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Phylogenetic Analysis of the Genera *Alteromonas*, *Shewanella*, and *Moritella* Using Genes Coding for Small-Subunit rRNA Sequences and Division of the Genus *Alteromonas* into Two Genera, *Alteromonas* (Emended) and *Pseudoalteromonas* gen. nov., and Proposal of Twelve New Species Combinations

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Small-subunit ribosomal DNA sequences were determined for 17 strains belonging to the genera *Alteromonas*, *Shewanella*, *Vibrio*, and *Pseudomonas*, and these sequences were analyzed by phylogenetic methods. The resulting data confirmed the existence of the genera *Shewanella* and *Moritella*, but suggested that the genus *Alteromonas* should be split into two genera. We propose that a new genus, the genus *Pseudoalteromonas*, should be created to accommodate 11 species that were previously *Alteromonas* species, including *Pseudoalteromonas atlantica* comb. nov., *Pseudoalteromonas aurantia* comb. nov., *Pseudoalteromonas carrageenovora* comb. nov., *Pseudoalteromonas citrea* comb. nov., *Pseudoalteromonas denitrificans* comb. nov., *Pseudoalteromonas espejiana* comb. nov., *Pseudoalteromonas haloplanktis* comb. nov. (with two subspecies, *Pseudoalteromonas haloplanktis* subsp. *haloplanktis* comb. nov. and *Pseudoalteromonas haloplanktis* subsp. *tetraodonis* comb. nov.), *Pseudoalteromonas luteoviolacea* comb. nov., *Pseudoalteromonas nigrifaciens* comb. nov., *Pseudoalteromonas rubra* comb. nov., and *Pseudoalteromonas undina* comb. nov., and one species that previously was placed in the genus *Pseudomonas*, *Pseudoalteromonas piscicida* comb. nov. We propose that *P. haloplanktis* (type strain, ATCC 14393) should be the type species of the genus *Pseudoalteromonas*. At this time the emended genus *Alteromonas* is restricted to a single species, *Alteromonas macleodii*.

Originally, the genus *Alteromonas* (4) consisted of four gram-negative, aerobic, nonpigmented, polarly flagellated species of marine bacteria, *Alteromonas macleodii* (the type species of the genus), *Alteromonas vaga*, *Alteromonas communis*, and *Alteromonas marinopraesens*. The name of the last species was later changed to *Alteromonas haloplanktis* (31). Subsequently, the genus *Alteromonas* was often used as a refuge for gram-negative, heterotrophic, aerobic bacteria with single polar flagella which differed from members of the genus *Pseudomonas* mainly in DNA G+C content (38 to 50 mol%, compared with 55 to 64 mol% for *Pseudomonas* spp.). As a result, 14 species were assigned to the genus *Alteromonas* (Table 1). In addition, on the basis of its nonfermentative metabolism, flagellar arrangement, and quinone composition, it was suggested that *Pseudomonas piscicida* (8) should be included in the genus *Alteromonas* (1, 6).

rRNA-DNA hybridization experiments (39) revealed that there was a high level of heterogeneity in the genus *Alteromonas* and that the following three rRNA groups could be distinguished; (i) *Alteromonas macleodii*, (ii) an *Alteromonas haloplanktis* cluster containing most *Alteromonas* species and *Pseudomonas piscicida*, and (iii) a group containing *Alteromonas putrefaciens* and *Alteromonas hanedai*. *Alteromonas vaga* and *Alteromonas communis*, which formed a distinct rRNA branch, were transferred to a new genus, the genus *Marinomonas*. Three species, *Alteromonas putrefaciens*, *Alteromonas hanedai*, and *Alteromonas colwelliana*, were subsequently reassigned to the new genus *Shewanella* on the basis of the results of a 5S rRNA sequence analysis (10, 28), and *Alteromonas tetraodonis* was reclassified as *Alteromonas haloplanktis* (2). Finally, the very low levels of genomic DNA homology between *Alteromonas macleodii* and all of the other species of the genus confirmed that these organisms were not related (2).

In this study we determined the nearly complete sequences of small-subunit ribosomal genes of 17 strains belonging to the genus *Alteromonas* and related genera (the genera *Shewanella*, *Vibrio* and *Pseudomonas*) to characterize more precisely the intra- and inter-generic relationships discussed above. These sequences were aligned by comparing them with other eubacterial small-subunit ribosomal DNA (rDNA) sequences, and phylogenetic relationships were determined by using different phylogenetic methods (the maximum-likelihood, maximum-parsimony, and neighbor-joining methods) to check the reliability of each topology. Each topology was then examined by performing a bootstrap analysis to assess its robustness.

MATERIALS AND METHODS

Bacterial strains and growth conditions. The strains used in this study are listed in Table 2. The bacteria were grown at 22°C on marine agar 2216 (Difco Laboratories, Detroit, Mich.) or were stored frozen at −70°C in marine broth (Difco) supplemented with 20% (vol/vol) glycerol.

DNA amplification and sequencing. The method used to prepare bacterial DNA for PCR was derived from the method of Sritharan and Barker (35). Colonies grown on marine agar were suspended in 200 μl of lysis mixture (10 mM Tris [pH 8.0], 1 mM EDTA, 1% Triton X-100) and boiled for 5 min. Following a single chloroform extraction, 5 μl of supernatant was used to amplify small-subunit rDNA as previously described (32). The amplification reaction produced 1.5-kb DNA molecules. After purification on a 1% low-melting-point agarose gel, the PCR products were directly sequenced as described previously (32). Thus, we determined a small-subunit rDNA sequence corresponding to positions 29 to 1,425 of the *Escherichia coli* sequence for each representative of the genera *Alteromonas* and *Shewanella*, as well as *Pseudomonas piscicida* and *Vibrio marinus*. The sequence of one *Alteromonas haloplanktis* strain (strain ATCC 14393[T]) [T = type strain]) has been published previously (21).

Phylogenetic analysis. Sequences were aligned and studied by using a set of programs developed in our laboratory (available from R. Christen). In this

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TABLE 1. Bacterial strains which previously have been assigned to the genus *Alteromonas* or considered related to this genus

First description		Last reassignment		Reference strain[a]
Name[b]	Reference	Name	Reference	
Alteromonas macleodii	4			ATCC 27126^T
Vibrio haloplanktis	45	*Alteromonas haloplanktis*	31	ATCC 14393^T
Alteromonas communis	4	*Marinomonas communis*	39	ATCC 27118^T
Alteromonas vaga	4	*Marinomonas vaga*	39	ATCC 27119^T
Alteromonas aurantia	19			ATCC 33046^T
Alteromonas citrea	17			ATCC 29719^T
Alteromonas colwelliana	40	*Shewanella colwelliana*	10	ATCC 39565^T
Alteromonas denitrificans	12			ATCC 43337^T
Alteromonas espejiana	9			ATCC 29659^T
Alteromonas hanedai	23	*Shewanella hanedai*	28	ATCC 33224^T
Alteromonas luteoviolacea	18			ATCC 33492^T
Alteromonas rubra	16			ATCC 29570^T
Alteromonas tetraodonis	34	*Alteromonas haloplanktis*	2	ATCC 51193^T
Alteromonas undina	9			ATCC 29660^T
Pseudomonas atlantica	43	*Alteromonas atlantica*	3	ATCC 19262^T
Pseudomonas carrageenovora	44	*Alteromonas carrageenovora*	3	ATCC 43555^T
Pseudomonas nigrifaciens	41	*Alteromonas nigrifaciens*	5	ATCC 19375^T
Pseudomonas putrefaciens	11	*Alteromonas putrefaciens*	26	ATCC 8071^T
		Shewanella putrefaciens	28	ATCC 8071^T
Flavobacterium piscicida	7	*Pseudomonas piscicida*	8	ATCC 15057^T
Vibrio marinus	14	*Moritella marinus*	36	ATCC 15381^T

[a] ATCC, American Type Culture Collection, Rockville, Md.

[b] The strains are divided into the following three groups: (i) the four original strains, (ii) strains which have been designated *Alteromonas* strain, and (iii) strains which have been considered related to the genus *Alteromonas*.

analysis we used the sequences determined in this study and small-subunit rDNA sequences of the following bacteria which were obtained from the EMBL: *Aeromonas allosaccharophila*, *Aeromonas caviae*, *Alteromonas haloplanktis*, *Arsenophonus nasoniae*, *E. coli*, *Haemophilus ducreyi*, *Hafnia alvei*, *Marinobacter hydrocarbonoclasticus*, *Marinomonas vaga*, *Pasteurella multocida*, *Photobacterium angustum*, *Vibrio nereis*, and an unnamed bacterium. The sequence of the unnamed bacterium was obtained by coupling PCR with molecular cloning; therefore, this sequence is the sequence of a bacterium that has not been isolated. The sequence of *Ruminobacter amylophilus* was obtained from the study of Martens et al. (30). A wild strain of *Pseudomonas piscicida* used in the phylogenetic analyses was isolated from water from the sea near Brest, France. In addition, the small-subunit rDNA sequence of *Pseudomonas piscicida* ATCC 15057 was also obtained. The two *Pseudomonas piscicida* sequences were identical except for some undetermined nucleotides in the wild strain sequence. The following sequence domains used to construct the dendrogram shown in for Fig. 1 were conserved regions in the small-subunit rDNA sequences: positions 42 to 69, 100 to 135, 141 to 180, 241 to 454, 479 to 832, 862 to 1131, 1140 to 1252, and 1275 to 1426 (*E. coli* small-subunit rDNA sequence numbering). To construct the dendrogram shown in Fig. 2, we used positions 41 to 74, 93 to 196, 215 to 840, 862 to 1132, and 1137 to 1437.

Phylogenetic analyses were performed by using three different methods. A neighbor-joining method (33) was used in our preliminary analysis. The resulting topologies were then investigated by using maximum-likelihood and maximum-parsimony methods. For the maximum-likelihood analyses we used the fdnaml program of G. J. Olsen (University of Illinois, Urbana) and a Hewlett-Packard model 700 workstation, and for the maximum-parsimony analyses we used the PAUP program for the Macintosh (37). In the latter case, the analyses were performed by using the branch-and-bound option or the heuristic option when the branch-and-bound option was too time consuming. The robustness of each topology was evaluated by the maximum-parsimony method through 100 bootstrap replications (heuristic search). Trees were drawn by using the njplot program for the Macintosh developed by M. Gouy (URA 243 CNRS, Université Claude Bernard, Lyon, France), which allowed us to transform a formal tree representation (Newick's format) into MacDraw drawings.

Nucleotide sequence accession numbers. The EMBL accession numbers for the rDNA sequences determined in this study are shown in Table 2. The EMBL accession numbers for the other small-subunit rDNA sequences used in this study are as follows: *Aeromonas allosaccharophila*, S39232; *Aeromonas caviae*, X74674; *Alteromonas haloplanktis*, X67024; *Arsenophonus nasoniae*, M90801; *E. coli*, J01859; *Haemophilus ducreyi*, M63900; *Hafnia alvei*, M59155; *Marinobacter hydrocarbonoclasticus*, X67022; *Marinomonas vaga*, X67025; *Pasteurella multocida*, M35018; *Photobacterium angustum*, X74685; *V. nereis*, X74716; and unnamed bacterium, Z25522.

RESULTS AND DISCUSSION

All of the sequences studied were aligned by comparing them with a database containing about 3,000 aligned eubacterial small-subunit rDNA sequences. The results of a broad phylogenetic analysis clearly confirmed that all of the species which we studied belonged to the gamma subgroup of the phylum *Proteobacteria* of the *Eubacteria* (data not shown) and, more precisely, to the well-defined robust monophyletic taxon also designated the gamma 3 subgroup (15, 32, 42). The phylogenetic positions of the genera *Alteromonas* and *Shewanella* within the gamma 3 subgroup are shown in Fig. 1, an unrooted tree in which the results of a neighbor-joining analysis (topology shown in Fig. 1) are combined with the results obtained by maximum-likelihood and maximum-parsimony methods. We included representatives of all of the major taxa previously identified as members of the gamma 3 clade (the families *Vibrionaceae*, *Enterobacteriaceae*, *Pasteurellaceae*, and *Aeromonadaceae*) in these analyses.

The results of all of the analyses confirmed that the three *Shewanella* species form an independent clade that can be recognized as a genus (Fig. 1). All of these species formed a robust monophyletic taxon (as determined by all methods and 81% of the bootstrap replications) that branched deeply and did not cluster with any other sequence. *Shewanella hanedai* and *Shewanella benthica* were closely related as determined by all three methods, a result supported by 92% of the bootstrap replications. Therefore, our data confirmed the results of previous rRNA-DNA hybridization experiments (39) and 5S rRNA (28) and partial small-subunit rRNA sequence (24) analyses.

Figure 1 shows that the sequence of *V. marinus* did not cluster with the sequence of any other member of the *Vibrionaceae* available at this time (32). The separate position of *V. marinus* has also been observed in 5S rRNA sequence studies

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TABLE 2. Bacterial strains for which complete or nearly complete small-subunit rDNA sequences are available

Taxon	Source[a]	Strain	Other designation	EMBL nucleotide sequence accession no.[b]
Alteromonas macleodii	IAM	IAM 12920^T	ATCC27126^T	X82145
Pseudoalteromonas atlantica	IAM	IAM 12927^T	ATCC19262^T	X82134
Pseudoalteromonas aurantia	ATCC	ATCC 33046^T		X82135
Pseudoalteromonas carrageenovora	IAM	IAM 12662^T	ATCC43555^T	X82136
Pseudoalteromonas citrea	NCIMB	NCIMB 1889^T	ATCC29719^T	X82137
Pseudoalteromonas denitrificans	ATCC	ATCC 43337^T		X82138
Pseudoalteromonas espejiana	NCIMB	NCIMB 2127^T	ATCC29659^T	X82143
Pseudoalteromonas haloplanktis subsp. *haloplanktis*	ATCC	ATCC 14393^T		X67024
Pseudoalteromonas haloplanktis subsp. *tetraodonis*	IAM	IAM14160	ATCC 51193	X82139
Pseudoalteromonas luteoviolacea	NCIMB	MCIMB 1893^T	ATCC33492^T	X82144
Pseudoalteromonas nigrifaciens	NCIMB	MCIMB 8614^T	ATCC19375^T	X82146
Pseudoalteromonas piscicida	Wild			X82141
	ATCC	ATCC 15057^T		X82215
Pseudoalteromonas rubra	ATCC	ATCC 29570^T		X82147
Pseudoalteromonas undina	NCIMB	NCIMB 2128^T	ATCC29660^T	X82140
Shewanella benthica	ATCC	ATCC 43992^T		X82131
Shewanella hanedai	CIP	CIP 103207^T	ATCC33224^T	X82132
Shewanella putrefaciens	ATCC	ATCC 8071^T		X82133
Moritella marinus	NCIMB	NCIMB 1144^T	ATCC15381^T	X82134

[a] Bacteria were obtained from the following collections: ATCC, American Type Culture Collection, Rockville, Md.; IAM, Institute of Applied Microbiology, Tokyo, Japan; NCIMB, National Collection of Industrial and Marine Bacteria, Aberdeen, Scotland; CIP, Collection of Institut Pasteur, Paris, France.
[b] EMBL, European Molecular Biology Laboratory, Cambridge, United Kingdom.

(27, 28), partial small-subunit rRNA sequence studies (24), and DNA-DNA relatedness studies (36). Therefore, it has been proposed that *V. marinus* should be renamed *Moritella marinus* (36). Our complete *V. marinus* sequence matched a previously published partial sequence (24) but not the sequence determined by Ruimy et al. (32). As discussed by Ruimy et al., their sequence is probably not the sequence of *V. marinus*. On the basis of its true sequence, *V. marinus* branched deeply and did not cluster with any other genus, despite a slight association with the genus *Shewanella* and the "*Alteromonas*" cluster. The deep branching and the lack of association with any other genus confirmed that this bacterium should be placed in a separate genus. Therefore, we support the proposal to create the genus *Moritella*, which contains the single species *Moritella marinus* (36).

Alteromonas macleodii clearly did not belong to the monophyletic taxon which included all of the other "*Alteromonas*" species (Fig. 1). *Alteromonas macleodii* branched deeply and did not cluster with any other organism whose sequence was available. All of the other "*Alteromonas*" species, *Pseudomonas piscicida*, and the unnamed bacterium whose nucleotide sequence accession number was Z25522 formed a robust monophyletic taxon that was identified by all three methods and was supported by 98% of the bootstrap replications (100% when *Moritella* [*Vibrio*] *marinus* was excluded from the analysis [data not shown]). All of our molecular data showed that *Alteromonas macleodii* was distinct from all other "*Alteromonas*" species (2, 39) and suggested that there should be two genera for these species. Unfortunately, no other species that clusters with *Alteromonas macleodii* has been found; however, there is ample evidence that *Alteromonas macleodii* represents a distinct genus, although it differs phenotypically from the other "*Alteromonas*" species only in the range of substrates used (the range of substrates used by *Alteromonas macleodii* is greater than the range of substrates used by other "*Alteromonas*" species; it is able to use D-ribose, L-rhamnose, turanose, salicin, gluconate, DL-glycerate, L-valine, and L-ornithine as sole sources of carbon and energy). As *Alteromonas macleodii* is the type species of the genus, and Rule 39b of the *International Code of Nomenclature of Bacteria* (25) stipulates that the generic name must be retained for the type species, we propose that the genus *Pseudoalteromonas* gen. nov. should be created to accommodate the 12 other "*Alteromonas*" species.

Small-subunit rDNA sequences analyses revealed that there is an unambiguous affiliation between *Pseudomonas piscicida* and the new genus *Pseudoalteromonas*, which is consistent with rRNA cistron similarity data (39) and the isoprenoid quinone compositions of the organisms (1). Finally, because of its nonfermentative metabolism and flagellar arrangement, *Pseudomonas piscicida* appeared to resemble the majority of the species of this genus phenotypically (6). Because this bacterium undoubtedly belongs to the new genus *Pseudoalteromonas*, the generic name *Pseudomonas* should not be used for it any longer. Thus, it is appropriate to rename this bacterium *Pseudoalteromonas piscicida* gen. nov., comb. nov.

Within the new genus *Pseudoalteromonas*, phylogenetic relationships were difficult to resolve when distant outgroups were included, as in Fig. 1. Nevertheless, we distinguished (Fig. 1) two deeply branched species (the bacterium whose nucleotide sequence accession number was Z25522 and *Pseudoalteromonas denitrificans*) that were clearly outgroups with respect to all of the other species (as determined by all three methods and 73% of the bootstrap replications). A more detailed phylogenetic analysis of the *Pseudoalteromonas* cluster was performed by using *Pseudoalteromonas denitrificans* as the outgroup (Fig. 2). The new genus *Pseudoalteromonas* could be divided into the following four monophyletic taxa, which were identified by all three phylogenetic methods: (i) *Pseudoalteromonas denitrificans*; (ii) two pigmented species, *Pseudoalteromonas citrea* and *Pseudoalteromonas aurantia* (100% of the bootstrap values); (iii) three other pigmented species, *Pseudoalteromonas piscicida*, *Pseudoalteromonas rubra*, and *Pseudoalteromonas luteoviolacea* (98% of the bootstrap values); and (iv) all nonpigmented *Pseudoalteromonas* species (84% of the bootstrap values). The last group included closely related species, and the phylogenetic relationships of these taxa were difficult to determine on the basis of small-subunit rDNA sequences. Within the nonpigmented *Pseudoalteromo-*

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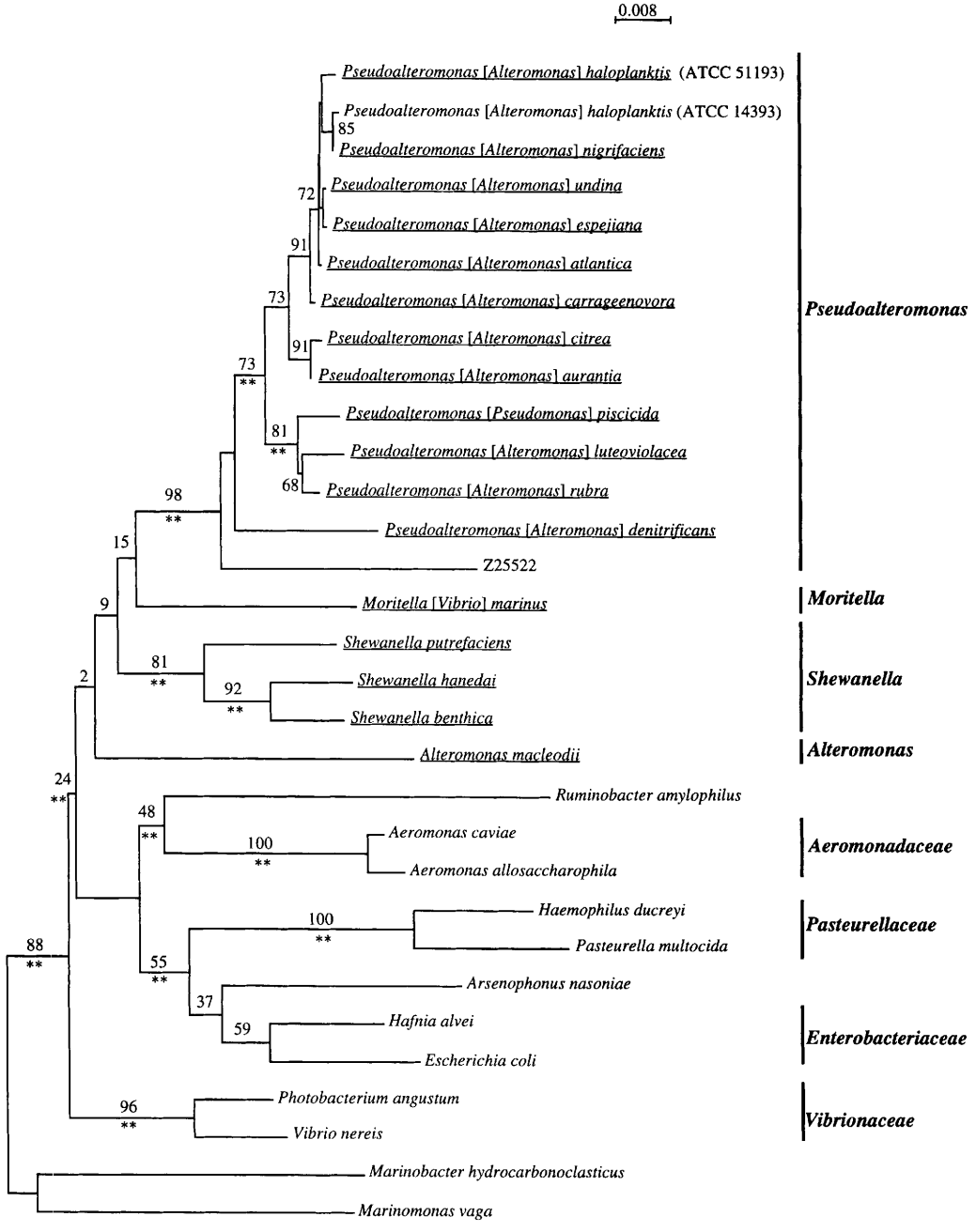

FIG. 1. Phylogenetic positions of *Alteromonas*, *Moritella*, and *Shewanella* species within the gamma 3 subgroup of the phylum *Proteobacteria*. An unrooted phylogenetic tree was obtained by performing a neighbor-joining analysis; branches that were significantly positive at a level of $P < 0.01$ as determined by a maximum-likelihood method are indicated by two asterisks. There are numbers above the branches that were also identified by the maximum-parsimony method (most parsimonious tree), and these numbers indicate how the branches were supported by the bootstrap analysis results. The sequences of the underlined species were determined in this study. *Marinobacter hydrocarbonoclasticus* and *Marinomonas vaga* were used as outgroups for the gamma 3 subgroup of the *Proteobacteria*.

nas species group, DNA-DNA hybridization experiments revealed that *Pseudoalteromonas haloplanktis* ATCC 14393^T and *Pseudoalteromonas haloplanktis* subsp. *tetraodonis* ATCC 51193 exhibited levels of relatedness ranging from 82 to 84% (2). Considering that there were a number of differences between the small-subunit rDNA sequences of these organisms (14 differences in 1,429 nucleotides), that biochemical analyses revealed a number of traits which can be used to differentiate these taxa (Table 3), and that their level of genomic DNA relatedness is less than 85%, we propose that they should be placed in different subspecies. Thus, we propose that strain ATCC 51193 is a *Pseudoalteromonas haloplanktis* subsp. *tetraodonis* comb. nov. strain and that strain ATCC 14393^T is a *Pseudoalteromonas haloplanktis* subsp. *haloplanktis* comb. nov. strain.

We propose that *Pseudoalteromonas haloplanktis* (type strain, ATCC 14393) should be the type species of the genus *Pseudoalteromonas* because (i) it was the first species described in this new genus (31), (ii) it has been used more widely than any other species for laboratory studies of marine bacteria (13,

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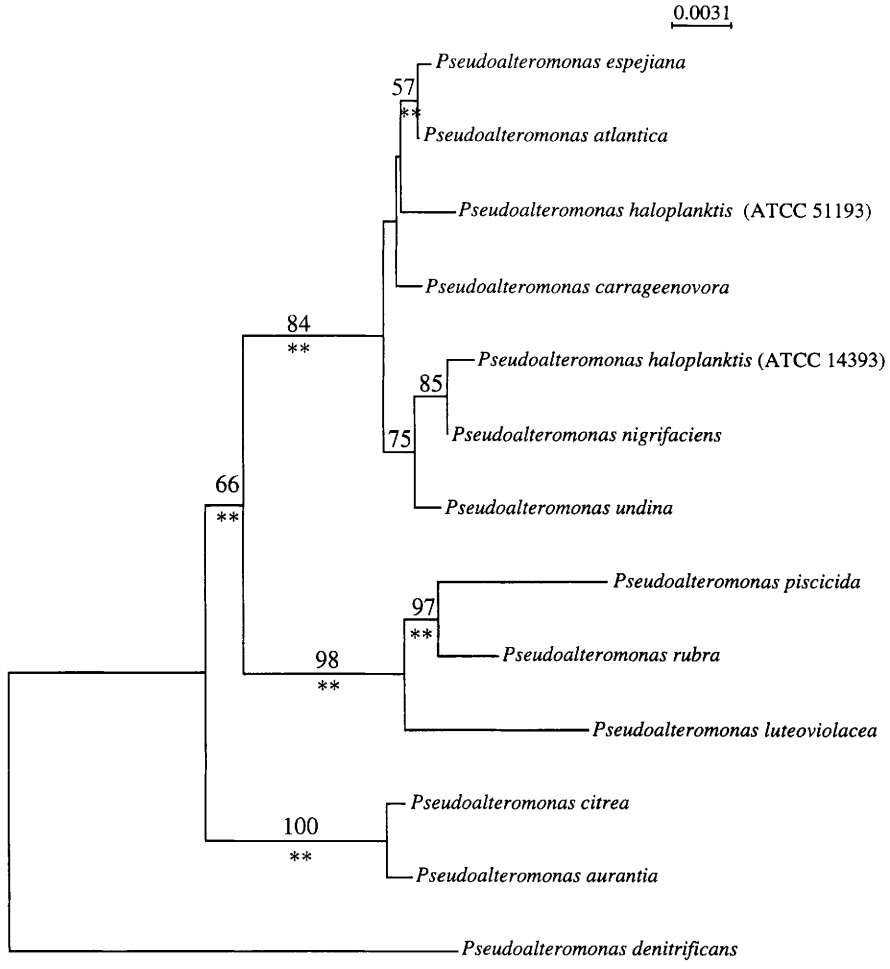

FIG. 2. Phylogenetic relationships among *Pseudoalteromonas* species. See the legend to Fig. 1.

29, 38), (iii) it is nonpigmented (most likely an ancestral characteristic of this genus), and (iv) it is centrally located in molecular phylogenies.

Finally, the bacterium whose sequence has been deposited under accession number Z25522 in the EMBL data bank, which has not been isolated in culture yet, clustered with the new genus *Pseudoalteromonas*, but a name cannot be proposed since the phenotype of this organism is not known.

Description of the genus *Pseudoalteromonas* gen. nov. *Pseudoalteromonas* (Pseu. do. al. te. ro. mon' as. Gr. adj. *pseudes*, false; L.n. *Alteromonas*, genus of gram-negative, aerobic, marine bacteria; L.n. *Pseudoalteromonas*, false *Alteromonas*). The phenotypic description of the genus *Pseudoalteromonas* is the same as the description published previously in *Bergey's Manual of Systematic Bacteriology* (6) and *The Prokaryotes* (20) for the genus *Alteromonas*, except for traits that are specific to *Alteromonas macleodii* (see below). The cells of all *Pseudoalteromonas* species are gram-negative, non-spore-forming, straight or curved rods that are 0.2 to 1.5 by 1.8 to 3 μm. The cells of most species are motile by means of single unsheathed polar flagella; *Pseudoalteromonas luteoviolacea* and *Pseudoalteromonas denitrificans* have sheathed flagella. Not luminescent. Several species produce pigments. Strictly aerobic. Chemoorganotrophs with respiratory but not fermentative metabolism. Oxidase positive. Catalase activity is generally weak and irregular. All species grow at 20°C. Only one species (*Pseudoalteromonas denitrificans*) is capable of denitrification. None of the strains has a constitutive arginine dihydrolase system. Strains do not accumulate poly-β-hydroxybutyrate. All species require a seawater base for growth. Many strains require organic growth factors. The following combination of properties is found in all 12 known species: positive for gelatinase, lipase, lecithinase, and DNase activities and utilization of D-glucose as a sole source of carbon; and negative for utilization of D-ribose, L-rhamnose, turanose, salicin, D-gluconate, glucuronate, DL-glycerate, erythritol, sorbitol, *meso*-inositol, adonitol, L-valine, L-ornithine, and *m*-hydroxybenzoate. The G+C content of the DNA ranges from 37 to 50 mol%.

The type species is *Pseudoalteromonas haloplanktis*; the type strain of this species is strain ATCC 14393 (= strain 215 of Baumann et al. [4]).

In addition to the type species, the genus comprises *Pseudoalteromonas atlantica* (3), *Pseudoalteromonas aurantia* (19), *Pseudoalteromonas carrageenovora* (3), *Pseudoalteromonas citrea* (17), *Pseudoalteromonas denitrificans* (12), *Pseudoalteromonas espejiana* (9), *Pseudoalteromonas luteoviolacea* (18), *Pseudoalteromonas nigrifaciens* (5), *Pseudoalteromonas piscicida* (7), *Pseudoalteromonas rubra* (16), and *Pseudoalteromonas undina* (9).

Description of *Pseudoalteromonas haloplanktis* subsp. *haloplanktis* (ZoBell and Upham) comb. nov. The description of *Pseudoalteromonas haloplanktis* subsp. *haloplanktis* comb. nov.

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TABLE 3. Characteristics that differentiate *Pseudoalteromonas haloplanktis* subsp. *haloplanktis* and *Pseudoalteromonas haloplanktis* subsp. *tetraodonis*

Characteristic[a]	*Pseudoalteromonas haloplanktis* subsp. *haloplanktis*	*Pseudoalteromonas haloplanktis* subsp. *tetraodonis*
Melaninlike dark pigment	+	−
Urease activity	+	−
Litmus milk coagulation	−	+
Assimilation of:		
Heptanoate	+	−
DL-3-Hydroxybutyrate	−	+
D-Malate	−	+
L-Lysine	−	+
L-Arginine	−	+
D-Glucosamine	−	+
N-Acetyl-D-glucosamine	−	+
Fructose	+	−
Cellobiose	+	−
Sucrose	−	+
Threalose	−	+

[a] Data from reference 3.

is identical to the description given by ZoBell and Upham (45). The type strain is strain ATCC 14393.

Description of *Pseudoalteromonas haloplanktis* subsp. *tetraodonis* (Simidu, Kita-Tsukamoto, Yasumoto, and Yotsu) comb. nov. The description of *Pseudoalteromonas haloplanktis* subsp. *tetraodonis* comb. nov. is identical to the description given by Simidu et al. (34). The type strain is strain ATCC 51193.

Description of *Pseudoalteromonas atlantica* (Akagawa-Matsushita, Matsuo, Koga, and Yamasato) comb. nov. The description of *Pseudoalteromonas atlantica* comb. nov. is identical to the description given by Akagawa-Matsushita et al. (3). The type strain is strain ATCC 19262.

Description of *Pseudoalteromonas aurantia* (Gauthier and Breittmayer) comb. nov. The description of *Pseudoalteromonas aurantia* comb. nov. is identical to the description given by Gauthier and Breittmayer (19). The type strain is strain ATCC 33046.

Description of *Pseudoalteromonas carrageenovora* (Akagawa-Matsushita, Matsuo, Koga, and Yamasato) comb. nov. The description of *Pseudoalteromonas carrageenovora* comb. nov. is identical to the description given by Akagawa-Matsushita et al. (3). The type strain is strain ATCC 43555.

Description of *Pseudoalteromonas citrea* (Gauthier) comb. nov. The description of *Pseudoalteromonas citrea* comb. nov. is identical to the description given by Gauthier (17). The type strain is strain ATCC 29719.

Description of *Pseudoalteromonas denitrificans* (Enger, Nygaard, Solberg, Schei, Nielsen, and Dundas) comb. nov. The description of *Pseudoalteromonas denitrificans* comb. nov. is identical to the description given by Enger et al. (12). The type strain is strain ATCC 43337.

Description of *Pseudoalteromonas espejiana* (Chan, Baumann, Garza, and Baumann) comb. nov. The description of *Pseudoalteromonas espejiana* comb. nov. is identical to the description given by Chan et al. (9). The type strain is strain ATCC 29659.

Description of *Pseudoalteromonas luteoviolacea* (Gauthier) comb. nov. The description of *Pseudoalteromonas luteoviolacea* comb. nov. is identical to the description given by Gauthier (18). The type strain is strain ATCC 33492.

Description of *Pseudoalteromonas nigrifaciens* (White) comb. nov. The description of *Pseudoalteromonas nigrifaciens* comb. nov. is identical to the description given by White (41). The type strain is strain ATCC 19375.

Description of *Pseudoalteromonas rubra* (Gauthier) comb. nov. The description of *Pseudoalteromonas rubra* comb. nov. is identical to the description given by Gauthier (16). The type strain is strain ATCC 29570.

Description of *Pseudoalteromonas undina* (Chan, Baumann, Garza, and Baumann) comb. nov. The description of *Pseudoalteromonas undina* comb. nov. is identical to the description given by Chan et al. (9). The type strain is strain ATCC 29660.

Description of *Pseudoalteromonas piscicida* (Bein) comb. nov. The description of *Pseudoalteromonas piscicida* comb. nov. is identical to the description given by Bein (7). The type strain is strain ATCC 15057.

Emended description of the genus *Alteromonas*. Gram-negative, non-spore-forming straight rods that are 0.7 to 1 μm in diameter and 2 to 3 μm long. Motile by means of a single unsheathed polar flagellum. Not luminescent and not pigmented. Strictly aerobic. Chemoorganotroph with respiratory but not fermentative metabolism. Oxidase positive and catalase negative. Growth occurs at 20 to 35°C but not at 4°C. Does not denitrify. No constitutive arginine dihydrolase system. Does not accumulate poly-β-hydroxybutyrate from the monomer β-hydroxybutyrate. Requires a seawater base for growth, but not organic growth factors. The G+C content of the DNA is 44 to 47 mol%.

The type species is *Alteromonas macleodii*, whose type strain is strain ATCC 27126 (= strain 107 of Baumann et al. [4]).

The characteristics of the type species are the same as the characteristics of the genus.

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