Genotypic Relationships and Taxonomic Localization of Unclassified *Pseudomonas* and *Pseudomonas*-Like Strains by Deoxyribonucleic Acid:Ribosomal Ribonucleic Acid Hybridizations

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The deoxyribonucleic acid (DNA):ribosomal ribonucleic acid (rRNA) hybridization technique was used to reveal the relationships and taxonomic positions of an additional 83 strains belonging to 43 saprophytic or pathogenic *Pseudomonas* species and 29 named and unnamed *Pseudomonas*-like strains. The DNA:rRNA hybrids were characterized by the following two parameters: (i) the temperature at which one-half of the hybrid was eluted and (ii) the percentage of rRNA binding (the amount of rRNA bound per 100 µg of filter-fixed DNA). We also used, for a limited number of strains, numerical analysis of carbon assimilation tests to delineate the finer taxonomic relationships of organisms. Of the 83 strains examined, 78 could be definitely assigned either to an rRNA branch or to an rRNA superfamily within the *Proteobacteria*. Only 25 of our strains belong in the genus *Pseudomonas sensu stricto* (our *Pseudomonas fluorescens* rRNA branch). In general, about two-thirds of the named *Pseudomonas* species have been misclassified and are distributed over at least seven genera all through the *Proteobacteria*. These organisms need to be reclassified and generically renamed according to their phylogenetic relationships. However, more detailed phenotypic and genotypic studies are necessary before definite nomenclatural proposals can be made. A comprehensive list of the phylogenetic affiliations of the *Pseudomonas* species is included.

From the original creation of *Pseudomonas* Migula 1894 until now, this genus has been a dumping ground for incompletely described, aerobic, polarly flagellated, gram-negative, rodlike bacteria. In the past and even today organisms isolated from a heterogeneous variety of ecological niches were and still are classified without sufficient grounds as new *Pseudomonas* species. One of the reasons for this situation is the incomplete generic definition.

In the United States, the Berkeley group has reported in several papers (42, 43, 48) on the taxonomy of the genus *Pseudomonas*. The several hundred strains included in the important study of these workers involved only a relatively small number of species. Their new generic definition and subdivision of *Pseudomonas* was reflected in *Bergey's Manual of Determinative Bacteriology*, 8th ed. (20). In an important reduction in the number of *Pseudomonas* species, more than 90% of the clinical, phytopathological, and saprophytic pseudomonads were relegated to four addenda to the genus *Pseudomonas* and were thus only marginally retained in this genus (20). Most of these organisms have no clear taxonomic status because their names were not retained on the Approved Lists of Bacterial Names (38, 46) nor were they on Validation Lists 17 to 23 (24-30). In *Bergey's Manual of Systematic Bacteriology*, Palleroni (41) listed 62 of these species in Section V of the genus *Pseudomonas*, although their natural relationships with other taxa are still largely unknown.

We have shown in the past (11-15, 21, 45, 51, 54, 55) that the deoxyribonucleic acid (DNA):ribosomal ribonucleic acid (rRNA) hybridization technique used by workers in our group (9) is a powerful tool for establishing bacteriological

relationships at the levels of subgenus to order. On the whole, our results agree well with those delineated by oligonucleotide cataloging and sequencing of 16S rRNA (47, 59). In our first paper on *Pseudomonas* (14), we confirmed in this genus *sensu* Doudoroff and Palleroni (20) five different rRNA branches. These branches correspond extremely well with the Palleroni rRNA homology groups (41, 43), although the latter were derived from a very small number of strains. However, we proved that these groups are genotypically too far removed from each other to be united in a single genus; furthermore, we established their exact relationship with other gram-negative genera (14). In our opinion the real genus *Pseudomonas* has to be limited to our *Pseudomonas fluorescens* rRNA branch, which contains section I of Palleroni (41) and many other species. In our second study (15) we localized by using DNA:rRNA hybridization most of the unclassified phytopathogenic pseudomonads in one of our *Pseudomonas* rRNA branches.

The present paper is an extension of our previous phylogenetic studies on *Pseudomonas* (14, 15, 17) and deals with the taxonomic locations of saprophytic species and a few clinical named *Pseudomonas* species from addenda I, III, and IV in *Bergey's Manual of Determinative Bacteriology*, 8th ed. (20), or section V in *Bergey's Manual of Systematic Bacteriology* (41) or both in our rRNA framework (Fig. 1). The taxonomic positions of several unnamed or misnamed bacteria which turned out to belong to one of our *Pseudomonas* rRNA branches are also discussed.

MATERIALS AND METHODS

Bacterial strains. The strains which we used, along with their present taxonomic status and former taxonomic status,

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FIG. 1. Locations of named and misnamed *Pseudomonas* species in a condensed and incomplete summary of rRNA cistron similarities among gram-negative taxa, expressed as $T_{m(e)}$ values of DNA:rRNA hybrids. ×, Misnamed species. The species involved are compiled in Tables 1 through 3. The Roman numerals indicate the rRNA superfamilies; the dashed lines indicate unpublished data. The dendrogram shows the extreme heterogeneity of the present presumed genus *Pseudomonas* and therefore also the present incorrect taxonomic status of the majority of the *Pseudomonas* species. In our opinion the authentic genus *Pseudomonas* should be limited to at most the *Pseudomonas fluorescens* rRNA branch.

TABLE 1. Reference organisms used for the preparation of ^{14}C - or ^3H -labeled 23S or 16S rRNA: nomenclatural status and origin

Name ^a	Status in Bergey's Manual of Determinative Bacteriology, 8th ed. ^b	Status in Bergey's Manual of Systematic Bacteriology, vol. 1 ^c	Strain no. as received ^d	LMG no. ^d
<i>Acetobacter aceti</i> *	<i>Acetobacter</i>	<i>Acetobacter</i>	NCIB 8621t1 ^T	1261t1 ^T
<i>Acinetobacter calcoaceticus</i> *	<i>Acinetobacter</i>	<i>Acinetobacter</i>	ATCC 23055t1 ^T	1046t1 ^T
<i>Aeromonas hydrophila</i> *	<i>Aeromonas</i>	<i>Aeromonas</i>	ATCC 7966 ^T	2844 ^T
<i>Agrobacterium tumefaciens</i> *	<i>Agrobacterium</i>	<i>Agrobacterium</i>	ICPB TT111	196
[<i>Alcaligenes</i>] <i>eutrophus</i> *	<i>Alcaligenes</i>	<i>Alcaligenes incertae sedis</i>	ATCC 17697 ^T	1199 ^T
<i>Alcaligenes faecalis</i> *	<i>Alcaligenes</i>	<i>Alcaligenes</i>	NCIB 8156 ^T	1229 ^T
[<i>Alcaligenes</i>] <i>paradoxus</i> *	<i>Alcaligenes</i>	<i>Alcaligenes incertae sedis</i>	ATCC 17713t1 ^T	1797t1 ^T
<i>Alteromonas haloplanktis</i> *		<i>Alteromonas</i>	ATCC 14393 ^T	2852 ^T
<i>Alteromonas macleodii</i> *		<i>Alteromonas</i>	ATCC 27126 ^T	2843 ^T
<i>Deleya aquamarina</i> ** ^c	<i>Alcaligenes</i>	<i>Alcaligenes</i>	NCMB 557t1 (= ATCC 14400)	2853t1
<i>Escherichia coli</i> *	<i>Escherichia</i>	<i>Escherichia</i>	B	2093
<i>Flavobacterium aquatile</i> *	<i>Flavobacterium</i>	<i>Flavobacterium</i>	NCIB 8694 ^T	2952 ^T
[<i>Flavobacterium</i>] <i>capsulatum</i> *	<i>Flavobacterium</i>	<i>Flavobacterium</i>	DSM 30196 ^T	2830 ^T
<i>Marinomonas vaga</i> ‡		<i>Alteromonas</i>	ATCC 27119 ^T	2845 ^T
<i>Oceanospirillum linum</i> *	<i>Spirillum</i>	<i>Oceanospirillum</i>	ATCC 11336 ^T	5214 ^T
<i>Pasteurella multocida</i> *	<i>Pasteurella</i>	<i>Pasteurella</i>	HIM 688-7 ^T (= NCTC 10322 ^T)	2851 ^T
[<i>Pseudomonas</i>] <i>acidovorans</i> *	<i>Pseudomonas</i> section III	<i>Pseudomonas</i> section III	14 (Stanier) ^T (= ATCC 15668 ^T)	1226 ^T
<i>Pseudomonas fluorescens</i> *	<i>Pseudomonas</i> section I	<i>Pseudomonas</i> section I	MMCA 40 ^T (= ATCC 13525 ^T)	1794 ^T
[<i>Pseudomonas</i>] <i>solanacearum</i> *	<i>Pseudomonas</i> section III	<i>Pseudomonas</i> section II	NCPPB 325 ^T	2299 ^T
<i>Rhizobium loti</i> ‡		<i>Rhizobium loti</i>	NZP 2037	6123
<i>Shewanella putrefaciens</i> ‡	<i>Pseudomonas</i> addendum III	<i>Alteromonas</i>	ATCC 8071t1 ^T	2268t1 ^T
<i>Vibrio parahaemolyticus</i> *	<i>Vibrio</i>	<i>Vibrio</i>	ATCC 17802 ^T	2850 ^T
<i>Xanthomonas campestris</i> *	<i>Xanthomonas</i>	<i>Xanthomonas</i>	NCPPB 528 ^T	568 ^T

^a *, Name on Approved Lists of Bacterial Names (38, 46); †, name validly published in the International Journal of Systematic Bacteriology since 1 January 1985; ‡, name on a validation list in the International Journal of Systematic Bacteriology after 1 January 1985 (24–30).

^b See reference 6.

^c See reference 34.

^d For abbreviations see Table 2, footnote d.

^e We believe that strain NCMB 557t1 (formerly [*Alcaligenes*] *aquamarinus*) belongs in the genus *Deleya* because it is completely integrated into this genus on the basis of DNA:rRNA data (32) and phenotypic data (unpublished data).

TABLE 2. Organisms tested: nomenclatural status, origin, and growth media

Name ^a	Status in <i>Pseudomonas</i> in Bergey's Manual of Determinative Bacteriology, 8th ed. ^b	Status in Bergey's Manual of Systematic Bacteriology, vol. 1 ^c	Strain no. as received ^d	LMG no. ^d	Growth medium
[<i>Pseudomonas</i>] <i>aminovorans</i> *	Addendum I	<i>Pseudomonas</i> section V	NCTC 10684 ^T (= ATCC 23314 ^T)	2122 ^T	Z5
"[<i>Pseudomonas</i>] <i>atlantica</i> "	Addendum III	<i>Alteromonas</i> incertae sedis	CIP 59.31	2139	Z19
"[<i>Pseudomonas</i>] <i>atlantica</i> "	Addendum III	<i>Alteromonas</i> incertae sedis	ATCC 19262	2140	Z19
"[<i>Pseudomonas</i>] <i>azotocolligans</i> "	Addendum I		ATCC 12417	2142	A
"[<i>Pseudomonas</i>] <i>bathycetes</i> "			ATCC 23597	2145	Z11
[<i>Pseudomonas</i>] <i>beijerinckii</i> *	Addendum I	<i>Pseudomonas</i> section V	ATCC 19372 ^T	2148 ^T	T
[<i>Pseudomonas</i>] <i>boreopolis</i> *	Addendum I	<i>Pseudomonas</i> section V	NRRL B-550 ^T (= NCIB 9401 ^T)	979 ^T	Z5
"[<i>Pseudomonas</i>] <i>carrageenovora</i> "			NCMB 302	2154	Z21
"[<i>Pseudomonas</i>] <i>caudata</i> "	Addendum II		NCMB 1499	2149	Z21
"[<i>Pseudomonas</i>] <i>coenobios</i> "	Addendum I		ATCC 14402	2169	Z11
"[<i>Pseudomonas</i>] <i>creosotensis</i> "	Addendum I		ATCC 14582	2174	Z11
"[<i>Pseudomonas</i>] <i>cruciviae</i> "	Addendum III		NCTC 10687	2175	
"[<i>Pseudomonas</i>] <i>denitrificans</i> "	Addendum I		CCEB 525	2179	B
[<i>Pseudomonas</i>] <i>doudoroffii</i> *		<i>Pseudomonas</i> section V	ATCC 27123 ^T	2180 ^T	Z11
[<i>Pseudomonas</i>] <i>echinoides</i> *	Addendum I	<i>Pseudomonas</i> section V	ATCC 14820 ^T	2181 ^T	Z5
[<i>Pseudomonas</i>] <i>elongata</i> *	Addendum I	<i>Pseudomonas</i> section V	ATCC 10144 ^T	2182 ^T	Z11
[<i>Pseudomonas</i>] <i>flectens</i> *	Addendum I		NCPPB 539 ^T	2187 ^T	
<i>Pseudomonas fragi</i> *	Addendum I	<i>Pseudomonas</i> section V	CCEB 387 ^T (= ATCC 4973 ^T)	2191 ^T	Z3
[<i>Pseudomonas</i>] <i>huttiensis</i> *	Addendum I	<i>Pseudomonas</i> section V	ATCC 14670 ^T	2199 ^T	Z5
<i>Deleya</i> (<i>Pseudomonas</i>) <i>marina</i> †		<i>Pseudomonas</i> section V	ATCC 25374 ^T	2217 ^T	Z11
<i>Deleya</i> (<i>Pseudomonas</i>) <i>marina</i> †		<i>Pseudomonas</i> section V	ATCC 27129t1	2218t1	Z11
"[<i>Pseudomonas</i>] <i>marinoglutinosa</i> "	Addendum II		NCMB 1770t1	2219t1	Z11
"[<i>Pseudomonas</i>] <i>marinoglutinosa</i> "	Addendum II		NCMB 1770t2	2219t2	Z11
"[<i>Pseudomonas</i>] <i>membranula</i> "	Addendum II		NCMB 562	2221	Z11
<i>Pseudomonas mucidolens</i> *	Addendum I	<i>Pseudomonas</i> section V	NCTC 8068 ^T (= ATCC 4685 ^T)	2223 ^T	B
"[<i>Pseudomonas</i>] <i>myxogenes</i> "	Addendum I		NRRL B-2086	2224	Z5
[<i>Pseudomonas</i>] <i>nautica</i> *		<i>Pseudomonas</i> section V	ATCC 27132 ^T	2226 ^T	Z11
"[<i>Pseudomonas</i>] <i>nigrifaciens</i> "	Addendum I	<i>Alteromonas</i> incertae sedis	NCTC 10691	2227	Z11
"[<i>Pseudomonas</i>] <i>nigrifaciens</i> "	Addendum I	<i>Alteromonas</i> incertae sedis	ATCC 25013t1	2228t1	Z20
"[<i>Pseudomonas</i>] <i>nigrifaciens</i> "	Addendum I	<i>Alteromonas</i> incertae sedis	ATCC 25013t2	2228t2	Z20
<i>Pseudomonas oleovorans</i> *	Addendum I	<i>Pseudomonas</i> section V	MMCA 4 ^T (= ATCC 8062 ^T)	2229 ^T	Z5
"[<i>Pseudomonas</i>] <i>oxalaticus</i> "	Addendum I		NCIB 8642	2235	B
[<i>Pseudomonas</i>] <i>paucimobilis</i> *		<i>Pseudomonas</i> section V	NCTC 11030 ^T	1227 ^T	Z5
[<i>Pseudomonas</i>] <i>paucimobilis</i> *		<i>Pseudomonas</i> section V	NCTC 11031	2239	Z5
[<i>Pseudomonas</i>] <i>paucimobilis</i> *		<i>Pseudomonas</i> section V	NCTC 11032	2240	Z5
"[<i>Pseudomonas</i>] <i>pavonacea</i> "	Addendum I		CCEB 533	2241	Z5
"[<i>Pseudomonas</i>] <i>pavonacea</i> "	Addendum I		NCIB 9395	2242	T
<i>Pseudomonas stutzeri</i> * (formerly <i>Pseudomonas perfectomarina</i> †)	Addendum I		ATCC 14405	2243	Z11
"[<i>Pseudomonas</i>] <i>perlurida</i> "	Addendum I		ATCC 490	2244	B
[<i>Pseudomonas</i>] <i>phenazinium</i> *			NCIB 11027 ^T	2247 ^T	Z5
[<i>Pseudomonas</i>] <i>pictorum</i> *	Addendum I	<i>Pseudomonas</i> section V	CCM 284 ^T (= ATCC 23328 ^T)	981 ^T	Z5
"[<i>Pseudomonas</i>] <i>piscicida</i> "	Addendum III	<i>Alteromonas</i> incertae sedis	NCMB 848	2248	Z11
"[<i>Pseudomonas</i>] <i>piscicida</i> "	Addendum III	<i>Alteromonas</i> incertae sedis	NCMB 2037t1	2249t1	Z11
"[<i>Pseudomonas</i>] <i>piscicida</i> "	Addendum III	<i>Alteromonas</i> incertae sedis	NCMB 2037t2	2249t2	Z11
"[<i>Pseudomonas</i>] <i>piscicida</i> "	Addendum III	<i>Alteromonas</i> incertae sedis	ATCC 15251	2251	Z11
"[<i>Pseudomonas</i>] <i>reptilivora</i> "	Addendum I		NRRL B-963	2273	Z5
<i>Pseudomonas resinovorans</i> *	Addendum I	<i>Pseudomonas</i> section V	ATCC 14235 ^T	2274 ^T	Z5
"[<i>Pseudomonas</i>] <i>riboflavina</i> "	Addendum III		ATCC 9526	2277	Z5
<i>Shewanella putrefaciens</i> ‡ (formerly "[<i>Pseudomonas</i>] <i>rubescens</i> ")	Addendum III		CCEB 519	2279	B
"[<i>Pseudomonas</i>] <i>septica</i> "	Addendum I		ATCC 14545	2290	Z5
"[<i>Pseudomonas</i>] <i>stereotropis</i> "	Addendum II		NCMB 1771	2325	Z11
<i>Pseudomonas synxantha</i> *	Addendum I	<i>Pseudomonas</i> section V	NCIB 8178 ^T	2190 ^T	B
<i>Pseudomonas taetrolens</i> *	Addendum I	<i>Pseudomonas</i> section V	CCEB 381 ^T (= ATCC 4683 ^T)	2336 ^T	B
"[<i>Pseudomonas</i>] <i>trifolii</i> "	Addendum I		ATCC 14537	2598	Z5
"[<i>Achromobacter</i>] <i>albus</i> "			NCIB 9988	2836	B
"[<i>Achromobacter</i>] <i>butyri</i> "			NCIB 9404	2833	B

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TABLE 2—Continued

Name ^a	Status in <i>Pseudomonas</i> in Bergey's Manual of Determinative Bacteriology, 8th ed. ^b	Status in Bergey's Manual of Systematic Bacteriology, vol. 1 ^c	Strain no. as received ^d	LMG no. ^d	Growth medium
"[<i>Achromobacter</i>] <i>cycloclastes</i> "			CRM ACY	2841	B
"[<i>Achromobacter</i>] <i>cystinovorum</i> "			NCIB 4854	1795	B
"[<i>Achromobacter</i>] <i>formosus</i> "			NCIB 9987	2835	B
"[<i>Achromobacter</i>] <i>liquefaciens</i> "			NCIB 9989	2837	B
[<i>Achromobacter</i>] species			M6 (Moore)	2840	B
[<i>Achromobacter</i>] species			NCMB 622	2838	B
[<i>Achromobacter</i>] species			P18/27 (Pane)	2839	B
"[<i>Achromobacter</i>] <i>venosus</i> "			NCIB 9985	2834	B
[<i>Bordetella</i>] species			API 1470476	2842	B
[<i>Agrobacterium</i>] species			111 (Sundman)	164	B
[<i>Agrobacterium</i>] species			112 (Sundman)	166	B
<i>Cellvibrio mixtus</i> subsp. <i>mixtus</i> ‡	Addendum IV		NCIB 8634	2847	Z17
<i>Cellvibrio</i> sp.	Addendum IV		NCIB 8975	2849	Z18
<i>Cellvibrio mixtus</i> subsp. <i>mixtus</i> ‡	Addendum IV		NCMB 8633	2848	Z17
Purple cream organism			F4530 (Rhodes)	2846	B
Leaf nodule organism			PeH ₂ 20	2806	B
Unnamed			349 (Lizarraga)		
Unnamed			1371 (Lizarraga)		
Unnamed			1613 (Lizarraga)		
Unnamed			2006 (Lizarraga)		
Unnamed			2014 (Lizarraga)		
Unnamed			2026 (Lizarraga)		
Unnamed			2128 (Lizarraga)		
Unnamed			2145 (Lizarraga)		
Unnamed			3400 (Lizarraga)		
Unnamed			3403 (Lizarraga)		
Unnamed			3407 (Lizarraga)		

^a *, Name on Approved Lists of Bacterial Names (38, 46); †, name validly published in the International Journal of Systematic Bacteriology since 1 January 1985; ‡, name on a validation list in the International Journal of Systematic Bacteriology after 1 January 1985 (24–30).

^b See reference 20.

^c See reference 34.

^d Abbreviations: API, API Systems, La-Balme-les-Grottes, Montalieu-Vercieu, France; ATCC, American Type Culture Collection, Rockville, Md.; CCEB, Culture Collection of Entomogenous Bacteria, Prague, Czechoslovakia; CCM, Czechoslovak Collection of Microorganisms, Brno, Czechoslovakia; CIP, Collection de l'Institut Pasteur, Paris, France; DSM, Deutsche Sammlung von Mikroorganismen, Braunschweig, Federal Republic of Germany; HIM, Hygiene Institute and Medicinal Research Service, Marburg, Federal Republic of Germany; ICPB, International Collection of Phytopathogenic Bacteria, Davis, Calif.; LMG, Culture Collection, Laboratorium voor Microbiologie, Gent, Belgium; MMCA, Medical Microbiology Culture Collection, Aarhus, Denmark; NCIB, National Collection of Industrial Bacteria, Torry Research Station, Aberdeen, Scotland; NCMB, National Collection of Marine Bacteria, Torry Research Station, Aberdeen, Scotland; NCPPB, National Collection of Plant Pathogenic Bacteria, Harpenden, England; NCTC, National Collection of Type Cultures, London, England; NRRL, Agricultural Research Service Culture Collection, Peoria, Ill.; NZP, Culture Collection, Department for Scientific and Industrial Research, Palmerston North, New Zealand.

are listed in Tables 1 and 2. The taxon names in quotation marks have not been validated; we use brackets for generic names of organisms which we found to be misnamed. The mass cultures were grown on media as reported previously (11–14, 54).

Preparation of labeled rRNA. Either ¹⁴C- or ³H-labeled rRNAs were prepared by using the previously described method (9) from the following strains: *Pseudomonas fluorescens* LMG 1794^T (T = type strain), [*Pseudomonas*] *acidovorans* LMG 1226^T, [*Pseudomonas*] *solanacearum* LMG 2299^T, *Xanthomonas campestris* LMG 568^T, *Escherichia coli* LMG 2093, *Aeromonas hydrophila* LMG 2844^T, *Vibrio parahaemolyticus* LMG 2850^T, *Alteromonas haloplanktis* LMG 2852^T, *Shewanella putrefaciens* LMG 22681^T, *Alteromonas macleodii* LMG 2843^T, *Acinetobacter calcoaceticus* LMG 10461^T, [*Flavobacterium*] *capsulatum* LMG 2830^T, "*Deleya aquamarina*" LMG 2853t1, *Acetobacter aceti* LMG 2161t1^T, *Agrobacterium tumefaciens* LMG 196, *Flavobacterium aquatile* LMG 2952^T, *Pasteurella multocida* LMG 2851^T, *Rhizobium loti* LMG 6123, *Oceanospirillum linum* LMG 5214, *Alcaligenes faecalis* LMG 1229^T, [*Alcali-*

genes] *eutrophus* LMG 1199^T, and [*Alcaligenes*] *paradoxus* LMG 1797t1^T.

Preparation of high-molecular-weight DNA and DNA:rRNA hybridization technique. For the preparation of DNA, the fixation of high-molecular-weight DNA on membrane filters, the saturation hybridization between ¹⁴C- or ³H-labeled 23S or 16S rRNA and filter-fixed DNA, the determination of the thermal stability of the hybrids, and the chemical determination of the DNA on the membrane filters, we used the methods described previously (9, 13, 14).

Mean DNA base composition (G+C content). Guanine-plus-cytosine (G+C) contents were determined in this study or were taken from our previous papers. We used the methods described previously (14).

Carbon substrate utilization tests and numerical analysis. Auxanographic API galleries were used to determine the growth of 22 strains on 49 carbohydrates (API 50CH galleries), 49 organic acids (API 50A0 galleries), and 49 amino acids and amines (API 50AA galleries) (API System, La Balme-les-Grottes, Montalieu-Vercieu, France). Tests were performed, read, and coded as described previously (22).

TABLE 3. Allocation of named and generically misnamed *Pseudomonas* species in different rRNA branches and rRNA superfamilies, as determined by DNA:rRNA hybridization

In rRNA superfamily I	
(i)	<i>Alteromonas haloplanktis</i> rRNA branch: "[<i>Pseudomonas</i>] atlantica" LMG 2140, "[<i>Pseudomonas</i>] carrageenovora," "[<i>Pseudomonas</i>] nigrificiens," "[<i>Pseudomonas</i>] marinoglutinosa," and "[<i>Pseudomonas</i>] piscicida" ^a
(ii)	<i>Enterobacteriaceae</i> rRNA branch: "[<i>Pseudomonas</i>] trifolii" ^b
(iii)	<i>Vibrionaceae</i> rRNA branch: "[<i>Pseudomonas</i>] creosotensis" ^c
(iv)	<i>Shewanella putrefaciens</i> rRNA branch: "[<i>Pseudomonas</i>] putrefaciens" and "[<i>Pseudomonas</i>] rubescens" ^a
(v)	<i>Aeromonadaceae</i> rRNA branch: [<i>Pseudomonas</i>] <i>doudoroffii</i> ^c
In rRNA superfamily II	
(i)	<i>Pseudomonas fluorescens</i> rRNA branch (the authentic genus <i>Pseudomonas</i>)
(a)	All <i>Pseudomonas</i> species from section I ^d
(b)	<i>Pseudomonas agarici</i> , <i>Pseudomonas amygdali</i> , <i>Pseudomonas asplenii</i> , <i>Pseudomonas caricapapayae</i> , <i>Pseudomonas cattleyae</i> (not the type strain), <i>Pseudomonas coronafaciens</i> , <i>Pseudomonas corrugata</i> , <i>Pseudomonas fuscovaginae</i> , "[<i>Pseudomonas</i>] lapsa," "[<i>Pseudomonas</i>] maculicola," <i>Pseudomonas marginalis</i> , <i>Pseudomonas meliae</i> , "[<i>Pseudomonas</i>] oryzicola," "[<i>Pseudomonas</i>] panici," "[<i>Pseudomonas</i>] pastinacae," "[<i>Pseudomonas</i>] primulae," "[<i>Pseudomonas</i>] ribicola," "[<i>Pseudomonas</i>] sesami," <i>Pseudomonas syringae</i> pv. <i>aceris</i> , <i>Pseudomonas syringae</i> pv. <i>antirrhini</i> , <i>Pseudomonas syringae</i> pv. <i>berberidis</i> , <i>Pseudomonas syringae</i> pv. <i>cannabina</i> , <i>Pseudomonas syringae</i> pv. <i>eriobotryae</i> , <i>Pseudomonas syringae</i> pv. <i>passiflorae</i> , <i>Pseudomonas syringae</i> pv. <i>striafaciens</i> , <i>Pseudomonas syringae</i> pv. <i>ulmi</i> , <i>Pseudomonas syringae</i> pv. <i>viburni</i> , <i>Pseudomonas tolaasii</i> , <i>Pseudomonas viridiflava</i> , "[<i>Pseudomonas</i>] viridilivida," and "[<i>Pseudomonas</i>] washingtoniae" ^e
(c)	" <i>Pseudomonas caudata</i> ," " <i>Pseudomonas denitrificans</i> ," <i>Pseudomonas fragi</i> , <i>Pseudomonas mucidolens</i> , " <i>Pseudomonas myxogenes</i> ," <i>Pseudomonas oleovorans</i> , " <i>Pseudomonas reptilovora</i> ," <i>Pseudomonas resinovorans</i> , " <i>Pseudomonas septica</i> ," <i>Pseudomonas synxantha</i> , and <i>Pseudomonas taetrolensis</i> ^c
(ii)	<i>Xanthomonas</i> rRNA branch
(a)	[<i>Pseudomonas</i>] <i>maltophilia</i> (= <i>Xanthomonas maltophilia</i>) ^f
(b)	[<i>Pseudomonas</i>] <i>betle</i> , "[<i>Pseudomonas</i>] <i>gardneri</i> ," [<i>Pseudomonas</i>] <i>hibiscicola</i> , "[<i>Pseudomonas</i>] <i>mangiferaeindicae</i> ," "[<i>Pseudomonas</i>] <i>viticola</i> ," and "[<i>Pseudomonas</i>] <i>vitiswoodrowii</i> " ^e
(c)	[<i>Pseudomonas</i>] <i>boreopolis</i> and [<i>Pseudomonas</i>] <i>pictorum</i> ^c
(iii)	<i>Deleya</i> rRNA branch: "[<i>Pseudomonas</i>] <i>bathycetes</i> ," [<i>Pseudomonas</i>] <i>beijerinckii</i> , and [<i>Pseudomonas</i>] <i>marina</i>
(iv)	<i>Oceanospirillum</i> rRNA branch: perhaps (at the base) [<i>Pseudomonas</i>] <i>elongata</i> LMG 2182 ^T , "[<i>Pseudomonas</i>] <i>atlantica</i> " LMG2139, and "[<i>Pseudomonas</i>] <i>nautica</i> " LMG2226 ^T ^g
(v)	<i>Acinetobacter rDNA</i> branch: "[<i>Pseudomonas</i>] <i>cruciviae</i> " and "[<i>Pseudomonas</i>] <i>pavonacea</i> " ^h
In rRNA superfamily III	
(i)	[<i>Pseudomonas</i>] <i>acidovorans</i> rRNA complex
(a)	Species from [<i>Pseudomonas</i>] section III ^d
(b)	"[<i>Pseudomonas</i>] <i>alboprecipitans</i> ," [<i>Pseudomonas</i>] <i>cattleyae</i> (type strain), [<i>Pseudomonas</i>] <i>pseudoalcaligenes</i> subsp. <i>citrulli</i> , and [<i>Pseudomonas</i>] <i>rubrilineans</i> ^c
(ii)	[<i>Pseudomonas</i>] <i>solanacearum</i> rRNA complex
(a)	[<i>Pseudomonas</i>] species from section II ^d
(b)	"[<i>Pseudomonas</i>] <i>alliicola</i> ," [<i>Pseudomonas</i>] <i>andropogonis</i> , [<i>Pseudomonas</i>] <i>glumae</i> , [<i>Pseudomonas</i>] <i>rubrisubalbicans</i> , "[<i>Pseudomonas</i>] <i>stizolobii</i> ," and [<i>Pseudomonas</i>] <i>woodsii</i> ^c
(c)	[<i>Pseudomonas</i>] <i>huttiensis</i> , "[<i>Pseudomonas</i>] <i>oxalaticus</i> ," and [<i>Pseudomonas</i>] <i>phenazinium</i> ^c
In rRNA superfamily IV	
(i)	<i>Rhizobium loti</i> rRNA branch: [<i>Pseudomonas</i>] <i>aminovorans</i> ^c
(ii)	<i>Brucella</i> rRNA branch: "[<i>Pseudomonas</i>] <i>arsenoxydans</i> " ⁱ
(iii)	[<i>Flavobacterium</i>] <i>capsulatum</i> rRNA branch: "[<i>Pseudomonas</i>] <i>azotocolligans</i> " and [<i>Pseudomonas</i>] <i>paucimobilis</i> ^c
(iv)	<i>Acetobacter</i> rRNA branch: "[<i>Pseudomonas</i>] <i>melophthora</i> " and "[<i>Pseudomonas</i>] <i>pomi</i> " ^j
At the base of rRNA superfamily IV	
(i)	[<i>Pseudomonas</i>] <i>vesicularis</i> and [<i>Pseudomonas</i>] <i>diminuta</i> ^k
(ii)	[<i>Pseudomonas</i>] <i>echinoides</i> and "[<i>Pseudomonas</i>] <i>riboflavina</i> " ^c
Gram-positive bacteria: <i>Arthrobacter</i> rRNA branch, "[<i>Pseudomonas</i>] <i>perturida</i>"^c	
Not assigned to any of the known rRNA branches: "[<i>Pseudomonas</i>] <i>coenobios</i>," [<i>Pseudomonas</i>] <i>flectens</i>, "[<i>Pseudomonas</i>] <i>membranula</i>, and "[<i>Pseudomonas</i>] <i>stereotropis</i>"^c	

^a Reference 54; this paper.^b This paper; De Ley and Tytgat, manuscript in preparation.^c This paper.^d Reference 41.^e Reference 15.^f Reference 50.^g Reference 44; this paper.^h Reference 55.ⁱ Reference 10.^j Reference 21.^k Reference 14.

TABLE 4. Organisms belonging to the *Pseudomonas fluorescens* rRNA branch (the authentic genus *Pseudomonas*): DNA base compositions and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%) ^a	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA										
			<i>Pseudomonas fluorescens</i> LMG 1794 ^T		<i>[Pseudomonas] acidovorans</i> LMG 1226 ^T		<i>[Pseudomonas] solanacearum</i> LMG 2299 ^T		<i>Shewanella putrefaciens</i> LMG 2268t1 ^T		<i>Alcaligenes faecalis</i> LMG 1229 ^T		
			<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	
" <i>Pseudomonas septica</i> "	2290	61.3	80.0	0.09									
<i>Pseudomonas synxantha</i>	2190 ^T	61.0	79.0	0.14	61.0	0.08							
<i>Pseudomonas taetrolens</i>	2336 ^T	59.8	79.0	0.11									
<i>Pseudomonas stutzeri</i>	2243	62.5	78.5	0.12	62.5	0.08							
<i>Pseudomonas fragi</i>	2191 ^T	60.6	78.0	0.18	61.5	0.14							
<i>Pseudomonas mucidolens</i>	2223 ^T	61.0	78.0	0.14	61.0	0.07							
<i>Pseudomonas resinovorans</i>	2274 ^T	63.7	77.5	0.10									
<i>Pseudomonas oleovorans</i>	2229 ^T	63.5	77.0	0.11									
" <i>Pseudomonas myxogenes</i> "	2224	59.4	77.0	0.05									
" <i>Pseudomonas reptilivora</i> "	2273	62.7	76.5	0.16									
" <i>Pseudomonas denitrificans</i> "	2179	62.3	75.5	0.11	61.5	0.06							
" <i>Pseudomonas caudata</i> "	2149	54.8	73.5	0.10	59.1	0.05			65.5	0.06			
"[<i>Achromobacter</i>] <i>albus</i> "	2836	61.8	79.5	0.15							61.0	0.07	
"[<i>Achromobacter</i>] <i>formosus</i> "	2835	61.5	79.5	0.13							61.0	0.06	
"[<i>Achromobacter</i>] <i>venosus</i> "	2834	61.8	79.0	0.09							62.0	0.07	
[<i>Achromobacter</i>] species	2840	62.2	78.5	0.11							62.0	0.06	
[<i>Achromobacter</i>] species	2838	58.2	78.0	0.13							62.5	0.07	
"[<i>Achromobacter</i>] <i>butyri</i> "	2833	60.5	77.5	0.12							61.5	0.06	
"[<i>Achromobacter</i>] <i>liquefaciens</i> "	2837	66.0	76.5	0.07							62.5	0.04	
[<i>Achromobacter</i>] species	2839	65.0	76.5	0.11							62.5	0.06	
"[<i>Achromobacter</i>] <i>cycloclastes</i> "	2841	64.2	75.5	0.09							63.0	0.06	
Unnamed (Lizarraga 3403)		64.0	79.0	0.08									
Unnamed (Lizarraga 3407)		63.5	77.5	0.09									
Unnamed (Lizarraga 3400)		63.7	77.0	0.07									
Purple cream organism	2846	59.9	79.0	0.12	60.5	0.08	63.0	0.09					

^a In Tables 4 through 19 some of the G+C content data were taken from previous papers (10, 12, 16, 21, 45, 54, 55).

FIG. 2. Dendrogram showing the phenotypic relationships among the strains investigated, based on the Gower similarity coefficient (S_G) and unweighted average linkage cluster analysis. Four phenons are delineated above an S_G level of 72%. Abbreviations: A., *Acinetobacter*; ACHR., *Achromobacter*; BORD., *Bordetella*; D., *Deleya*; P., *Pseudomonas*.

The Gower similarity coefficient was calculated between each pair of strains. Clustering was performed by using the unweighted average linkage technique and the Siemens model 7570 computer of the Centraal Digitaal Rekencentrum, Rijksuniversiteit, Gent, Belgium.

RESULTS AND DISCUSSION

The results of the DNA:rRNA hybridizations and mean G+C values are shown in the tables below. The DNA:rRNA hybrids were characterized by the following two parameters: (i) the temperature at which 50% of the hybrid was eluted [$T_{m(e)}$ value] and (ii) the percentage of rRNA binding (i.e., the amount [in micrograms] of labeled rRNA bound [after

TABLE 5. Organisms belonging to the acidovorans rRNA branch: DNA base compositions and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%)	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA			
			<i>[Pseudomonas] acidovorans</i> LMG 1226 ^T		<i>[Alcaligenes] paradoxus</i> LMG 1797t1 ^T	
			<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding
[<i>Bordetella</i>] species	2842	67.4	81.0	0.12	76.0	0.11
"[<i>Achromobacter</i>] <i>cystinovorum</i> "	1795	68.7	80.5	0.11	77.0	0.10

TABLE 6. Organisms belonging to the *solanacearum* rRNA branch: DNA base compositions and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%)	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA							
			<i>Pseudomonas fluorescens</i> LMG 1794 ^T		[<i>Pseudomonas</i>] <i>acidovorans</i> LMG 1226 ^T		[<i>Pseudomonas</i>] <i>solanacearum</i> LMG 2299 ^T		[<i>Alcaligenes</i>] <i>eutrophus</i> LMG 1199 ^T	
			<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding
“[<i>Pseudomonas</i>] <i>oxalaticus</i> ”	2235	66.2	65.0	0.06	69.5	0.09	76.0	0.11	76.0	0.19
[<i>Pseudomonas</i>] <i>phenazinum</i>	2247 ^T	61.6	64.0	0.06	69.5	0.07	75.0	0.09	74.5	0.07
[<i>Pseudomonas</i>] <i>huttiensis</i>	2199 ^T	63.7	63.5	0.08	71.0	0.08	74.5	0.09	71.5	0.10
[<i>Agrobacterium</i>] sp.	164	62			70.5	0.08	76.0	0.11		
[<i>Agrobacterium</i>] sp.	166	62.5	62.5	0.06	70.0	0.06	75.0	0.09		

ribonuclease treatment] to 100 µg of DNA retained on the membrane filter). For each labeled reference rRNA, the $T_{m(e)}$ values were plotted versus the percentages of rRNA binding, yielding rRNA similarity maps. Why $T_{m(e)}$ is the most useful parameter for taxonomic conclusions has been explained previously (11, 13, 14). The strains were clustered in a $T_{m(e)}$ dendrogram (Fig. 1). Organisms forming DNA:rRNA hybrids with a $\Delta T_{m(e)}$ of at most 12°C versus the $T_{m(e)}$ of the homologous duplex constitute what we call an rRNA branch. Each rRNA branch is named after a reference taxon used to prepare a labeled reference rRNA. The latter was prepared preferably from a type strain of a type species; in a few exceptional cases labeled reference rRNA was prepared from a reference strain or a reliable working strain. A group of rRNA branches containing taxa which are phenotypically and genotypically similar and which are removed from each other at a $\Delta T_{m(e)}$ of 5 to 8°C is what we call an rRNA complex (e.g., the *Alcaligenes-Bordetella* complex, the *Agrobacterium-Rhizobium* complex, etc). In a few cases we attempted to translate these phylogenetic relationships into taxonomic categories. In a number of cases either isolated rRNA branches or rRNA complexes correspond to taxonomic families; examples of the former are the *Enterobacteriaceae* and the *Vibrionaceae*, and examples of the latter the *Alcaligenaceae* and the *Rhizobiaceae*. A number of rRNA branches and rRNA complexes group together at a $\Delta T_{m(e)}$ of about 12 to 14°C in larger units which we call (8) rRNA superfamilies; these superfamilies probably corre-

spond to either taxonomic subclasses, orders, or suborders. So far, we have discovered six rRNA superfamilies, designated superfamilies I to VI, in the gram-negative bacteria. Four of these superfamilies correspond to the alpha (superfamily IV), beta (superfamily III), and gamma (superfamilies I and II) subdivisions of Woese (59), which, together with the delta subdivision, were recently united in the new class *Proteobacteria* (47).

The taxonomic positions of the strains included in this study are discussed below according to their rRNA branch. A comprehensive list of named and misnamed *Pseudomonas* species, together with their positions in the various rRNA branches, is given in Table 3.

Organisms belonging to the *Pseudomonas fluorescens* rRNA branch. We pointed out previously (12, 14) that the authentic genus *Pseudomonas* should be limited to the *Pseudomonas fluorescens* rRNA branch and that the members of the *Azotobacteraceae* as defined in *Bergey's Manual of Systematic Bacteriology* (53) are the closest relatives of this group. The emended genus *Pseudomonas* consists of (i) all *Pseudomonas* species from section I in *Bergey's Manual of Systematic Bacteriology* (41), (ii) previously unclassified plant-pathogenic species (15), and (iii) the following strains examined in the present study (in decreasing order of relatedness to reference strain *Pseudomonas fluorescens* LMG 1794^T): “*Pseudomonas septica*” LMG 2290, *Pseudomonas synxantha* LMG 2190^T, *Pseudomonas taetrolens* LMG 2336^T, *Pseudomonas stutzeri* (formerly *Pseudomonas per-*

TABLE 7. Organisms belonging to the *Alteromonas haloplanktis* rRNA branch: DNA base compositions and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%)	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA									
			<i>Pseudomonas fluorescens</i> LMG 1794 ^T		<i>Alteromonas macleodii</i> LMG 2843 ^T		<i>Alteromonas haloplanktis</i> LMG 2852 ^T		<i>Shewanella putrefaciens</i> LMG 2268t1 ^T		<i>Marinomonas vaga</i> LMG 2845 ^T	
			<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding
“[<i>Pseudomonas</i>] <i>atlantica</i> ”	2140	43.5	65.0	0.09			77.5	0.21				
“[<i>Pseudomonas</i>] <i>marinoglutinosa</i> ”	2219t1	42.2					76.0	0.25				
“[<i>Pseudomonas</i>] <i>marinoglutinosa</i> ”	2219t2	42.1					76.5	0.28				
“[<i>Pseudomonas</i>] <i>nigrifaciens</i> ”	2228t1	40.4					76.5	0.25				
“[<i>Pseudomonas</i>] <i>nigrifaciens</i> ”	2228t2						76.0	0.25				
“[<i>Pseudomonas</i>] <i>nigrifaciens</i> ”	2227	41.0	67.0	0.12	70.0	0.15	74.0	0.17				
“[<i>Pseudomonas</i>] <i>carrageenovora</i> ”	2154	40.0					76.0	0.28				
“[<i>Pseudomonas</i>] <i>piscicida</i> ”	2251	44.4	66.5	0.09			75.5	0.19				
“[<i>Pseudomonas</i>] <i>piscicida</i> ”	2248	44.5			66.5	0.11	71.0	0.14	66.5	0.11	63.0	0.10
“[<i>Pseudomonas</i>] <i>piscicida</i> ”	2249t1	42.4			66.0	0.12	71.5	0.17	65.5	0.11	65.0	0.11
“[<i>Pseudomonas</i>] <i>piscicida</i> ”	2249t2	41.9					69.0	0.11	65.0	0.10	63.0	0.11

TABLE 8. Organism belonging to the *Vibrionaceae* rRNA branch: DNA base composition and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%)	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA													
			<i>Pseudomonas fluorescens</i> LMG 1794 ^T		<i>Deleya aquamarina</i> LMG 2853t1		<i>Alteromonas macleodii</i> LMG 2843 ^T		<i>Alteromonas haloplanktis</i> LMG 2852 ^T		<i>Vibrio parahaemolyticus</i> LMG 2850 ^T		<i>Shewanella putrefaciens</i> LMG 2268t1 ^T		<i>Marinomonas vaga</i> LMG 2845 ^T	
			<i>T</i> _{m(e)} (°C)	% rRNA binding	<i>T</i> _{m(e)} (°C)	% rRNA binding	<i>T</i> _{m(e)} (°C)	% rRNA binding	<i>T</i> _{m(e)} (°C)	% rRNA binding	<i>T</i> _{m(e)} (°C)	% rRNA binding	<i>T</i> _{m(e)} (°C)	% rRNA binding	<i>T</i> _{m(e)} (°C)	% rRNA binding
“ <i>[Pseudomonas] creosotensis</i> ”	2174	45.6	67.5	0.13	68.5	0.14	68.0	0.15	70.5	0.18	77.5	0.12	71.5	0.17	68.0	0.24

TABLE 9. Organism belonging to the *Shewanella putrefaciens* rRNA branch: DNA base composition and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%)	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA							
			<i>Pseudomonas fluorescens</i> LMG 1794 ^T		<i>Alteromonas macleodii</i> LMG 2843 ^T		<i>Alteromonas haloplanktis</i> LMG 2852 ^T		<i>Shewanella putrefaciens</i> LMG 2268t1 ^T	
			<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding
<i>Shewanella putrefaciens</i>	2279	46.1	66.5	0.07	69.0	0.14	69.0	0.18	79.0	0.28

fectomarina [18]) LMG 2243, *Pseudomonas fragi* LMG 2191^T, *Pseudomonas mucidolens* LMG 2223^T, *Pseudomonas resinovorans* LMG 2274^T, *Pseudomonas oleovorans* LMG 2229^T, “*Pseudomonas myxogenes*” LMG 2224, “*Pseudomonas reptilovora*” LMG 2273, “*Pseudomonas denitrificans*” LMG 2179, the misnamed *Achromobacter* strains “*[Achromobacter] albus*” LMG 2836, “*[Achromobacter] formosus*” LMG 2835, “*[Achromobacter] venosus*” LMG 2834, *[Achromobacter]* species strains LMG 2840, *[Achromobacter]* species strain LMG 2838, “*[Achromobacter] butyri*” LMG 2833, “*[Achromobacter] liquefaciens*” LMG 2837, *[Achromobacter]* species strain LMG 2839, and “*[Achromobacter] cycloclastes*” LMG 2841, the unnamed organisms Lizzaraga 3403 and Lizzaraga 3400, and the purple cream organism strain LMG 2846 (Table 4). Because all of these organisms have *T_{m(e)}* values between 80 and 75.5°C and rRNA binding ranging from 0.05 to 0.18%, they clearly belong in the authentic genus *Pseudomonas*. “*Pseudomonas caudata*” LMG 2149, with a *T_{m(e)}* value of 73.5°C, is at the lower border of this rRNA branch.

For the organisms with *T_{m(e)}* values between 75 and 76.5°C, the relationship with the members of the *Azotobacteraceae* has to be investigated.

Often bacteria, in particular pathogenic bacteria, have been grouped together because of similar habitats. However, the ecological niches of the pseudomonads listed above are

quite different. Some of them, such as *Pseudomonas stutzeri* LMG 2243, “*Pseudomonas caudata*” LMG 2149, and the isolates of Lizzaraga, are of marine origin; others, such as *Pseudomonas fragi*, *Pseudomonas synxantha*, *Pseudomonas mucidolens*, *Pseudomonas taetrolens*, and “*Pseudomonas myxogenes*,” were isolated from foods or beverages; still others, e.g., “*Pseudomonas reptilovora*” and “*Pseudomonas septica*,” were isolated from reptiles and insects, respectively; and finally, “*Pseudomonas denitrificans*,” *Pseudomonas oleovorans*, and *Pseudomonas resinovorans* were isolated from soil, with the latter two organisms showing unusual nutritional capacities in degrading oil or oil fragments. For some of these organisms a natural relationship with *Pseudomonas fluorescens* has been suggested or may be deduced from data in the literature. Based on cofactor specificity and regulatory properties of dehydrogenase proteins in the biosynthesis of tyrosine, *Pseudomonas fragi*, *Pseudomonas synxantha*, *Pseudomonas taetrolens* LMG 2336^T, and *Pseudomonas stutzeri* LMG 2243 have been tentatively placed in group I of Byng et al. (7, 57). Furthermore, *Pseudomonas taetrolens* LMG 2336^T is identical to Stanier strain 92, which is indistinguishable from *Pseudomonas putida* (48), a species also belonging in the *Pseudomonas fluorescens* rRNA branch (14). “*Pseudomonas denitrificans*” LMG 2179 belongs to Palleroni rRNA homology group I and exhibits an average of ca. 30% DNA

TABLE 10. Organisms belonging to the *Enterobacteriaceae* rRNA branch: DNA base compositions and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%)	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA					
			<i>Pseudomonas fluorescens</i> LMG 1794 ^T		<i>[Pseudomonas] acidovorans</i> LMG 1226 ^T		<i>Escherichia coli</i> LMG 2093	
			<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding
“ <i>[Pseudomonas] trifolii</i> ”	2598	55.7	70.5	0.11	63.0	0.10	77.0	0.15
Leaf nodule organism	2806	55.5	66.0	0.09	62.5	0.09	77.0	0.14

TABLE 11. Organism belonging to the *Aeromonadaceae* rRNA branch: DNA base composition and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%)	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA			
			<i>Pseudomonas fluorescens</i> LMG 1794 ^T	<i>Escherichia coli</i> LMG 2093	<i>Aeromonas mucidolens</i> LMG 2843 ^T	<i>Aeromonas halophilantis</i> LMG 2852 ^T
			$T_{m(e)}$ (°C)	$T_{m(e)}$ (°C)	$T_{m(e)}$ (°C)	$T_{m(e)}$ (°C)
			% rRNA binding	% rRNA binding	% rRNA binding	% rRNA binding
<i>[Pseudomonas] doudoroffii</i>	2180 ^T	59.7	67.5	71.0	70.5	70.5
			0.16	0.18	0.19	0.20
			71.0	70.5	70.5	71.0
			0.17	0.21	0.21	0.21
			69.5	69.5	69.5	69.5
			0.20	0.20	0.20	0.20
			65.0	65.0	65.0	65.0
			0.13	0.13	0.13	0.13
			74.0	74.0	74.0	74.0
			0.25	0.25	0.25	0.25
			69.0	69.0	69.0	69.0
			0.06	0.06	0.06	0.06

homology to *Pseudomonas fluorescens* biotype A (19). The description of *Pseudomonas mucidolens* conforms to that of the denitrifying biovars of *Pseudomonas fluorescens* (41). For the other organisms, the natural relationship was previously unknown. The conclusions from our DNA:rRNA data were confirmed for 10 strains by the numerical analysis of the carbon assimilation tests (Fig. 2). *Pseudomonas synxantha* LMG 2190^T, *Pseudomonas mucidolens* LMG 2223^T, and "[*Achromobacter*] formosus" LMG 2835 are the closest phenotypic neighbors of *Pseudomonas fluorescens* LMG 1794^T. The auxanographic technique also indicated that the following *Achromobacter* strains are authentic pseudomonads, as they clustered in phenon 1 together with the type strain of *Pseudomonas fluorescens* (Fig. 2): "[*Achromobacter*] venosus" LMG 2834, "[*Achromobacter*]" species strain LMG 2840, "[*Achromobacter*] albus" LMG 2836, "[*Achromobacter*] butyri" LMG 2833, and [*Achromobacter*] species strain LMG 2838. The strains of the *Pseudomonas fluorescens* rRNA branch which we investigated are phenotypically clearly distinct from strains of the rRNA branches containing [*Pseudomonas*] *acidovorans*, *Acinetobacter calcoaceticus*, and "*Deleya aquamarina*" (Fig. 2).

Misnamed pseudomonads belonging to the acidovorans rRNA complex. In general, the organisms of the acidovorans rRNA branch are very heterogeneous (Table 5). They are physiologically, as well as morphologically, diverse bacteria, including photosynthetic and heterotrophic organisms, polarly or peritrichously flagellated straight rods, spirilla or *Vibrio*-like organisms (A. Willems, M. Gillis and J. De Ley, manuscript in preparation). Obviously, they represent several genera. Two of the subbranches have already been proposed as *Comamonas* nom. rev. (17, 52) and as *Xylophilus* (58). The *Pseudomonas* species of this rRNA branch are all generically misnamed. We prefer to postpone the creation of new genus names because the relationships within this rRNA branch are being examined closely by members of our research group. "[*Achromobacter*] cystinovorum" LMG 1795 and [*Bordetella*] species strain LMG 2842 belong in this rRNA branch and were clearly misnamed, with $T_{m(e)}$ values of 80.5 and of 81°C, respectively, versus [*Pseudomonas*] *acidovorans*. These strains are also phenotypically highly related to the type strain of [*Pseudomonas*] *acidovorans* (Fig. 2, phenon 4).

Misnamed pseudomonads belonging to the solanacearum rRNA complex. The nomenclatural remarks for the solanacearum rRNA branch are the same as those given above for the acidovorans rRNA branch. Five of the organisms tested, "[*Pseudomonas*] *oxalaticus*" LMG 2235, [*Pseudomonas*] *phenazinium* LMG 2247^T, [*Pseudomonas*] *huttiensis* LMG 2199^T, and [*Agrobacterium*] species strains LMG 164 and 166, are located in this branch with $T_{m(e)}$ values between 76 and 74.5°C versus [*Pseudomonas*] *solanacearum* (Table 6). At the same level we previously found [*Alcaligenes*] *eutrophus*, as well as the plant pathogens [*Pseudomonas*] *glumae*, [*Pseudomonas*] *gladioli*, [*Pseudomonas*] *cepacia*, [*Pseudomonas*] *woodsii*, [*Pseudomonas*] *rubrisubalbicans*, and [*Pseudomonas*] *andropogonis* (14, 15). Previously published data confirm some of the relationships which we found. The type strain of [*Pseudomonas*] *huttiensis* belongs in group II of Byng et al. (7). A recent taxonomic study (31) revealed a close relationship (50% DNA homology) between [*Alcaligenes*] *eutrophus* and "[*Pseudomonas*] *oxalaticus*," which has been confirmed by immunological studies (E. Falsen, personal communication). Our DNA:rRNA hybridization data (Table 6) showed that "[*Pseudomonas*] *oxalaticus*" is equally far removed from [*Pseudomonas*] *solanacearum* and

TABLE 12. Organisms belonging to none of the established rRNA branches (members of the first or second rRNA superfamily): DNA base compositions and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%)	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA									
			<i>Pseudomonas fluorescens</i> LMG 1794 ^T		<i>Vibrio parahaemolyticus</i> LMG 2850 ^T		<i>Escherichia coli</i> LMG 2093		<i>Alteromonas macleodii</i> LMG 2843 ^T		<i>Alteromonas haloplanktis</i> LMG 2852 ^T	
			<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding
“ <i>[Pseudomonas]</i> atlantica”	2139	45.4			70.0	0.16	67.5	0.17	67.0	0.21	69.5	0.25
<i>[Pseudomonas]</i> elongata	2182 ^T	58.2	69.5	0.10			70.0	0.10				
<i>[Pseudomonas]</i> nautica	2226 ^T	59.2	70.5	0.07					67.5	0.08	68.0	0.07
<i>Cellvibriomixtus</i> subsp. <i>mixtus</i>	2847	49.5			66.0	0.08	66.5	0.07	65.5	0.08		
<i>Cellvibriomixtus</i> subsp. <i>mixtus</i>	2848	51.5	66.5	0.08	66.0	0.05	68.0	0.05	64.0	0.06		
<i>Cellvibrio</i> sp.	2849	48.2			68.0	0.08	67.0	0.07	65.0	0.07		
Unnamed (Lizarraga 1371)			71.5	0.06							68.0	0.08
Unnamed (Lizarraga 1613)		57.8	71.0	0.05							65.5	0.07
Unnamed (Lizarraga 2006)			73.0	0.06								
Unnamed (Lizarraga 2128)			71.5	0.05					65.0	0.05	68.5	0.07
Unnamed (Lizarraga 2026)			72.0	0.05							70.0	0.07
Unnamed (Lizarraga 2014)		56.6	72.5	0.05								
Unnamed (Lizarraga 2145)		56.8	71.0	0.04							67.0	0.06
Unnamed (Lizarraga 349)		64.0	71.0	0.15							67.0	0.14

[Alcaligenes] eutrophus [*T_{m(e)}* = 76°C]. More DNA:DNA hybridizations and an extensive phenotypic analysis are required to elucidate this taxonomic problem. *[Pseudomonas] phenazinium* produces iodinin on a medium containing L-threonine or glycine (4); it falls at the border of the *[Pseudomonas] solanacearum* rRNA branch and is not related to other iodinin producers which are outside this rRNA superfamily (11). Organisms described as ligninolytic bacteria from Finland (49) were originally tentatively included in *Agrobacterium*, but previous DNA:rRNA results (13) excluded them from this genus and from rRNA superfamily IV. The taxonomic position of these bacteria was determined in this study. In contrast to former results (11), it was found recently that the bifurcation of the *Janthinobacterium* rRNA branch from the *[Pseudomonas] solanacearum* rRNA branch also occurs at a *T_{m(e)}* level of ±74°C. These findings will be discussed in a forthcoming paper.

Misnamed pseudomonads belonging to the *Alteromonas haloplanktis* rRNA branch. The genus *Alteromonas*, as localized genotypically by Van Landschoot and De Ley (54), consists of the *Alteromonas macleodii* and *Alteromonas haloplanktis* rRNA branches delineated above a *T_{m(e)}* of 70°C. The gap between these two *Alteromonas* rRNA branches is expressed phenotypically by some minor differences (1).

A total of 11 strains from five different misnamed *Pseudomonas* species belong in the genus *Alteromonas* (Table 7).

The rRNA hybrids of eight strains, “*[Pseudomonas] atlantica*” LMG 2140, the two colony types of “*[Pseudomonas] marinoglutinosa*” LMG 2219, the two colony types of “*[Pseudomonas] nigrifaciens*” LMG 2228, “*[Pseudomonas] nigrifaciens*” LMG 2227, “*[Pseudomonas] carrageenovora*” LMG 2154, and “*[Pseudomonas] piscicida*” LMG 2251, have parameters [*T_{m(e)}* values 74.0 to 77.5°C; rRNA binding values, 0.17 to 0.28%] that fit the range of the *Alteromonas haloplanktis* group [*T_{m(e)}* values, 73.5 to 79.0°C; rRNA binding values, 0.17 to 0.31%]. Three other strains of “*[Pseudomonas] piscicida*” (LMG 2248, LMG 2249t1, and LMG 2249t2) are below the *Alteromonas haloplanktis* area on the rRNA similarity map, but still have *T_{m(e)}* values (69.0 to 71.5°C) which allow their inclusion in the genus *Alteromonas*. The strains of these five misnamed *Pseudomonas* species fit the general description of the genus *Alteromonas*; they are gram-negative, aerobic, polarly flagellated, heterotrophic bacteria with G+C contents ranging from 40 to 50 mol% (Tables 2 and 7). One strain “*[Pseudomonas] nigrifaciens*” LMG 2227, is not of marine origin but was isolated from salted butter. On phenotypic grounds and on the basis of a G+C content of 42.9 mol%, Baumann et al. (1) assigned this strain to the genus *Alteromonas*.

Misnamed pseudomonads belonging to the rRNA branch of the *Vibrionaceae*. The marine isolate “*[Pseudomonas] creosotensis*” LMG 2174, which is tolerant of substantial creosote concentrations, is located in the rRNA branch of the

TABLE 13. Organisms belonging to the *Xanthomonas* rRNA branch: DNA base compositions and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%)	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA					
			<i>Pseudomonas fluorescens</i> LMG 1794 ^T		<i>[Pseudomonas] acidovorans</i> LMG 1226 ^T		<i>Xanthomonas campestris</i> LMG 568 ^T	
			<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding
<i>[Pseudomonas] boreopolis</i>	979 ^T	67.8	68.0	0.05	61.0	0.04	77.0	0.05
<i>[Pseudomonas] pictorum</i>	981 ^T	65.7	66.5	0.10			77.0	0.12

TABLE 12—Continued

Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA													
<i>Deleya aquamarina</i> LMG 2853t1		<i>Shewanella putrefaciens</i> LMG 2268t1 ^T		<i>Xanthomonas campestris</i> LMG 568 ^T		<i>Marinomonas vaga</i> LMG 2845 ^T		<i>Aeromonas hydrophila</i> LMG 2844 ^T		<i>Pasteurella multocida</i> LMG 2851 ^T		<i>Oceanospirillum linum</i> LMG 5214 ^T	
<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding
68.0	0.09	71.0	0.27			65.0	0.22			66.0	0.17	68.0	0.15
71.5	0.06	68.0	0.24	65.0	0.05	69.5	0.12	68.0	0.14			70.0	0.08
65.0	0.09			65.0	0.07	69.5	0.10	69.0	0.06			70.5	0.03
												67.5	0.03
65.0	0.07			65.5	0.06	68.5	0.12					69.5	0.03
												66.5	0.02
						69.0	0.08						
						70.5	0.17						
73.5	0.19												

Vibrionaceae with a $T_{m(e)}$ of 77.5°C versus *Vibrio parahaemolyticus* (Table 8). This organism is certainly not a member of the genus *Pseudomonas*. Its G+C content (45.6 mol%) also excludes it from the genus *Pseudomonas*. The exact generic and specific status of this bacterium in the family *Vibrionaceae* has to be determined.

Misnamed pseudomonads belonging to the *Shewanella* (formerly *Pseudomonas* and *Alteromonas*) *putrefaciens* rRNA branch. “[*Pseudomonas*] *rubescens*” LMG 2279 (54) has a $T_{m(e)}$ value of 79°C, which is very similar to the $T_{m(e)}$ value of the homologous duplex (79.5°C) of *Shewanella putrefaciens* LMG 2268t1^T (Table 9). This close relationship between the “[*Pseudomonas*] *rubescens*” strain and the type strain of *Shewanella putrefaciens* has been pointed out phenotypically (35) and by DNA:DNA hybridizations (40).

Misnamed pseudomonads belonging to the rRNA branch of the *Enterobacteriaceae*. “[*Pseudomonas*] *trifolii*” LMG 2598 groups with a $T_{m(e)}$ of 77°C versus *Escherichia coli* in the rRNA branch of the *Enterobacteriaceae* (Table 10). Thus, our results do not contradict the proposed and generally accepted inclusion of “[*Pseudomonas*] *trifolii*” in *Erwinia herbicola* (33). Recently, Verdonck et al. (56) showed that this strain belongs phenotypically in *Erwinia herbicola* phenon 9. The position of leaf nodule organism LMG 2806 has been discussed previously in more detail (16).

Misnamed pseudomonads belonging to the rRNA branch of the *Aeromonadaceae*. [*Pseudomonas*] *doudoroffii* LMG 2180^T, with a $T_{m(e)}$ of 74.0°C and 0.25% rRNA binding versus *Aeromonas hydrophila* (Table 11), is located at the lower border of the rRNA branch of the *Aeromonadaceae*. Therefore, this species cannot belong to the same lineage as *Pseudomonas aeruginosa*, as was proposed by Baumann et al. (2). We believe that [*Pseudomonas*] *doudoroffii* LMG 2180^T is not a member of the genus *Pseudomonas*. It is not clear yet whether this bacterium may be included in the genus *Aeromonas* or whether it deserves separate generic rank. An extensive study comparing this species with authentic *Aeromonas* species is required for a definite conclusion.

Misnamed pseudomonads located at the junction of the first and second rRNA superfamilies. The organisms located at the junction of the first and second rRNA superfamilies are shown in Table 12. None of these strains definitely belongs to either one of our rRNA branches; thus, they are certainly not members of the genus *Pseudomonas*. The Lizarraga strains (349, 1371, 1613, 2006, 2014, 2026, 2128, and 2145), with $T_{m(e)}$ values ranging from 71 to 73°C versus *Pseudomonas fluorescens*, probably belong in the second rRNA superfamily. The other strains “[*Pseudomonas*] *atlantica*” LMG 2139, [*Pseudomonas*] *elongata* LMG 2182^T, [*Pseudomonas*]

TABLE 14. Organisms belonging to the *Deleya* rRNA branch: DNA base compositions and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA														
Name	LMG no.	G+C content (mol%)	<i>Pseudomonas fluorescens</i> LMG 1794 ^T		<i>Deleya aquamarina</i> LMG 2853t1		<i>Alteromonas macleodii</i> LMG 2843 ^T		<i>Alteromonas haloplanktis</i> LMG 2852 ^T		<i>Shewanella putrefaciens</i> LMG 2268t1 ^T		<i>Marinomonas vaga</i> LMG 2845 ^T	
			<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding
“[<i>Pseudomonas bathycetes</i> ”	2145	56.0			80.5	0.17					67.5	0.14	70.0	0.20
[<i>Pseudomonas beijerinckii</i>	2148 ^T	58.6	70.0	0.16	74.5	0.16								
<i>Deleya marina</i>	2218t1	63.3	70.5	0.15	75.5	0.15								
<i>Deleya marina</i>	2217 ^T	63.6			75.5	0.16	67.0	0.14	66.5	0.14			71.0	0.18

TABLE 15. Organisms belonging to the *Acinetobacter* rRNA branch: DNA base compositions and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%)	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA											
			<i>Pseudomonas fluorescens</i> LMG 1794 ^T		<i>Alteromonas macleodii</i> LMG 2843 ^T		<i>Alteromonas haloplanktis</i> LMG 2852 ^T		<i>Marinomonas vaga</i> LMG 2845 ^T		<i>Acinetobacter calcoaceticus</i> LMG 1046t1 ^T		<i>Xanthomonas campestris</i> LMG 568 ^T	
			<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding	<i>T_{m(e)}</i> (°C)	% rRNA binding
“[<i>Pseudomonas pavonacea</i>]”	2242	45.9	66.0	0.17	62.0	0.14	64.0	0.19	70.0	0.28	76.0	0.35		
“[<i>Pseudomonas pavonacea</i>]”	2241	45.6			64.0	0.08	60.5	0.19	66.0	0.25	75.5	0.37		
“[<i>Pseudomonas cruciviae</i>]”	2175	39.7	66.5	0.10	64.0	0.09			67.5	0.14	75.5	0.21	64.0	0.07

nautica LMG 2226^T, and *Cellvibrio mixtus* subsp. *mixtus* LMG 2847, LMG 2848, and LMG 2849), all exhibit *T_{m(e)}* values around 70°C versus the reference strains from the first and second rRNA superfamilies. In a taxonomic study, [*Pseudomonas*] *nautica* has been included in the same lineage as *Pseudomonas aeruginosa* (2). This organism was also included in group I (the *Pseudomonas fluorescens* group) of Whitaker et al. (57). Our results do not confirm this assignment. The correct taxonomic position and generic name of this misnamed organism remain to be established. In 1985 Blackall et al. (5) revived the genus *Cellvibrio*. Numerical analysis of morphological and biochemical data showed that the revived genus is different from the *Pseudomonas* species included here, indicating that the *Cellvibrio* strains are not at all related to the genus *Pseudomonas*.

Misnamed pseudomonads belonging to the *Xanthomonas* rRNA branch. Two strains isolated from soil (23), [*Pseudomonas*] *boreopolis* LMG 979^T and [*Pseudomonas*] *pictorum* LMG 981^T, have *T_{m(e)}* values of 77°C versus *X. campestris* (Table 13); they are generically misnamed and belong in the genus *Xanthomonas*. Both of these strains are about the same distance from *X. campestris* as *Xanthomonas maltophilia* (50). Van den Mooter et al. (manuscript in preparation) have shown that these taxa are phenotypically different. Strains LMG 979^T and LMG 981^T probably deserve separate species or subspecies status in *Xanthomonas*.

Misnamed pseudomonads belonging to the *Deleya* rRNA branch. Baumann et al. (2) reclassified [*Alcaligenes*] *aestus*, [*Alcaligenes*] *cupidus*, [*Alcaligenes*] *pacificus*, and [*Alcaligenes*] *venustus* together with [*Pseudomonas*] *marina* in the new genus *Deleya*. Hybridizations with rRNA from *Deleya aquamarina* LMG 2853 confirmed that the marine *Alcaligenes* species (1) are not at all related to the authentic genus *Alcaligenes*, which belongs in the third rRNA superfamily. The *Deleya* strains (formerly the marine *Alcaligenes* strains)

constitute a separate rRNA branch in the second rRNA superfamily (32). Our hybridization data show that (i) [*Pseudomonas*] *marina* is indeed a member of the *Deleya* rRNA branch, with a *T_{m(e)}* of 75.5°C versus *Deleya aquamarina* LMG 2853, and (ii) "[*Pseudomonas*] bathycetes," with a *T_{m(e)}* of 80.5°C, and [*Pseudomonas*] *beijerinckii*, with a *T_{m(e)}* of 74.5°C, also belong in this rRNA branch (Table 14). The three misnamed pseudomonads were isolated from marine environments (*Deleya marina* and "[*Pseudomonas*] bathycetes") or salted beans ([*Pseudomonas*] *beijerinckii*). In our numerical analysis these organisms grouped together at a similarity level of more than 80% with "*Deleya aquamarina*" LMG 2853 in phenon 2 (Fig. 2).

Misnamed pseudomonads belonging to the *Acinetobacter* rRNA branch. We examined two strains of "[*Pseudomonas*] pavonacea" (36), an original Levine strain from creamery waste (strain LMG 2242; G+C content, 45.9 mol%) and strain LMG 2241 (G+C content, 45.6 mol%) (37), and one strain of the phenol- and cresol-attacking soil bacterium "[*Pseudomonas*] cruciviae," strain LMG 2175 (23) (Table 15). With *T_{m(e)}* values of 75.5 to 76°C these organisms fit in the genus *Acinetobacter* [*T_{m(e)}* range, 74.5 to 79.5°C]. In 1961 Lysenko (37) showed that "[*Pseudomonas*] pavonacea" is phenotypically different from the rest of the genus *Pseudomonas*. Furthermore, there are some phenotypic differences among "[*Pseudomonas*] pavonacea," "[*Pseudomonas*] cruciviae," and *Acinetobacter*; both misnamed pseudomonads have two striking features, motility and the presence of oxidase, which are lacking in *Acinetobacter* species. In our phenotypic analysis (Fig. 2) "[*Pseudomonas*] pavonacea" LMG 2242 and "[*Pseudomonas*] cruciviae" LMG 2175 clustered at a similarity level of 80% with *Acinetobacter calcoaceticus* LMG 1046t1^T in phenon 3, indicating that these strains are highly related.

Misnamed pseudomonads belonging to the *Rhizobium loti*

TABLE 16. Organism belonging to the *Rhizobium loti* rRNA branch: DNA base composition and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%)	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA									
			<i>Pseudomonas fluorescens</i> LMG 1794 ^T		[<i>Pseudomonas</i>] <i>acidovorans</i> LMG 1226 ^T		[<i>Flavobacterium</i>] <i>capsulatum</i> LMG 2830 ^T		<i>Agrobacterium tumefaciens</i> LMG 196		<i>Rhizobium loti</i> LMG 6123	
			<i>T</i> _{m(e)} (°C)	% rRNA binding	<i>T</i> _{m(e)} (°C)	% rRNA binding	<i>T</i> _{m(e)} (°C)	% rRNA binding	<i>T</i> _{m(e)} (°C)	% rRNA binding	<i>T</i> _{m(e)} (°C)	% rRNA binding
[<i>Pseudomonas</i>] <i>aminovorans</i>	2122 ^T	62.1	59.0	0.03	58.5	0.05	69.5	0.16	72.5	0.08	76.5	0.06

TABLE 17. Organisms belonging to the [*Flavobacterium*] *capsulatum* rRNA branch: DNA base compositions and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%)	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA					
			<i>Pseudomonas fluorescens</i> LMG 1794 ^T		[<i>Pseudomonas</i>] <i>acidovorans</i> LMG 1226 ^T		[<i>Flavobacterium</i>] <i>capsulatum</i> LMG 2830 ^T	
			<i>T</i> _{m(c)} (°C)	% rRNA binding	<i>T</i> _{m(c)} (°C)	% rRNA binding	<i>T</i> _{m(c)} (°C)	% rRNA binding
“[<i>Pseudomonas</i>] <i>azotocolligans</i> ”	2142	65.6					76.0	0.04
[<i>Pseudomonas</i>] <i>paucimobilis</i>	1227 ^T	64.4	59.5	0.06	61.0	0.07	75.0	0.06
[<i>Pseudomonas</i>] <i>paucimobilis</i>	2239	62.7	59.5	0.05			75.5	0.10
[<i>Pseudomonas</i>] <i>paucimobilis</i>	2240	64.6	59.5	0.06			76.0	0.13

TABLE 18. Organisms belonging to rRNA superfamily IV: DNA base compositions and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

Name	LMG no.	G+C content (mol%)	Source of ¹⁴ C- or ³ H-labeled 23S or 16S rRNA									
			<i>Pseudomonas fluorescens</i> LMG 1794 ^T		<i>[Pseudomonas] acidovorans</i> LMG 1226 ^T		<i>Agrobacterium tumefaciens</i> LMG 196		<i>[Flavobacterium] capsulatum</i> LMG 2830 ^T		<i>Acetobacter acetii</i> LMG 12611 ^T	
			<i>T_m(e)</i> (°C)	% rRNA binding	<i>T_m(e)</i> (°C)	% rRNA binding	<i>T_m(e)</i> (°C)	% rRNA binding	<i>T_m(e)</i> (°C)	% rRNA binding	<i>T_m(e)</i> (°C)	% rRNA binding
[" <i>Pseudomonas</i> "] <i>riboflavina</i> ^{''}	2277	61.5	61.0	0.04	55.5	0.03	67.5	0.08	63.5	0.03	65.5	0.04
<i>[Pseudomonas]</i> <i>echinoides</i>	2181 ^T	65.3	56.5	0.03	56.0	0.04					65.5	0.04

rRNA branch. [*Pseudomonas*] *aminovorans* LMG 2122^T, with a $T_{m(e)}$ of 76.5°C and 0.06% rRNA binding (Table 16), falls on the *Rhizobium loti* rRNA branch but outside *Rhizobium loti* sensu stricto (10). The relationship of this organism with other members of the *Rhizobium-Agrobacterium-Brucella* complex should be examined more closely.

Misnamed pseudomonads belonging to the [Flavobacterium] capsulatum rRNA branch. The [Flavobacterium] capsulatum rRNA branch is located in the fourth rRNA superfamily (3). The reference organism which we used is a misnamed *Flavobacterium* strain (Table 17). Two of the misnamed *Pseudomonas* species, [*Pseudomonas*] paucimobilis [$T_{m(e)}$ values, 75 to 76°C] and “[*Pseudomonas*] azotocolligans” [$T_{m(e)}$, 76°C], are located in this rRNA branch. The [*Pseudomonas*] paucimobilis strains which we used were isolated from clinical sources. Yabuuchi et al. (60) reidentified the generically misnamed organism [Flavobacterium] devorans

LMG 4017^T as a strain of [*Pseudomonas*] *paucimobilis*. Owen and Jackman (39) confirmed this similarity between the type strains of [*Flavobacterium*] *devorans* and [*Pseudomonas*] *paucimobilis* by DNA:DNA hybridization. Our DNA:rRNA hybridization data (3) (Table 17) show that the [*Pseudomonas*] *paucimobilis* strains are as close to the reference organism [*Flavobacterium*] *capsulatum* as [*Flavobacterium*] *devorans* is. "[*Pseudomonas*] *azotocolligans*" is a free-living nitrogen-fixing organism. It is clearly neither a pseudomonad nor a member of the *Azotobacteraceae*, which is located in the second rRNA superfamily (12, 14). Owen and Jackman (39) argued that a certain background (8 to 12%) DNA:DNA similarity between [*Pseudomonas*] *paucimobilis* on the one hand and [*Flavobacterium*] *capsulatum*, "[*Pseudomonas*] *azotocolligans*," and [*Pseudomonas*] *echinoides* on the other hand, together with chemotaxonomic data (like the presence of the yellow pigment nostoxanthin),

TABLE 19. Organisms belonging to none of the established rRNA superfamilies: DNA base compositions and properties of DNA:rRNA hybrids with labeled rRNAs from reference strains

[illegible]

may support the creation of a new genus for these organisms. Our data confirm the rather close relationship among [*Pseudomonas*] *paucimobilis*, [*Pseudomonas*] *capsulatum*, and "[*Pseudomonas*] *azotocolligans*." It is not yet clear whether [*Pseudomonas*] *echinoides* also belongs in this group (see below).

Misnamed pseudomonads belonging to rRNA superfamily IV. Our hybridization data did not allow definite assignment of "[*Pseudomonas*] *riboflavina*" LMG 2277 or [*Pseudomonas*] *echinoides* LMG 2181^T to one of the established rRNA branches. However, $T_{m(e)}$ values between 65 and 70°C (Table 18) for DNA:rRNA hybrids of these organisms versus the reference rRNAs of *Agrobacterium tumefaciens*, [*Flavobacterium*] *capsulatum*, and *Acetobacter aceti* indicate that both of these misnamed *Pseudomonas* species are members of rRNA superfamily IV.

Misnamed pseudomonads not located in any of the known gram-negative rRNA superfamilies. We have not been able to localize "[*Pseudomonas*] *coenobios*" LMG 2169, "[*Pseudomonas*] *membranula*" LMG 2221, [*Pseudomonas*] *flectens* LMG 2187, and "[*Pseudomonas*] *stereotropis*" LMG 2325 in our rRNA framework (Table 19). The taxonomic position of these organisms remains unclear. They have been misnamed, and they do not belong in the genus *Pseudomonas*. "[*Pseudomonas*] *perlurida*" LMG 2244 belongs to the gram-positive bacteria; it is located versus *Arthrobacter oxydans* LMG 3816 (= CBRI 21010) at a $T_{m(e)}$ of around 70°C on the rRNA similarity dendrogram (data not shown). It is perhaps related to the *brevibacteria*.

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