Proposal to Recognize the Family Aeromonadaceae fam. nov.

R. R. COLWELL,* M. T. MACDONELL,† AND J. DE LEY²

Department of Microbiology, The University of Maryland, College Park, Maryland 207421 and Laboratorium voor Microbiologie en Microbiele Genetica, Faculteit der Wetenschappen, Rijksuniversiteit, B-9000 Gent, Belgium²

The genus Aeromonas is currently allocated, primarily on the basis of phenotypic expression, to the eubacterial family Vibrionaceae. However, a sizeable collection of molecular genetic evidence, including 16S ribosomal ribonucleic acid catalog, 5S ribosomal ribonucleic acid sequence, and ribosomal ribonucleic acid-deoxyribonucleic acid hybridization data, indicates that Aeromonas spp. possess an evolutionary history sufficiently different from that of the Vibrionaceae to warrant removal from this family. The phylogenetic locus (i.e., intermediate between the families Enterobacteriaceae and Vibrionaceae) and phylogenetic depth of the genus Aeromonas suggest that Aeromonas spp. represent a discrete family of eubacteria, for which the name Aeromonadaceae fam. nov. is proposed.

Kluyver and van Niel (10) proposed the genus Aeromonas to accommodate enteric bacterium-like microorganisms which were associated with freshwater aquatic environments and were motile by means of polar flagella (14). The partitioning of this group of bacteria was intended to portray phylogenetic relationships. The identification of species comprising the genus Aeromonas has varied significantly since the creation of the genus in 1936. As a consequence, the taxonomic history of the genus Aeromonas has been one of confusion and controversy (7, 8, 13--22), involving not only definition of the species assigned to the genus but also the taxonomic locus of the genus with respect to the families Enterobacteriaceae and Vibrionaceae as they are presently defined (2, 10). A major problem faced in defining the precise taxonomic position of Aeromonas hydrophila and related species sharing a similar evolutionary history is that these species possess phenotypic properties defined, a priori, to be characteristic of each of two distinct eubacterial families, the Vibrionaceae and the Enterobacteriaceae.

<table>
<thead>
<tr>
<th>TABLE 1. Family Vibrionaceae*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genus</td>
</tr>
<tr>
<td>Vibrio</td>
</tr>
<tr>
<td>Photobacterium</td>
</tr>
<tr>
<td>Listonella</td>
</tr>
<tr>
<td>Shewanella</td>
</tr>
<tr>
<td>Plesiomonas*</td>
</tr>
<tr>
<td>Aeromonas*</td>
</tr>
</tbody>
</table>

* The following is a general description of the family Vibrionaceae: gram-negative straight or curved rods; motile by polar flagella; do not form endospores or microcrysts; chemoorganotrophic and facultatively anaerobic; capable of respiratory and fermentative metabolism; oxygen is a universal electron acceptor; do not denitrify; most are oxidase positive; all utilize D-glucose as a sole source of carbon and energy; most require 2 to 3% NaCl or seawater for optimum growth; primarily associated with aquatic habitats; several species are pathogenic to humans, fish, eels, and frogs; DNA base composition, 38 to 63 mol% guanine plus cytosine.

† Removal from the family Vibrionaceae has been recommended (13).

‡ We recommend elevation to the family level.

Substantial molecular genetic evidence now exists which suggests that species currently assigned to the genus Aeromonas (e.g., A. hydrophila, A. salmonicida, A. sobria, A. caviae, and A. media) possess a phylogenetic history sufficiently different from that of the enteric species from the Vibrionaceae (Table 1) and elevation to the level of family. Support for such a change in the taxonomy of Aeromonas can be found in the results of deoxyribonucleic acid (DNA)-ribosomal ribonucleic acid (rRNA) competition studies (2); such data for species of the genera Vibrio (Beneckea) and Aeromonas and the family Enterobacteriaceae support our conclusion that Vibrio spp., Aeromonas spp. and enteric species share the relationships shown in Fig. 1, which is based on rRNA-DNA hybridiza-

* Corresponding author.

† Present address: Center of Marine Biotechnology, The University of Maryland, College Park, MD 20742.
species of the families Enterobacteriaceae and Vibrionaceae that minor differences in secondary structures are implied (11). Secondary structure differences alone corroborate significant separation in the evolutionary histories of {Aeromonas} spp. and both the Vibrionaceae and the Enterobacteriaceae. The determination of rRNA cistron similarities among numerous named strains and type strains by DNA-rRNA hybridization revealed the existence of at least five large rRNA superfamilies sensu De Ley (4) among the gram-negative bacteria (4-6, 25). Figure 3 shows the relatedness of the main large groups in superfamily I. All strains of {Aeromonas} constitute a branch which is approximately equidistant from the Entero bacteriaceae and the Vibrionaceae. These data demonstrate that the present genus {Aeromonas} deserves to be elevated to family level.

Results of DNA-DNA hybridization among strains of the genera {Aeromonas} and {Vibrio} (24) indicate a very low level of relatedness between {Aeromonas} and Vibrio species, between which the average relative binding ratio is no greater than that observed between such distantly related strains as {Pseudomonas aeruginosa} and Vibrio spp. (i.e., <10%). Furthermore, studies in which comparisons were made among the immunologic distances of glutamine synthetases and superoxide dismutases for species of the genera Vibrio, {Aeromonas}, and {Photobacterium} and species of the {Enterobacteriaceae} indicated that {Aeromonas} spp. are approximately equidistant from both Vibrio and enteric species (1).

On a basis of the information described above, we suggest that sufficient evidence exists to justify the conclusion that the species of the genus {Aeromonas} represent a phylogenetically distinct family of eubacteria. Therefore, we propose creation of the family {Aeromonadaceae} for these and similar species, including new species to be described elsewhere (J. D. Deming, M. T. MacDonell, W. S. Straube, and R. R. Colwell, manuscript in preparation).

Description of {Aeromonadaceae} fam. nov. {Aeromonas} (ae.ro.mo.na.da'ce.ae. M.L. fem. n. {Aeromonas} type genus of family; suffix -aceae to denote family; M.L. fem. pl. n. {Aeromonadaceae} {Aeromonas} family). Gram-negative straight or curved rods. Motile by means of polar flagella. Do not form endospores or microcysts. Chemoorganotrophs and facultative anaerobes capable of respira-

---

**FIG. 1.** Dendrogram showing relationships among species of the families Enterobacteriaceae and Vibrionaceae and the genus {Aeromonas}. The relationships shown are based on DNA-rRNA competition data (2).

**FIG. 2.** Evolutionary trees indicating relationships among species of the families Enterobacteriaceae and Vibrionaceae and the genus {Aeromonas}, based on rRNA homologies. (A) Phylogenetic relationships among prokaryotic taxa based on 16S rRNA catalogs. Adapted from reference 23. Note the relationships among the enteric bacteria, vibrios, and aeromonads, suggesting that {Aeromonas} spp. share a more recent common ancestor with species of the Enterobacteriaceae than with species of the Vibrionaceae. Abbreviations: Aq., Aquaspirillum; P., Pseudomonas; R., Rhodospirillum; X., Xanthomonas; S-dep, sulfur-dependent group. (B) Evolutionary tree depicting phylogenetic relationships among the enteric bacteria, vibrios, photobacteria, and aeromonads, based on SS rRNA sequence analyses. The tree was derived from evolutionary distance coefficients (9) by using the difference matrix clustering program KITSCH (PHYLIP phylogeny inference package; J. Felsenstein, University of Washington). For a detailed discussion of the taxonomy of the family Vibrionaceae as indicated by comparative sequence analysis of SS rRNAs, see reference 13. Abbreviations: A., {Aeromonas} (except {A. aerogenes}, {Aerobacter aerogenes}); E., {Escherichia}; P., {Photobacterium} (except {P. mirabilis}, {Proteus mirabilis}; and {P. shigelloides}, {Plesiomonas shigelloides}); S. marcescens, {Serratia marcescens}; S. typhimurium, {Salmonella typhimurium}; V., Vibrio; Y., {Yersinia}. Note that {Listonella} species appear as Vibrio.
A. Enterobacteriaceae
- Vibrio
- Photobacterium
  - P. fluorescens
  - P. aeruginosa
  - P. testosteroni
  - P. cepacia
- P. diminuta
- Rhizobium
- Ag. itersonii
- Chromatium
- Legionella
- Nitrosomonas
- Nitrobacter
- R. rubrum
- Cytophaga
- Bacteroides
- Cyanobacteria
- Methanococcus
- Sulfolobus
- Chlorobium
- Archaebacteria

B. Progenote
- A. aerogenes
- P. mirabilis
- S. typhimurium
- P. shigelloides
- S. marcescens
- A. salmonicida
- A. hydrophila
- A. media
- V. psychrophoerythrus
- BNL-1
- V. proteolyticus
- V. harveyi
- V. carchariae
- V. diazotrophicus
- V. parahaemolyticus
- V. metschnikovii
- V. mimicus
- V. cincinnatiensis
- V. gazogenes
- V. anguillarum
- V. fluvialis
- V. pelagius
- V. damselae
- V. fluvialis
- V. fluvialis
- V. fluvialis
- V. fluvialis
- V. fluvialis
- V. fluvialis
- V. fluvialis
- V. fluvialis
- V. fluvialis
- V. fluvialis
tory and fermentative metabolism. Oxygen is a universal electron acceptor. Reduce nitrate. Do not denitrify. Most are oxidase positive. Most utilize D-glucose as a sole or principal source of carbon and energy. Most utilize ammonium salts as sole sources of nitrogen. A few have relatively simple organic growth factor requirements. Primarily aquatic inhabitants found in freshwater and in association with aquatic animals; also found in sewage. Psychrophilic and mesophilic; motile and nonmotile strains are included. Several species are pathogenic for humans, fish, eels, and frogs, as well as other vertebrates and invertebrates. The guanine-plus-cytosine content of the DNA ranges from 40 to 63 mol%.

The type genus is *Aeromonas* Kluyver and van Niel, 1936, 398.

The genus *Aeromonas* (Ae.ro.mo'nas. Gr. n. aer, air, gas; Gr. n. monas, unit, monad; M.L. fem. n. Aeromonas gas-producing monad) is described in reference 16.

Support for this research was provided in part by National Science Foundation grant BSR-82-08418, by Office of Naval Research Contract N000-14-81-K0638, and by Agency for International Development Grant DPE-5542-GSS-4060-00. Support provided by the University of Maryland Sea Grant College is also appreciated. J.D.L. is indebted to the Fonds voor Geneeskundig Wetenschappelijk Onderzoek (Belgium) for several research and personnel grants.

We gratefully acknowledge P. R. Brayton for assistance with preparation of figures.

**LITERATURE CITED**


