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REVIEW PAPERS

A New Family, *Alteromonadaceae* fam. nov., Including Marine Proteobacteria of the Genera *Alteromonas, Pseudoalteromonas, Idiomarina*, and *Colwellia*

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Abstract—The taxonomic positions of the marine genera *Alteromonas*, *Pseudoalteromonas*, *Idiomarina*, and *Colwellia* within the gamma subclass of the class *Proteobacteria* were specified on the basis of their phenotypic, genotypic, and phylogenetic characteristics. Gram-negative aerobic bacteria of the genera *Alteromonas*, *Pseudoalteromonas*, and *Idiomarina* and facultatively anaerobic bacteria of the genus *Colwellia* were found to form a phylogenetic cluster with a 16S rRNA sequence homology of 90% or higher. The characteristics of these genera presented in this paper allow their reliable taxonomic identification. Based on the analysis of our experimental data and analyses available in the literature, we propose to combine the genera *Alteromonas*, *Pseudoalteromonas*, *Idiomarina*, and *Colwellia* into a new family, *Alteromonadaceae* fam. nov., with the type genus *Alteromonas.*

Key words: marine proteobacteria, *Alteromonadaceae* fam. nov., *Alteromonas, Pseudoalteromonas, Idiomarina, Colwellia.*

Gram-negative heterotrophic bacteria are an essential part of marine microbial populations, whose habitats are very diverse and include coastal and open-water areas, deep-sea and hydrothermal basins, and marine sediments. Some of these bacteria are associated with invertebrates, fish, and algae [1, 2]. In recent years, these bacteria have attracted the attention of researchers in relation to the production of various physiologically active compounds [3–5]. Gram-negative marine heterotrophic bacteria belong to the gamma subclass of the class *Proteobacteria* [6]. Many of these bacteria have very similar morphologies, physiologies, and biochemistries, which impedes their identification.

The aim of the present work was to analyze the pheno- and genotypic characteristics and the phylogenetic relationship of the four marine genera, *Alteromonas*, *Pseudoalteromonas*, *Idiomarina*, and *Colwellia*, which belong to the gamma subclass of the class *Proteobacteria.*

The first volume of *Bergey's Manual of Systematic Bacteriology* (1984) describes only one genus of gram-negative aerobic heterotrophic marine bacteria with one polar flagellum (*Alteromonas* Baumann, Baumann, Mandel, and Allen 1972 [7]), whose members are phenotypically similar to pseudomonads, but differ from them in the lower content of G+C in their DNA. This genus originally included the species *A. macleodii*, *A. haloplanktis*, "*A. marinopraesens*" (reclassified into *A. haloplanktis* [8]), *A. communis*, and *A. vaga* [2]. Later, a number of other species were described, namely, *A. rubra, A. citrea, A. luteoviolacea, A. aurantia* [2], *A. espejiana, A. undina* [9], "*Alteromonas putrefaciens*" [10], "*Alteromonas thalassomethanolica*"[11], and *A. nigrifaciens* [12–14]. rRNA–DNA hybridization [15] showed a high level of genetic heterogeneity among the members of the genus and allowed the following rRNA homology clusters to be revealed: (1) the *A. macleodii* cluster; (2) the *A. haloplanktis* cluster, which included the majority of *Alteromonas* species and one species from the genus *Pseudomonas*, "*P. piscicida*" [16, 17]; (3) the *A. putrefaciens* and *A. hanedai* cluster [18]; and (4) the *A. vaga* and *A. communis* cluster, which was classified as a new genus, "*Marinomonas*" [15]. Based on 5S rRNA sequences, the species *A. putrefaciens*, *A. hanedai*, and *A. colwelliana* [19] were combined into a new genus, *Shewanella* [20]. By the early 1990s, the genus *Alteromonas* had been supplemented with several novel species, *A. denitrificans* [21], *A. atlantica*, *A. carrageenovora* [22], *A. tetraodonis* [23], "*A. rava*" [24], *A. fuliginea*, *A. distincta*, *A. elyakovii* [25–27], and "*Alteromonas agarliquefaciens*" [28].

In 1995, based on the analysis of 16S rRNA gene sequences, the genus *Alteromonas* was revised. The revised *Alteromonas* genus contained only one species, *A. macleodii*, while a new genus *Pseudoalteromonas*,

Table 1. Marine bacteria of *Alteromonadaceae* fam. nov.

Strain	Source	Location	Ref.
Alteromonas macleodii ATCC 27126^T	Seawater	Hawaiian Islands	[7]
Alteromonas macleodii subsp. *fijiensis* CNCM I-1627^T	Hydrothermal vents, 2000 m	Fiji Islands	[36]
Alteromonas infernus CNCM I-1628^T	Hydrothermal vents, 2000 m	Guayama reefs	[37]
Pseudoalteromonas distincta KMM 638^T	Sea sponge	Komandor Islands	[25, 33]
Pseudoalteromonas elyakovii KMM 162^T	Mussel *Crenomytilus grayanus*	Sea of Japan	[27, 34]
Pseudoalteromonas haloplanktis subsp. *haloplanktis* IAM 12915^T	Coastal and open oceanic waters; damaged tissues of fish and lobsters; marine sediments	Eastern and Western North American coasts; Indian Ocean; Hawaiian Islands; Sea of Japan	[7]
Pseudoalteromonas haloplanktis subsp. *tetraodonis* IAM^T (ATCC 51193^T)	Surface mucus of the fish *Fugu poecilonotus*	Sea of Japan	[23, 35, 29]
Pseudoalteromonas atlantica ATCC 19262^T	Algal surface	Chiba prefecture coast (Japan)	[22]
Pseudoalteromonas antarctica CECT 4664^T	Marine sediment	Antarctica	[38]
Pseudoalteromonas aurantia ATCC 33046^T	Surface of rocks and algae; marine sediment; coastal waters	French Mediterranean coast	[2]
Pseudoalteromonas carrageenovora ATCC 43555^T	Algal surface	Sea of Japan	[22]
Pseudoalteromonas citrea ATCC 29719^T	Surface of rocks, algae, and fish; marine sediment, coastal waters	French Mediterranean coast; Russian coast of the Sea of Japan	[2, 32]
Pseudoalteromonas denitrificans ATCC 43337^T	Seawater, 90–100 m	West Norwegian coast	[21]
Pseudoalteromonas espejiana ATCC 29659^T	Seawater	Western North American coast, Chile	[9]
Pseudoalteromonas luteoviolacea ATCC 33492^T	Surface of rocks, algae, and animals; marine sediment, coastal waters	French Mediterranean coast; the Sea of Japan	[2]
Pseudoalteromonas nigrifaciens ATCC 19375^T	Seawater; marine animals; type strain was isolated from saline butter	Russian coast of the Sea of Japan	[12, 14]
Pseudoalteromonas rubra ATCC 29570^T	Surface of rocks, algae, and animals; marine sediment, coastal waters	French Mediterranean coast	[2]
Pseudoalteromonas undina ATCC 29660^T	Seawater	Eastern North American coast	[9]
Pseudoalteromonas piscicida ATCC 15057^T	Red tide water; surface of wounded fish	Southwestern coast of Florida	[16]
Pseudoalteromonas bacteriolytica IAM 14595^T	Kelp *Laminaria japonica*	Sea of Japan	[40]
Pseudoalteromonas prydzensis ACAM 620^T	Antarctic ice and water under the ice	Antarctic coast	[39]
Pseudoalteromonas tunicata CCUG 26757^T	Surface of the tunicata *Ciona intestinalis*	Western Sweden coast	[43]
Pseudoalteromonas peptidolytica	Seawater	Sea of Japan	[41]
Idiomarina abyssalis KMM 227^T	Seawater, 4000 m	Pacific Ocean	[44]
Idiomarina zobellii KMM 231^T	Seawater, 5000 m	Pacific Ocean	[44]
Colwellia hadaliensis BNL 1	Seawater, 7410 m	Puerto Rico Trench	[42]
Colwellia psychrerythraea ATCC 27364^T	Seawater, 6000 m; sea ice	Pacific Ocean; Antarctica	[42]
Colwellia psychrotropica ACAM 179^T	Seawater/sea ice	Antarctica	[50]
Colwellia demingiae ACAM 459^T	Seawater and sea ice	Antarctica	[50]
Colwellia hornerae ACAM 607^T	Sea ice	Antarctica	[50]
Colwellia rossensis ACAM 608^T	Sea ice	Antarctica	[50]
Colwellia maris JCM 10085^T	Sea ice	The Sea of Okhotsk coast; Hokkaido	[51]

Table 2. Differentiating characteristics of the genera of *Alteromonadaceae* fam. nov.

	Alteromonas	*Pseudoalteromonas*	*Idiomaria*	*Colwellia*
Cell size, μm	0.7–1.0	0.2–1.5	0.7–0.9	0.5–5.0
Flagellation:				
polar	+	+	+	+
bipolar	–	–	–	–
lateral	–	+	–	–
outer coat	–	–	+/–	
Pigmentation	–	–/+	–	–
Metabolism	Aerobic	Aerobic	Aerobic	Facultatively anaerobic
Growth-supporting NaCl concentrations, %	1–6	1–9	1–15	1–6.5
Maximum growth temperature, °C	35–40	35–40	35	10–25
Minimum growth temperature, °C	10	4–10	4	20
Hydrolysis of:				
chitin	–	V	V	V
agar	–	+	–	–
gelatin, Tween-80	+	+	+	V
Utilization:				
D-glucose, D-fructose	+	+	–	V
D-mannose	–	V	–	–
sucrose	+	V	–	–
cellobiose	+	V	–	–
lactose	+	V	–	–
D-gluconate	+	V	–	ND
fumarate	–	V	–	ND
glycerol	+	–	–	V
Susceptibility to load, μg per disk:				
Kanamycin (30), Benzylpenicillin (10), Ampicillin (10), Oxacillin (20)	+	V	–	
Streptomycin (10)	+	V	V	
Erythromycin (30)	+	+	+	
Gentamicin (10)	+	+	V	
Lincomycin (15)	–	–	–	
Tetracycline (30)	+	+	–	
O/129 (150)	–	–	–	
Major fatty acids	Unbranched	Unbranched	Unbranched	Monounsaturated, saturated, polyunsaturated
Major isoprenoid quinones	Q_8	Q_8	ND	Q_8
G+C content of DNA, mol %	44–47	37–50	48–50	35–46

Note: "ND" stands for "no data available." "V" denotes a variable reaction.

which included the rRNA homology group II species, was formed [29]. It should be noted that the species "*Pseudomonas marinoglutinosa*," which was first described more than half a century ago [30], has recently been reported as *Pseudoalteromonas marinoglutinosa* [31]. According to our DNA–DNA hybridization measurements and phylogenetic studies, the species name *Alteromonas fuliginea* should be used as a junior synonym of the species name *Pseudoalteromonas citrea* [32], while the species *A. distincta* and *A. elyakovii* should be transferred to the genus *Pseudoalteromonas* [33, 34].

The species *A. tetraodonis* [23] has recently been reclassified into *A. haloplanktis* subsp. *tetraodonis*

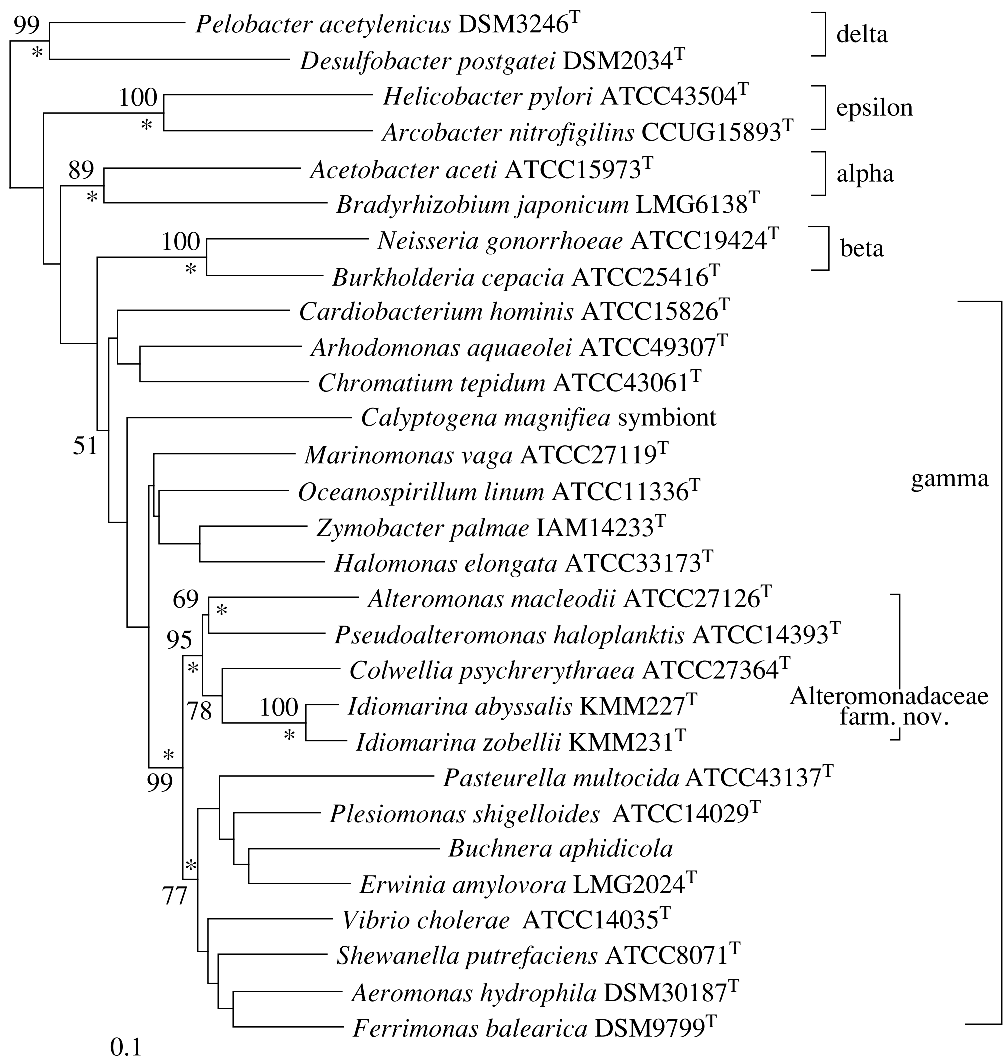
[35]. However, our studies show that the taxonomic status of *A. tetraodonis* should be *Pseudoalteromonas tetraodonis* comb. nov. In recent years, several novel species of marine *Proteobacteria* had been described, such as *"A. infernus"* and *"A. macleodii* subsp. *fijiensis,"* which were isolated from deep-sea hydrothermal basins [36, 37]; *Pseudoalteromonas antarctica* [38] and *Pseudoalteromonas prydzensis* [39], which were isolated from antarctic coastal waters; *Pseudoalteromonas bacteriolytica* [40], which was isolated from the damaged kelp *Laminaria japonica* taken from the Sea of Japan; and *Pseudoalteromonas peptidolytica* [41], which was isolated from seawater. The facultatively anaerobic species *Pseudoalteromonas tunicata*, which is similar to bacteria of the genus *Colwellia* [42], was isolated from an ascidian residing in coastal waters of western Sweden [43].

This year, Ivanova *et al.* [44] described a new genus of aerobic marine proteobacteria, *Idiomarina*, which included two species, *I. abyssalis* and *I. zobellii*, which were isolated from seawater samples taken from depths of 4000 and 5000 m, respectively. The species were phenotypically close to bacteria of the genera *Alteromonas*, *Pseudoalteromonas*, and *Marinomonas*, but differed from them in their cellular fatty acid profiles and inability to use carbohydrates as the sole sources of carbon and energy. The species were distinguished by their characteristic morphology: *I. zobellii* cells were fimbriated, while *I. abyssalis* cells were enclosed in sheaths. The sources and habitats of marine bacteria of the family *Alteromonadaceae* are summarized in Table 1. We did not include the new genus *Glaciecola* [45] into this family: *Glaciecola* is phylogenetically very close to the genus *Alteromonas* and its assignment to *Alteromonadaceae* would be questionable.

Species of the genera *Alteromonas*, *Pseudoalteromonas*, and *Idiomarina* are heterotrophic, gram-negative, rod-shaped, obligately marine bacteria that require sodium cations for growth. Bacteria of these genera have one usually uncoated polar flagellum. However, some strains of the species *P. luteoviolacea*, all strains of *P. denitrificans*, and the type strain of *P. tunicata* have coated flagella; the flagella of the type strain of *P. distincta* are lateral; bacteria of the species *I. zobellii* are fimbriated; and some species are encapsulated. With the exception of *P. tunicata*, all species of the three genera under discussion are aerobic, mesophilic, and are able to grow under normal atmospheric pressure. All species can hydrolyze gelatin and Tween-80 and utilize glucose and fructose (except for those of the genus *Idiomarina*). Many species cannot utilize mannose. All the species of the genera *Alteromonas*, *Pseudoalteromonas*, and *Idiomarina* are resistant to O/129 (except for *P. tunicata*) at a load of 150 μg per disk and to lincomycin, but are sensitive to erythromycin. The genera can be distinguished by the following phenotypic and chemotaxonomic characteristics. Bacteria of the genus *Alteromonas* can grow at a temperature of 10°C and in the presence of NaCl at concentrations varying from 1 to 6%, and they can utilize a variety of carbohydrates and are unable to hydrolyze chitin and agar. Bacteria of the genus *Pseudoalteromonas* can grow at NaCl concentrations from 1 to 9%; their ability to hydrolyze high molecular weight compounds is species-specific. The identification of these bacteria without invoking DNA–DNA hybridization data is intricate. Bacteria of the genus *Idiomarina* can grow at NaCl

Table 3. Cellular fatty acids of *Alteromonadaceae* fam. nov. (data from publications [44–46, 50, 51])

Fatty acid	*Alteromonas macleodii* ATCC 27126^T	Species of		
		Pseudo-alteromonas	*Idiomarina*	*Colwellia*
11 : 0-3OH	0.2	0–0.4	0	0
12 : 0-3OH	0.4	0.4–1.97	0	0
12 : 0	1.2	0.6–2.0	0.2	0
11 : 0	0	0	0.1	0
12 : 1	0	0–1.1	0	0
*i*13 : 0	0.2	0.1–0.2	1.0	0
13 : 0	0.4	0	0.1	0
13 : 1	0	0.1–0.5	0	0
–*i*14 : 0	0.2	0–0.2	0.1	0
14 : 0	3.5	1.1–3.9	0.6	0.8–8.0
14 : 1 (*n*-7)	0.9	0.4–1.4	0.1–0.2	2.0–9.3
***i*15 : 0**	**0**	**0.1–0.2**	**33.7–40.6**	**0**
*a*15 : 0	0.5	0.1–0.8	0.6	0
15 : 0	3.2	2.2–8.5	0	1.7–14.3
15 : 1 (*n*-6)	0.2	0–0.8	0.1–0.3	0–1.1
15 : 1 (*n*-8)	2.3	0.6–7.3	1.1–1.3	1.9–20.3
*i*16 : 0	0.8	0.2–2.12	0	0–10.3
16 : 0	**23.8**	**14.0–33.8**	**4.6–6.3**	**0**
16 : 1 (*n*-5)	0	0–0.3	0	0
16 : 1 (*n*-7)	**37.1**	**35–49.1**	**7.0–8.3**	**15.4–43.4**
16 : 1 (*n*-9)	0	0	0.5–0.6	1.8–11.8
***i*17 : 0**	**0**	**0–0.5**	**11.9–12.5**	**0**
*a*17 : 0	0.6	0–1.0	0.2	0
17 : 0	4.5	0.5–5.5	0.5–0.6	0–2.5
17 : 1 (*n*-6)	0.3	0–0.8	1.5–3.4	0–1.9
17 : 1 (*n*-8)	7.0	1.6–12.3	0.8–1.1	0–5.6
*i*18 : 0	0.4	0–0.2	0	0
18 : 0	1.0	0.5–1.9	0.8–1.8	0.1–2.4
18 : 1 (*n*-7)	9.4	1.3–5.7	5.9–6.7	0.3–4.2
18 : 1 (*n*-9)	0.3	0.2–0.6	0.9–1.4	0–1.4
18 : 1 (*n*-11)	0.6	0–0.8	0	0
19 : 1	0.2	0.03	0	0
20 : 5 (*n*-3)	0	0	0	0–1.5
22 : 6 (*n*-3)	0	0	0	1.7–4.1



Phylogenetic tree showing the position of *Alteromonadaceae* fam. nov. in the class *Proteobacteria*. The asterisks mark the phylogenetic clusters that were revealed by different methods [47–49]. Bootstrap values are given to confirm the topology of the dendrogram. The accession numbers of the nucleotide sequences used for the tree construction are as follows: X70955 (*Pelobacter acetylenicus*), M26633 (*Desulfobacter postgatei*), Z25737 (*Helicobacter pylori*), Ll4627 (*Arcobacter nitrofigilis*), D30768 (*Acetobacter aceti*), S46916 (*Bradyrhizobium japonicum*), M86915 (*Neisseria gonorrhoeae*), L28675 (*Burkholderia cepacia*), M35014 (*Cardiobacterium hominis*), AJ000726 (*Arhodomonas aquaeolei*), M59150 (*Chromatium tepidum*), AF035730 (*Calyptogena magnifica*), X67025 (*Marinomonas vaga*), M22365 (*Oceanospirillum linum*), D14555 (*Zymobacter palmae*), M93355 (*Halomonas elongata*), X82145 (*Alteromonas macleodii*), X67024 (*Pseudoalteromonas haloplanktis*), AF0011375 (*Colwellia psychrerythraea*), AF0552740 (*Idiomarina abyssalis*), AF052741 (*Idiomarina zobellii*), E05329 (*Pasteurella multocida*), AB025970 (*Plesiomonas shigelloides*), Z19056 (*Buchnera aphidicola*), Z96088 (*Erwinia amylovora*), X76337 (*Vibrio cholerae*), X82123 (*Shewanella putrefaciens*), X74676 (*Aeromonas hydrophila*), and X93021 (*Ferrimonas balearica*).

concentrations from 1 to 15%, and they are psychrotolerant, nonpigmented, and unable to utilize carbohydrates (Table 2).

The cellular fatty acid profile of the bacteria under study is a valuable taxonomic marker [44, 46]. In the type strain *Alteromonas macleodii* ATCC 27126^T, the specific fatty acids are 14 : 0, 17 : 0, 17 : 1(*n*-8), and 18 : 1(*n*-7); and the major fatty acids are 16 : 0 and 16 : 0(*n*-7) (23.8 and 37.1%, respectively). In species of the genus *Pseudoalteromonas*, the profile of specific fatty acids is different and the major fatty acids are present in greater amounts than in ATCC 27126^T (the only exception is 18 : 1(*n*-7), whose amount is lower). In bacteria of the genus *Idiomarina*, the major fatty acids are *i*15 : 0 and *i*17 : 0 (40.6 and 12.5%, respectively), whereas the amounts of 16 : 0, 16 : 1(*n*-7), and 18:1(*n*-7) are considerably lower (6–8%) than in ATCC 27126^T (Table 3).

Phylogenetic analyses performed as described in [47–49] showed that the genera *Alteromonas*, *Pseudoalteromonas*, and *Idiomarina* represent a distinct cluster within the gamma subclass of the class *Proteobacteria*, with a 16S rRNA homology level of 96.9%, which corresponds to 45 differences per 1462 nucleotides sequenced (see figure). The genus *Col-*

wellia [42], which originally included two facultatively anaerobic bacteria (*C. psychrerythraea* and *C. hadaliensis*), turned out to be the closest phylogenetic neighbor of the genus *Idiomarina* with a 16S rRNA homology level of 90.1–90.5% (see figure). The first strains of this genus were isolated from the water samples taken in the Mariana Trench and near the coast of the United States. The type strain of the species *C. psychrerythraea* was found to be an obligate barophile. In 1998, Bowman *et al.* described four novel psychrophilic species of this genus and new strains of the species *C. psychrerythraea* [50]. None of these antarctic isolates was barophilic and all of them synthesized docosahexaenoic acid (22 : 6ω3) in amounts of up to 8% of the total cellular content of fatty acids (Table 3). Bowman *et al.* believe that the specific low-temperature habitats of these bacteria made them capable of synthesizing polyunsaturated fatty acids, which favor the integrity of cell membranes at low temperatures under high hydrostatic pressures. Table 2 also presents some other differentiating characteristics of the four genera of the family *Alteromonadaceae*. It should be noted that the species *Colwellia maris* was originally assigned to the genus *Vibrio* [51].

Thus, the genera *Alteromonas*, *Pseudoalteromonas*, *Idiomarina*, and *Colwellia* comprise a monophyletic evolutionary line (this inference has a 95–100% confidence level) [44]. The 16S rRNA similarity values of these genera are 90% or higher. According to the criterion of Fox *et al.* [52], such close genetic relatedness of the genera makes it possible to combine them into one family. Inasmuch as the genus *Alteromonas* was the first to be described, and the type species of this genus, *A. macleodii*, was extensively studied in many laboratories, we propose to name this family *Alteromonadaceae*, with the type genus *Alteromonas*. A description of the genus *Alteromonas* can be found in the book *The Prokaryotes* [2] and in [29]. The latter also describes the genus *Pseudoalteromonas*. The genera *Idiomarina* and *Colwellia* are described in [44] and [42], respectively.

Description of *Alteromonadaceae* fam. nov. *Alteromonadaceae* (Al. te. ro. mo. na. da’ce. ae. M. L. fem. n. *Alteromonas*, the genus of gram-negative, aerobic, marine bacteria, the type genus of the family; suffix *aceae*, denoting family; M. L. fem. pl. n. *Alteromonadaceae*, the *Alteromonas* family). Gram-negative, rod-shaped bacteria. Motile by single flagellum (sometimes coated), some of the species have lateral flagella, fimbriae, or outer sheath-like structures. Do not form endospores or microcysts. Some species produce capsules. Require Na^+ cations for growth, some strains are capable of growing in media containing 15% NaCl. Chemoorganotrophs. Oxygen is used as the electron acceptor. Aerobic or facultatively anaerobic. Usually do not denitrify. Arginine dihydrolase is absent. Most species utilize glucose and fructose and do not utilize mannose. In most species, the major isoprenoid quinone is Q_8. The major fatty acids are *i*15 : 0, 16 : 0, and 16 : 1(*n*-7). The G+C content of DNA ranges from 35 to 50 mol %. The family members were isolated from coastal, open, and deep-sea waters; sediments; marine invertebrates; fish; algae; and temperate and Antarctic marine environments. The family is a member of the gamma subclass of the *Proteobacteria* in accordance with the nucleotide sequence characteristics (sensu C. Woese [53]). The family comprises four genera, *Alteromonas*, *Pseudoalteromonas*, *Idiomarina*, and *Colwellia*. The type genus is *Alteromonas* Baumann, Baumann, Mandel, Allen 1972, emend. Gauthier, Gauthier, Christen 1995.

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