]						**100**		
10	*Sphingomonas paucimobilis* IFO13935^T	<1[a]		<1[a]							**100**	
11	*Erythromicrobium ramosum* DSM8510^T	38[a]	24[b]	29[a]	40[b]				25[b]			**100**

Original data:
[a]Hiraishi et al. (2002)
[b]Rainey et al. (2003)
[c]Yoon et al. (2004b)
[d]Yoon et al. (2006)

Table 9.9

Properties of the sequenced genomes of members of the *Erythrobacteraceae* (as of May 2013)

	Erythrobacter litoralis HTCC2594[a]	*Erythrobacter* sp. strain NAP1[b]	*Erythrobacter* sp. strain SD-21[c,d]	*Porphyrobacter* sp. strain AAP82[d,e]
Accession number	CP000157.1	AAMW00000000	ABCG00000000	ANFX00000000
RefSeq	NC_007722.1	NZ_AAMW00000000	NZ_ABCG00000000	NZ_ANFX00000000
Genome length (bp)	3,052,398	3,264,238	2,970,874	2,899,072
G+C content	63.1	61	62.9	67.3
Protein sequence	3.011	3.177	2.941	NR
rRNA	3	3	1	3
tRNA	45	45	41	44
Gene	3.059	3223	2986	2789
Chromosomes	1	NR	NR	NR
Scaffolds	–	2	19	52

Data taken from:
[a]Oh et al. (2009)
[b]Koblízek et al. (2011)
[c]J. Craig Venter Institute (https://moore.jcvi.org/moore/)
[d]GeneBank (http://www.ncbi.nlm.nih.gov/genome/browse/)
[e]Rapid Annotation Subsystem Technology (RAST)
NR not reported

database (http://www.ncbi.nlm.nih.gov/genome/browse/), but no valid publication has been reported yet. This AAP bacterium represents an important microbial component in the upper layers of the water column in various freshwater lakes. The AAP82 strain genome is available in 52 scaffolds and contains 2,899,072 bp, 2789 coding sequences, one copy of each of the rRNA genes, 44 genes for tRNAs, and G+C content of 67.3 % (RAST server; Aziz et al. 2008).

The comparative analyses among these four genomes of the *Erythrobacteraceae* family has been represented by Genome Atlas (*Fig. 9.2*) based on the GeneWiz browser 0.94 server. *Sphingomonas wittichii* RW1 was used as the reference genome.

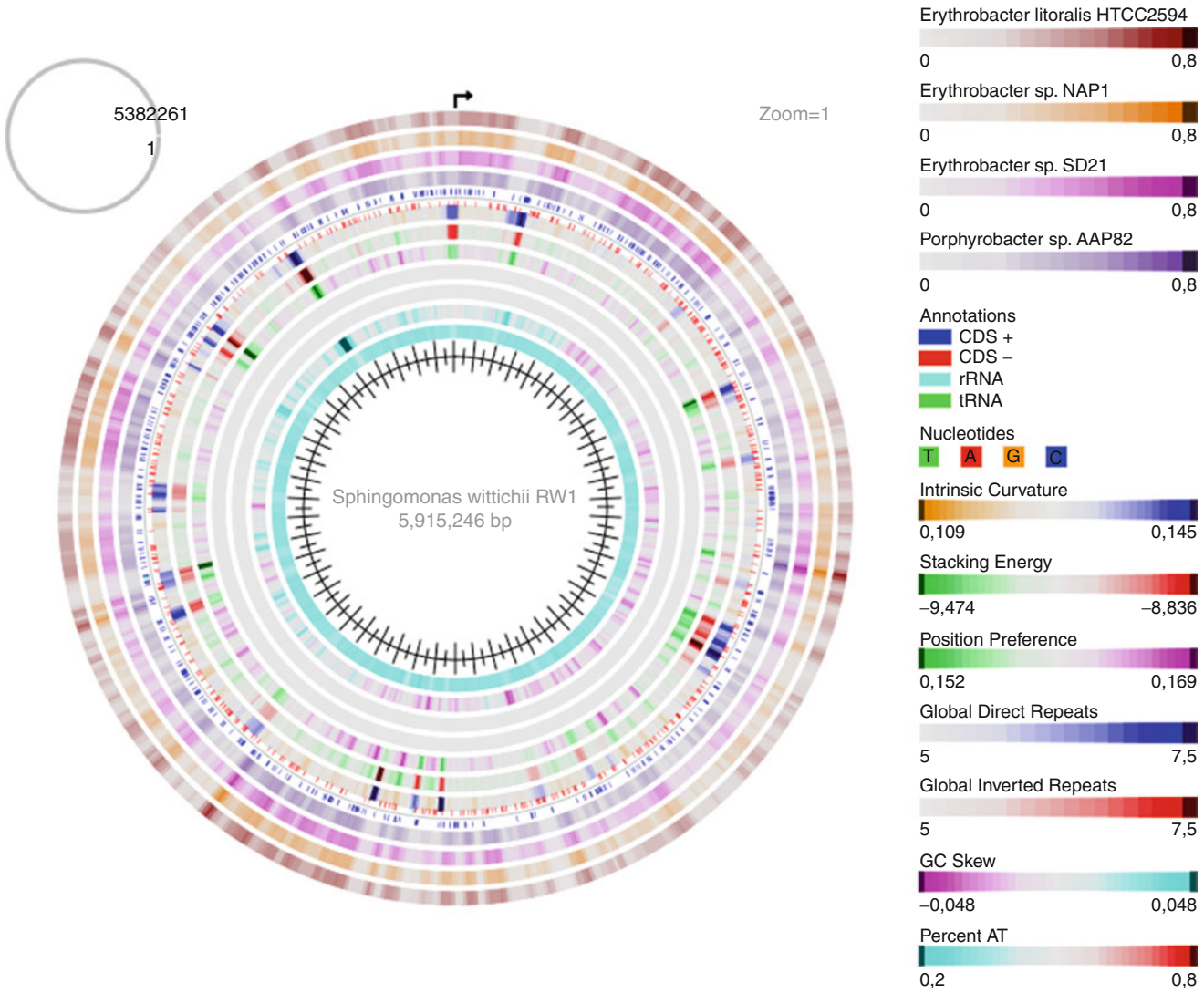

Fig. 9.2
Genome Atlas. The Atlas shows the genome comparison among *Erythrobacter litoralis* HTCC2594, *Erythrobacter* sp. strain NAP1, *Erythrobacter* sp. strain SD-21 and *Porphyrobacter* sp. strain AAP82 chromosomes. *Sphingomonas wittichii* RW1 was used as reference genome

Phages

Two prophage sequences are reported in the genome of *Erythrobacter litoralis* strain HTCC2594: a large prophage region (157,555–185,998 bp) and a medium prophage region (2,812,472–2,826,784 bp) (Oh et al. 2009). Based on the Rast Server annotation (Aziz et al. 2008), which uses the subsystem feature counts, three sequences have been allocated in the phages: a prophages category from *Erythrobacter* sp. NAP1 and two from *Erythrobacter* sp. SD-21 genomes. The main functions of the proteins in this category were phage packaging machinery and phage capsid proteins. The comparative chromosomal region for the phage genes among the three *Eryhtrobacter* strains is represented in *Fig. 9.3*. No sequence has been reported for *Porphyrobacter* sp. strain AAP82 in phages, prophages, transposable elements, or plasmids categories.

Phenotypic Analyses

Family *Erythrobacteraceae* Lee, Liu, Anzai, Kim, Aono and Oyaizu (2005). Emend Xu, Wu, Wang, Wang, Oren and Wu (2009)

Erythrobacteraceae (E.ry.thro.bac.te.ra'ceae. N.L. masc. n. *Erythrobacter* type genus of the family; -aceae ending to denote a family; N.L. fem. pl. n. *Erythrobacteraceae* the *Erythrobacter* family.

The main features of *Erythrobacteraceae* family members are summarized below and listed in *Tables 9.1*, *9.2*, *9.3*, *9.4*, and *9.5*. The family *Erythrobacteraceae* was circumscribed on the basis of the phylogenetic analysis of 16S rRNA gene sequences, hybridizations based on similarities between DNA–DNA (DDH), and phenotypic characteristics. The family is

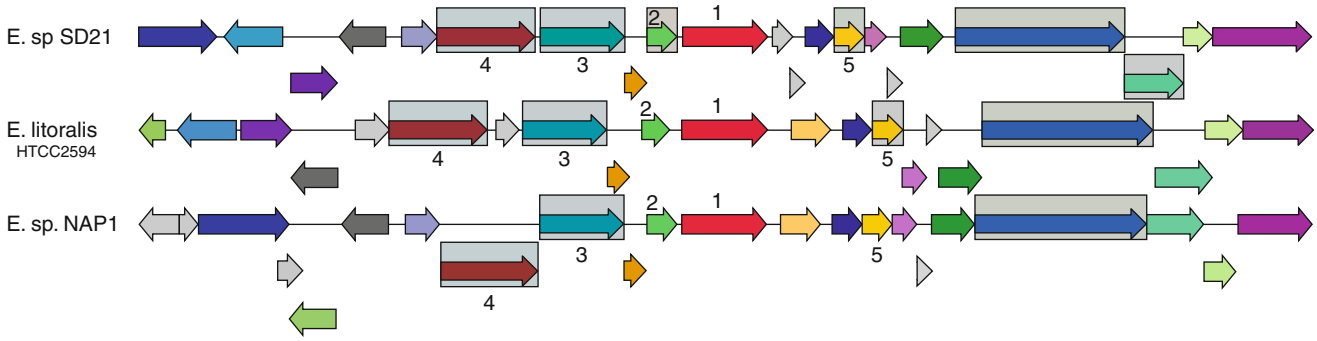

Fig. 9.3

Comparative chromosome region for phage genes among three *Erythrobacter* strains. The function predicted is represented by number: *1* Phage major capsid protein, *2* Gene transfer prohead protease, *3* Phage portal protein, *4* Gene transfer agent terminase protein, *5* Gene transfer tail protein. Sets of genes with similar sequence are grouped with the same number and color. Genes whose relative position is conserved are functionally coupled and share gray background boxes

phenotypically, metabolically, and ecologically similar. It basically includes aerobic chemoorganotrophs, but one genus may be facultative photoheterotrophs.

Type genus: *Erythrobacter.*

Genus *Erythrobacter* Shiba and Simidu (1982)

Erythrobacter (Gr. adj. *eiythrus* red; M. L. masc. n. *bacter* rod or staff; M. L. mas. n. *Erythrobacter* red rod)

Cells are yellow, orange, orange-yellow, or red-orange; ovoid to rod-shaped; and 0.3–3.0 by 0.5–5.0 um. The cells contain ubiquinone-10 (Q-10) as the predominant respiratory lipoquinone. Optimal growth occurs at temperatures between 25 °C and 37 °C and at pH values between 7.0 and 8.0. They are Gram-negative, non-spore-forming, and multiply by binary fission. Cells are motile by means of polar or subpolar flagella, or they are nonmotile. Most species contain carotenoids, require NaCl for growth, utilize glucose but do not hydrolyze starch or gelatin, and do not reduce nitrate. The Voges-Proskauer test is mostly negative. They are aerobic chemoorganotrophs; only two species present bacteriochlorophyll *a*. No growth is reported anaerobically in the light and no autotrophic growth occurs with H_2. Although small amounts of acid are produced from a wide range of carbohydrates under microaerobic conditions, metabolism is predominantly respiratory. Most species are mainly susceptible to chloramphenicol. Methanol is not utilized. Oxidase and catalase can be produced. The G+C of the DNA is 58.9–67 mol%.

Type species: *Erythrobacter longus.*

The genus currently contains 13 species, although only 2 of which were effectively published: *E. longus* (Shiba and Simidu 1982); *E. litoralis* (Yurkov et al. 1994); *E. citreus* (Denner et al. 2002); *E. flavus* (Yoon et al. 2003); *E. aquimaris* (Yoon et al. 2004a); *E. gaetbuli* and *E. seohaensis* (Yoon et al. 2005b); *E. vulgaris* (Ivanova et al. 2006); *E. gangjinensis* (Lee et al. 2010); *E. nanhaisediminis* (Xu et al. 2010); *E. pelagi* (Wu et al. 2012); "*E. jejuensis*" (Yoon et al. 2013); and "*E. marinus*" (Jung et al. 2012). *Erythrobacter luteolus* was isolated from a tidal flat of the Yellow Sea in Korea (Yoon et al. 2005a) has been transferred to *Altererythrobacter luteolus* comb. nov. (Kwon et al. 2007). *Tables 9.1* and *9.2* summarize the properties of the *Erythrobacter* genus.

Genus *Altererythrobacter* Kwon, Woo, Yang, Kang, Kang, Kim, Sato and Kato (2007). Emend Xue, Zhang, Cai, Dai, Wang, Rahman, Peng and Fang (2012)

Altererythrobacter (Al.ter.e.ryth'ro.bac'ter. L. adj. *alius*, *alterius* another, other, different; N.L. masc. n. *Erythrobacter* a genus name; N.L. masc. n. *Altererythrobacter* another or different *Erythrobacter*, because the genus shows high similarity to the genus *Erythrobacter* but does not share its phyletic line).

Cells are Gram-negative and motile or nonmotile; the color of cell suspensions and colonies can be yellow, orange-red, or ochre. Strains produce catalase and can be positive or negative for oxidase. Methanol-soluble pigments are species-dependent and are characterized by absorption maxima at 447 and 473 nm. They do not contain *BChl a* as a photosynthetic pigment. The major polar lipids are phosphatidylethanolamine, phosphatidylglycerol, diphosphatidylglycerol, and sphingoglycolipid. Anaerobic growth does not occur on marine agar (MA) or on MA supplemented with nitrate. The dominant fatty acid is C18:1 ω7*c*. They do not produce H_2S or indole, do not utilize manose, and do not hydrolyze gelatin. The dominant respiratory quinone is Q10. The optimal growth temperature occurs in mesophilic conditions. All species can grow in the presence of NaCl, although it is not essential in many cases. The DNA G+C content is 54.5–67.2 mol%.

Type species: *Altererythrobacter epoxidivorans.*

The genus currently contains 12 species, although only 2 of which were effectively published: *A. luteolus* (Yoon et al. 2005a; Kwon et al. 2007); *A. epoxidivorans* (Kwon et al. 2007);

A. indicus (Kumar et al. 2008); *A. marinus* (Lai et al. 2009); *A. marensis* (Seo and Lee 2010); *A. aestuarii* (Park et al. 2011); *A. dongtanensis* (Fan et al. 2011); *A. ishigakiensis* (Matsumoto et al. 2011); *A. namhicola* (Park et al. 2011); *A. xinjiangensis* (Xue et al. 2012); "*A. gangjinensis*" (Jeong et al. 2013); "*A. troitsensis*" (Nedashkovskaya et al. 2013).

Tables 9.1 and *9.3* summarize the properties of *Altererythrobacter*.

Genus *Croceicoccus* Xu, Wu, Wang, Wang, Oren and Wu (2009)

Croceicoccus [Cro.ce.i.coc'cus. L. adj. *croceus* yellow, golden; N.L. masc. n. *coccus* (from Gr. masc. n. *kokkos*) grain or berry; N.L. masc. n. *Croceicoccus* referring to a yellow coccoid-shaped bacterium].

Cells are Gram-negative and non-spore-forming cocci. Cells are motile and occur in pairs. Young cultures show pleomorphic coccoid cells (0.8–1.0 mm). Colonies on complex agar containing peptone, casamino acids, and yeast extract are 1–2 mm in diameter, circular, smooth, elevated, opaque, and yellow pigmented. They are oxidase negative, catalase positive, divide by binary division, and are capable of producing multifibrillar stalk-like fascicle structures on the cell surface. Cells are aerobic and chemoheterotrophic. They contain carotenoids but not *BChl a*. No growth occurs anaerobically in the light.

Ubiquinone-10 is the major respiratory quinone. The polar lipid profiles comprise phosphatidylglycerol, two unidentified glycolipids, phosphatidylcholine, and an unidentified phospholipid. The major fatty acids are anteiso-C_{15}: 0, iso-C_{14} : 0 and iso-C_{15} : 0. Cells are susceptible to ampicillin (10 mg), bacitracin (0.04 U), cefalexin (30 mg), ceftriaxone (30 mg), chloramphenicol (30 mg), erythromycin (15 mg), gentamicin (10 mg), minocycline (30 mg), neomycin (30 mg), novobiocin (30 mg), penicillin (10 mg), streptomycin (10 mg), and tetracycline (30 mg). The phylogenetic position is in the α-4 subgroup of the class *Alphaproteobacteria*. The G+C of the DNA of the type strain of the single species is 71.5 mol%.

Type species: *Croceicoccus marinus*.

Tables 9.1 and *9.4* summarizes the properties of *Croceicoccus marinus* and *Erythromicrobium ramosum*.

Genus *Erythromicrobium* Yurkov, Stackebrandt, Holmes, Fuerst, Hugenholtz, Golecki, Gad'on, Gorlenko, Kompantseva and Drews (1994)

Erythromicrobium (E.ry.thro.mi.cro'bi.um. Gr. adj. *erythrus*, red; Gr. adj. *micros*, small; Gr. n. *bios*, life; N.L. n. *Erythromicrobium*, red microbe).

The description of *Erythromicrobium* is supported by biochemical, morphological, and 16S rDNA sequence data. Cells are Gram-negative, rod-shaped cells, 0.6–1.0 by 1.3–2.5 μm, and usually motile by means of flagella. Branching may occur. The cells are orange and contain *BChl a* and carotenoids. The major carotenoids are the very polar compound erythroxanthin sulfate and bacteriorubixanthinal. Optimal growth occurs at temperatures between 25 °C and 30 °C and at pH values between 7.0 and 8.5. Multiplication occurs by binary or ternary fission. Cells are aerobic chemoorganotrophs and facultative photoheterotrophs. No growth occurs anaerobically in the light. Ribulose diphosphate carboxylase is not detected. No fermentation or denitrification activities occur. Methanol is not utilized. Cells are phylogenetically related to members of the *Proteobacteria* α-4 subclass. They are frequently found in freshwater habitats and are not halophilic. The G+C of the DNA of the type strain of the single species is 64.2 mol%.

Type species: *Erythromicrobium ramosum*.

Erythromicrobium ramosum is the only valid species published in this genus (Yurkov et al. 1994). "*Erythromicrobium sibiricum*," "*Erythromicrobium ursincola*", "*Erythromicrobium ezovicum*," and "*Erythromicrobium hydrolyticum*" were tentatively allocated in this genus by Yurkov et al. (1991). However, later "*E. sibiricum*" and "*E. ursincola*" were taxonomic transferred from this genus to new genera, *Sandaracinobacter* and *Erythromonas*, respectively, and validly published by Yurkov et al. in 1997. *Tables 9.1* and *9.4* summarize the properties of *Erythromicrobium ramosum* and *Croceicoccus marinus*.

Genus *Porphyrobacter* Fuerst, Hawkins, Holmes, Sly, Moore and Stackebrandt (1993)

Porphyrobacter (Por.phy.ro.bac.ter. Gr. adj. *porphyreos*, purple; Gr. n. *bacter*, rod; M.L. masc. n. *Porphyrobacter*, porphyrin-producing rod, referring to bacteriochlorophyll production).

Cells are members of the α-subclass of *Proteobacteria*. They are Gram-negative, ovoid-to-short rods, pleomorphic, 0.5–1.0 × 0.5–2.8 μm, and reproduce by polar growth, budding, or asymmetric cell division. Colonies on complex media containing peptone are circular, smooth, opaque, and orange or red. They are neutrophilic freshwater bacteria, mesophilic to moderately thermophilic. Growth occurs at 10–60 °C, with an optimum temperature between 30 °C and 37 °C for most species. Cells are motile by peritrichous flagella or nonmotile. They are capable of producing structures that are multifibrillar stalk-like fascicles and crateriforms on the cell surface. Cells do not form any type of internal membranes. Spores and capsules are not formed. They are aerobic and chemoheterotrophic.

Cells synthesize *BChl a* on low-nutrient media under aerobic and semiaerobic conditions. Carotenoids are present. They are positive for calatase, D-glucose utilization, and hydrolyze of aesculine, but negative for citrate, L-arabinose, and D-fructose utilization. Cells do not grow phototrophically under anoxic conditions in the light. Simple organic compounds, peptone, and yeast extract are used as electron donors and carbon sources. Straight-chain octadecenoic acid ($C_{18:1}$) is the major cellular fatty acid. 2-Hydroxy fatty acids and sphingoglycolipids are present, but 3-hydroxy fatty acids are absent. Ubiquinone-10 is the major quinine. Some strains may require vitamins for growth. The G+C of the DNA is 66.8–63.8 mol%.

Type species: *Porphyrobacter neustonensis.*

The genus currently contains six species with validly published names: *P. neustonensis* (Fuerst et al. 1993); *P. tepidarius* (Hanada et al. 1997); *P. sanguineus* (Ahrens 1968; Ahrens and Rheinheimer 1967; Hiraishi et al. 2002); *P. cryptus* (Rainey et al. 2003); *P. donghaensis* (Yoon et al. 2004b); *P. dokdonensis* (Yoon et al. 2006).

Tables 9.1 and *9.5* summarize the properties of the *Porphyrobacter* genus.

Isolation, Enrichment, and Maintenance Procedures

Members of this taxon have been isolated mainly from aquatic environments. However, there are also isolation reports from desert sand and rice in the *Altererythrobacter* genus. Growth media and culture conditions commonly used for the isolation of freshwater aerobic bacteria can be used for obtainment of *Erythrobacteraceae* members. Marine surface water, sediment, invertebrates, and freshwater environments are possible isolation sources for these organisms. MA and marine broth (MB) are the main culture media used to isolate and cultivate isolates. However, other media have been reported to be useful for isolation of *Erythrobacteraceae* members.

R_2A (Difco) plates supplemented with 1 % NaCl and solidified with 1.5 % gellan have been used to isolate *Altererythrobacter dongtanensis* (Fan et al. 2011). Tryptone soy agar was used to isolate *Altererythrobacter indicus* (Kumar et al. 2008) and *Altererythrobacter xinjiangensis* (Xue et al. 2012).

R_3A media solidified with agar (2 %, w/v) (Reasoner and Geldreich 1985; Williams and da Costa 1992) was used to isolate *Porphyrobacter cryptus* (Rainey et al. 2003). PE medium containing sodium glutamate, sodium succinate, sodium acetate, yeast extract, casamino acids, and a vitamin mixture (Hanada et al. 1995, 1997) supplemented with 1.5 % agar was used for isolation of *Porphyrobacter tepidarius.* Lake water agar (Franzmann and Skerman 1981) was used to isolate *Polphyrobacter neustonensis* (Fuerst et al. 1993). *P. sanguineum* strains were grown in MP medium, which consisted of marine broth and 0.5 % peptone water (1:1, vol/vol) (Hiraishi et al. 2002).

Erythromicrobium ramosum was isolated in a medium containing (per liter) 1.0 g of yeast extract, 1.0 g of bacto peptone, 1.0 g of sodium acetate, 0.3 g of KCl, 0.5 g of $MgS0_4.7H_20$, 0.05 g of $CaC1_2.2H_20$, 0.3 g of NH_4Cl, 0.3 g of K_2HP0_4, 20 pg of vitamin B12, and 1 ml of a trace element solution (Drews 1983; Yurkov et al. 1994). *Croceicoccus marinus* (Xu et al. 2009) was isolated by using ZoBell marine-casamino acids medium, which contained (per liter distilled water): NaCl, 19.45 g; $MgCl_2$, 8.8 g; Na_2SO_4, 3.24 g; $CaCl_2$, 1.8 g; KCl, 0.55 g; $NaHCO_3$, 0.16 g; $C_6H_5FeO_7$. $5H_2O$, 0.1 g; KBr, 0.08 g; $CsCl_2$, 34 mg; H_3BO_3, 22 mg; Na_2SiO_3, 4.0 mg; NaF, 2.4 mg; NH_4NO_3, 1.6 mg; Na_3PO_4, 8.0 mg; peptone, 0.5 g; yeast extract, 0.1 g; and casamino acids 0.1 g at a pH of 7.2 (ZoBell 1941).

Maintenance

It has been found that liquid cultures (taken from the late logarithmic growth phase) and agar surface cultures remained viable after storage at 4 °C for at least 2 months (Yurkov and Beatty 1998). Members of this family do not require special procedures for maintenance in medium and long-term storage. Strains may be preserved in screw-capped vials by freezing cell suspensions of liquid cultures or supplemented with MB (cultures mid-logarithmic growth phase) in 20 % (v/v) glycerol as a protective agent at −20 °C or at −70 °C. Long-term preservation is by lyophilization or by freezing cell suspensions in liquid nitrogen or at −80 °C in the presence of a cryoprotectant (Yurkov and Beatty 1998).

Physiological and Biochemical Features

Ecology

The habitat range of the family *Erythrobacteraceae* includes mainly aquatic environments. The original cultures were isolated from high-tidal seaweeds (Shiba and Simidu 1982), freshwater (Fuerst et al 1993; Yurkov et al 1994), cold-seep sediment (Kwon et al. 2007), and deep-sea sediment (Xu et al. 2009). This applies to most species described or reclassified recently. For instance, *Erythrobacter marinus*, *E. pelagi*, and *Porphyrobacter dokdonensis* were isolated from seawater (Yoon et al. 2006; Jung et al. 2012; Wu et al. 2012); *Altererythrobacter dongtanensis* and *A. aestuarii* were isolated from a tidal flat (Fan et al. 2011; Park et al. 2011), and *A. ishigakiensis* was isolated from marine sediment (Matsumoto et al. 2011). To date, all *Erythrobacter* species were retrieved from seawater environments, including marine invertebrates (*E. vulgaris*; Ivanova et al. 2006), as well as the monospecific *Croceicoccus* (*C. marinus*; Xu et al. 2009). The representative monospecific *Erythromicrobium* was isolated from freshwater (*E. ramosum*, Yurkov et al. 1994). *Porphyrobacter* genus includes members isolated from freshwater, brackish, and marine environments. To this genus belong isolates found in hot springs: *P. tepidarius* was isolated from a brackish hot spring (Hanada et al. 1997) and *P. cryptus* from a hot spring at Alcafache in central Portugal (Rainey et al. 2003). Both are moderately thermophilic. *Altererythrobacter* genus includes exceptions in addition to aquatic habitats: *A. indicus*, isolated from wild rice rhizosphere (Kumar et al. 2008) and *A. xinjiangensis*, isolated from desert sand (Xue et al. 2012).

The NCBI taxonomy browser *Erythrobacter* list includes isolates from a broader source than those of the type strains: marine aerosols (HQ188568); bacterioneuston (AY576736); coastal subseafloor (AB094461); soda pond (FN395246); biofilm on a copper-based antifouling paint (JN594622); *Scrippsiella* sp. laboratory culture (DQ486511); Dunhuang Mogao Grottoes 245# (JN244985); ancient salt deposits of the Yipinglang Salt Mine (EF177676); magnetite mine drainage (HQ652571); and chemocline of the hypersaline deep-sea Urania basin (AF321064).

The same search for *Porphyrobacter* resulted the following unusual sources: mine tailings ore and sand (JQ429465); an air sample collected 25 m above sea level (GQ484916); ozone-biological activated carbon filters for drinking water treatment (DQ884358); industrial site soil containing high amounts of heavy oil and heavy metals (HQ588835); Hamelin Pool stromatolites in Shark Bay, Australia (EF150743); aerobic fermentation of a mixture of bovine dung and urine, cow's milk, and yogurt (GQ246725); commercial nitrifying inoculum (AM236300); aquatic microbial mat from Antarctica (FR772128); arsenate resistant culture from estuary (AY788979); HAA degrading bacteria from drinking water (JN547328); oak (*Quercus alba*) leaf infusion (EF685171); ancient salt deposits of the Yipinglang Salt Mine (EF177679); and endophytic from a pine tree with Pine Wilt Disease (FJ784659). The NCBI taxonomy browser also includes *P. meromictius* isolated from a $Na_2SO_4^-$ dominated meromictic lake (Mahoney Lake in the Okanagan Valley of British Columbia, Canada) but the name is not valid (Rathgeber et al. 2007).

Erythromicrobium was found in mud volcano soil in Baratang Island, India (FN397674) and in arsenic-contaminated soil (AFI42455). The NCBI taxonomy browser also includes *E. ezovicum* and *E. hydrolyticum*, which are not valid names. These strains were reported to pertain to Vladimir Yurkov's personal collection and were related to tellurite resistance and reduction (Yurkov et al 1996). *Altererythrobacter* has also been recovered from Polycyclic Aromatic Hydrocarbons (PAHs) and crude oil degrading consortia enriched from marine sediments (GQ505272); mud volcano soil in Baratang Island, India (FN397680); aquatic microbial mat from Antarctica (FR772131); root interior of *Cymbidium goeringii* (GQ476825); and farming field soil (JN848799).

The genera *Erythrobacter*, *Porphyrobacter* and *Erythromicrobium* include AAP members. AAPs contain *BChl a* as a main light-harvesting pigment; however, in contrast to purple nonsulfur photosynthetic bacteria, these are obligate aerobes (Yurkov and Beatty 1998). They are facultative photoheterotrophs, metabolizing organic carbon when available, but are capable of photosynthetic light utilization when organic carbon is scarce. The first AAP bacteria discovered was *Erythrobacter longus* (Shiba et al. 1979; Shiba and Simidu 1982). *Porphyrobacter* and *Erythromicrobium* members present *BChl a* (Yoon et al. 2006; Yurkov et al. 1994; Yurkov and Gorlenko 1993), whereas the *Erythrobacter* genus includes 2 species (out of 13) that synthesize *BChl a*: the former isolated *E. longus* retrieved from high-tidal seaweeds of Tokyo Bay (Shiba and Simidu 1982) and *E. litoralis* found in marine cyanobacterial mat in a supralitoral zone (Yurkov et al. 1994). It had been suggested that cultivated *Erythrobacter* species represent the predominant AAPs in the upper ocean and should be main players in carbon cycling in the ocean, mainly in the euphotic zone (Shiba et al. 1991; Fenchel 2001; Kolber et al. 2001; Karl 2002). Later, culture-independent genomic analyses targeting photosynthetic operon genes (i.e., *puf*M) showed dissimilar results. No sequences recovered in Monterey Bay waters or in the central North Pacific Ocean (Karl and Lukas 1996) were similar to those of *Erythrobacter* species (Béjà et al. 2002).

An extensive study included samples from the Pacific, Atlantic, and Indian Oceans and West Pacific marginal seas, including the East and South China Seas – covering tropical, subtropical, and temperate zones, as well as coastal, shelf, and oceanic waters; it was able to account *Erythrobacter*- and *Roseobacter*-like sequences for approximately a quarter of the totality sequences obtained in the study (Jiao et al. 2007). For nearshore/offshore samples from a Pacific Ocean transect, only one station (out of three) presented sequences (32 %) most similar to those from cultured *Erythrobacter*, but altogether with *Rhodobacter* and *Roseobacter* genera (Ritchie and Johnson 2012). It is now clear that *Erythrobacter* species are not the oceanic-dominating AAP population and the counterparts include a wide variety of bacterial types. Therefore, the relative contribution of *Erythrobacter* spp. to oceanic carbon cycling may not be as large as previously suggested. The studies quantify *Bchl a*, and it is widespread among a phylogenetically diverse group – the AAP bacteria – in which oceanic representation of *Erythrobacter* spp. is not a consensus and may be variable (Béjà et al. 2002; Rathgeber et al. 2004; Venter et al. 2004; Jiao et al. 2007; Yutin et al. 2007; Ritchie and Johnson 2012).

Pathogenicity: Clinical Relevance

No information on pathogenicity for members of *Erythrobacteriaceae* is available heretofore (as of February 2013). The detection of naturally occurring β-lactamases in *Erythrobacter* spp. gave rise to the idea that this group, as many other marine bacteria, plays an important role as reservoir of β-lactam resistance genes, namely the oceanic resistome. A beta-lactamase II from *Erythrobacter litoralis* HTCC 2594 (ELbla2) showing *in silico* similarity with New Delhi metallo-beta-lactamase (MBL) was expressed in *E. coli* cells. These two mature proteins were purified from cultures and both presented as a monomer of 25 kDa. Antimicrobial susceptibility assay revealed that both shared similar substrate specificities, being sensitive to aztreonam and tigecycline (Zheng et al. 2011). Further, several chromosomally located MBLs have been identified from *Erythrobacter* spp. by bioinformatic analyses followed by cloning and expressing in *E. coli* cells. These MBLs showed a large diversity and belonged to subclasses B1 or B3. None of them could be considered a progenitor of the plasmid-mediated carbapenemases disseminated worldwide.

Clones expressing the MBL from *E. flavus* and *E. longus* presented decreased sensitivity to carbapenems (Girlich et al. 2012). It was hypothesized that resistance genes are transferred to the human gut microbiota by means of the consumption of nonsterilized seafood (e.g., seaweeds) (Hehemann et al. 2010; Zheng et al. 2011), given that the virus-like gene transfer system identified, likely Gene Transfer Agent (GTA) systems, are common in marine bacteria (e.g., *E. litoralis*) (Biers et al., 2008), and

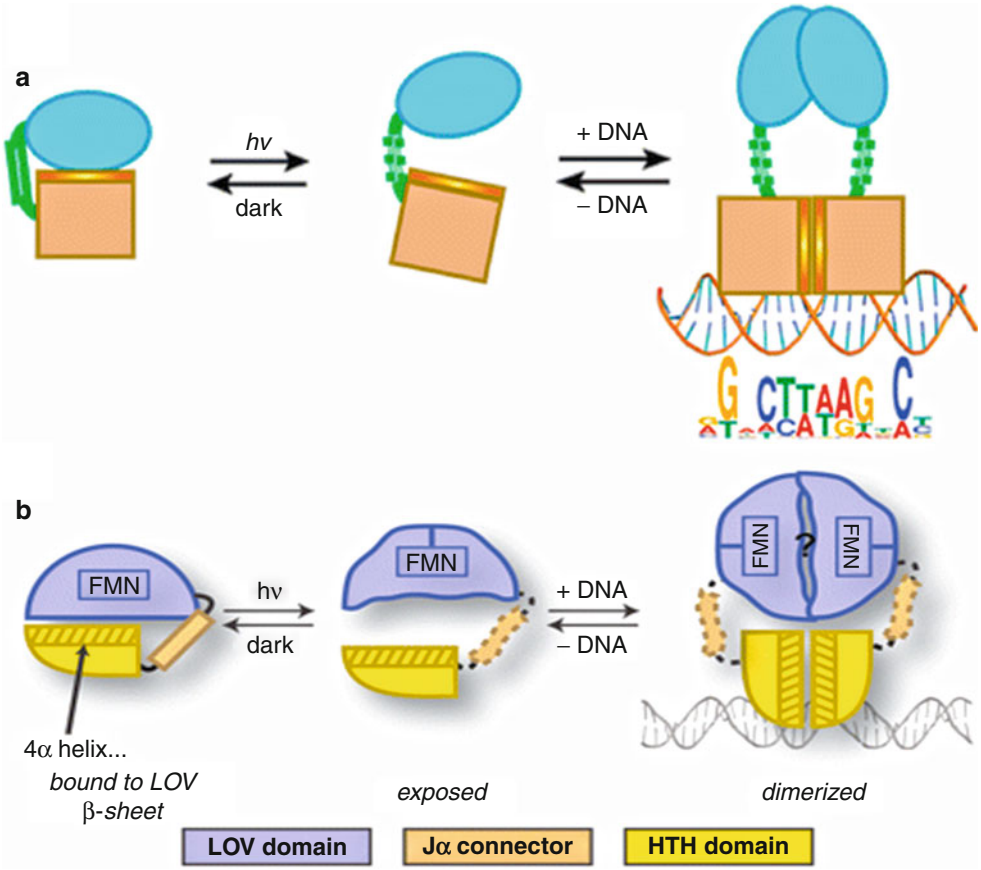

Fig. 9.4

(a) Light-oxygen-voltage (LOV) domains activation schematic model. LOV module inactive in the dark (*left*) and after blue light. activation (*center*): direct DNA binding (*right*) to regulate diverse functions (Adapted from Rivera-Cancel et al. (2012)). (b) Model for *E. litoralis* HTCC2594 LOV domain (EL222) activation. In the dark EL222 is incapable of binding DNA as the LOV domain interacts with the helix-turn-helix (HTH) module. Photo activation induces the formation of a cystein/flavin adduct in the LOV domain resulting in conformational changes that release LOV/HTH interactions. The 4α-helix is free to participate in HTH homodimerization upon binding DNA substrates (Adapted from Nash et al. (2011))

that GTAs account for an horizontal gene transfer frequency that is a million times the frequencies of transformation and transduction (McDaniel et al. 2010).

Application

A summary of the main application properties for the *Erythrobacteraceae* members is presented in *Table 9.10*.

Bioremediation

There are field and experimental evidences of the potential of *Erythrobacteraceae* members for bioremediation of heavy metals and a variety of xenobiotics, including hydrocarbons, aromatics and halogenates. For instance, *Erythrobacter* members were detected as part of the population related to alkane degradation from shoreline environments (Costa da Morte, Northwestern Spain) affected by the Prestige oil spill (Alonso-Gutiérrez et al. 2009). *Erythrobacter longus* and *E. citreus* were the closest phylogenetic neighbors related to the dominant clones identified after a bioremediated microcosm (nitrogen supplemented) experiment (Röling et al. 2002). A petroleum-aromatic-degrading active *Altererythrobacter* isolate is suggested to be a possible agent of bioremediation in and around nutrient-rich tropical marine environments (Teramoto et al. 2010). A *Porphyrobacter* strain, Oxy6 (according to 16S rRNA–based molecular phylogenetic analysis), isolated from subtropical Western Atlantic seawater, showed an ability to methyl halides degradation. This strain was even able to co-oxidize CH_3Br while growing on toluene. A variety of toluene pathway intermediates, such as benzyl alcohol, benzylaldehyde, benzoate, and catechol, could also be oxidized. Furthermore, the bacterium also oxidized *o*-xylene and the xylene monooxygenase pathway intermediate 3-methylcatechol. Considering the widespread

Table 9.10
Summary of the main application properties for the *Erythrobacteraceae* members

Bacteria name	Application	Function
Erythrobacter longus	Bioremediation	Alkane degradation[a, b]
Erythrobacter citreus		
Altererythrobacter		Petroleum-aromatic-degrading active[c]
Porphyrobacter strain – Oxy6		Methyl halides degradation[d], co-oxidize CH_3Br[d], oxidize *o*-xylene[d] and xylene monooxygenase (XMO)[d]
Erythrobacter litoralis		Resistance to tellurite and accumulation of metallic tellurium crystals[e]
Erythromicrobium ramosum		
Erythrobacter longus	Carotenoids	Twenty different carotenoids such as β-carotene and monocyclic carotenoids (e.g., rubixanthan)[f]
Erythrobacter JPCC M sp. strain 1436		Astaxanthin productivity[g]
Erythrobacter sp. strain SNB-035	Cytotoxic Compounds	Benzothiazoles Erythrazoles A-B, Erythrolic acid D (a meroterpenoid)[h]
E. litoralis strain HTCC 2594	LOV Domains	LOV-histidine kinase (LOV-HK) domain (which mediates light-activated histidine phosphorylation)[i,] EL222 DNA-binding protein (LOV domain binds and inhibits a helix-turn-helix (HTH) DNA binding domain in the dark)[j,k]

[a]Röling et al. (2002)
[b]Alonso-Gutiérrez et al. (2009)
[c]Teramoto et al. (2010)
[d]Goodwin et al. (2005)
[e]Yurkov et al. (1996), Yurkov and Beatty (1998)
[f]Takaichi et al. (1990)
[g]European Patent Register Publication Number EP 2157169A1 (2010)
[h]Hu and MacMillan (2011), Hu et al. (2012)
[i]Swartz et al. (2007)
[j]Nash et al. (2011)
[k]Rivera-Cancel et al. (2012)

inhibitory effect of toluene on seawater samples and the substrate oxidation pattern of this *Porphyrobacter* sp., the authors suggested a possible link between aromatic hydrocarbon utilization and the biogeochemical cycle of methyl halides (Goodwin et al. 2005).

Erythrobacter and *Erythromicrobium* isolates demonstrated high-level resistance to tellurite and accumulation of metallic tellurium crystals. In *Erythrobacter litoralis* and *Erythromicrobium ramosum* isolates, crystals occupied 20–30 % of the cell volume. This reduction of tellurite to the relatively inert metallic tellurium [Te(IV) to Te(0)] with accumulation as intracellular deposits is suited to the development of microbiological methods for environmental remediation. Tellurite compounds are toxic to other bacteria and other organisms, including humans. Furthermore, bacterial cells can be harvested for pure tellurium metal in the mineral ore (Yurkov et al. 1996; Yurkov and Beatty 1998).

Carotenoids

A remarkable characteristic of many members of Erythrobacteriaceae is the pigmentation (pink/red/orange/yellow) due to the production of carotenoids (Takaichi et al. 1988, 1990, 1991; Hanada et al. 1997; Yurkov et al. 1994; Denner et al. 2002; Xu et al. 2009). *Erythrobacter longus* produces approximately 20 different carotenoids, such as β-carotene and monocyclic carotenoids (e.g., rubixanthan) (Takaichi et al. 1990). The carotenoid biosynthesis genes lycopene cyclase (*crtY*) and phytoene desaturase (*crtI*), from *E. longus* strain Och101, were cloned, sequenced, and expressed in *Escherichia coli*. The *E. coli* HB101 employed contained the other required biosynthetic genes from *Erwinia herbicola*. Zeaxanthin and lycopene were produced and accumulated in the transformed cells, but transformants containing *crtY* and *crtI* genes from *E. herbicola* gave a higher pigment yield. The weak expression of *E. longus crt* genes in *E. coli* was attributed to codon usage bias (Matsumura et al. 1997).

Erythrobacter JPCC M sp. strain 1436 was included in a patent process for its astaxanthin productivity, reported to be 35 % or more by mass of the all produced pigments. According to 16S rDNA sequence similarity, the closest neighbor was *Erythrobacter luteolus* SW-109^T (GenBank AY739662), with a low nucleotide identity of 95.7 %. Based on 16S rDNA phylogeny, the authors considered *Erythrobacter* JPCCM sp. strain 1436 (accession number NITE BP-340), a novel species belonging to the genus *Erythrobacter*, at the time of priority application (April 2007). The process was entitled "Astaxanthin-producing

bacterium, bacterium culture product, astaxanthin-containing composition, and method for production of astaxanthin"; the European Patent Register Publication Number is EP 2157169 A1 (February 2010). The invention is claimed to be useful for the production of supplement foods and feedstuffs (color-enhancing feedstuffs).

Cytotoxic Compounds

Erythrobacter sp. strain SNB-035, isolated from mangrove sediments in Trinity Bay (Galveston, TX), yielded cytotoxic compounds: the benzothiazoles erythrazoles A-B and erythrolic acid D, a meroterpenoid. Cytotoxicity was observed against non-small cell lung cancer cell lines. Erythrazole B was cytotoxic, with IC_{50} values of 1.5, 2.5, and 6.8 μM against H1325, H2122, and HCC366, respectively. Erythrolic acid D was cytotoxic, with a modest IC_{50} value of 2.5 μM against HCC44. Strain SNB-035 shares 98 % 16S rRNA identity with *E. citreus*. (Hu and MacMillan 2011; Hu et al. 2012).

Light-Oxygen-Voltage Domains

Light-oxygen-voltage (LOV) domains are photosensory-signaling modules acting as blue light–dependent regulators of numerous activities, such as enzymes and DNA binding. LOV domains are widespread and highly conserved in eukaryotes, prokaryotes (including cyanobacteria), and archaeans; thus, they are suited for model-based studies. They can be readily produced in *E. coli* in amounts sufficient for biochemical and spectroscopic analysis. LOV domains can also be engineered into a variety of exogenous targets, allowing similar regulation for new protein-based reagents (Briggs et al. 2007; Möglich and Moffat 2010; Strickland et al. 2012). *Erythrobacter litoralis* presents the LOV-histidine kinase (LOV-HK) domain, which mediates light-activated histidine phosphorylation. *E. litoralis* strain HTCC 2594 has had full-length modules expressed in *E. coli* (EL346-LOV-HK and EL368-LOV-HK). The same was performed with modules from *Brucella melitensis* (animal pathogen) and *Pseudomonas syringae* (plant pathogen), allowing descriptive and comparative analysis (Swartz et al. 2007; Briggs et al. 2007; Tseng et al. 2010). EL222, a DNA-binding protein from the same E. *litoralis* strain, is also a model system. Despite its compactness (222 amino acids), it includes both sensor and effector domains. Nash et al. (2011) demonstrated that this LOV domain binds and inhibits a helix-turn-helix (HTH) DNA binding domain in the dark, releasing these interactions upon illumination. Furthermore, the same research group identified optimal DNA binding sites for EL222 and demonstrated the light-dependent activation of transcription (*Fig. 9.4*). EL222 LOV-HTH native targets are yet to be determined; nevertheless, the portability of the system, the direct regulation of DNA binding with light, together with the fact that the DNA binding sites are identified, make it attractive for engineering in heterologous systems (Rivera-Cancel et al. 2012).

Enzymes

Three epoxide hydrolases (EHases) genes (eeh1, eeh2, and eeh3) of *Erythrobacter litoralis* HTCC2594 were cloned in *E. coli*, and the recombinant proteins (rEEH1, rEEH2, and rEEH3) were purified. The functionality of purified proteins was proved by hydrolytic activities towards styrene oxide (SO). EEH1 preferentially hydrolyzed (R)-styrene oxide, whereas EEH3 preferred to hydrolyze (S)-SO, representing enantioselective hydrolysis of styrene oxide. EEH2 could hydrolyze (R)- and (S)-SO at an equal rate. The hydrolysis rate of EEH1 towards various epoxide substrates was superior to those of EEH2 or EEH3 (Woo et al. 2007). *Erythrobacter* sp. JCS358 also presents enantioselective epoxide hydrolyzing activity. Its performance was outstanding among marine strains isolated by the capability of living on SO and further screened for retaining enantioselective EHase activities towards SO (Hwang et al. 2008). *Altererythrobacter epoxidivorans* JCS350^T was described as presenting EHase activity, but it was not reported if this activity was enantioselective (Kwon et al. 2007). Pharmaceutical industries are eager for enantioselective EHases for the production of enantiopure epoxides.

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