Ribosomal Ribonucleic Acid Cistron Similarities of Phytopathogenic *Pseudomonas* Species

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Deoxyribonucleic acid (DNA)-ribosomal ribonucleic acid (rRNA) hybridizations were carried out between 23S ^{14}C - or ^3H -labeled rRNAs from type strains *Pseudomonas fluorescens* ATCC 13525, *Pseudomonas acidovorans* ATCC 15668, *Pseudomonas solanacearum* ATCC 11696, and *Xanthomonas campestris* NCPPB 528 and DNA from one or more strains of several taxonomically assigned or unassigned phytopathogenic *Pseudomonas* species. The strains were assigned to one of the following rRNA branches: (i) the *P. fluorescens* rRNA branch (the authentic pseudomonads), containing also *Pseudomonas agarici*, *Pseudomonas amygdali*, *Pseudomonas asplenii*, *Pseudomonas caricapapayae*, *Pseudomonas cichorii*, *Pseudomonas corrugata*, *Pseudomonas fuscovaginae*, *Pseudomonas marginalis* (*P. marginalis* pathovar *marginalis*, *P. marginalis* pathovar *alfalfae*, and *P. marginalis* pathovar *pastinacae*), *Pseudomonas meliae*, the *Pseudomonas syringae* group (including "*Pseudomonas aceris*," "*Pseudomonas antirrhini*," "*Pseudomonas apii*," "*Pseudomonas berberidis*," "*Pseudomonas cannabina*," "*Pseudomonas coronafaciens*," "*Pseudomonas eriobotryae*," "*Pseudomonas lapsa*," "*Pseudomonas maculicola*," "*Pseudomonas oryzicola*," "*Pseudomonas panici*," "*Pseudomonas passiflorae*," "*Pseudomonas primulae*," "*Pseudomonas ribicola*," "*Pseudomonas sesami*," "*Pseudomonas striafaciens*," *P. syringae*, "*Pseudomonas ulmi*," and "*Pseudomonas viburni*"), *Pseudomonas tolaasii*, *Pseudomonas viridiflava*, and "*Pseudomonas washingtoniae*"; (ii) the *P. solanacearum* rRNA branch, containing *P. solanacearum*, *Pseudomonas andropogonis* (synonym, "*Pseudomonas stizolobii*"), *Pseudomonas caryophylli*, *Pseudomonas cepacia*, *Pseudomonas gladioli* (synonyms, "*Pseudomonas alliicola*" and "*Pseudomonas marginata*"), *Pseudomonas glumae*, *Pseudomonas rubrisubalbicans*, and *Pseudomonas woodsii*; (iii) the *P. acidovorans* rRNA branch, containing also "*Pseudomonas albobacillans*" (synonym of *Pseudomonas avenae*), *Pseudomonas pseudoalcaligenes* subsp. *citrulli*, *Pseudomonas rubrilineans*, and "*Pseudomonas setariae*"; and (iv) the *Xanthomonas* rRNA branch, containing *X. campestris*, *Pseudomonas betle*, "*Pseudomonas gardneri*," *Pseudomonas hibiscicola*, "*Pseudomonas mangiferaeindicae*," "*Pseudomonas viticola*," and "*Pseudomonas vitiswoodrowii*." *Pseudomonas flectens* and *Pseudomonas cissicola* definitely have to be removed from the genus *Pseudomonas*. *Pseudomonas cattleiae*, and "*Pseudomonas viridilivida*" are heterogeneous and require additional examination.

The genus *Pseudomonas*, as defined in *Bergey's Manual of Determinative Bacteriology*, 8th ed. (23), and *Bergey's Manual of Systematic Bacteriology* (57), consists of a very large and heterogeneous assemblage of polarly flagellated gram-negative bacteria. Valuable phenotypic studies on the taxonomy within this genus were carried out by several workers (34, 35, 44, 69, 70). The extensive phenotypic characterization of a large number of *Pseudomonas* strains by Stanier et al. (84) resulted in improved classification into species and species groups.

Additional approaches have been used to clarify the relationships among the taxa in the genus *Pseudomonas*. In general, deoxyribonucleic acid (DNA) base compositions (mean molar percent guanine plus cytosine [G+C]) (46) and the results of DNA-DNA hybridization (58) agreed with the phenotypic classification scheme. DNA-ribosomal ribonucleic acid (rRNA) hybridization (59) revealed the existence of five rRNA homology groups of named *Pseudomonas*. These findings were supported by the results of immunological characterization of the host factor required for coliphage Q β ribonucleic acid replication (24), the results of cellular fatty acid composition studies (36), and enzymic data (15).

Recently, De Vos and De Ley (22) confirmed the existence of the same five rRNA groups by using another DNA-rRNA hybridization technique. However, by including many more strains and in particular many strains of a great variety of gram-negative taxa, these authors found that

these rRNA groups are less related to each other than they are to other gram-negative genera (Fig. 1). Therefore, De Vos and De Ley rejected the present classification of *Pseudomonas* species in a single genus. The following division was proposed: (i) the *Pseudomonas fluorescens* rRNA branch, which De Vos and De Ley considered to be the authentic genus *Pseudomonas*, containing the type species, *Pseudomonas aeruginosa* (this branch corresponds to Section I of *Pseudomonas* in *Bergey's Manual of Systematic Bacteriology* [57]); (ii) the *Pseudomonas acidovorans* rRNA branch, corresponding to Section III of *Pseudomonas* (57); (iii) the *Pseudomonas solanacearum* rRNA branch, corresponding to Section II of *Pseudomonas* (57) (the latter two branches should be removed from the genus *Pseudomonas*); (iv) the *Xanthomonas* rRNA branch, containing "*Pseudomonas*" *maltophilia*, which has been reclassified as *Xanthomonas maltophilia* (89); and (v) *Pseudomonas vesicularis* and *Pseudomonas diminuta*, which do not belong in the genus *Pseudomonas* at all.

A great number of phytopathogenic *Pseudomonas* species have been created by using the so-called new host-new species concept. Because of poor descriptions, a limited number of these species were accepted on the Approved Lists of Bacterial Names (81), on the Validation Lists, and by publication in the International Journal of Systematic Bacteriology since 1980. A great number have not yet been officially accepted, although they have important phytopathological and economic properties (26, 102). A certain number of phytopathogenic *Pseudomonas* species have been

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FIG. 1. rRNA cistron similarity dendrogram of various gram-negative bacteria, based on $T_{m(e)}$ values (in degrees Celsius) of DNA-rRNA hybrids. All data were determined by members of our research group. The solid bars indicate the $T_{m(e)}$ ranges within individual rRNA branches. The branching levels were calculated from previously published data (18, 20–22, 30, 89, 90, 97), as well as from unpublished data (dotted lines) obtained by our research group by using the unweighted average pair group method.

assigned to taxonomic positions within the framework of *Bergey's Manual of Determinative Bacteriology*, 8th ed. (23), and *Bergey's Manual of Systematic Bacteriology* (57); others still remain taxonomically unattached (e.g., those listed in the Addenda I and III of *Bergey's Manual of Determinative Bacteriology*, 8th ed. [23], and in Section V of *Bergey's Manual of Systematic Bacteriology* [57]). Division into a fluorescent group and a nonfluorescent group (102) has been proposed for practical identification purposes.

From our previous DNA-rRNA hybridization experiments (22) it appeared that phytopathogenic *Pseudomonas* species belong in different rRNA branches. It was the purpose of the study described here to determine the correct taxonomic positions at the generic and subgeneric levels of a large number of the above-mentioned phytopathogenic *Pseudomonas* species and strains by means of DNA-rRNA hybridization.

MATERIALS AND METHODS

Bacterial strains. The strains which we used are listed in Table 1. For practical reasons, in our discussion below we use the original species names as they appear in Table 1. For mass cultures, the bacteria were grown in Roux flasks on media solidified with 2 to 2.5% agar. The compositions of the media used have been described previously (18, 20–22, 30, 99). When different colony types were isolated from the subcultures which we received, they were kept as separate strains only when the electropherograms of their soluble cell proteins were different.

Preparation of labeled rRNA and DNA and hybridization conditions. rRNAs labeled with ^{14}C or ^3H were prepared from type strains *P. fluorescens* ATCC 13525, *P. acidovorans* ATCC 15668, *P. solanacearum* ATCC 11696, and *Xanthomonas campestris* NCPPB 528 as described previously (22). For all DNA preparations except one we used the

methods described previously (22); for the preparation of DNA from the type strain of "*Pseudomonas viridilivida*," strain NCPPB 1963, we treated the DNA with lysozyme and *n*-dodecylamine in sucrose-TES₄ [0.1 M tris(hydroxymethyl)aminomethane-hydrochloride (pH 8.0) with 0.07 disodium ethylenediaminetetraacetic acid and 0.05 M NaCl] as described by Meynell (48). The methods used for the preparation of high-molecular-weight DNA were those used by De Vos and De Ley (22), whereas the methods used for fixation of single-stranded high-molecular-weight DNA on membrane filters, saturation hybridization between ^{14}C - or ^3H -labeled rRNA and filter-fixed DNA, determination of the thermal stability of the hybrids, and quantitative chemical determination of the DNA on the filters were the methods used by De Ley and De Smedt (17); these methods have been used previously in studies done by workers in our laboratory (18, 20, 21, 30, 89, 90, 97).

Average molar percent G + C. Average DNA base compositions either were determined or were taken from previous papers. We used the methods described previously (22). The data are shown in Table 2.

RESULTS AND DISCUSSION

The results of the DNA-rRNA hybridizations are shown in Table 2. The hybrids were characterized by the following two parameters: the temperature at which 50% of the hybrid was eluted (the $T_{m(e)}$ value) and the percentage of rRNA binding (i.e., the amount of labeled rRNA bound after ribonuclease treatment per 100 μg of DNA retained on the filter). For each labeled reference rRNA, the $T_{m(e)}$ values were plotted versus the percentages of rRNA binding on what we call an rRNA similarity map (Fig. 2 through 5). The $T_{m(e)}$ value is the most decisive taxonomic parameter discussed extensively in our previous papers (18, 21, 22). The

TABLE 1. Organisms used and their nomenclatural status, strain numbers, origins and growth media

Sequence no.	Species name as originally described ^a	Name according to Young et al. ^b	Classification in:		Strain	Host plant or origin and place and year of isolation	Growth medium ^c
			<i>Bergey's Manual of Determinative Bacteriology</i> , 8th ed.	<i>Bergey's Manual of Systematic Bacteriology</i>			
1	" <i>P. aceris</i> " (1)	<i>P. syringae</i> pathovar <i>aceris</i>	Addendum I	Section I	NCPPB 958 ^d	<i>Acer</i> sp., United States, year unknown	B
2	<i>P. acidovorans</i> (AL) (19)		Section III	Section III	ATCC 15668 ^{Te}	Acetamide-enriched soil, Holland, 1926	B
3	<i>P. agarici</i> (AL) (100)	<i>P. agarici</i>		Section V	NCPPB 1999 ¹	<i>Agaricus bisporus</i> United Kingdom, 1966	Z5
4	<i>P. agarici</i> (AL) (100)				NCPPB 2289 ^T	<i>Agaricus bisporus</i> , New Zealand, 1969	Z5
5	<i>P. agarici</i> (AL) (100)				NCPPB 2471 ¹¹	<i>Agaricus bisporus</i> , United Kingdom, 1972	Z5
6	<i>P. agarici</i> (AL) (100)				NCPPB 2471 ¹²	<i>Agaricus bisporus</i> , United Kingdom, 1972	Z5
7	" <i>P. alboprecipitans</i> " (73)	<i>P. avenae</i>	Addendum I	Section V	NCPPB 1011 ^T	<i>Zea mays</i> , United States, 1958	B
8	" <i>P. alboprecipitans</i> " (73)				NCPPB 2399	<i>Oryza sativa</i> , Philippines, year unknown	Z5
9	" <i>P. alboprecipitans</i> " (73)				NCPPB 2401	<i>Zea mays</i> , Japan, 1966	Z5
10	" <i>P. alliicola</i> " (12)	<i>P. gladioli</i> pathovar <i>alliicola</i>	Section II	Section II	NCPPB 947 ^d	Host plant unknown, United States, 1939	Z5
11	<i>P. amygdali</i> (AL) (66)	<i>P. amygdali</i>		Section V	NCPPB 2607 ^T	<i>Prunus dulcis</i> , Greece, 1967	Z3
12	<i>P. amygdali</i> (AL) (66)				NCPPB 2608	<i>Prunus dulcis</i> , Greece, 1967	Z3
13	<i>P. amygdali</i> (AL) (66)				NCPPB 2610	<i>Prunus dulcis</i> , Greece, 1968	Z3
14	<i>P. andropogonis</i> (AL) (83)	<i>P. andropogonis</i>	Addendum I	Section V	NCPPB 933	<i>Zea mays</i> , United States, 1959	B
15	<i>P. andropogonis</i> (AL) (83)				NCPPB 934 ^T	<i>Sorghum bicolor</i> , United States, 1959	B
16	" <i>P. antirrhini</i> " (91)	<i>P. syringae</i> pathovar <i>antirrhini</i>		Section I	NCPPB 1761	<i>Antirrhinum majus</i> , United Kingdom, 1965	B
17	" <i>P. apii</i> " (37)	<i>P. syringae</i> pathovar <i>apii</i>	Addendum I	Section I	NCPPB 1626 ^d	<i>Apium graveolens</i> var. <i>dulce</i> , United States, 1942	B
18	<i>P. asplenii</i> (AL) (4)	<i>P. asplenii</i>	Addendum I	Section V	NCPPB 1947 ^T	<i>Asplenium nidus</i> , place and year of isolation unknown	B
19	" <i>P. berberidis</i> " (95)	<i>P. syringae</i> pathovar <i>berberidis</i>	Addendum I	Section I	NCPPB 1871	<i>Berberis thunbergii</i> , United States, 1942	Z5
20	" <i>P. berberidis</i> " (95)				NCPPB 2724 ^d	<i>Berberis</i> sp., New Zealand, 1972	Z5
21	<i>P. betle</i> (AL) (67)	<i>P. betle</i>	Addendum III		NCPPB 323 ^T	<i>Piper betle</i> , Sri Lanka, 1953	B
22	" <i>P. cannabina</i> " (86)	<i>P. syringae</i> pathovar <i>cannabina</i>	Addendum I	Section I	NCPPB 1410	<i>Cannabis sativa</i> , Hungary, 1957	B
23	" <i>P. cannabina</i> " (86)				NCPPB 2069	<i>Cannabis sativa</i> , Yugoslavia, year unknown	Z5
24	<i>P. caricapapayae</i> (AL) (71)	<i>P. caricapapayae</i>		Section V	NCPPB 1872	<i>Carica papaya</i> , Brazil, 1955	B
25	<i>P. caricapapayae</i> (AL) (71)				NCPPB 1873 ^T	<i>Carica papaya</i> , Brazil, 1966	Z5
26	<i>P. caryophylli</i> (AL) (12)	<i>P. caryophylli</i>	Section II	Section II	NCPPB 349	<i>Dianthus caryophyllus</i> , Denmark, year unknown	PAF
27	<i>P. caryophylli</i> (AL) (12)				NCPPB 609	<i>Dianthus caryophyllus</i> , United Kingdom, 1958	Z3
28	<i>P. caryophylli</i> (AL) (12)				NCPPB 2151 ^T	<i>Dianthus caryophyllus</i> , United States, 1951	Z5
29	<i>P. cattleyae</i> (AL) (63)	<i>P. cattleyae</i>	Addendum I	Section V	NCPPB 961 ^T	Unknown	Z5

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TABLE 1—Continued

Sequence no.	Species name as originally described ^a	Name according to Young et al. ^b	Classification in:		Strain	Host plant or origin and place and year of isolation	Growth medium ^c
			Bergey's Manual of Determinative Bacteriology, 8th ed.	Bergey's Manual of Systematic Bacteriology			
30	<i>P. cattleyae</i> (AL) (63)				NCPPB 1874	<i>Phalaenopsis</i> sp., United States, 1950	Z5
31	<i>P. cattleyae</i> (AL) (63)				PDDCC 3992	<i>Cattleya</i> sp., United States, year unknown	PAF
32	<i>P. cepacia</i> (VL) (13)	<i>P. cepacia</i>	Section II	Section II	Ballard 717 ^T	<i>Allium cepa</i> , place and year of isolation unknown	Z5
33	<i>P. cepacia</i> (VL) (13)				Stanier 382	Forest soil, Trinidad, 1958	B
34	<i>P. cepacia</i> (VL) (13)				NCTC 10661	Forest soil, Trinidad, 1958	Z5
35	<i>P. cichorii</i> (AL) (88)	<i>P. cichorii</i>	Section I	Section I	NCPPB 906	<i>Chrysanthemum morifolium</i> , United States, 1957	B
36	<i>P. cichorii</i> (AL) (88)				NCPPB 943 ^T	<i>Cichorium endivia</i> , Germany, 1929	Z5
37	<i>P. cichorii</i> (AL) (88)				NCPPB 1512	<i>Chrysanthemum morifolium</i> , United States, 1962	B
38	<i>P. cissicola</i> (AL) (93)	<i>P. cissicola</i>	Addendum III	Section V	NCPPB 2982 ^T	<i>Cissus japonica</i> , Japan, 1974	Z5
39	<i>P. cissicola</i> (AL) (93)				PDDCC 4290	<i>Cissus japonica</i> , Japan, 1974	PAF
40	" <i>P. coronafaciens</i> " (27)	<i>P. syringae</i> pathovar <i>coronafaciens</i>	Section I	Section I	NCPPB 1328	<i>Bromus</i> sp., Canada, 1962	Z5
41	<i>P. corrugata</i> (VL) (75)	<i>P. corrugata</i>		Section V	NCPPB 2445 ^T	<i>Lycopersicon lycopersicum</i> , United Kingdom, 1972	Z5
42	<i>P. corrugata</i> (VL) (75)				NCPPB 2447	<i>Lycopersicon lycopersicum</i> , United Kingdom, 1972	PAF
43	<i>P. corrugata</i> (VL) (75)				NCPPB 2455	<i>Lycopersicon lycopersicum</i> , United Kingdom, 1972	Z5
44	" <i>P. eriobotryae</i> " (92)	<i>P. syringae</i> pathovar <i>eriobotryae</i>	Addendum I	Section I	NCPPB 2331 ^d	<i>Eriobotrya japonica</i> , United States, 1970	Z5
45	<i>P. flectens</i> (AL) (38)	<i>P. flectens</i>	Addendum I		NCPPB 538	<i>Phaseolus vulgaris</i> , Australia, 1957	PAF
46	<i>P. flectens</i> (AL) (38)				NCPPB 539 ^T	<i>Phaseolus vulgaris</i> , Australia, 1956	Z3
47	<i>P. fluorescens</i> (AL) (49)		Section I	Section I	ATCC 13525 ^T	Prefilter tanks, United Kingdom, 1951	B
48	<i>P. fuscovaginae</i> (VL) (51)				PDDCC 5939	<i>Oryza sativa</i> , Japan, year unknown	PAF
49	" <i>P. gardneri</i> " (85)				NCPPB 881 ^f	<i>Lycopersicon lycopersicum</i> , Yugoslavia, 1953	B
50	<i>P. gladioli</i> (AL) (80)	<i>P. gladioli</i> pathovar <i>gladioli</i>	Section II	Section II	NCPPB 1891 ^T	<i>Gladiolus</i> sp., United States, year unknown	Z5
51	<i>P. glumae</i> (AL) (40)	<i>P. glumae</i>		Section V	NCPPB 2391	<i>Oryza sativa</i> , Japan, 1967	Z5
52	<i>P. glumae</i> (AL) (40)				NCPPB 2981 ^T	<i>Oryza sativa</i> , Japan, 1967	Z5
53	<i>P. hibiscicola</i> (AL) (52)	<i>P. hibiscicola</i>	Addendum I		NCPPB 1683 ^T	<i>Hibiscus rosasinensis</i> , India, 1964	B
54	" <i>P. lapsa</i> " (2)	<i>P. syringae</i> pathovar <i>lapsa</i>	Addendum I	Section I	NCPPB 2096 ^d	<i>Zea</i> sp. hybrid seed, place and year of isolation unknown	B
55	" <i>P. maculicola</i> " (47)	<i>P. syringae</i> pathovar <i>maculicola</i>	Addendum I	Section I	NCPPB 1776	<i>Brassica oleracea</i> var. <i>botrytis</i> , United Kingdom, 1965	B
56	" <i>P. mangiferaeindicae</i> " (62)	<i>X. campestris</i> pathovar <i>mangiferaeindicae</i>	Addendum I	<i>X. campestris</i>	NCPPB 490 ^d	<i>Mangifera indica</i> , place and year of isolation unknown	B

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TABLE 1—Continued

Sequence no.	Species name as originally described ^a	Name according to Young et al. ^b	Classification in:		Strain	Host plant or origin and place and year of isolation	Growth medium ^c
			Bergey's Manual of Determinative Bacteriology, 8th ed.	Bergey's Manual of Systematic Bacteriology			
57	" <i>P. mangiferae</i> indicae" (62)				NCPPB 2387	<i>Mangifera indica</i> , India, 1970	Z5
58	" <i>P. mangiferae</i> indicae" (62)				NCPPB 2438	<i>Mangifera indica</i> , South Africa, 1971	Z5
59	<i>P. marginalis</i> (AL) (10)	<i>P. marginalis</i> pathovar <i>alfalfae</i>	Section I	Section I	PDDCC 5708 ^d	<i>Medicago sativa</i> , United States, 1971	PAF
60	<i>P. marginalis</i> (AL) (10)	<i>P. marginalis</i> pathovar <i>marginalis</i>	Section I	Section I	PDDCC 3553 ^T	<i>Cichorium intybus</i> , United States, 1949	PAF
61	<i>P. meliae</i> (VL) (54)				NCPPB 3033 ^T	<i>Melia azedarach</i> , Japan, 1974	PAF
62	" <i>P. oryzicola</i> " (39)	<i>P. syringae</i> pathovar <i>syringae</i>	Addendum I		NCPPB 388 ^f	<i>Oryza sativa</i> , Hungary, year unknown	B
63	" <i>P. oryzicola</i> " (39)				NCPPB 1417	<i>Oryza sativa</i> , Hungary, 1956	B
64	" <i>P. panici</i> " (28)	<i>P. syringae</i> pathovar <i>panici</i>		Section I	NCPPB 1498 ^d	Unknown	B
65	" <i>P. passiflorae</i> " (68)	<i>P. syringae</i> pathovar <i>passiflorae</i>	Addendum I	Section I	NCPPB 224	<i>Passiflora edulis</i> , New Zealand, year unknown	B
66	" <i>P. passiflorae</i> " (68)				NCPPB 1386	<i>Passiflora edulis</i> , New Zealand, 1962	B
67	" <i>P. pastinacae</i> " (14)	<i>P. marginalis</i> pathovar <i>pastinacae</i>	Addendum I	Section I	NCPPB 806 ^d	<i>Pastinaca sativa</i> , United States, 1959	B
68	" <i>P. primulae</i> " (3)	<i>P. syringae</i> pathovar <i>primulae</i>	Addendum I	Section I	NCPPB 133 ^d	<i>Primula</i> sp., United States, year unknown	B
69	<i>P. pseudoalcaligenes</i> subsp. <i>citrulli</i> (AL) (78)			Section I	PDDCC 6521	<i>Citrullus lanatus</i> , United States, 1978	PAF
70	<i>P. pseudoalcaligenes</i> subsp. <i>citrulli</i> (AL) (78)				PDDCC 6522	<i>Citrullus lanatus</i> , United States, 1977	PAF
71	" <i>P. ribicola</i> " (7)	<i>P. syringae</i> pathovar <i>ribicola</i>	Addendum I	Section I	NCPPB 963 ^d	<i>Ribes aureum</i> , place and year of isolation unknown	B
72	<i>P. rubrilineans</i> (AL) (41)	<i>P. rubrilineans</i>		Section V	NCPPB 359	<i>Saccharum officinarum</i> , Mauritius, year unknown	Z5
73	<i>P. rubrilineans</i> (AL) (41)				NCPPB 920 ^T	<i>Saccharum officinarum</i> , Reunion, 1960	B
74	<i>P. rubrilineans</i> (AL) (41)				NCPPB 1118	<i>Saccharum officinarum</i> , India, 1961	PAF
75	<i>P. rubrisubalbicans</i> (AL) (16)	<i>P. rubrisubalbicans</i>	Addendum I	Section V	NCPPB 1027 ^T	<i>Saccharum officinarum</i> , United States, 1961	Z5
76	" <i>P. sesami</i> " (45)	<i>P. syringae</i> pathovar <i>sesami</i>	Addendum I	Section I	NCPPB 1016 ^d	<i>Sesamum orientale</i> , Yugoslavia, 1961	B
77	" <i>P. setariae</i> " (55)	<i>P. setariae</i>	Addendum I		NCPPB 1392 ^d	<i>Oryza sativa</i> , Japan, 1955	B
78	<i>P. solanacearum</i> (AL) (82)	<i>P. solanacearum</i>	Section III	Section II	NCPPB 173	<i>Solanum tuberosum</i> , Kenya, year unknown	Z5
79	<i>P. solanacearum</i> (AL) (82)				NCPPB 215	<i>Lycopersicon lycopersicum</i> , Rhodesia, year unknown	Z5
80	<i>P. solanacearum</i> (AL) (82)				NCPPB 253	<i>Casuarina equisetifolia</i> , Mauritius, 1949	Z5
81	<i>P. solanacearum</i> (AL) (82)				NCPPB 282	<i>Solanum tuberosum</i> , Colombia, 1950	B
82	<i>P. solanacearum</i> (AL) (82)				ATCC 11696 ^T	<i>Lycopersicon lycopersicum</i> , United States, year unknown	Z5
83	<i>P. solanacearum</i> (AL) (82)				NCPPB 339	Host plant unknown Israel, year unknown	Z5
					NCPPB 446	<i>Musa</i> sp., Trinidad, 1957	Z5

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TABLE 1—Continued

Sequence no.	Species name as originally described ^a	Name according to Young et al. ^b	Classification in:		Strain	Host plant or origin and place and year of isolation	Growth medium ^c
			Bergey's Manual of Determinative Bacteriology, 8th ed.	Bergey's Manual of Systematic Bacteriology			
84	<i>P. solanacearum</i> (AL) (82)						
85	<i>P. solanacearum</i> (AL) (82)				NCPPB 613	<i>Solanum tuberosum</i> , Brazil, 1958	B
86	<i>P. solanacearum</i> (AL) (82)				NCPPB 787	<i>Musa</i> sp., Costa Rica, year unknown	Z5
87	<i>P. solanacearum</i> (AL) (82)				NCPPB 789	<i>Musa</i> sp., Honduras, year unknown	Z5
88	<i>P. solanacearum</i> (AL) (82)				NCPPB 792	<i>Tectona grandis</i> , Malaysia, year unknown	B
89	<i>P. solanacearum</i> (AL) (82)				NCPPB 909	<i>Solanum tuberosum</i> , Egypt, 1961	Z5
90	<i>P. solanacearum</i> (AL) (82)				NCPPB 1019	<i>Lycopersicon lycopersicum</i> , Portugal, 1960	B
91	<i>P. solanacearum</i> (AL) (82)				NCPPB 1029	<i>Pelargonium capitatum</i> , Reunion, 1961	Z5
92	<i>P. solanacearum</i> (AL) (82)				Kelman 3	<i>Musa</i> sp., Costa Rica, year unknown	Z5
93	<i>P. solanacearum</i> (AL) (82)				Kelman 25	<i>Lycopersicon lycopersicum</i> , North Carolina, year unknown	Z5
94	<i>P. solanacearum</i> (AL) (82)				Kelman 81	<i>Solanum tuberosum</i> , Colombia, year unknown	Z5
95	" <i>P. striafaciens</i> " (29)	<i>P. syringae</i> pathovar <i>striafaciens</i>	Addendum I	Section I	NCPPB 1898 ^f	Unknown	B
96	" <i>P. stizolobii</i> " (98)		Addendum I		NCPPB 1024t ^f	<i>Mucuna deeringianum</i> , Zimbabwe, 1961	B
97	<i>P. syringae</i> (AL) (96)	<i>P. syringae</i> pathovar <i>syringae</i>	Section I	Section I	NCPPB 281 ^T	<i>Syringa vulgaris</i> , United Kingdom, 1950	Z3
98	<i>P. tolaasii</i> (AL) (56)	<i>P. tolaasii</i>	Section I	Section V	NCPPB 741t1	<i>Agaricus bisporus</i> , The Netherlands, 1951	Z5
99	<i>P. tolaasii</i> (AL) (56)				NCPPB 1116	<i>Agaricus bisporus</i> , United Kingdom, 1961	Z5
100	<i>P. tolaasii</i> (AL) (56)				NCPPB 1311	<i>Agaricus bisporus</i> , United Kingdom, 1962	Z5
101	<i>P. tolaasii</i> (AL) (56)				NCPPB 2192 ^T	<i>Agaricus bisporus</i> , United Kingdom, 1965	Z5
102	<i>P. tolaasii</i> (AL) (56)				NCPPB 2193	<i>Agaricus bisporus</i> , United Kingdom, 1968	Z5
103	" <i>P. ulmi</i> " (87)	<i>P. syringae</i> pathovar <i>ulmi</i>	Addendum I	Section I	NCPPB 632 ^d	<i>Ulmus</i> sp., Yugoslavia, 1958	Z5
104	" <i>P. viburni</i> " (94)	<i>P. syringae</i> pathovar <i>viburni</i>	Addendum I	Section I	NCPPB 1921 ^d	<i>Viburnum</i> sp. United States, year unknown	Z5
105	<i>P. viridiflava</i> (AL) (11)	<i>P. viridiflava</i>	Addendum I	Section I	NCPPB 1248t1	<i>Chrysanthemum morifolium</i> , United Kingdom, year unknown	Z5
106	<i>P. viridiflava</i> (AL) (11)				NCPPB 1810t1	<i>Phaseolus vulgaris</i> , United Kingdom, 1965	Z5
107	<i>P. viridiflava</i> (AL) (11)				NCPPB 2024	<i>Viola tricolor</i> , West Germany, 1967	Z5
108	" <i>P. viridilivida</i> " (9)	<i>P. viridilivida</i>	Addendum I		NCPPB 152t1	<i>Lactuca sativa</i> , United Kingdom, 1942	Z5
109	" <i>P. viridilivida</i> " (9)				NCPPB 1923	<i>Lactuca sativa</i> , United States, 1915	Z5
110	" <i>P. viridilivida</i> " (9)				NCPPB 1963 ^d	<i>Lactuca sativa</i> , United States, year unknown	Z5
111	" <i>P. viticola</i> " (53)	<i>X. campestris</i> pathovar <i>viticola</i>		<i>X. campestris</i>	NCPPB 2475 ^d	<i>Vitis vinifera</i> , India, 1969	Z5

Continued on following page

TABLE 1—Continued

Sequence no.	Species name as originally described ^a	Name according to Young et al. ^b	Classification in:		Strain	Host plant or origin and place and year of isolation	Growth medium ^c
			Bergey's Manual of Determinative Bacteriology, 8th ed.	Bergey's Manual of Systematic Bacteriology			
112	" <i>P. viticola</i> " (53)	<i>X. campestris</i> pathovar <i>vitis-woodrowii</i>	Addendum I	<i>X. campestris</i>	NCPPB 2614	<i>Vitis vinifera</i> , India, 1972	PAF
113	" <i>P. viticola</i> " (53)				NCPPB 2616	<i>Vitis vinifera</i> , India, 1972	PAF
114	" <i>P. vitiswoodrowii</i> " (61)				NCPPB 1014 ^d	<i>Vitis woodrowii</i> , India, year unknown	B
115	" <i>P. vitiswoodrowii</i> " (61)	<i>X. campestris</i> pathovar <i>campestris</i>	Addendum I	<i>X. campestris</i>	NCPPB 2490	<i>Vitis vinifera</i> , India, 1970	Z5
116	" <i>P. washingtoniae</i> " (65)				NCPPB 967	Host plant and place of isolation unknown, 1944	B
117	<i>P. woodsii</i> (AL) (83)				NCPPB 968 ^T	<i>Dianthus caryophyllus</i> , United States, 1957	B
118	<i>P. woodsii</i> (AL) (83)	<i>X. campestris</i> pathovar <i>campestris</i>	Addendum I	<i>X. campestris</i>	NCPPB 2157	<i>Dianthus barbatus</i> , place of isolation unknown, 1944	Z3
119	<i>P. woodsii</i> (AL) (83)				NCPPB 2441	<i>Setcreasea purpurea</i> , United States, 1969	PAF
120	<i>X. campestris</i> (AL) (60)				NCPPB 528 ^T	<i>Brassica oleracea</i> var. <i>gemmifera</i> , United Kingdom, 1957	

^a For practical reasons, we used the species names as originally described. (AL), Species listed on the Approved Lists of Bacterial Names (81); (VL), species listed on one of the validation lists. Names in quotation marks are not on either the Approved Lists or any validation list, and they have not been published in the International Journal of Systematic Bacteriology since January 1980. The numbers in parentheses are reference numbers.

^b See reference 102.

^c The compositions of media B, X, Z3, Z5, and PAF have been described elsewhere (21, 22, 30, 99).

^d Reference strain according to Young et al. (102).

^e T = type strain.

^f Cotype, reference strain, or neotype strain.

percentage of rRNA binding is not a measure of rRNA cistron homology since it depends not only on base sequence matching, but also on the number of rRNA cistrons per genome, the size of the genome, and the state of replication of the DNA. However, it is a useful parameter to separate taxa with the same $T_{m(e)}$ value. Workers in our research group have shown that the DNA-rRNA hybridization method generally does not allow species separation within an rRNA branch. Therefore, other techniques are required.

Most of the phytopathogenic *Pseudomonas* species could be placed into one of the following four rRNA branches: the *P. fluorescens* branch, the *P. solanacearum* branch, the *P. acidovorans* branch, and the *Xanthomonas* branch. The position of each species or strain is discussed briefly below. We included as many type strains as possible. For the species which have not been formally accepted on the Approved Lists or the Validation Lists, we included the reference strains, neotype strains, or cotypes, although we know that they have no taxonomic standing at present. For a number of species only one or a few strains were available.

Phytopathogenic pseudomonads belonging to the *P. fluorescens* rRNA branch. The *P. fluorescens* rRNA branch contains the majority of the phytopathogenic pseudomonads. These organisms are *Pseudomonas agarici* (four strains studied), *Pseudomonas amygdali* (three strains), *Pseudomonas asplenii* (one strain), *Pseudomonas caricapapayae* (two strains), *Pseudomonas cichorii* (three strains), *Pseudomonas corrugata* (three strains), *Pseudomonas fuscovaginae* (one strain), *Pseudomonas marginalis* (two strains), (*P. marginalis* pathovar *marginalis* and *P. margin-*

alis pathovar *alfalfae*), *Pseudomonas meliae* (one strain), "*Pseudomonas pastinacae*" (one strain), the *Pseudomonas syringae* group (including "*Pseudomonas aceris*" [one strain], "*Pseudomonas antirrhini*" [one strain], "*Pseudomonas apii*" [one strain], "*Pseudomonas berberidis*" [two strains], "*Pseudomonas cannabina*" [two strains], "*Pseudomonas coronafaciens*" [one strain], "*Pseudomonas eriobotryae*" [one strain], "*Pseudomonas lapsa*" [one strain], "*Pseudomonas maculicola*" [one strain], "*Pseudomonas oryzicola*" [two strains], "*Pseudomonas panici*" [one strain], "*Pseudomonas passiflorae*" [two strains], "*Pseudomonas primulae*" [one strain], "*Pseudomonas ribicola*" [one strain], "*Pseudomonas sesami*" [one strain], "*Pseudomonas striafaciens*" [one strain], *P. syringae* [one strain], "*Pseudomonas ulmi*" [one strain], and "*Pseudomonas viburni*" [one strain]), *Pseudomonas tolaasii* (five strains), *Pseudomonas viridiflava* (three strains) and "*Pseudomonas washingtoniae*" (one strain). Two strains of *Pseudomonas cattleyae* (strains NCPPB 1874 and PDDCC 3992, but not the type strain) and two strains of "*P. viridilivida*" (strains NCPPB 1923 and NCPPB 152t₁, but not the strain of Young et al. [102]) also belong in this group (see below). These species are genetically closely related to the following non-phytopathogenic members of this rRNA branch: *P. aeruginosa*, *P. fluorescens*, *Pseudomonas putida*, *Pseudomonas chlororaphis*, *Pseudomonas aureofaciens*, *Pseudomonas stutzeri*, *Pseudomonas mendocina*, *Pseudomonas alcaligenes*, and *Pseudomonas pseudoalcaligenes* (22).

It is our opinion that the genus *Pseudomonas* should be limited to the *P. fluorescens* rRNA branch (22), which

TABLE 2. DNA base compositions and properties of DNA-rRNA hybrids with labeled reference rRNAs from the type strains of *P. fluorescens*, *P. solanacearum*, *P. acidovorans*, and *X. campestris*

Sequence no.	Species ^a	Strain	G+C content (mol%)	Hybridization with rRNA from:							
				<i>P. fluorescens</i> ATCC 13525 ^T		<i>P. solanacearum</i> ATCC 11696 ^t		<i>P. acidovorans</i> ATCC 15668 ^T		<i>X. campestris</i> NCPPB 528 ¹	
				<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
1	" <i>P. aceris</i> "	NCPPB 958 ^b	61.1	78.5	0.09			61.5	0.08		
4	<i>P. agarici</i>	NCPPB 2289 ^{Tc}	61.1	80.0	0.09			60.5	0.07		
3	<i>P. agarici</i>	NCPPB 1999t1	59.9	78.0	0.20						
5	<i>P. agarici</i>	NCPPB 2471t1	58.8	78.5	0.18						
6	<i>P. agarici</i>	NCPPB 2471t2	59.9	78.5	0.19						
11	<i>P. amygdali</i>	NCPPB 2607 ^T	58.5	74.5	0.13	56.5	0.07				
12	<i>P. amygdali</i>	NCPPB 2608	57.7	75.5	0.11						
13	<i>P. amygdali</i>	NCPPB 2610	55.2	76.0	0.09						
16	" <i>P. antirrhini</i> "	NCPPB 1761	60.4	78.5	0.08			64.0	0.09		
17	" <i>P. apii</i> "	NCPPB 1626 ^b	60.8	79.0	0.09			63.0	0.08		
18	<i>P. asplenii</i>	NCPPB 1947 ^T		79.0	0.10			61.0	0.09		
20	" <i>P. berberidis</i> "	NCPPB 2724 ^b	59.7	79.0	0.11			62.0	0.07		
19	" <i>P. berberidis</i> "	NCPPB 1871	60.1	78.5	0.11						
22	" <i>P. cannabina</i> "	NCPPB 1410	60.3	79.0	0.08			61.0	0.07		
23	" <i>P. cannabina</i> "	NCPPB 2069	59.3	78.5	0.10			59.0	0.06		
25	<i>P. caricapapayae</i>	NCPPB 1873 ^T	58.9	77.5	0.09						
24	<i>P. caricapapayae</i>	NCPPB 1872	59.4	79.0	0.14			64.0	0.09		
30	<i>P. cattleyae</i>	NCPPB 1874	63.9	78.0	0.11			65.0	0.12		
31	<i>P. cattleyae</i>	PDDCC 3992	57.4	76.0	0.13						
36	<i>P. cichorii</i>	NCPPB 943 ^T	58.9	78.0	0.19						
35	<i>P. cichorii</i>	NCPPB 906	59.7 ^d	76.0 ^d	0.13 ^d						
37	<i>P. cichorii</i>	NCPPB 1512	60.3 ^d	77.5 ^d	0.13 ^d			61.5 ^d	0.09 ^d		
40	" <i>P. coronafaciens</i> "	NCPPB 1328	59.3	78.0	0.15						
41	<i>P. corrugata</i>	NCPPB 2445 ^T	60.8	78.0	0.13	60.5	0.07				
42	<i>P. corrugata</i>	NCPPB 2447	60.8	78.0	0.10						
43	<i>P. corrugata</i>	NCPPB 2455	58.4	77.0	0.12						
44	" <i>P. erioobotryae</i> "	NCPPB 2331 ^b	58.3	78.5	0.10						
47	<i>P. fluorescens</i>	ATCC 13525 ^T	60.2 ^d	81.0 ^d	0.14 ^d	62.5 ^d	0.09 ^d	61.0 ^d	0.10 ^d	69.0 ^d	0.08 ^d
48	<i>P. fuscovaginae</i>	PDDCC 5939	60.3	77.5	0.12						
54	" <i>P. lapsa</i> "	NCPPB 2096 ^b	59.4	76.0	0.12						
55	" <i>P. maculicola</i> "	NCPPB 1776	61.3	80.0	0.08			63.5	0.07		
59	<i>P. marginalis</i>	PDDCC 5708 ^b	60.1	78.5	0.16						
60	<i>P. marginalis</i>	PDDCC 3553 ^T	59.1	77.5	0.13						
61	<i>P. meliae</i>	NCPPB 3033 ^T	57.9	77.0	0.19						
62	" <i>P. oryzicola</i> "	NCPPB 388 ^c	60.7	78.0	0.10			62.5	0.09		
63	" <i>P. oryzicola</i> "	NCPPB 1417	60.8	77.5	0.09			62.5	0.09		
64	" <i>P. panici</i> "	NCPPB 1498 ^b	60.7	78.5	0.09			60.5	0.07		
65	" <i>P. passiflorae</i> "	NCPPB 224	59.4	77.5	0.20						
66	" <i>P. passiflorae</i> "	NCPPB 1386	60.3	79.0	0.09			62.0	0.10		
67	" <i>P. pastinacae</i> "	NCPPB 806 ^b	62.7	80.5	0.09			63.0	0.07		
68	" <i>P. primulae</i> "	NCPPB 133 ^b	60.4	79.0	0.08			63.0	0.09		
71	" <i>P. ribicola</i> "	NCPPB 963 ^b	60.6	77.5	0.05			63.0	0.09		
76	" <i>P. sesami</i> "	NCPPB 1016 ^b	59.4	78.0	0.09			60.5	0.07		
95	" <i>P. striafaciens</i> "	NCPPB 1898 ^c	59.1	78.5	0.09			63.0	0.09		
97	<i>P. syringae</i>	NCPPB 281 ^T	59.9 ^d	78.0 ^d	0.14 ^d			59.0 ^d	0.08 ^d		
101	<i>P. tolaasii</i>	NCPPB 2192 ^T	61.3	80.0	0.14						
98	<i>P. tolaasii</i>	NCPPB 741t1	61.1	79.5	0.13						
99	<i>P. tolaasii</i>	NCPPB 1116	61.1	80.0	0.13						
100	<i>P. tolaasii</i>	NCPPB 1311	60.8	80.0	0.14						
102	<i>P. tolaasii</i>	NCPPB 2193	61.3	79.5	0.14						
103	" <i>P. ulmi</i> "	NCPPB 632 ^b	58.7	78.5	0.09			63.0	0.08		
104	" <i>P. viburni</i> "	NCPPB 1921 ^b	60.1	79.0	0.10			62.5	0.10		
105	<i>P. viridiflava</i>	NCPPB 1248t1		77.5	0.15						
106	<i>P. viridiflava</i>	NCPPB 1810t1	59.9	77.5	0.13						
107	<i>P. viridiflava</i>	NCPPB 2024		77.5	0.14						
108	" <i>P. viridilivida</i> "	NCPPB 152t1	57.4	76.0	0.13						
109	" <i>P. viridilivida</i> "	NCPPB 1923	61.3	77.5	0.18						
116	" <i>P. washingtoniae</i> "	NCPPB 967	61.2	80.5	0.10			63.0	0.09		
10	" <i>P. alliiicola</i> "	NCPPB 947 ^T	67.2			74.0	0.08				
15	<i>P. andropogonis</i>	NCPPB 934 ^T	59.0	64.5	0.05	74.5	0.08	71.5	0.06		
14	<i>P. andropogonis</i>	NCPPB 933	61.3	65.0	0.05	75.0	0.08	72.0	0.08	59.0	0.04
28	<i>P. caryophylli</i>	NCPPB 2151 ^T	63.3 ^d	62.0 ^d	0.06 ^d	75.5 ^d	0.09 ^d	70.5 ^d	0.06 ^d		

Continued on following page

TABLE 2—Continued

Sequence no.	Species ^a	Strain	G+C content (mol%)	Hybridization with rRNA from:							
				<i>P. fluorescens</i> ATCC 13525 ^T		<i>P. solanacearum</i> ATCC 11696 ^T		<i>P. acidovorans</i> ATCC 15668 ^T		<i>X. campestris</i> NCPPB 528 ^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
26	<i>P. caryophylli</i>	NCPPB 349				74.5	0.08				
27	<i>P. caryophylli</i>	NCPPB 609	65.0			76.5	0.07				
32	<i>P. cepacia</i>	Ballard 717 ^T	67.5 ^d	64.0 ^d	0.07 ^d	76.0 ^d	0.08 ^d	72.5 ^d	0.08 ^d		
33	<i>P. cepacia</i>	Stanier 382	67.4 ^d	64.5 ^d	0.07 ^d	76.0 ^d	0.09 ^d	71.0 ^d	0.07 ^d		
34	<i>P. cepacia</i>	NCTC 10661	66.9 ^d	62.0 ^d	0.04 ^d			72.0 ^d	0.08 ^d		
50	<i>P. gladioli</i>	NCPPB 1891 ^T	68.8 ^d	63.5 ^d	0.06 ^d	76.0 ^d	0.07 ^d	69.5 ^d	0.06 ^d		
52	<i>P. glumae</i>	NCPPB 2981 ^T	68.4			75.0	0.10				
51	<i>P. glumae</i>	NCPPB 2391	67.7			75.0	0.11				
75	<i>P. rubrisubalbicans</i>	NCPPB 1027 ^T	62.5			75.0	0.07	71.0	0.08		
82	<i>P. solanacearum</i>	ATCC 11696 ^T	66.1 ^d	63.0 ^d	0.05 ^d	81.5 ^d	0.08 ^d	72.0 ^d	0.07 ^d	62.5 ^d	0.05 ^d
78-81, 83-94	<i>P. solanacearum</i>		66.3—68.1 ^d			80.0—81.5 ^d	0.07—0.12 ^d	69.5—72.0 ^d	0.04—0.07 ^d		
96	" <i>P. stizolobii</i> "	NCPPB 102412 ^c	59.4	65.0	0.04	74.0	0.08				
117	<i>P. woodsii</i>	NCPPB 968 ^T	59.8	64.0	0.04	75.5	0.07	71.5	0.07		
118	<i>P. woodsii</i>	NCPPB 2157				75.0	0.08				
119	<i>P. woodsii</i>	NCPPB 2441				75.5	0.06				
2	<i>P. acidovorans</i>	ATCC 15668 ^T	66.6 ^d	61.0 ^d	0.07 ^d	70.5 ^d	0.07 ^d	80.5 ^d	0.12 ^d	61.0 ^d	0.04 ^d
7	" <i>P. alboprecipitans</i> "	NCPPB 1011 ^T	70.8	63.5	0.05			78.0	0.09		
8	" <i>P. alboprecipitans</i> "	NCPPB 2399	67.8	64.0	0.06			77.0	0.07		
9	" <i>P. alboprecipitans</i> "	NCPPB 2401	66.6					75.5	0.08		
29	<i>P. cattleyae</i>	NCPPB 961 ^T	68.6	61.0	0.06	70.4	0.07	73.5	0.09		
69	<i>P. pseudoalcaligenes</i> subsp. <i>citrulli</i>	PDDCC 6521	68.1	64.0	0.07	72.5	0.06	77.0	0.07		
70	<i>P. pseudoalcaligenes</i> subsp. <i>citrulli</i>	PDDCC 6522	67.2	63.5	0.07			77.0	0.08		
73	<i>P. rubrilineans</i>	NCPPB 920 ^T	69.0	57.5	0.03	72.5	0.05	77.5	0.06		
72	<i>P. rubrilineans</i>	NCPPB 359	68.1					76.0	0.08		
74	<i>P. rubrilineans</i>	NCPPB 1118	69.6					76.5	0.07		
77	" <i>P. setariae</i> "	NCPPB 1392 ^b	69.1			72.5	0.12	78.0	0.08		
120	<i>X. campestris</i>	NCPPB 528 ^T	65.2 ^d	69.0 ^d	0.07 ^d			63.0 ^d	0.06 ^d	81.0 ^d	0.09 ^d
21	<i>P. betle</i>	NCPPB 323 ^T	68.7	67.0	0.09			59.5	0.09	79.0	0.10
49	" <i>P. gardneri</i> "	NCPPB 881 ^c	64.2	66.5	0.04			62.0	0.04	81.0	0.05
53	<i>P. hibiscicola</i>	NCPPB 1683 ^T	67.9	67.5	0.08			63.5	0.11	78.0	0.09
56	" <i>P. mangiferaeindicae</i> "	NCPPB 490 ^b	65.8	69.5	0.04			64.0	0.05	80.5	0.05
57	" <i>P. mangiferaeindicae</i> "	NCPPB 2387	65.7							80.0	0.07
58	" <i>P. mangiferaeindicae</i> "	NCPPB 2438	63.9							78.0	0.06
111	" <i>P. viticola</i> "	NCPPB 2475 ^b	65.2							80.0	0.07
112	" <i>P. viticola</i> "	NCPPB 2614	65.1							76.0	0.06
113	" <i>P. viticola</i> "	NCPPB 2616	64.7							79.0	0.07
114	" <i>P. vitiswoodrowii</i> "	NCPPB 1014 ^b	65.7	69.0	0.04			58.5	0.03	78.5	0.07
115	" <i>P. vitiswoodrowii</i> "	NCPPB 2490	65.2							79.0	0.07
38	<i>P. cissicola</i>	NCPPB 2982 ^T	55.7	60.5	0.07	62.5	0.08				
39	<i>P. cissicola</i>	PDDCC 4290	56.9	61.5	0.06						
46	<i>P. flectens</i>	NCPPB 539 ^T	31.8	59.5	0.10			54.5	0.09		
45	<i>P. flectens</i>	NCPPB 538	44.8			55.0	0.13				
110	" <i>P. viridilivida</i> "	NCPPB 1963 ^b	68.9	55.0	0.08	58.5	0.07				

^a For more information see Table 1.^b Reference strain according to Young et al. (102).^c T = type strain.^d Data from reference 22.^e Cotype, reference strain, or neotype strain.

corresponds to Section I of *Pseudomonas* in *Bergey's Manual of Systematic Bacteriology* (57). Therefore, all of the above-mentioned phytopathogenic strains and species are authentic members of this genus. The species or pathovar names of these phytopathogenic organisms should be retained as separate entities until future extensive phenotypic and genotypic experiments reveal synonymies, if any. Our findings should induce extensive experimentation on the relationships among these species and pathovars. The *P.*

fluorescens rRNA branch contains saprophytes, human and animal pathogens, clinical isolates, epiphytes, and phytopathogens with *T*_{m(e)} values ranging from 74.5 to 81.0°C. The G+C contents vary between 55.2 and 66.8 mol%.

Some of our findings agree with data in the literature. In *Bergey's Manual of Systematic Bacteriology* *P. syringae*, *P. cichorii*, *P. marginalis*, and *P. tolaasii* are classified in Section I of *Pseudomonas* (57), which belongs completely in the *P. fluorescens* rRNA branch (22, 59). Young et al. (102)

FIG. 2. Similarity map of DNA-rRNA hybrids between the radioactively labeled 23S rRNA fraction of *P. fluorescens* ATCC 13525^T and DNAs from phytopathogenic *Pseudomonas* strains (represented by their sequence numbers) (see Tables 1 and 2). Values for hybrids with DNAs from a number of bacteria belonging to different taxa (unmarked symbols) were taken from a previous paper (22). Abbreviations: Ps, *Pseudomonas*; Azom-Azot, *Azomonas-Azotobacter*; Xanth, *Xanthomonas*; Enterob, *Enterobacteriaceae*; Vibron, *Vibrionaceae*; Chrom-Janth, *Chromobacterium-Janthinobacterium*; Alc-Achr, *Alcaligenes-Achromobacter*; Acetic ac bact, acetic acid bacteria.

and Dye et al. (26) proposed 40 to 41 pathovars in *P. syringae*, which is also commonly called the *P. syringae* group. The grouping of these pathovars in one species is at least partially supported by phenotypic (74) and genotypic data (DNA-DNA hybridization) (64). We examined various strains of 19 of the pathovars and localized them without exception in the *P. fluorescens* branch. Lukezic (43) found a level of phenotypic similarity of ca. 80% between *P. corrugata* and *P. syringae*. The localization of *P. amygdali* by Psallidas and Panagopoulos (66) in group Ia of Lelliott et al. (42) and group IA of Misaghi and Grogan (50) (i.e., the groups containing the pathogen *P. syringae* and related organisms) suggested a close relationship with *P. fluorescens*. *P. agarici* and *P. asplenii* were assigned to group I of Byng et al. (15), who determined relatedness among pseu-

domonads and xanthomonads from various enzymic patterns during tyrosine biosynthesis. Group I of Byng et al. (15) corresponds to our *P. fluorescens* rRNA branch. Billing (6) reported that *P. viridiflava* is phenotypically closely related to *P. syringae*. According to Young (101), "*P. washingtoniae*" must be regarded as a synonym of *P. fluorescens*.

The presence or absence of yellowish green fluorescent pigments on King medium B is considered to be a primary criterion in separating the phytopathogenic pseudomonads for identification (33, 76, 79). However, this single feature induces identification problems with nonfluorescent strains, which resemble fluorescent strains in several phenotypic features. Our DNA-rRNA hybridization data reveal a quite clear-cut situation. All yellowish green fluorescent pseu-

FIG. 3. Similarity map of DNA-rRNA hybrids between the radioactively labeled 23S rRNA fraction of *P. solanacearum* ATCC 11696^T and DNAs from organisms belonging to different taxa. For further explanation see the legend to Fig. 2. Abbreviations: Ps, *Pseudomonas*; Alc-Achr, *Alcaligenes-Achromobacter*; Chrom-Janth, *Chromobacterium-Janthinobacterium*; Xanth, *Xanthomonas*; E coli, *Escherichia coli*.

domonads are genetically related and belong in our *P. fluorescens* rRNA branch. The nonfluorescent phytopathogenic pseudomonads belong to one of the following four genetically different groups: the *P. fluorescens* rRNA branch, the *P. solanacearum* rRNA branch, the *P. acidovorans* rRNA branch or the *Xanthomonas* rRNA branch. Thus, as far as we know, the *P. fluorescens* rRNA branch contains

both fluorescent and nonfluorescent members which are genetically closely related and appear to be different because of only one feature, the production of yellowish green fluorescent pigments. In both the fluorescent non-phytopathogenic and phytopathogenic species of the *P. fluorescens* rRNA branch there are nonfluorescent strains. In this rRNA branch there are also non-phytopathogenic and

FIG. 4. Similarity map of DNA-rRNA hybrids between the radioactively labeled 23S rRNA fraction of *P. acidovorans* ATCC 15668^T and DNAs from organisms belonging to different taxa. For further explanation see the legend to Fig. 2. Abbreviations: Ps, *Pseudomonas*; Chrom-Janth, *Chromobacterium-Janthinobacterium*; Alc-Achr, *Alcaligenes-Achromobacter*; Xanth, *Xanthomonas*; Enterob, *Enterobacteriaceae*; Vibron, *Vibrionaceae*; Acet ac bact, acetic acid bacteria.

phytopathogenic species containing no fluorescent strains; examples of the latter are *P. amygdali*, "*P. cannabina*," *P. corrugata*, *P. meliae*, and "*P. sesami*." This information should be useful for adapting and improving the present key for identification of phytopathogenic pseudomonads.

Phytopathogenic organisms belonging to the *P. solanacearum* rRNA branch. Together with *P. solanacearum* itself (17 strains studied; $T_{m(e)}$ values, 80.0 to 81.5°C), three other phytopathogenic *Pseudomonas* species, *Pseudomonas cepacia* (3 strains; $T_{m(e)}$ value, 76.0°C), *Pseudomonas caryophylli* (3 strains; $T_{m(e)}$ values, 74.5 to 76.5°C), and *Pseudomonas gladioli* (1 strain; $T_{m(e)}$ value, 76.0°C), belong to the *P. solanacearum* rRNA branch (22), which corresponds to Section II of *Pseudomonas* in *Bergey's Manual of Systematic Bacteriology* (57). Based on phenotypic characterization and DNA-DNA homology studies, "*Pseudomonas alliiicola*" appeared to be a synonym of "*Pseudomonas marginata*" (5), which was in turn considered to be a subjective synonym of *P. gladioli* (32) on phenotypic

grounds. The Young reference strain of "*P. alliiicola*" falls in this rRNA branch with a $T_{m(e)}$ value of 74.0°C, as expected. In addition, *Pseudomonas andropogonis* (two strains), which is a synonym of "*Pseudomonas stizolobii*" (one strain) (31), *Pseudomonas glumae* (two strains), *Pseudomonas woodsii* (three strains), and the type strain of *Pseudomonas rubrisubalbicans* (one strain) also belong in the *P. solanacearum* rRNA branch ($T_{m(e)}$ values around 75°C compared with *P. solanacearum*). At present the classification of the above-mentioned phytopathogenic species within the *P. solanacearum* rRNA branch is not clear.

The *P. solanacearum* rRNA branch now contains 8 to 11 named phytopathogenic *Pseudomonas* species. We previously stated (22) that this rRNA branch is not related to the authentic pseudomonads. Future extensive studies on the *P. solanacearum* rRNA branch will have to include the species mentioned above.

Phytopathogenic organisms belonging to the *P. acidovorans* rRNA branch. Thus far, the *P. acidovorans* rRNA branch

FIG. 5. Similarity map of DNA-rRNA hybrids between the radioactively labeled 23S rRNA fraction of *X. campestris* NCPPB 528^T and DNAs from organisms belonging to different taxa. For further explanation see the legend to Fig. 2. Abbreviations: Xanth, *Xanthomonas*; Frat, *Frateriia*; Ps, *Pseudomonas*; Enterob, *Enterobacteriaceae*; Vibron, *Vibrionaceae*; Chrom-Janth, *Chromobacterium-Janthinobacterium*; Acetic ac bact, acetic acid bacteria.

contains only one phytopathogenic species, "*Pseudomonas alboprecipitans*," which was assigned to it by Byng et al. (15) based on comparative enzymology. Section III of *Pseudomonas* in *Bergey's Manual of Systematic Bacteriology* (57) contains no phytopathogens. Our data (Table 2) clearly show that three strains of "*P. alboprecipitans*" (a subjective synonym of *Pseudomonas avenae* according to Schaad et al. [77]), *P. pseudoalcaligenes* subsp. *citrulli* (two strains), *Pseudomonas rubriligneans* (three strains), and "*Pseudomonas setariae*" (one strain) belong to this rRNA branch. Young et al. (102) classified all of these organisms except *P. pseudoalcaligenes* subsp. *citrulli* among the nonfluorescent plant-pathogenic *Pseudomonas* species; *P. pseudoalcaligenes* subsp. *citrulli* had not been described at that time. One would expect the latter taxon to be closely related to *P. pseudoalcaligenes* subsp. *pseudoalcaligenes*, which belongs to the *P. fluorescens* rRNA branch. However, *P. pseudoalcaligenes* subsp. *citrulli* (78) is not a member of the *P. fluorescens* rRNA branch ($T_{m(e)}$ value, 63.5 to 64°C

compared with *P. fluorescens*). Therefore, we reject the present classification of the melon pathogens as subspecies of *P. pseudoalcaligenes*. Their exact species status is being investigated in our laboratory and will be reported separately.

It is not surprising that the melon pathogens were erroneously assigned to the *P. alcaligenes*-*P. pseudoalcaligenes* group of Stanier et al. (84). Indeed, these authors (84) reported that this group, as well as the *P. acidovorans*-*Pseudomonas testosteroni* (84) group, contained nutritionally restricted bacteria. Assignment of organisms to either one of these groups is based mainly on the absence of physiological and biochemical features and may therefore be questionable.

Schaad et al. (78) mentioned a certain phenotypic resemblance between *P. pseudoalcaligenes* subsp. *citrulli* and *P. avenae*, which is itself a member of the *P. acidovorans* rRNA branch. This supports our DNA-rRNA hybridization data. One of the major differences was the disagreement in

G+C content (70 to 75 mol% G+C for *P. avenae* and 66 ± 1.6 mol% G+C for the melon pathogens). However, in our hands the DNA base composition of *P. avenae* (our "*P. alboprecipitans*" strains) was definitely lower (between 70.8 and 66.6 mol% G+C), which does not a priori exclude a close relationship between the two taxa.

Phytopathogenic organisms belonging to the *Xanthomonas* rRNA branch. The present generic definitions of *Xanthomonas* and *Pseudomonas* do not allow a sharp separation between these two genera. Unequivocal identification in either one of these genera is difficult for some organisms. Thus, it is possible (8, 57) that some of the phytopathogenic pseudomonads in fact belong in the genus *Xanthomonas*. Recently, workers in our research group proposed to extend the definition of *Xanthomonas* by including $T_{m(e)}$ values from DNA-rRNA hybridizations performed with rRNA from the type strain of *Xanthomonas campestris* (89).

Our DNA-rRNA hybridization data revealed that some pseudomonads are misnamed and should be located in the *Xanthomonas* rRNA branch (Table 2); these organisms are "*Pseudomonas gardneri*," *Pseudomonas betle*, *Pseudomonas hibiscicola*, "*Pseudomonas mangiferaeindicae*," "*Pseudomonas viticola*," and "*Pseudomonas vitiswoodrowii*." For some of these taxa a close relationship with members of the genus *Xanthomonas* has been mentioned previously. "*P. gardneri*" was considered by Dye (25) to be a synonym of "*Xanthomonas vesicatoria*," which is itself a pathovar of *X. campestris* (8, 102). Byng et al. (15) also assigned this organism to the *Xanthomonas* group. Robbs et al. (72) classified "*P. mangiferaeindicae*" as *X. campestris* f. sp. *mangiferaeindicae*, whereas Young et al. (102) and Bradbury (8) considered it a pathovar of *X. campestris*. "*P. viticola*" and "*P. vitiswoodrowii*" have both been classified as pathovars of *X. campestris* (8, 102).

On the Approved Lists of Bacterial Names (81) *P. betle* and *P. hibiscicola* were retained as separate *Pseudomonas* species. Young et al. (102) classified these organisms as atypical plant-pathogenic *Pseudomonas* species. Our results show that both of these species should be renamed in the genus *Xanthomonas*. Their correct position in this genus has to be established.

All of our genotypic data on the *Xanthomonas* rRNA branch have been confirmed by an extensive phenotypic study of the entire genus *Xanthomonas* (M. Van den Mooter, J. Swings, and J. De Ley, manuscript in preparation). Definite taxonomic and nomenclatural proposals will be made elsewhere.

Phytopathogenic *Pseudomonas* species with uncertain taxonomical status. *Pseudomonas cissicola* and *Pseudomonas flectens* exhibited no relationship with any of the four rRNA branches considered above. *P. cissicola* was placed in Addendum III to *Pseudomonas* in *Bergey's Manual of Determinative Bacteriology*, 8th ed. (23), and in Section V of *Pseudomonas* in *Bergey's Manual of Systematic Bacteriology* (57), indicating its uncertain taxonomic status. *P. flectens* was regarded as an atypical member of *Pseudomonas* by Young et al. (102), and it was not retained in *Bergey's Manual of Systematic Bacteriology* (57). From our data we conclude that *P. cissicola* and *P. flectens* should definitely be removed from the genus *Pseudomonas*. Their correct taxonomic positions remain unknown. The two *P. flectens* strains which we used are probably different since their G+C contents differed by 13 mol%.

P. cattleyae and "*P. viridilivida*" are discussed together because both of these species contain strains belonging to different rRNA branches. Young et al. (102) placed both of

these species in their group of nonfluorescent phytopathogens. However, each species contains at least two strains (*P. cattleyae* NCPPB 1874 and PDDCC 3992, "*P. viridilivida*" NCPPB 152t1 and NCPPB 1923) which form fluorescent pigments and show a close relationship with the *P. fluorescens* rRNA branch ($T_{m(e)}$ values, 76.0 to 78.0°C). The type strain of *P. cattleyae*, strain NCPPB 961, is a member of the *P. acidovorans* rRNA branch, whereas the former type strain of "*P. viridilivida*," strain NCPPB 1963 (= DSM 50318), is gram positive. Thus, it is certainly not a member of the genus *Pseudomonas*. A more extensive study must be made to draw definite taxonomic conclusions from these findings and to propose the appropriate nomenclatural changes.

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