Genomic-based taxonomic classification of the family Erythrobacteraceae

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Abstract
The family Erythrobacteraceae, belonging to the order Sphinogononadales, class Alphaproteobacteria, is globally distributed in various environments. Currently, this family consist of seven genera: Altererythrobacter, Croceibacterium, Croceicoccus, Erythrobacter, Erythromicrobium, Porphyrobacter and Opengyuania. As more species are identified, the taxonomic status of the family Erythrobacteraceae should be revised at the genomic level because of its polyphyletic nature evident from 16S rRNA gene sequence analysis. Phylogenomic reconstruction based on 288 single-copy orthologous clusters led to the identification of three separate clades. Pairwise comparisons of average nucleotide identity, average amino acid identity (AAI), percentage of conserved protein and evolutionary distance indicated that AAI and evolutionary distance had the highest correlation. Thresholds for genera boundaries were proposed as 70% and 0.4 for AAI and evolutionary distance, respectively. Based on the phylogenomic and genomic similarity analysis, the three clades were classified into 16 genera, including 11 novel ones, for which the names Alteraurantiacibacter, Altericroceibacterium, Alteripontixanthobacter, Aurantiacibacter, Paraurantiacibacter, Parerythrobacter, Parapontixanthobacter, Pelagerythrobacter, Tsuneonella and Pontixanthobacter are proposed. We reclassified all species of Erythromicrobium and Porphyrobacter as species of Erythrobacter. This study is the first genomic-based study of the family Erythrobacteraceae, and will contribute to further insights into the evolution of this family.

INTRODUCTION
The family Erythrobacteraceae, belonging to the order Sphinogononadales, class Alphaproteobacteria [1], is distributed globally, inhabiting various environments including subterrestrial, lake, intertidal areas, mangrove, coastal and deep-sea sediments [2–10], soil [11–13], desert sands [14, 15], stadium seat [16], seawater [17–19], estuary water [20–22], fresh water [23, 24], hot springs [25–27], air [28] as well as plants and animals [29–36] (Table S1, available in the online version of this article). The members of the family Erythrobacteraceae are Gram-stain-negative, rod or pleomorphic coccoïd-shaped, pink-, red-, orange- or yellow-pigmented, and aerobic chemoorganotrophs [1]. The majority require NaCl for growth [1]. Ubiquinone-10 (Q-10) is the major respiratory quinone [1, 2, 30]. The family was established by Lee et al. who included the genera Erythrobacter (Erb. litoralis and Erb. longus), Erythromicrobium (Erm. ramosum) and Porphyrobacter.
(Por. neustonensis and Por. tepidarius) based on 16S rRNA gene phylogeny in 2005 [37]. Four other genera including Altererythrobacter (Aeb.), Croceibacterium (Crb.), Cröcicoccus (Ccc.) and Qipengyuania (Qpy.) were later proposed by Kwon et al. [38], Liu et al. [30], Xu et al. [4] and Feng et al. [2], respectively, based on 16S rRNA gene phylogeny [2, 4, 30, 38]. At the time of writing (September 2019), the genera Altererythrobacter, Croceibacterium, Cröcicoccus, Erythrobacter, Erythromicrobiurn, Porphyrobacter and Qipengyuania consist of 41, two, four, 23, one, eight and one species, respectively [9, 10, 17, 19, 22, 30, 35, 39–43]. With the increase in the number of species proposed, the taxonomic status of the family Erythrobacteraceae should be revised in view of the polyphyletic nature of the group based on 16S rRNA gene sequence comparison [16, 30, 44]. The family Erythrobacteraceae includes aerobic anoxygenic phototrophic bacteria (AAPB), which can harvest light energy and play a significant role in the carbon cycling of the oceans globally [45–47]. Members of the family also show bioremediation and industrial potential, such as degradation of benzo[a]pyrene [48] and oil [49], and production of erythrazoles [50] and erythrolactic acids [51]. A comprehensively taxonomic investigation of the family Erythrobacteraceae could not only lead to an improved classification of its members, but also broaden our understanding of their ecology and potential biotechnological applications.

Development of genome sequencing technologies has made bacterial genomic data more and more accessible, resulting in a revolution in bacterial taxonomy [52–54]. Phylogenomic reconstruction can provide a higher-resolution phylogeny than that based on 16S rRNA gene or several housekeeping genes [55–58]. In addition, genomic similarity calculations including average nucleotide identity (ANI), average amino acid identity (AAI) and percentage of conserved protein (POCP) provide numerical thresholds for delineation of each taxon [59–61]. Therefore, a genome-wide investigation of the taxonomy of the family Erythrobacteraceae was performed to revise the taxonomic status of this family.

METHODS

Collection of Erythrobacteraceae type strains

In addition to the 47 Erythrobacteraceae type strains for which genome sequences were available, 27 type strains were obtained from culture collections including the China General Microbiological Culture Collection (CGMCC), the Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH (DSMZ), the Japan Collection of Microorganisms (JCM), the Korean Collection for Type Cultures (KCTC), the Korea Environmental Microorganism Bank (KEMB), the Collection of the Laboratorium voor Microbiologie en Microbiële Genetic (LMG) and the Marine Culture Collection of China (MCCC) or received as gifts from other scholars (Table 1 and Acknowledgements). These type strains were cultivated under appropriate conditions proposed previously [3, 12, 14, 20, 28, 31–33, 36, 44, 62–77] for subsequent genomic sequencing.

Sequencing and assembly of genomic sequences

Genomic sequencing and assembly were performed as described previously [78]. Cells were harvested by centrifuge at 12,000 g for 30 s. Genomic DNA was extracted by using AxyPre Bacterial Genomic DNA Miniprep Kit (Corning Life Sciences) according to its manual. Genomes were sequenced on the HiSeq 2000 system (Illumina) by Solexa paired-end sequencing technology with a paired-end library with insert length of 500 bp by the Novogene Corporation (Beijing, PR China). Draft genomes were assembled by using SPAdes version 3.11.1 [79] based on clean reads generated from raw reads by quality trimming. The collection of assembled and obtained genomes covered 92% (74/80) of the Erythrobacteraceae type strains, comprising 88% (36/41), 100% (2/2), 100% (4/4), 96% (22/23), 100% (1/1), 100% (8/8) and 100% (1/1) of the genera Altererythrobacter, Croceibacterium, Cröcicoccus, Erythrobacter, Erythromicrobiurn, Porphyrobacter and Qipengyuania.

Genomic annotation and comparative genomic analysis

Genomes for annotation and comparative analysis were selected following assessment of genomic completeness (>95%) and contamination (<5%) using CheckM software version 1.0.7 [80] with the command ‘checkm lineage_wf -x fasta bins/ checkm/’. rRNA and tRNA genes were searched by the command RNAmmer 1.2 package [81] and the tRNAscan-SE web server (http://lowelab.ucsc.edu/trNAscan-SE/) [82], respectively. Annotated 16S rRNA genes were used to compare sequence identities on the EzBioCloud web server (www.ezbiocloud.net/identify) [83] to confirm that a genome represented its corresponding type strain. Coding sequences (CDSs) were predicted and annotated by using Rapid Annotation using Subsystem Technology (RAST) web server version 2.0 (http://rast.nmpdr.org/rast.cgi) [84]. The DNA G+C contents were also calculated on the RAST web server version 2.0.

Comparative genomic analysis was performed as previously described [85, 86]. Orthologous clusters (OCs) were identified by comparing whole protein sequences translated from CDSs pairwise with the execution of Proteinortho version 5.16b [87] with command ‘-e 1e-5 -cov=50 -identity=50’, which is accordance with the threshold values for a group of OCs sharing identities more than 50% and coverage longer than half of their sequence lengths. Subsequently, single-copy OCs were filtered by an in-house Perl script.

16s rRNA gene phylogenetic and phylogenomic reconstructions

In accordance with previous polyphasic taxonomic studies of the members in the family Erythrobacteraceae [19, 22, 35, 40, 88], Rhodospirillum rubrum ATCC 11170” was chosen as an outgroup, with its 16S rRNA gene sequence and genomic sequences obtained from the NCBI GenBank database under the accession numbers D30778 and CP000230–CP000231, respectively. 16S rRNA gene phylogeny was
Table 1. Genomic information for *Erythrobacteraceae* strains included in this study

DOE-JGI, U.S. Department of Energy, Joint Genome Institute; KRIBB, Korea Research Institute of Bioscience and Biotechnology; SDU, Shandong University.

| Strain                  | NCBI GenBank Accession | Genome size (Mbp) | Gene count | Contig count | G+C content (%) | Reference |
|-------------------------|------------------------|-------------------|------------|--------------|-----------------|-----------|
| Aeb. aeriis 100921-2T   | WTZA0000000000         | 2.75              | 2793       | 2            | 66.3            | This study |
| Aeb. aerophilus Ery1T    | QXFK0000000000         | 3.65              | 3638       | 19           | 65.4            | [17]      |
| Aeb. aestuarii JCM 16339T | WTTY000000000         | 2.87              | 2823       | 2            | 57.2            | This study |
| Aeb. amylyticus NS1T    | CP032570               | 2.79              | 2791       | 1            | 67.0            | [10]      |
| Aeb. aquamixtaceae KCTC 52765T | WTYX000000000     | 2.98              | 2933       | 4            | 58.5            | This study |
| Aeb. aquimixtcola SSKS-13T | SSNH000000000     | 3.43              | 3349       | 5            | 63.9            | [40]      |
| Aeb. atlanticus 26DY36T | CP011452, CP011453    | 3.51              | 3423       | 2            | 61.9            | [120]     |
| Aeb. aurantiacis MCCC 1A09962T | WTYW000000000    | 2.90              | 2907       | 7            | 61.2            | This study |
| Aeb. bacillus M0322T    | WTYV0000000000       | 3.77              | 3734       | 22           | 66.0            | This study |
| Aeb. confluens KCTC 52259T | WTYU000000000       | 2.93              | 2892       | 5            | 59.1            | This study |
| Aeb. dongtanensis KCTC 22672T | CP016591            | 3.01              | 2976       | 1            | 65.8            | [121]     |
| Aeb. endophyticus LMG 29518T | WTYT000000000       | 3.47              | 3314       | 13           | 58.6            | This study |
| Aeb. epoxidovoris CGMCC 1.7731T | CP012669            | 2.79              | 2819       | 1            | 61.5            | [48]      |
| Aeb. flavus MSI-4T      | PHSO000000000        | 3.28              | 3154       | 29           | 60.5            | [7]       |
| Aeb. gangiinensis JCM 17802T | WTYS000000000       | 2.89              | 2889       | 1            | 55.5            | This study |
| Aeb. halomnias LMG 29519T | WTYR000000000       | 2.81              | 2778       | 2            | 63.6            | This study |
| Aeb. indicus DSM 18604T | WTYQ000000000       | 3.11              | 3011       | 20           | 55.8            | This study |
| Aeb. insulae BPTF-M16T  | QURO000000000       | 3.32              | 3997       | 1055         | 52.8            | [41]      |
| Aeb. ishigakiensis NBRC 107699T | CP015963           | 2.68              | 2670       | 1            | 56.9            | [122]     |
| Aeb. lutolus SW-109T    | WTPY000000000       | 2.89              | 2841       | 3            | 59.3            | This study |
| Aeb. lutipolagi GH1-16T | SKCJ000000000       | 3.10              | 3114       | 2            | 60.6            | [42]      |
| Aeb. mangrovei C9-11T   | CP022889             | 2.70              | 2650       | 1            | 63.5            | [6]       |
| Aeb. marinensis KCTC 22370T | CP011805           | 2.88              | 2784       | 1            | 64.7            | KRIBB     |
| Aeb. marinus H32T       | WTYO000000000       | 3.00              | 2898       | 16           | 68.2            | This study |
| Aeb. maritimus HME9302T | QBKA000000000       | 2.68              | 2737       | 2            | 60.8            | [43]      |
| Aeb. nankinola JCM 16345T | CP016545            | 2.59              | 2590       | 1            | 65.0            | This study |
| Aeb. oceananis MCCC 1A09965T | WTYN000000000     | 2.87              | 2892       | 14           | 63.9            | This study |
| Aeb. rigui KCTC 42620T  | RSEL000000000       | 2.86              | 2903       | 30           | 66.7            | This study |
| Aeb. salegens MCCC 1K01500T | WTYM000000000     | 3.63              | 3630       | 69           | 64.6            | This study |
| Aeb. sediminis KCTC 42453T | WTYL000000000       | 3.16              | 3102       | 6            | 61.5            | This study |
| Aeb. solit MCCC 1K02066T | WTYK000000000       | 3.08              | 2998       | 15           | 67.0            | This study |
| Aeb. troitsensis JCM 17037T | LMAU000000000     | 2.90              | 2848       | 9            | 64.7            | [123]     |
| Aeb. xiamenensis CGMCC 1.12494T | FXWG000000000   | 3.09              | 3064       | 5            | 61.8            | DOE-JGI  |
| Aeb. xinjiangensis CCTCC AB 207166T | RSEK000000000   | 3.11              | 3153       | 59           | 64.2            | [17]      |

Continued
| Strain                        | NCBI GenBank Accession | Genome size (Mbp) | Gene count | Contig count | G+C content (%) | Reference     |
|------------------------------|------------------------|-------------------|------------|--------------|-----------------|--------------|
| *Aeb. xixiisoli* S36<sup>T</sup> | WTYJ00000000           | 3.88              | 3768       | 9            | 63.3            | This study    |
| *Crb. feralae* SX2RGS8<sup>T</sup> | QZVQ00000000           | 3.61              | 3434       | 36           | 66.5            | [30]          |
| *Crb. mercuriale* Coronado<sup>T</sup> | JTDN00000000           | 3.48              | 3205       | 10           | 67.3            | [124]         |
| *Ccc. marinus* E4A9<sup>T</sup> | CP019602-CP019604      | 4.11              | 3956       | 3            | 64.5            | [125]         |
| *Ccc. mobilis* Ery22<sup>T</sup> | LYWZ00000000           | 4.21              | 4061       | 32           | 62.5            | [5]           |
| *Ccc. napthovorans* PQ-2<sup>T</sup> | CP011770-CP011772      | 3.86              | 4007       | 3            | 62.6            | [110]         |
| *Ccc. pelagius* Ery9<sup>T</sup> | LYWY00000000           | 3.31              | 3264       | 40           | 62.8            | [5]           |
| *Erb. aquimaris* JCM 12189<sup>T</sup> | WTYI00000000           | 2.66              | 2680       | 3            | 61.8            | This study    |
| *Erb. aquimixtico* JSSK-14<sup>T</sup> | RAHX00000000           | 2.55              | 2633       | 2            | 63.0            | [35]          |
| *Erb. arachoides* RC4-10-4<sup>T</sup> | WTYH00000000           | 2.94              | 2929       | 1            | 65.4            | This study    |
| *Erb. atlanticus* s21-N3<sup>T</sup> | CP011310,CP015441      | 3.23              | 3296       | 2            | 58.3            | [109]         |
| *Erb. citreus* CGMCC 1.8703<sup>T</sup> | WTYG00000000           | 3.03              | 3045       | 24           | 64.2            | This study    |
| *Erb. gaetbuli* DSM 16225<sup>T</sup> | WTYF00000000           | 2.78              | 2752       | 4            | 64.1            | This study    |
| *Erb. ganginensis* CGMCC 1.15024<sup>T</sup> | CP018097,CP018098      | 2.72              | 2695       | 2            | 62.7            | [126]         |
| *Erb. jejesensis* JCM 16677<sup>T</sup> | WTYE00000000           | 4.15              | 4124       | 1            | 60.2            | This study    |
| *Erb. litoralis* DSM 8509<sup>T</sup> | CP017057               | 3.25              | 3164       | 1            | 65.2            | [127]         |
| *Erb. longus* DSM 6997<sup>T</sup> | JMW00000000            | 3.60              | 3430       | 14           | 57.4            | [127]         |
| *Erb. luteus* KA37<sup>T</sup> | LBHB00000000           | 2.89              | 2876       | 22           | 67.2            | [118]         |
| *Erb. lutimaris* S-5<sup>T</sup> | QRB00000000            | 3.31              | 3219       | 12           | 65.5            | SDU           |
| *Erb. marinus* KCTC 23554<sup>T</sup> | LDCP00000000           | 2.84              | 2818       | 5            | 59.1            | This study    |
| *Erb. marisflavi* KEM-5<sup>T</sup> | VCA00000000            | 2.67              | 2656       | 18           | 61.7            | [22]          |
| *Erb. nanhasediminis* CGMCC 1.7715<sup>T</sup> | FOWZ00000000           | 2.90              | 2870       | 12           | 62.0            | DOE-JGI       |
| *Erb. odithensis* KCTC 23981<sup>T</sup> | QYOS00000000           | 3.19              | 3137       | 25           | 63.7            | [9]           |
| *Erb. pelagi* JCM 17468<sup>T</sup> | WTYD00000000           | 3.03              | 2936       | 9            | 64.2            | This study    |
| *Erb. seohaensis* SW-135<sup>T</sup> | CP024920               | 2.94              | 2919       | 1            | 61.7            | [78]          |
| *Erb. spongiae* HN-E23<sup>T</sup> | RDFZ00000000           | 2.86              | 2867       | 2            | 65.5            | [35]          |
| *Erb. vulgaris* DSM 17792<sup>T</sup> | WTYC00000000           | 3.23              | 3212       | 19           | 60.6            | This study    |
| *Erb. xanthus* CCTCC AB 2015396<sup>T</sup> | QXFM00000000           | 4.38              | 4320       | 151          | 64.5            | [9]           |
| *Erb. zhengii* V18<sup>T</sup> | QXFL00000000           | 3.80              | 3812       | 29           | 62.7            | [9]           |
| *Erm. ramosum* JCM 10282<sup>T</sup> | WTYB00000000           | 3.24              | 3175       | 10           | 64.3            | This study    |
| *Por. algicida* KEMB 9005–328<sup>T</sup> | WTYA00000000           | 3.22              | 3255       | 21           | 60.7            | This study    |
| *Por. colymbi* JCM 18338<sup>T</sup> | MUYK00000000           | 4.31              | 4092       | 53           | 66.5            | [85]          |
| *Por. cryptus* DSM 12079<sup>T</sup> | AUHC00000000           | 2.95              | 2902       | 36           | 67.9            | DOE-JGI       |
| *Por. dokonensis* DSM 17193<sup>T</sup> | MUYD00000000           | 3.00              | 2885       | 13           | 64.8            | [85]          |
| *Por. donghaensis* DSM 16220<sup>T</sup> | MUYG00000000           | 3.37              | 3199       | 11           | 66.2            | [85]          |
| *Por. neustonensis* DSM 9434<sup>T</sup> | CP016033               | 3.09              | 2955       | 1            | 65.3            | [128]         |

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reconstructed as described by Xu et al. [89]. Gene sequences of 80 Erythrobacteraceae type strains and an outgroup were aligned with CLUSTAL_W [90] built in the MEGA7 software [91]. Then, aligned sequences were processed into maximum-likelihood phylogenetic analysis [92], using MEGA7 software with the substitution model and the bootstrap value set as Kimura's two-parameter model [93] and 1000 replicates, respectively.

Protein and gene sequences of filtered single-copy OCs were both performed in the phylogenomic analyses. Protein sequences were aligned by using MAFFT version 7 [94] with the parameter ‘-auto’, while gene sequences were aligned by mapping nucleotides on amino acids based on aligned protein sequences through PAL2NAL program version 14 [95]. Aligned sequences were refined to select the most reliable positions through trimAL version 1.4.1 [96] with the parameter ‘-automated1’ and concatenated through our in-house perl script. Concatenation and partition methods were both applied in this study. The best substitution models for were proposed by IQ-Tree 1.6.1 software [97] with the command ‘-m MFP’. Subsequently, LG+F+R9 and GTR+F+R8 were estimated as the best substitution models for concatenations of amino acid and nucleotide sequences, respectively, and the best substitution models for partition methods are listed in Table S2. Maximum-likelihood phylogenomic trees were reconstructed by using IQ-Tree 1.6.1 software [97] with the bootstrap value set to 100 replicates.

**Genomic similarity analysis**

ANI, AAI and POCP values were used to calculate genomic similarities. ANI values were calculated by the orthologous average nucleotide identity tool (OrthoANI version 0.93.1) [98] implemented with the BLAST algorithm [99]. AAI values were obtained using the Kostas lab AAI calculator web server (http://enve-omics.ce.gatech.edu/aaial) [100]. POCP values were obtained according to the formula ‘POCP=(C1 + C2)/(T1 + T2)×100 %’ where C1 and C2 indicated the conserved number of predicted proteins in the two pairwise compared genomes, respectively, as well as T1 and T2 stands for the total number of predicted proteins in the two pairwise compared genomes, respectively [59], following comparative genomic analysis by using Proteinortho version 5.16b with the command ‘-e=1e-5 -cov=50 -identity=40’. In addition, the t-tests of AAI, ANI and POCP values of inter- and intra-group were calculated by using the function ‘t.test’ within R version 3.4.2 [101].

**DISCUSSION**

**Characteristics of Erythrobacteraceae genomes**

All obtained genomes were of high quality with genomic completeness of 97.6–99.9% (average 99.3%; median 99.4%) and contamination of 0–4.9% (average 0.7%; median 0.4%), as shown in Table S2. Sequence identity analysis of annotated 16S rRNA genes from the genomes sequenced in this study indicated that each represented its type strain with high identities of 99.2–100.0% (Table S3). Several strains, including *Aeb. confluentis* KCTC 52259T, *Aeb. indicus* DSM 18604T, *Aeb. luteolus* SW-109T, *Erb. citreus* CGMCC 1.8703T and *Erb. jejuensis* JCM 16677T, had multi-copy 16S rRNA genes, whose sequences were identical.

Genomic sizes, gene counts and G+C contents were 2.24–4.38 Mbp (average 3.16 Mbp; median 3.06 Mbp), 2400–4320 (average 3117; median 2987) and 52.8–68.2% (average 63.0%; median 63.6%), respectively (Table 1). Comparative genomic analysis revealed that the pan-genome of the family *Erythrobacteraceae* harboured 49,006 OCs, among which 763 OCs were shared by all type strains, which also had 1,233–2,375 accessory and 157–1,500 unique OCs (Fig. 1). The percentages of accessory, core and unique OCs in each type strain varied greatly with values of 18.7–32.5, 42.6–66.7 and 6.0–38.1%, respectively, which showed a rich genetic diversity in this family. A total of 288 single-copy OCs (Table S4) were included in our phylogenomic analyses.

**16S rRNA gene phylogeny**

As stated before, several genera within the family *Erythrobacteraceae* did not form an independent clade in the 16S rRNA gene phylogenetic tree (Fig. S1): (1) the genus *Erythrobacter*, being the type genus of the family, could be divided into four clades, one of which was grouped with the genera *Erythromicrobium* and *Porphyrobacter*; (2) the genus *Altererythrobacter* showed five clades which also included the genera *Croceicoccus* and *Qipengyuania*; (3) the genera *Erythromicrobium* and *Qipengyuania*, each consisting of a single species, were clustered in clades mostly containing of *Porphyrobacter* and *Altererythrobacter*, respectively. The genera

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**Table 1. Continued**

| Strain               | NCBI GenBank Accession | Genome size (Mbp) | Gene count | Contig count | G+C content (%) | Reference             |
|----------------------|------------------------|-------------------|------------|--------------|----------------|-----------------------|
| *Por. sanguineus* JCM 20691T | MUYH0000000000 | 3.02              | 2931       | 34           | 63.6            | [85]                  |
| *Por. tepidarius* DSM 10594T | MUYJ0000000000 | 3.22              | 3151       | 32           | 65.9            | [85]                  |
| *Qpy. sediminis* CGMCC 1.12928T | CP037948            | 2.42              | 2400       | 1            | 66.87           | [129]                 |
Fig. 1. Accessory, core and unique OCs distributed in each type strain belonging to the family *Erythrobacteraceae*. 
Croceibacterium and Croceicoccus formed two independent clades, and they did not belong to monophyletic clades which could be separated from other genera. Thus, 16S rRNA gene sequences did not confirm monophyletic relationships within the genera of the family [2, 4, 30, 37, 38]. Only 19 nodes accounting for 26.0% exhibited bootstrap values higher than 70%, indicating that this phylogenetic tree was not reliable enough to correctly reveal the taxonomic status of the genera of the family.

Phylogenomic and genomic similarity analyses proposing three clades

Four phylogenomic trees, based on 288 single-copy OC, amino acid or nucleotide sequences, with annotations and substitution models are shown in Table S4 and had similar topological structures with 59 nodes accounting for 80.8%, and were identical in all four calculated phylogenetic relationship parameters (Fig. 2 and Figs. S2–4). In all four phylogenomic trees, the bootstrap value of most nodes (66/73–68/73) exceeded 70%, indicating those phylogenies were robust. Compared with 16S rRNA gene phylogeny, those similar and robust phylogenomic trees could provide a reliable taxonomic status for the family Erythrobacteraceae.

Based on these phylogenomic trees, the family Erythrobacteraceae can be divided into three separate clades, Clades I, II and III, consisting of 47, 23 and four species, respectively (Fig. 2). Genomic similarity analyses by AAI, ANI and POCP calculations also supported that the three clades were significantly separated with \( p \text{-value}<2.2 \times 10^{-16} \) (Fig. 3). Clades I and II contained most species. Clade III only contained four Croceicoccus species, indicating that the taxonomic status of this genus should not be changed.

AAI value and evolutionary distance classifying genera

A robust core-genome phylogeny of the family was obtained. Although there is no generally recognized genus boundary, recent studies suggested AAI (60–80%) and POCP (50%) could be thresholds for distinguishing genera [59, 61]. Evolutionary distance is also a relatively conserved criterion for inferring evolutionary relationships [102]. Pairwise comparisons of ANI, AAI, POCP and evolutionary distance indicated that the pair of AAI and evolutionary distance had a much higher correlation coefficient \( (r_{cc} = 0.85) \) than other pairs (Fig. 4). Type strains shared pairwise >50% of POCP values, which is similar to the result of a phylogenomic study of the Roseobacter group [58], suggesting that POCP values could not be applied for delineating genera within the family Erythrobacteraceae. AA1 was more suitable to distinguish each taxon in the family than ANI and POCP (Figs. S5–S7). Thus, AAI and evolutionary distance were selected to classify genera of Erythrobacteraceae.

Since phylogenetic tree topology is a major criterion for classifying genera, we propose that one genus should be clustered into one group only. Based on this criterion, Clade I is then composed of 10 genera (Fig. 5), including Genus I-1 (Aeh. flavus

Fig. 2. A maximum-likelihood tree based on the partition of 288 single-copy OC protein sequences showing the phylogenetic relationship of type strains belonging to the family Erythrobacteraceae. Bootstrap values are based on 100 replicates. Bar., 0.1 substitutions per nucleotide position. The backgrounds coloured brown, green and grey indicate Clades I, II and III, respectively. Rhodospirillum rubrum ATCC 11170\(^\ast\) was used as an outgroup (not shown).
**Fig. 3.** Histograms of AAI, ANI and POCP values regarding inter- and intra-clade. Red and blue indicate inter-clade and intra-clade, respectively.

**Fig. 4.** Pairwise correlations of ANI, AAI, POCP and evolutionary distance calculated from the genomes of *Erythrobacteraceae* type strains.
DSM 17193, *Por. sanguineus* JCM 20691, *Erb. litoralis* DSM 8509 and *Erb. longus* DSM 69977, Genus I-VIII (*Aeb. luteolus* SW-109, *Aeb. aquamixtiae* KCTC 52763, *Aeb. aetiaqueae* KCTC 42006, *Aeb. ganggijensis* JCM 17802, *Aeb. confluentis* KCTC 52259 and *Aeb. sediminis* KCTC 42453), Genus I-IX (*Aeb. oceanensis* MCCC 1A09965) and Genus I-X (*Aeb. aurantiacus* MCCC 1A09972). The type strains of each of these genera exhibited pairwise evolutionary distance < 0.4%, except for *Aeb. oceanensis* MCCC 1A09965 and *Qpy. sediminis* M1. These two type strains also showed a pairwise AAI value of 67.3%, while the pairwise AAI value for the majority of this clade (96.8%, 1047/1081) were higher than 70%. Clade III consisted of one genus, whose species had AAI values of 68.1–77.5% and evolutionary distances of 0.13–0.27. Based on the analysis of these two clades, the genus boundary for the family is here proposed as AAI values of 70% and an evolutionary distance of 0.4 (Fig. 6).

Based on these criteria, Clade II with all nodes with bootstrap values of > 85% could be divided into five genera (Fig. 5), consisting of Genus II-I (*Aeb. endophyticus* LMG 29518, *Aeb. indicus* DSM 18604 and *Aeb. xinjiangensis* CCTCC AB 207166), Genus II-II (*Aeb. atlanticus* 2DY36, *Crb. ferulae* SX2RGS8, *Crb. mercuriale* Coronado, *Aeb. xixiisoli* S36, *Aeb. salegens* MCCC 1K01500, *Aeb. soli* MCCC 1K02066), Genus II-III (*Aeb. aquimixticola* SSKS-13, *Aeb. aestuarii* JCM 16339), Genus II-IV (*Erb. spongiae* HN-3E23, *Erb. zhongii* V18, *Erb. odiashensis* KCTC 23981, *Erb. gangjensis* CGMCC 1.15204, *Erb. arachoides* RC4-10-4, *Erb. luteus* KA37, *Erb. atlanticus* s21-N3, *Erb. marinus* KCTC 23554, *Erb. aquimixtica* JSSK-14 and *Erb. xanthus* CCTCC AB 2015396) and Genus II-V (*Aeb. namhlicola* 16345).

We therefore propose that phylogenomic topology supplemented with AAI values and evolutionary distance values could replace the phylogeny based on 16S rRNA gene sequences in the taxonomy of the family *Erythrobacteraceae*.
Genotype and phenotype support the proposal of new genera

Comparison of genomic contents within the family Erythrobacteraceae revealed that 12443 OCs could be indicators for distinguishing newly proposed genera. While considerable metabolic diversity is found within the family, metabolic pathways involving carbon, nitrogen, phosphorus and sulfur could not be applied to refine the taxonomic status of this family. Therefore, the pathways of aerobic anoxygenic photosynthesis and flagella biosynthesis, which contain multiple genes and reactions [47, 103], were selected to investigate their value as indicators for their taxonomic status.

Aerobic anoxygenic photosynthesis is encoded by a series of genes that were found in all Genus I-VI species, Aeb. ishigakiensis NBRC 107699T (Genus I-V), Erb. marinus KCTC 23554T (Genus II-III) and Erb. odishensis KCTC 239891T (Genus II-III), as shown in Table 2. Phenotypic characteristics revealed that Genus I-VI consisted of AAPB [23, 24, 26, 27, 29, 31, 104–106], while other genera did not include AAPB. Moreover, phylogenetic analysis indicated that genes for aerobic anoxygenic photosynthesis of Aeb. ishigakiensis NBRC 107699T, Erb. marinus KCTC 23554T and Erb. odishensis KCTC 239891T were paralogs of such genes in Genus I-VI (Fig. S8).

Flagella can be used for locomotion and sensing, which improves the survival of prokaryotes [107, 108]. Comparison of gene contents showed that several strains in Genus I-II (Por. algicida KEMB 9005-328T), Genus I-VI (Erb. litoralis DSM 8509T, Erb. longus DSM 6997T, Erm. ramosum JCM 10282T, Por. colymbi JCM 18338T, Por. cryptus DSM 12079T, Por. neustonensis DSM 9434T and Por. sanguineus JCM 20691T), Genus I-X (Aeb. marinus H32T), Genus II-II (Aeb. atlanticus 26DY36T and Aeb. soli MCCC 1K02066T), Genus II-IV (Erb. atlanticus s21-N3T) and Genus III (Ccc. mobilis Ery22T and Ccc. napthovorans PQ-2T) had genes related to flagella biosynthesis. Microscopic observations showed flagella in those strains [5, 8, 14, 23, 24, 26, 29, 31, 44, 104, 109, 110], except for Aeb. marinus H32T.

Based on the phylogenomic and genomic similarity analyses, we propose that the family Erythrobacteraceae could be reclassified into 16 genera including 11 novel genera, for which the names Alteraurantiacibacter, Altericroceibacterium, Alteriqipengyuania, Alteripontixanthobacter, Aurantiacibacter, Paraaurantiacibacter, Parapontixanthobacter, Parerythrobacter, Pelagerythrobacter, Pontixanthobacter and Tsuneonella are proposed. Because the species of Erythromicrobiium and Porphyrobacter were merged into the genus Erythrobacter, those two genera are no longer necessary in taxonomic discussions, but their names remain validly published and can still be used.

DESCRIPTION OF TSUNEONELLA GEN. NOV.

Tsuneonella (Tsuneo.nella. N.L. fem. n. Tsuneonella, named in honour of Tsuneo Shiba who established genus Erythrobacter).

Cells are Gram-stain-negative, ovoid to rod, non-sporing and non-motile. Aerobic or facultatively aerobic. Contains carotenoid pigments but not bacteriochlorophyll a. The predominant ubiquinone is Q-10. The major fatty acid (>10 %) is summed feature 8 (C18:1ω7c and/or C18:1ω6c). The major polar lipids are diphasphatidylglycerol and phosphatidylethanolamine. The genus represents a distinct branch in the family Erythrobacteraceae of the class Alphaproteobacteria based on the core-genomic phylogeny. The DNA G+C content is 60.5–67.0% (by genome). The type species is Tsuneonella dongtanensis.

DESCRIPTION OF TSUNEONELLA AERIA COMB. NOV.

Tsuneonella aeria (a.e’ri.a. L. fem. adj. aeria pertaining to the air, aerial).

Basonym: Altererythrobacter aerius Xue et al. 2016.

The description is the same as for Aeb. aerius [28]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Tsuneonella. The type strain, 100921-2T (=CFCC 14287T=KCTC 42844T), was isolated from air at the foot of Xiangshan Mountain, Beijing, PR China. The DNA G+C content of the type strain is 66.3% (by genome).

DESCRIPTION OF TSUNEONELLA AMYLOLYTICA COMB. NOV.

Tsuneonella amylolytica (a.my.lo.ly’ti.ca. Gr. neut. n. amylon starch; Gr. fem. adj. lytikè able to loosen, able to dissolve; N.L. fem. adj. amylolytica starch dissolving).

Basonym: Altererythrobacter amylolyticus Qu et al. 2019.

The description is the same as for Aeb. amylolyticus [10]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Tsuneonella. The type strain, NS1T (=CGMCC 1.13679T=NBRC 113553T), was isolated from sediment of Taihu Lake in Jiangsu Province, PR China. The DNA G+C content of type strain is 67.0% (by genome).

DESCRIPTION OF TSUNEONELLA DONGTANENSIS COMB. NOV.

Tsuneonella dongtanensis (dong.tan.en’sis. N.L. fem. adj. dongtanensis pertaining to Dongtan, a wetland region in Chongming Island, Shanghai, PR China).

Basonym: Altererythrobacter dongtanensis Fan et al. 2011.

The description is the same as for Aeb. dongtanensis [111]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Tsuneonella. The type strain, JM27T (=KCTC 22672T=CCTCC AB 209199T), was isolated from a tidal flat (Dongtan Wetland, Chongming Island, Shanghai, PR China). The DNA G+C content of the type strain is 65.8% (by genome).
| Pathway                        | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|-------------------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|
| **Aerobic anoxygenic photosynthesis** |   |   |   |   |   |   |   |   |   |    |    |    |    |    |    |    |
| bchD                          | − | − | + | − | + | + | + | − | − | − | − | − | + | − | − | − |
| bchE                          | − | − | + | − | + | + | + | − | − | − | − | − | + | − | − | − |
| bchG                          | − | − | + | − | + | + | + | − | − | − | − | − | + | − | − | − |
| bchL                          | − | − | + | − | + | + | + | − | − | − | − | − | + | − | − | − |
| bchM                          | − | − | + | − | + | + | + | − | − | − | − | − | + | − | − | − |
| bchN                          | − | − | + | − | + | + | + | − | − | − | − | − | + | − | − | − |
| bchP                          | − | − | + | − | + | + | + | − | − | − | − | − | + | − | − | − |
| bchX                          | − | − | + | − | + | + | + | − | − | − | − | − | + | − | − | − |
| bchY                          | − | − | + | − | + | + | + | − | − | − | − | − | + | − | − | − |
| bchZ                          | − | − | + | − | + | + | + | − | − | − | − | − | + | − | − | − |
| hemD                          | + | + | − | + | + | + | + | + | + | + | + | + | + | + | + | + |
| hemF                          | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| psFL                          | − | − | − | − | + | − | − | − | − | − | − | − | − | − | − | − |
| **Phenotype**                 | − | − | − | − | − | + | − | − | − | − | − | − | − | − | − | − |
| **Flagella biosynthesis**     |   |   |   |   |   |   |   |   |   |    |    |    |    |    |    |    |    |
| flgA                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flgB                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flgC                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flgD                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flgE                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flgF                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flgG                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flgH                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flgI                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flgL                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flgK                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flgL                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flhA                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flhB                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flhC                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flhD                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flhE                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flhF                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flhG                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| flhL                          | − | + | − | − | − | − | − | − | − | − | − | − | − | − | − | − |

Continued
DESCRIPTION OF **TSUNEONELLA FLAVA**

**COMB. NOV.**

*Tsuneonella flava* (fla’va. L. fem. adj. flava yellow, the colour of colonies and pigments of the bacterium).

Basonym: *Altererythrobacter flavus* Ma et al. 2018.

The description is the same as for *Aeb. flavus* [44]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Tsuneonella*. The type strain, MS1-4^T^ (=MCCC 1K02683^T^=NBRC 112977^T^), was isolated from mangrove sediment of the Jiulong River Estuary, Fujian Province, PR China. The DNA G+C content of the type strain is 60.5 % (by genome).

DESCRIPTION OF **TSUNEONELLA MANGROVI**

**COMB. NOV.**

*Tsuneonella mangrovi* (man. gro’vi. N.L. gen. n. mangrovi of or belonging to a mangrove wetland).

Basonym: *Altererythrobacter mangrovi* Liao et al. 2017.

The description is the same as for *Aeb. mangrovi* [6]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Tsuneonella*. The type strain, C9-11^T^ (=MCCC 1K03311^T^=JCM 32056^T^), was isolated from mangrove sediment sample collected from Yunxiao Mangrove National Nature Reserve in Zhangzhou, Fujian Province, PR China. The DNA G+C content of the type strain is 63.5 % (by genome).

DESCRIPTION OF **TSUNEONELLA RIGUI**

**COMB. NOV.**

*Tsuneonella rigui* (ri’gu.i. L. gen. n. rigui of a well-watered place).

Basonym: *Altererythrobacter rigui* Kang et al. 2016.

The description is the same as for *Aeb. rigui* [112]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Tsuneonella*. The type strain, WW3^T^ (=KCTC 42620^T^=JCM 30975^T^), was isolated from freshwater of Woopo wetland, Republic of Korea. The DNA G+C content of the type strain is 66.7 % (by genome).

DESCRIPTION OF **TSUNEONELLA TROIITSSENSIS**

**COMB. NOV.**

*Tsuneonella troitsensis* (troi. tsen’sis. N.L. fem. adj. troitsensis referring to Troitsa Bay, from where the organism was isolated).

Basonym: *Altererythrobacter troitsensis* Nedashkovskaya et al. 2013.

The description is the same as for *Aeb. troitsensis* [34]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Tsuneonella*. The type strain, KMM 6042^T^ (=KCTC 12303^T^=JCM 17037^T^), was isolated from the sea urchin *Strongylocentrotus intermedius*. The DNA G+C content of the type strain is 64.7 % (by genome).

EMENDED DESCRIPTION OF **QIPENGYUANIA FENG ET AL. 2015**

The description is as given by Feng et al. [2] with the following amendment. Cells are aerobic or facultatively aerobic. Contains carotenoid pigments but not bacteriochlorophyll a. Positive or negative for oxidase. The major fatty acid (>10%) is summed feature 8 (C_18:1_ω7c and/or C_18:1_ω6c). The major polar lipids are phosphatidylcholine, phosphatidylethanolamine and phosphatidylglycerol. The genus represents a distinct branch in the family *Erythrobacteraceae* of the class *Alphaproteobacteria* based on the core-genomic phylogeny. The DNA G+C content is 60.6–66.7 % (by genome). The type species for the genus is *Qipengyuania sediminis*.

DESCRIPTION OF **QIPENGYUANIA ALGICIDA**

**COMB. NOV.**

*Qipengyuania algicida* (al.gi.cida. L. fem. n. alga alga; L. suff. –cida from L. v. caedere to kill; N.L. fem. n. algicida a killer of algae).

Basonym: *Porphyrobacter algicida* Kristyanto et al. 2017.

The description is the same as for *Por. algicida* [44]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Qipengyuania*. The type strain, Yeonmyeong 2-22^T^ (=KEMB 9005–328^T^=JCM 31499^T^), was isolated from surface seawater collected from...
Goeje Island in the South Sea, Republic of Korea. The DNA G+C content of the type strain is 60.7% (by genome).

**DESCRIPTION OF QIPENGYANIA AQUIMARIS COMB. NOV.**

Qipengyuania aquimarís (a.qui.ma’ris. L. fem. n. aqua water; L. neut. n. mare the sea; N.L. gen. n. aquimarís of the water of the sea).

Basonym: Erythrobacter aquimarís Yoon et al. 2004.

The description is the same as for Erb. aquimarís [73]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Qipengyuania. The type strain, SW-110⁻ (≡KCCM 41818⁻=JCM 12189⁷), was isolated from sea water of a tidal flat of the Yellow Sea in the Republic of Korea. The DNA G+C content of the type strain is 61.8% (by genome).

**DESCRIPTION OF QIPENGYANIA CITREA COMB. NOV.**

Qipengyuania citreà (ci’tre.a. L. fem. adj. citrea, describing the lemon-yellow pigmentation).

Basonym: Erythrobacter citreus Denner et al. 2002.

The description is the same as for Erb. citreus [75]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Qipengyuania. The type strain, RE35/F1⁻ (≡CIP 107092⁻=DSM 14432⁷=JCM 21816⁷), was isolated from the western Mediterranean Sea (Bay of Calvi, Corsica, France). The DNA G+C content of the type strain is 64.2% (by genome).

**DESCRIPTION OF QIPENGYANIA GAETBULI COMB. NOV.**

Qipengyuania gaetbuli (gaet. bu’li. N.L. gen. n. gaetbuli of gaetbul, the Korean name for a tidal flat).

Basonym: Erythrobacter gaetbuli Yoon et al. 2005.

The description is the same as for Erb. gaetbuli [3]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Qipengyuania. The type strain, SW-161⁻ (≡KCTC 12227⁻=DSM 16225⁷), was isolated from a tidal flat of the Yellow Sea in the Republic of Korea. The DNA G+C content of the type strain is 64.1% (by genome).

**DESCRIPTION OF QIPENGYANIA MARISFLAVI COMB. NOV.**

Qipengyuania marisflavi (mar.is.flavi. L. neut. n. mare the sea; L. masc. adj. flavus yellow; N.L. gen. n. marisflavi of the Yellow Sea).

Basonym: Erythrobacter marisflavi Park et al. 2019.

The description is the same as for Erb. marisflavi [22]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Qipengyuania. The type strain, KEM-5⁻ (≡KACC 19865⁵=KCTC 62896⁻=NBRC 113546⁵), was isolated from water collected from an estuary environment where the ocean and a river meet at Seocheon, Republic of Korea. The DNA G+C content of the type strain is 61.7% (by genome).

**DESCRIPTION OF QIPENGYANIA NANHAISEDIMINIS COMB. NOV.**

Qipengyuania nanhaisediminis (nan.hai.se.di’mi.nis. Chin. n. nanhai meaning ‘the South China Sea’; L. gen. n. sediminis of a sediment; N.L. gen. n. nanhaisediminis of a sediment from the South China Sea).

Basonym: Erythrobacter nanhaisediminis Xu et al. 2010.

The description is the same as for Erb. nanhaisediminis [113]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Qipengyuania. The type strain, T30⁻ (≡CGMCC 1.7715⁵=JCM 16125⁷), was isolated from the South China Sea. The DNA G+C content of the type strain is 62.0% (by genome).

**DESCRIPTION OF QIPENGYANIA OCEANENSIS COMB. NOV.**

Qipengyuania oceanensis (o.ce.a.nen’sis. L. fem. adj. oceanensis, belonging to the ocean).

Basonym: Altererythrobacter oceanensis Yang et al. 2014.

The description is the same as for Aeb. oceanensis [70]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Qipengyuania. The type strain, Y2⁻ (≡CGMCC 1.12752⁻=LMG 28109⁷), was isolated from a deep-sea sediment of the western Pacific Ocean. The DNA G+C content of the type strain is 63.9% (by genome).

**DESCRIPTION OF QIPENGYANIA PELAGI COMB. NOV.**

Qipengyuania pelagi (pe’la.gi. L. gen. n. pelagi of/from the sea, reflecting isolation of the type strain from seawater of the Red Sea).

Basonym: Erythrobacter pelagi Wu et al. 2012.

The description is the same as for Erb. pelagi [77]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Qipengyuania. The type strain, UST081027-248⁻ (≡JCM 17468⁵=NRRRL 59511⁷), was isolated from shallow seawater collected from the middle of the Red Sea. The DNA G+C content of the type strain is 64.2% (by genome).
EMENDED DESCRIPTION OF QIPENGYUANIA SEDIMINIS FENG ET AL. 2015

Qipengyuania sediminis (se.di.mi.nis. L. gen. n. sediminis of sediment)

The description is identical to that given for Qpy. sediminis [2], except for the DNA G+C content. The type strain, M1T (=CGMCC 1.12928=JCM 30182T), was isolated from a borehole sediment sample collected from Qiangtang Basin in Qinghai-Tibetan Plateau, PR China. The DNA G+C content of the type strain is 66.7% (by genome).

DESCRIPTION OF QIPENGYUANIA SEOHAENSI Comb. nov.

Qipengyuania seohaensis (seo.ha.en sis. N.L. fem. adj. seohaensis of Seohae, the Korean name of the Yellow Sea in Korea, from where the type strain was isolated).

Basonym: Erythrobacter seohaensis Yoon et al. 2005.

The description is the same as for Erb. seohaensis [3]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Qipengyuania. The type strain, SW-135T (=KCTC 12228=DSM 16221T=JCM 21815T), was isolated from a tidal flat of the Yellow Sea in the Republic of Korea. The DNA G+C content of the type strain is 61.7% (by genome).

DESCRIPTION OF QIPENGYUANIA VULGARIS Comb. nov.

Qipengyuania vulgaris (vul.ga'ris. L. fem. adj. vulgaris, ordinary, usual, common).

Basonym: Erythrobacter vulgaris Ivanova et al. 2006.

The description is the same as for Erb. vulgaris [36]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Qipengyuania. The type strain, 022-2-10T (=KMM 3465T=CIP 107841T=DSM 21815T), was isolated from a borehole sediment sample collected from Qiangtang Basin in Qinghai-Tibetan Plateau, PR China. The DNA G+C content of the type strain is 66.7% (by genome).

DESCRIPTION OF ALTERIQIPENGYUANIA GEN. NOV.

Alteriqipengyuania (Al.te.ri.qi.peng.yu.an'i.a. L. adj. alter, another, other, different; N.L. fem. n. Qipengyuania, a genus name; N.L. fem. n. Alteriqipengyuania, another or different Qipengyuania).

Cells are Gram-stain-negative, rod-shaped, non-spore-forming, non-motile and strictly aerobic. Oxidase- and catalase-positive. Contains carotenoid pigments but not bacteriochlorophyll a. Requires NaCl for growth. The predominant ubiquinone is Q-10. The major fatty acids (>10%) are C17:1ω6c and summed feature 8 (C18:1ω7c and/or C18:1ω6c). The genus represents a distinct branch in the family Erythrobacteraceae of the class Alphaproteobacteria based on the core-genomic phylogeny. The DNA G+C content is 63.6–65.50% (by genome). The type species is Alteriqipengyuania lutimaris.

DESCRIPTION OF ALTERIQIPENGYUANIA HALIMIONAE COMb. NOV.

Alteriqipengyuania halimionae (ha.li.mi'o'nae. N.L. gen. n. halimionae of the marsh plant Halimione portulacoides).

Basonym: Altererythrobacter halimionae Fidalgo et al. 2017.

The description is the same as for Aeb. halimionae [32]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Alteriqipengyuania. The type strain, CPA5T (=CECT 9130T=LMG 29519T), was isolated from the surface-sterilized aboveground tissues of the halophyte Halimione portulacoides. The DNA G+C content of the type strain is 65.5% (by genome).

DESCRIPTION OF ALTERIQIPENGYUANIA LUTIMARIS COMb. NOV.

Alteriqipengyuania lutimaris (lu.ti.ma'ris. L. neut. n. lutim mar; L. neut. n. mare the sea; N.L. gen. n. lutimaris of a marine mud).

Basonym: Erythrobacter lutimaris Jung et al. 2014.

The description is the same as for Erb. lutimaris [114]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Alteriqipengyuania. The type strain, S-5T (=KCTC 42109T=CECT 8624T), was isolated from a tidal flat sediment of Saemankum in the Republic of Korea. The DNA G+C content of the type strain is 63.6% (by genome).

DESCRIPTION OF PARERYTHROBACTER GEN. NOV.

Parerythrobacter (Par.e.ry.thro.bac'ter. Gr. prep. para, beside, alongside of, near, like; N.L. masc. n. Erythrobacter, a genus name; N.L. masc. n. Parerythrobacter, near or like Erythrobacter).

Cells are Gram-stain-negative, rod-shaped, non-spore-forming, non-motile and strictly aerobic. Oxidase- and catalase-positive. Contains carotenoid pigments but not bacteriochlorophyll a. Requires NaCl for growth. The predominant ubiquinone is Q-10. The major fatty acids (>10%) are C17:1ω6c and summed feature 8 (C18:1ω7c and/or C18:1ω6c). The major polar lipids are diphosphatidylglycerol, phosphatidylcholine, phosphatidylethanolamine, phosphatidylglycerol and sphingoglycolipid. The genus represents a distinct branch in the family Erythrobacteraceae of the class Alphaproteobacteria based on the core-genomic phylogeny. The DNA G+C content of the type strain is 60.2–60.6% (by genome). The type species is Parerythrobacter jejuensis.
DESCRIPTION OF PARERYTHROBACTER JEJUENSIS COMB. NOV.

Parerythrobacter jejueensis (je.ju.en’sis. N.L. masc. adj. jejueensis of or belonging to Jeju Island in the Republic of Korea, where the type strain was isolated).

Basonym: Erythrobacter jejueensis Yoon et al. 2013.

The description is the same as for Erb. jejueensis [76]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Parerythrobacter. The type strain, CNU001T (=KCTC 23090T=JCM 16677T), was isolated from seawater collected off Jeju Island, Republic of Korea. The DNA G+C content of the type strain is 62.0% (by genome).

DESCRIPTION OF PARERYTHROBACTER LUTIPELAGI COMB. NOV.

Parerythrobacter lutipelagi (lu.ti.pe.la’gi. L. neut. n. lutum, mud; L. neut. n. pelagus the sea; N.L. gen. n. lutipelagi of mud of the sea, where the type strain was isolated).

Basonym: Altererythrobacter lutipelagi Lee 2019.

The description is the same as for Aeb. lutipelagi [42]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Parerythrobacter. The type strain, GH1-16T (=KCTC 52845T=NBRC 113275T), was isolated from tidal mudflat sample collected at the seashore of Gangwha Island, Republic of Korea. The DNA G+C content of the type strain is 60.2% (by genome).

EMENDED DESCRIPTION OF THE GENUS ALTERERYTHROBACTER KWON ET AL. 2007, EMEND. XUE ET AL. 2012, EMEND. XUE ET AL. 2016

The description is as given by Kwon et al. 2007 [38], Xue et al. [15] and Xue et al. 2016 [28] with the following amendment. Cells are aerobic and non-motile. Oxidase- and catalase-positive. Requires NaCl for growth. The major fatty acid (>10%) is C_{18:1} ω7c. The major polar lipids are phosphatidylethanolamine, phosphatidylglycerol and sphingoglycolipid. The genus represents a distinct branch in the family Erythrobacteraceae of the class Alphaproteobacteria based on the core-genomic phylogeny. The DNA G+C content is 52.0–61.8% (by genome). The type species for the genus is Altererythrobacter epoxidivorans.

EMENDED DESCRIPTION OF ALTERERYTHROBACTER EPOXIDIVORANS KWON ET AL. 2007

Altererythrobacter epoxidivorans (e.po.xi.di.vo’rans. N.L. neut. n. epoxidum epoxide; L. pres. part. vorans devouring; N.L. part. adj. epoxidivorans epoxide-devouring).

The description is identical to that given for Aeb. epoxidivorans [38], except for the DNA G+C content. The type strain, JCS350T (=KCCM 42314T=JCM 13815T), was isolated from cold-seep sediments of Kagoshima Bay, Japan. The DNA G+C content of the type strain is 61.5% (by genome).

EMENDED DESCRIPTION OF ALTERERYTHROBACTER ISHIGAKIENSIS MATSUMOTO ET AL. 2011

Altererythrobacter ishigakiensis (i.shi.ga.ki.en’sis. N.L. masc. adj. ishigakiensis of or belonging to Ishigaki island, Okinawa, Japan, where the type strain was isolated).

The description is identical to that given for Aeb. ishigakiensis [115], except for the DNA G+C content. The type strain, JPCCM0017T (=NITE-AP48T=ATCC 2084T=NBRC 107699T), was isolated from the coastal area of Okinawa, Japan. The DNA G+C content of the type strain is 56.9% (by genome).

EMENDED DESCRIPTION OF ALTERERYTHROBACTER XIAMENENSIS LEI ET AL. 2014

Altererythrobacter xiamenensis (xia.men.en’sis. N.L. masc. adj. xiamensis of Xiamen, a city in Fujian, PR China, where the type strain was first isolated).

The description is identical to that given for Aeb. xiamenensis [18], except for the DNA G+C content. The type strain, LY02T (=CGMCC 1.12494T=KCTC 32398T=NBRC 109638T), was isolated from red tide seawater in Xiamen, Fujian Province, PR China. The DNA G+C content of the type strain is 61.8% (by genome).

EMENDED DESCRIPTION OF THE GENUS ERYTHROBACTER SHIBA ET AL. 1982

The description is as given by Shib et al. 1982 [29] with the following amendment. Cells are motile or non-motile. Positive or negative for oxidase. Requires NaCl for growth. The major fatty acids (>10%) are C_{18:1} ω7c and C_{17:1} ω6c. The major polar lipids include a sphingoglycolipid. The genus represents a distinct branch in the family Erythrobacteraceae of the class Alphaproteobacteria based on the core-genomic phylogeny. The DNA G+C content is 57.4–67.9% (by genome). The type species for the genus is Erythrobacter longus.

DESCRIPTION OF ERYTHROBACTER COLYMBI COMB. NOV.

Erythrobacter colymbi (co.lym’bi. L. gen. n. colymbi, of a swimming pool, thus indicating the site of isolation of the type strain).

Basonym: Porphyrobacter colymbi Rainey et al. 2003.

The description is the same as for Por. colymbi [24]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Erythrobacter. The type
strain, TPW-24T (=JCM 18338T=KCTC 32078T), was isolated from swimming pool water in Tokyo, Japan. The DNA G+C content of the type strain is 66.5% (by genome).

**DESCRIPTION OF ERYTHROBACTER CRYPTUS COMB. NOV.**

*Erythrobacter cryptus* (crypt'rus. N.L. masc. adj. cryptus from Gr. masc. adj. kryptos hidden, to indicate the cryptic relationship of this species to the closely related organisms).

Basomym: *Porphyrobacter cryptus* Rainey et al. 2003.
The description is the same as for *Por. cryptus* [26]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Erythrobacter*. The type strain, ALC-2T (=DSM 12079T=ATCC BAA-386T), was isolated from the hot spring at Alcafache in Portugal. The DNA G+C content of the type strain is 64.3% (by genome).

**DESCRIPTION OF ERYTHROBACTER DOKDONENSIS COMB. NOV.**

*Erythrobacter dokdonensis* (dok.do.nen’sis. N.L. masc. adj. dokdonensis of Dokdo, from where the strain was isolated).

Basomym: *Porphyrobacter dokdonensis* Yoon et al. 2006.
The description is the same as for *Por. dokdonensis* [106]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Erythrobacter*. The type strain, DSW-74T (=KCTC 12395T=DSM 17193T), was isolated from sea water off the island of Dokdo, Korea. The DNA G+C content of the type strain is 64.8% (by genome).

**DESCRIPTION OF ERYTHROBACTER DONGHAENSI S COMB. NOV.**

*Erythrobacter donghensis* (dong.ha.en’sis. N.L. masc. adj. donghaensis of Donghae, the Korean name for the East Sea in the Republic of Korea from which the strains were isolated).

Basomym: *Porphyrobacter donghensis* Yoon et al. 2004.
The description is the same as for *Por. donghensis* [105]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Erythrobacter*. The type strain, SW-132T (=KCTC 12229T=DSM 16226T), was isolated from sea water from the East Sea in the Republic of Korea. The DNA G+C content of the type strain is 66.2% (by genome).

**EMENDED DESCRIPTION OF ERYTHROBACTER LITORALIS YURKOV ET AL. 1994**

*Erythrobacter litoralis* (li.to.ra’lis. L. masc. adj. litoralis, at the beach or coast, referring to the supralitoral habitat).
The description is identical to that given for *Erb. litoralis* [31], except for the DNA G+C content. The type strain, T4T (=ATCC 700002T=CIP 106926T=DSM 8509T=JCM 10281T=NBRC 102620T), was isolated from a marine cyanobacterial mat in a supralitoral zone. The DNA G+C content of the type strain is 65.2% (by genome).

**EMENDED DESCRIPTION OF ERYTHROBACTER LONGUS SHIBA ET AL. 1982**

*Erythrobacter longus* (lon’gus. L. masc. adj. longus, long).
The description is identical to that given for *Erb. longus* [29], except for the DNA G+C content. The type strain, Och01T (=ATCC 33941T=CIP 104268T=DSM 6997T=JCM 6170T=NBRC 14126T), was isolated from high-tidal seaweed *Enteromorpha linza*. The DNA G+C content of the type strain is 57.4% (by genome).

**DESCRIPTION OF ERYTHROBACTER NEUSTONENSIS COMB. NOV.**

*Erythrobacter neustonensis* [neu.sto.nen’sis. N.L. masc. adj. derived from Gr. n. neustos, swimming (floating), referring to occurrence of the bacterium as a member of the neuston (organisms floating at the air–water interface surface layer of a body of water)].

Basomym: *Porphyrobacter neustonensis* Fuerst et al. 1993.
The description is the same as for *Por. neustonensis* [23]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Erythrobacter*. The type strain, ACM 2844T (=CIP 104070T=DSM 9434T), was isolated from air–water interface of freshwater subtropical pond in Brisbane, Australia. The DNA G+C content of the type strain is 65.3% (by genome).

**DESCRIPTION OF ERYTHROBACTER RAMOUS COMB. NOV.**

*Erythrobacter ramosus* (ra.mo’sus. L. masc. adj. ramosus, ramifying, referring to the morphology of the cells).

Basomym: *Erythromicrobium ramosum* Yurkov et al. 1994.
The description is the same as for *Erm. ramosum* [31]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Erythrobacter*. The type strain, E5T (=ATCC 700003T=CIP 106927T=DSM 8510T=JCM 10282T=NBRC 102621T), was isolated from a cyanobacterial mat from an alkaline spring. The DNA G+C content of the type strain is 64.3% (by genome).

**DESCRIPTION OF ERYTHROBACTER SANGUINEUS COMB. NOV.**

*Erythrobacter sanguineus* (san.gui.ne.us. L. masc. adj. sanguineus blood-coloured).

Basomym: *Porphyrobacter sanguineus* Hiraishi et al. 2002.
The description is the same as for *Por. sanguineus* [104]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Erythrobacter*. 

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The type strain, A91T (=ATCC 25659=DSM 11302=IAM 12620=ICPB 4167=NBRB 15763=JCM 20691T), was isolated from sea water collected in Baltic Sea. The DNA G+C content of the type strain is 63.6% (by genome).

**DESCRIPTION OF ERYTHROBACTER TEPIDARIUS COMB. NOV.**

*Erythrobacter tepidarius* (te.pi.da’ri.us. L. neut. n. tepidarium, a warm bath fed by natural thermal water; N.L. masc. adj. tepidarius, warm bathing).

Basonym: *Porphyrobacter tepidarius* Hanada *et al.* 1997.

The description is the same as for *Por. tepidarius* [27]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Erythrobacter*. The type strain, OT3T (=DSM 10594T), was isolated from a cyanobacterial mat in brackish water of a hot spring in Shizuoka Prefecture, Japan. The DNA G+C content of the type strain is 65.9% (by genome).

**DESCRIPTION OF PONTIXANTHOBACTER GEN. NOV.**

*Pontixanthobacter* (Pon. ti.xan.tho.bac’ter. L. masc. n. pontus, the sea; Gr. masc. adj. xanthos, yellow; N.L. masc. n. bacter, rod or staff; N.L. masc. n. Pontixanthobacter, a yellow bacterium from the sea).

Cells are Gram-stain-negative, ovoid to rod, non-spore-forming, non-motile and aerobic. Positive and negative for oxidase. Catalase-positive. Contains carotenoid pigments but not bacteriochlorophyll *a*. The predominant ubiquinone is Q-10. The major fatty acid (>10 %) is summed feature 8 (C18:1ω7c and/or C18:1ω6c). The major polar lipids are phosphatidylcholine, phosphatidylethanolamine, phosphatidylglycerol and sphingoglycolipid. The genus represents a distinct branch in the family *Erythrobacteraceae* of the class *Alphaproteobacteria* based on the core-genomic phylogeny. The DNA G+C content is 55.5–61.5% (by genome).

**DESCRIPTION OF PONTIXANTHOBACTER AESTIAQUAE COMB. NOV.**

*Pontixanthobacter aestiaquae* (aes.ti.a’qua.e. L. masc. n. aestus the sea tide; L. fem. n. *aqua* water; N.L. gen. n. aestiaquae of the water of the sea tide).

Basonym: *Altererythrobacter aestiaquae* Jung *et al.* 2014.

The description is the same as for *Aeb. aestiaquae* [62]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Pontixanthobacter*. The type strain, HDW-31T (=KCTC 42006=CECT 8527T), was isolated from seawater of Hwang-do in the Republic of Korea. The DNA G+C content of the type strain is 57.2% (by genome).

**DESCRIPTION OF PONTIXANTHOBACTER AQUAEMIXTAE COMB. NOV.**

*Pontixanthobacter aquaemixtae* (aqua.e.mi’xtae. L. fem. n. *aqua* water; L. fem. perf. part. *mixta* mixed; N.L. fem. gen. n. *aquaemixtae* of mixed waters).

Basonym: *Altererythrobacter aquaemixtae* Park *et al.* 2017.

The description is the same as for *Aeb. aquaemixtae* [64]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Pontixanthobacter*. The type strain, JSSK-8T (=KCTC 52763=NBRC 112764T), was isolated from the place where the ocean and a freshwater spring meet at Jeju Island, Republic of Korea. The DNA G+C content of the type strain is 58.5% (by genome).

**DESCRIPTION OF PONTIXANTHOBACTER CONFLUENTIS COMB. NOV.**

*Pontixanthobacter confluentis* (con.flu.en’tis. L. gen. n. confluentis of a meeting place of waters).

Basonym: *Altererythrobacter confluentis* Park *et al.* 2016.

The description is the same as for *Aeb. confluentis* [20]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Pontixanthobacter*. The type strain, KEM-4T (=KCTC 52259=NBRC 112305T), was isolated from water collected from an estuary environment where the ocean and a river meet at Seocheon, Republic of Korea. The DNA G+C content of the type strain is 59.1% (by genome).

**DESCRIPTION OF PONTIXANTHOBACTER GANGJINENSIS COMB. NOV.**

*Pontixanthobacter gangjinensis* (gang.jin.en’sis. N.L. masc. adj. gangjinensis pertaining to Gangjin bay where the type strain was isolated).

Basonym: *Altererythrobacter gangjinensis* Jeong *et al.* 2013.

The description is the same as for *Aeb. gangjinensis* [67]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Pontixanthobacter*. The type strain, KJ7T (=KACC 16190=JCM 17802T), was isolated from a tidal flat of the Gangjin bay in the Republic of Korea. The DNA G+C content of the type strain is 59.1% (by genome).

**DESCRIPTION OF PONTIXANTHOBACTER LUTEOLUS COMB. NOV.**

*Pontixanthobacter luteolus* (lu.te’o.lus. L. masc. adj. *luteolus*, yellowish).

Basonym: *Altererythrobacter luteolus* Yoon *et al.* 2005. emend. Kwon *et al.* 2007.

The description is the same as for *Aeb. luteolus* [38, 68]. Core-genomic phylogenetic analysis strongly supported
the placement of this species in the genus *Pontixanthobacter*. The type strain, SW-109$^T$ (=KCTC 12311$^T$=JCM 12599$^T$), was isolated from a tidal flat of the Yellow Sea in the Republic of Korea. The DNA G+C content of the type strain is 59.3% (by genome).

**DESCRIPTION OF *PONTIXANTHOBACTER SEDIMINIS* COMB. NOV.**

*Pontixanthobacter sediminis* (se.di.mi.nis. L. gen. n. sediminis of sediment).

Basonym: *Altererythrobacter sediminis* Kim et al. 2016.

The description is the same as for *Aeb. sediminis* [72]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Pontixanthobacter*. The type strain, CAU 1172$^T$ (=KCTC 42453$^T$=NBRC 110917$^T$), was isolated from a sample of lagoon sediment from along the east coast of the Republic of Korea. The DNA G+C content of the type strain is 61.5% (by genome).

**DESCRIPTION OF *ALTERIPONTIXANTHOBACTER GEN. NOV.***

*Alteripontixanthobacter* (Al.te.ri.pon.ti.xan.tho.bac.ter. L. adj. alter, another, other, different; N.L. masc. n. *Pontixanthobacter*, a genus name; N.L. masc. n. *Alteripontixanthobacter*, another or different *Pontixanthobacter*).

Cells are Gram-stain-negative, rod, non-spore-forming, non-motile and aerobic. Oxidase- and catalase-positive. Contains carotenoid pigments but not bacteriochlorophyll *a*. Requires NaCl for growth. Reduces nitrate to nitrite. The predominant ubiquinone is Q-10. The major fatty acids (>10 %) are summed feature 8 (C$_{18:1}\omega 7c$ and/or C$_{18:1}\omega 6c$), summed feature 3 (C$_{16:1}\omega 7c$ and/or C$_{16:1}\omega 6c$) and C$_{16:0}$. The major polar lipids are diphosphatidylglycerol, phosphatidylethanolamine, phosphatidylglycerol and sphingoglycolipid. The genus represents a distinct branch in the family *Erythrobacteraceae* of the class *Alphaproteobacteria* based on the core-genomic phylogeny. The DNA G+C content is 61.2% (by genome). The type species is *Parapontixanthobacter aurantiacus*.

**DESCRIPTION OF *PARAPONTIXANTHOBACTER AURANTIACUS* COMB. NOV.**

*Parapontixanthobacter aurantiacus* (au.ran.ti.a.cus. N.L. masc. adj. aurantiacus, orange-coloured).

Basonym: *Altererythrobacter aurantiacus* Zhang et al. 2016.

The description is the same as for *Aeb. aurantiacus* [65]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus *Parapontixanthobacter*. The type strain, O30$^T$ (=CGMCC 1.12762$^T$=JCM 19853$^T$=LMG 28110$^T$=MCCC 1A09962$^T$), was isolated from a deep-sea sediment of the west Pacific Ocean. The DNA G+C content of the type strain is 61.4% (by genome). The type species is *Parapontixanthobacter aurantiacus*.

**DESCRIPTION OF *PELAGERYTHROBACTER GEN. NOV.***

*Pelagerythrobacter* (Pe.lag.e.ry.th.ro.bac.ter. L. neut. n. pelagus the sea; N.L. masc. n. *Erythrobacter*, a genus name; N.L. masc. n. *Pelagerythrobacter, Erythrobacter* from the sea).

Cells are Gram-stain-negative, rod-shaped, non-spore-forming and aerobic. Motile or non-motile. Positive and negative for oxidase. Catalase-positive. Contains carotenoid pigments but not bacteriochlorophyll *a*. Requires NaCl for growth. The predominant ubiquinone is Q-10. The major fatty acid (>10 %) is C$_{18:1}\omega 7c$. The major polar lipids are diphosphatidylglycerol, phosphatidylethanolamine, phosphatidylglycerol and sphingoglycolipid. The genus represents a distinct branch in the family *Erythrobacteraceae* of the class *Alphaproteobacteria* based on the core-genomic phylogeny. The DNA G+C content of the type strain is 60.8% (by genome).
on the core-genomic phylogeny. The DNA G+C content is 64.7–68.2% (by genome). The type species is Pelagerythrobacter marinus.

DESCRIPTION OF PELAGERYTHROBACTER AEROPHILUS COMB. NOV.

Pelagerythrobacter aerophilus (a.e.ro’phi.lus. Gr. masc. n. aer, air; N.L. adj. philus from Gr. masc. adj. philos friend, loving; N.L. masc. adj. aerophilus, air-loving).

Basonym: Altererythrobacter aerophilus Meng et al. 2019.

The description is the same as for Aeb. aerophilus [17]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Pelagerythrobacter. The type strain, Ery1T (=KCTC 62387T=CGMCC 1.16499T=MCCC 1A01037T), was isolated from deep-sea seawater of the Mariana Trench. The DNA G+C content of the type strain is 65.4% (by genome).

DESCRIPTION OF PELAGERYTHROBACTER MARINUS COMB. NOV.

Pelagerythrobacter marinus (ma.ri’nus. L. masc. adj. marinus of the sea, marine).

Basonym: Altererythrobacter marinus Lai et al. 2009.

The description is the same as for Aeb. marinus [69]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Pelagerythrobacter. The type strain, H32T (=CCTCCAB 208229T=LMG 24629T=MCCC 1A01070T), was isolated from deep seawater of the Indian Ocean. The DNA G+C content of the type strain is 68.2% (by genome).

DESCRIPTION OF PELAGERYTHROBACTER MARENSIS COMB. NOV.

Pelagerythrobacter marensis (ma.ren’sis. N.L. masc. adj. marensis of Mara Island, Jeju, Republic of Korea, where the type strain was isolated).

Basonym: Altererythrobacter marensis Seo et al. 2010.

The description is the same as for Aeb. marensis [116]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Pelagerythrobacter. The type strain, MSW-14T (=KCTC 22370T=DSM 21428T), was isolated from seawater collected around Mara Island, Jeju, Republic of Korea. The DNA G+C content of the type strain is 64.7% (by genome).

DESCRIPTION OF ALTERICOCEIBACTERIUM GEN. NOV.

Altericroceibacterium (Al.te.ri.cro.ce.i bac.te’ri.um. L. masc. adj. alter another, other, different; N.L. neut. n. Croceibacterium, a genus name; N.L. neut. n. Altericroceibacterium, another or different Croceibacterium).

Cells are Gram-stain-negative, rod-shaped, non-spore-forming, aerobic and non-motile. Positive and negative for oxidase. Catalase-positive. Contains carotenoid pigments but not bacteriochlorophyll a. Requires NaCl for growth. The predominant ubiquinone is Q-10. The major fatty acid (>10%) is summed feature 8 (C18:1ω7c and/or C18:1ω6c). The major polar lipid is phosphatidylethanolamine. The genus represents a distinct branch in the family Erythrobacteraceae of the class Alphaproteobacteria based on the core-genomic phylogeny. The DNA G+C content is 55.8–64.2% (by genome). The type species is Altericroceibacterium indicum.

DESCRIPTION OF ALTERICOCEIBACTERIUM ENDOPHYTICUM COMB. NOV.

Altericroceibacterium endophyticum (en.do.phy’ti.cum. Gr. pref. endo within; Gr. n. phytos plant; N.L. neut. suff. -icum adjectival suffix used with the sense of belonging to; N.L. neut. adj. endophyticum within plant, endophytic).

Basonym: Altererythrobacter endophyticus Fidalgo et al. 2017.

The description is the same as for Aeb. endophyticus [32]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Altericroceibacterium. The type strain, BR75T (=CECT 9129T=LMG 29518T), was isolated from the surface-sterilized belowground tissues of the halophyte Halimione portulacoides. The DNA G+C content of the type strain is 58.6% (by genome).

DESCRIPTION OF ALTERICOCEIBACTERIUM INDICUM COMB. NOV.

Altericroceibacterium indicum (in’di.cum. L. neut. adj. indicum pertaining to India, where the type strain was isolated).

Basonym: Altererythrobacter indicus Kumar et al. 2008.

The description is the same as for Aeb. indicus [33]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Altericroceibacterium. The type strain, MSSRF26T (=LMG 23789T=DSM 18604T), isolated from the rhizosphere of mangrove-associated wild rice (Porteresia coarctata Tateoka). The DNA G+C content of the type strain is 55.8% (by genome).

DESCRIPTION OF ALTERICOCEIBACTERIUM XINJIANGENSE COMB. NOV.

Altericroceibacterium xinjiangense (xin.jiang.en’se. N.L. neut. adj. xinjiangense of or pertaining to Xinjiang, an autonomous region in north-west China).

Basonym: Altererythrobacter xinjiangensis Xue et al. 2012.

The description is the same as for Aeb. xinjiangensis [15]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Altericroceibacterium.
The type strain, S3-63T (=CCTCC AB 207166T=CIP 110125T), was isolated from sand from the desert of Xinjiang, PR China. The DNA G+C content of the type strain is 64.6% (by genome).

EMENDED DESCRIPTION OF THE GENUS CROCEIBACTERIUM LIU ET AL. 2019

The description is as given by Liu et al. [30] with the following amendment. Cells are pleomorphic. Some species can motile by means of polar flagella. Positive or negative for oxidase. The major fatty acid (>10%) is summed feature 8 (C_{18:1ω7c} and/or C_{18:1ω6c}). The major polar lipids are diphasatidylglycerol, phosphatidylethanolamine and phosphatidylglycerol. The genus represents a distinct branch in the family Erythrobacteraceae of the class Alphaproteobacteria based on the core-genomic phylogeny. The DNA G+C content is 61.9–67.0% (by genome). The type species for the genus is Croceibacterium ferulae (Erythrobacter ferulae).

DESCRIPTION OF CROCEIBACTERIUM ATLANTICUM COMB. NOV.

Croceibacterium atlanticum (atl.an’ti.cum. L. neut. adj. atlant-icum of or pertaining to the Atlantic Ocean, where the type strain was isolated).

Basonym: Altererythrobacter atlanticus Wu et al. 2014.

The description is the same as for Aeb. atlanticus [8]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Croceibacterium. The type strain, 26DY36T (=CGMCC 1.12411T=JCM 18865T), was isolated from a deep-sea sediment sample collected from the North Atlantic Rise. The DNA G+C content of the type strain is 61.9% (by genome).

DESCRIPTION OF CROCEIBACTERIUM SALEGENS COMB. NOV.

Croceibacterium salegens (sal.e’gens. L. masc. n. sal, salis salt; L. pres. part. egens needy; N.L. part. adj. salegens salt-needy).

Basonym: Altererythrobacter salegens Liang et al. 2017.

The description is the same as for Aeb. salegens [71]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Croceibacterium. The type strain, XY-R17T (=KCTC 52267T=MCCC 1K01500T), was isolated from the surface sediment of Mai Po Inner Deep Bay Ramsar Site in Hong Kong. The DNA G+C content of the type strain is 61.9% (by genome).

DESCRIPTION OF CROCEIBACTERIUM SOLI COMB. NOV.

Croceibacterium soli (so’li. L. gen. n. soli of soil).

Basonym: Altererythrobacter soli Zhao et al. 2017.

The description is the same as for Aeb. soli [14]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Croceibacterium. The type strain, MN-1T (=KCTC 52135T=MCCC 1K02066T), isolated from a desert sand sample collected from Tengger desert, north-western PR China. The DNA G+C content of the type strain is 67.0% (by genome).

DESCRIPTION OF CROCEIBACTERIUM XIXISOLI COMB. NOV.

Croceibacterium xixisoli (xi.xi.i.so’lii. L. gen. n. soli of soil. N.L. gen. n. xixisoli from Xixi soil).

Basonym: Altererythrobacter xixisoli Yuan et al. 2017.

The description is the same as for Aeb. xixisoli [12]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Croceibacterium. The type strain, S36T (=CGMCC 1.12804T=NBRC 110413T), was isolated from soil of the Xixi wetland in Hangzhou, eastern PR China. The DNA G+C content of the type strain is 63.3% (by genome).

DESCRIPTION OF ALTERAURANTIACIBACTER GEN. NOV.

Alteraaurantiacibacter (Al.ter.au.ran.ti.a.ci.bac’ter. L. masc. adj. alter another, other, different; N.L. masc. n. Aurantiacibacter, a genus name; N.L. masc. n. Alteraurantiacibacter, another or different Aurantiacibacter).

Cells are Gram-stain-negative, pleomorphic, non-spore-forming, aerobic and non-motile. Oxidase- and catalase-positive. Contains carotenoid pigments but not bacteriochlorophyll a. Requires NaCl for growth. The predominant ubiquinone is Q-10. The major fatty acid (>10%) is summed feature 8 (C_{18:1ω7c} and/or C_{18:1ω6c}). The major polar lipids are phosphatidylethanolamine and phosphatidylglycerol. The genus represents a distinct branch in the family Erythrobacteraceae of the class Alphaproteobacteria based on the core-genomic phylogeny. The DNA G+C content is 62.5–66.0% (by genome). The type species is Alteraurantiacibacter aestuarii.

DESCRIPTION OF ALTERAURANTIACIBACTER AESTUARII COMB. NOV.

Alteraaurantiacibacter aestuarii (aes tu.au.ri.ii. L. gen. n. aestuarii of a tidal flat, from where the type strain was isolated).

Basonym: Altererythrobacter aestuarii Park et al. 2011.

The description is the same as for Aeb. aestuarii [63]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Alteraurantiacibacter. The type strain, KYW147T (=KCTC 22735T=JCM 16339T), was isolated from a seawater sample collected from the South Sea, Republic of Korea. The DNA G+C content of the type strain is 62.5% (by genome).
DESCRIPTION OF ALTERAURANTIACIBACTER AQUIMIXTICOLA COMB. NOV.

Alteraurantiacibacter aquimixticoila (a.qui.mix.ti.co.la. L. fem. n. aqua water; L. masc. perf. part. mixtus mixed; L. suff. -cola inhabitant; N.L. masc. n. aquimixticoila an inhabitant of mixed waters).

Basonym: Altererythrobacter aquimixticoila Park et al. 2017.

The description is the same as for Erb. aquimixticoila [88]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Aurantiacibacter. The type strain, JSSK-14T (=KCTC 52764T=NBRC 112765T), was isolated from water from the place where the ocean and a freshwater spring meet at Jeju island, Republic of Korea. The DNA G+C content of the type strain is 63.0% (by genome).

DESCRIPTION OF ALTERAURANTIACIBACTER BUCTENSIS COMB. NOV.

Alteraurantiacibacter buctensis (buc.ten’sis. N.L. masc. adj. buctensis referring to the acronym BUCT, Beijing University of Chemical Technology, where the strain was identified).

Basonym: Altererythrobacter buctensis Zhang et al. 2016.

The description is the same as for Aeb. buctensis [66]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Alteraurantiacibacter. The type strain, MO322T (=CGMCC 1.12871T=JCM 30112T), was isolated from the Mohe Basin, PR China. The DNA G+C content of the type strain is 66.0% (by genome).

DESCRIPTION OF AURANTIACIBACTER GEN. NOV.

Aurantiacibacter (Au.ran.ti.a.ci.bac’ter. N.L. masc. adj. aurantiacus, orange-coloured; N.L. masc. n. bacter, rod or staff; N.L. masc. n. Aurantiacibacter, orange-coloured rod).

Cells are Gram-stain-negative, pleomorphic and non-spore-forming. Aerobic or facultative anaerobic. Positive or negative for oxidase. Catalase-positive. Contains carotenoid pigments but not bacteriochlorophyll a. The predominant ubiquinone is Q-10. The major fatty acid (>10%) is summed feature 8 (C\textsubscript{18:1}ω7c and/or C\textsubscript{18:1}ω6c). The major polar lipid is phosphatidylethanolamine. The genus represents a distinct branch in the family Erythrobacteraceae of the class Alphaproteobacteria based on the core-genomic phylogeny. The DNA G+C content is 58.3–67.2% (by genome). The type species is Aurantiacibacter gangjinensis.

DESCRIPTION OF AURANTIACIBACTER AQUIMIXTICOLA COMB. NOV.

Aurantiacibacter aquimixticoila (a.qui.mix.ti.co.la. L. fem. n. aqua water; L. masc. perf. part. mixtus mixed; L. suff. -cola from L. n. incola dweller, inhabitant; N.L. masc. n. aquimixticoila an inhabitant of mixed waters).

Basonym: Erythrobacter aquimixticoila Park et al. 2017.

The description is the same as for Erb. aquimixticoila [88]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Aurantiacibacter. The type strain, JSSK-14T (=KCTC 52764T=NBRC 112765T), was isolated from water from the place where the ocean and a freshwater spring meet at Jeju island, Republic of Korea. The DNA G+C content of the type strain is 63.0% (by genome).

DESCRIPTION OF AURANTIACIBACTER ARACHOIDES COMB. NOV.

Aurantiacibacter arachoides (a.ra cho’i.des. N.L. fem. n. arachis, peanut; L. suff. -oides, looking like; N.L. masc. adj. arachoides, looking like a peanut).

Basonym: Erythrobacter arachoides Xing et al. 2017.

The description is the same as for Erb. arachoides [74]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Aurantiacibacter. The type strain, RC4-10-4T (=CGMCC 1.15507T=JCM 31277T), was isolated from an ice core in the East Rongbuk Glacier, Tibetan Plateau. The DNA G+C content of the type strain is 65.4% (by genome).

DESCRIPTION OF AURANTIACIBACTER ATLANTICUS COMB. NOV.

Aurantiacibacter atlanticus (at.lan’ti.cus. N.L. masc. adj. atlanticus referring to the Atlantic Ocean, where the type strain was isolated).

Basonym: Erythrobacter atlanticus Zhuang et al. 2015.

The description is the same as for Erb. atlanticus [109]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Aurantiacibacter. The type strain, s21-N3T (=MCCC 1A00519T=KCTC 42697T) was isolated from deep-sea sediment of the Atlantic Ocean. The DNA G+C content of the type strain is 58.3% (by genome).

DESCRIPTION OF AURANTIACIBACTER GANGJINENSIS COMB. NOV.

Aurantiacibacter gangjinensis (gang.jin.en’sis. N.L. masc. adj. gangjinensis referring to Gangjin, the name of the bay in Korea from which the type strain was isolated).

Basonym: Erythrobacter gangjinensis Lee et al. 2010.

The description is the same as for Erb. gangjinensis [117]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Aurantiacibacter. The type strain, K7-2T (=KCTC 22330T=JCM 15420T), was isolated from seawater of Gangjin Bay, Republic of Korea. The DNA G+C content of the type strain is 62.7% (by genome).
DESCRIPTION OF AURANTIACIBACTER LUTEUS COMB. NOV.

Aurantiacibacter luteus (lu’te.us. L. masc. adj. luteus orange-coloured, referring to the colour of the colony).

Basonym: Erythrobacter luteus Lei et al. 2015.

The description is the same as for Erb. luteus [118]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Aurantiacibacter. The type strain, KA37T (=MCCC 1F01227T=KCTC 42179T), was isolated from a mangrove sediment sample collected from Yunxia mangrove National Nature Reserve, Fujian Province, PR China. The DNA G+C content of the type strain is 67.2% (by genome).

DESCRIPTION OF AURANTIACIBACTER MARINUS COMB. NOV.

Aurantiacibacter marinus (ma.rin’us. L. masc. adj. marinus of the sea, marine).

Basonym: Erythrobacter marinus Jung et al. 2012.

The description is the same as for Erb. marinus [119]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Aurantiacibacter. The type strain, HWDM-33T (=KCTC 23554T=CCUG 60528T), was isolated from seawater of Hwang-do, an island of the Yellow Sea, Republic of Korea. The DNA G+C content of the type strain is 59.1% (by genome).

DESCRIPTION OF AURANTIACIBACTER ODISHENSIS COMB. NOV.

Aurantiacibacter odishensis (o.dish.en’sis. N.L. masc. adj. odishensis of or belonging to Odisha, a coastal state in India rich in bacterial diversity).

Basonym: Erythrobacter odishensis Subhash et al. 2013.

The description is the same as for Erb. odishensis [13]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Aurantiacibacter. The type strain, JA747T (=KCTC 23981T=NBRC 108930T), was isolated from a soil sample of a solar saltern at Humna, Odisha, India. The DNA G+C content of the type strain is 63.7% (by genome).

DESCRIPTION OF AURANTIACIBACTER SPONGIAE COMB. NOV.

Aurantiacibacter spongiae (spon’gi.ae. L. gen. n. spongiae of a sponge, the source of the type strain).

Basonym: Erythrobacter spongiae Zhuang et al. 2019.

The description is the same as for Erb. spongiae [35]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Aurantiacibacter. The type strain, HN-E23T (=MCCC 1K03331T=LMG 30457T), was isolated from a sponge sample. The DNA G+C content of the type strain is 65.5% (by genome).
DESCRIPTION OF PARURAINTIACIBACTER NAMHICOLA COMB. NOV.

Paruraantiacibacter namhicola (nam.hi’co.la. N.L. n. namhiae Namhae, the Korean name of the South Sea; L. suff. -cola from L. n. incola a dweller, inhabitant; N.L. masc. n. namhicola a dweller of the South Sea, referring to the isolation of the type strain).

Basonym: Altererythrobacter namhicola Park et al. 2011.

The description is the same as for Aeb. namhicola [63]. Core-genomic phylogenetic analysis strongly supported the placement of this species in the genus Paruraantiacibacter. The type strain, KYW487 (=KCTC 22736=JCM 16345T), was isolated from a seawater sample collected from the South Sea, Republic of Korea. The DNA G+C content of the type strain is 65.0% (by genome).

EMENDED DESCRIPTION OF THE GENUS CROCEICOCCUS XU ET AL. 2009 EMEND. HUANG ET AL. 2015

The description is as given by Xu et al. [4] and Huang et al. [110] with the following amendments. Cells are coccoid to rods. The major fatty acid (>10 %) is C18:1ω7c. The genus represents a distinct branch in the family Erythrobacteraceae of the class Alphaproteobacteria based on the core-genomic phylogeny. The DNA G+C content is 62.5–64.5% (by genome). The type species for the genus is Croceicoccus marinus.

EMENDED DESCRIPTION OF CROCEICOCCUS MARINUS XU ET AL. 2009 EMEND. HUANG ET AL. 2015

Croceicoccus marinus (ma.ri’nu.s. L. masc. adj. marinus of or belonging to the sea, marine)

The description is identical to that given for Ccc. marinus [4, 110], except for the DNA G+C content. The type strain, E4A9T (=CGMCC 1.6776=JCM 14846T), was isolated from a deep-sea sediment sample collected from a polynetic node in the East Pacific Ocean. The DNA G+C content of the type strain is 64.5% (by genome).

EMENDED DESCRIPTION OF CROCEICOCCUS NAPHTHOVORANS HUANG ET AL. 2015

Croceicoccus naphthovorans (naph.tho.vo’ran.s. Gr. fem. n. naphtha oil; L. pres. part. vorans devouring; N.L. part. adj. naphthovorans oil-degrading).

The description is identical to that given for Ccc. naphthovorans [110], except for the DNA G+C content. The type strain, PQ-2T (=CGMCC 1.12805=NBRC 110381T) was isolated from marine biofilm collected from a boat shell at a harbour of Zoushan island in Zhejiang Province, PR China. The DNA G+C content of the type strain is 62.6% (by genome).

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Conflicts of interest

The authors declare that there are no conflicts of interest.
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