Reclassification of the Genus *Pasteurella* Trevisan 1887 on the Basis of Deoxyribonucleic Acid Homology, with Proposals for the New Species *Pasteurella dagmatis*, *Pasteurella canis*, *Pasteurella stomatis*, *Pasteurella anatis*, and *Pasteurella langaa*

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Deoxyribonucleic acid (DNA)-DNA hybridization was used to determine the genetic relationships among a variety of previously established or proposed species of *Pasteurella* and their positions within the family *Pasteurellaceae* Pohl 1981. Our results indicated that the genus *Pasteurella* sensu stricto, which can be separated from the *Actinobacillus* group, consists of at least the following 11 species: *Pasteurella multocida*, with three subspecies (*P. multocida* subsp. *multocida*, *P. multocida* subsp. *septica*, and *P. multocida* subsp. *gallicida*); *Pasteurella dagmatis* sp. nov., containing organisms previously labeled *Pasteurella* "gas," *Pasteurella* new species 1, or *Pasteurella pneumotropica* type Henriksen; *Pasteurella gallinarum*; *Pasteurella canis* sp. nov., previously labeled *P. multocida* biotype 6 or "dog type" strains; *Pasteurella stomatis* sp. nov., which contains *Pasteurella* strains isolated from dogs and cats; *Pasteurella avium* (Hinz and Kunjara) Muters et al. 1985; *Pasteurella volantium* Muters et al. 1985, a new species consisting of V-factor-requiring strains that occur in humans and birds; *Pasteurella anatis* sp. nov.; *Pasteurella langaa* sp. nov., containing strains previously designated taxa 1 and 4 of Bisgaard; and two new species, which were provisionally designated *Pasteurella* species A and *Pasteurella* species B. The previously recognized taxa *Pasteurella ureae*, *Pasteurella haemolytica* biotypes A and T, *Pasteurella testudinis*, and *P. pneumotropica* biotypes Jawetz and Heyl do not belong to the genus *Pasteurella* but are more closely related to the *Actinobacillus* group. The exact taxonomic positions of *Pasteurella aerogenes*, *P. multocida* biotype 1, group HB-5, "*Pasteurella piscicida*," the SP group, and the bovine lymphangitis group are still unknown, but these organisms do not belong to the genus *Pasteurella*.

Around 1880 certain microorganisms were described as probably associated with fowl cholera and hemorrhagic septicemia of cattle and other animals. In 1885 Kitt cultured the etiological agent (31). Not until around 1920 were similar or identical organisms reliably isolated and described from infections in humans (51, 63).

"*Micrococcus gallicidus*" Burrill 1883 (5) appears to be the first scientific name used for these bacteria. Later, this organism was assigned to various genera, including "*Bacterium*" (11, 31, 33, 34), "*Octopsis*" (65), "*Coccobacillus*" (14), and "*Eucystia*" (10). In 1887, Trevisan proposed the generic name *Pasteurella* to commemorate the work of Pasteur on these bacteria (66).

During the years that followed, many organisms with a variety of species names were assigned to the genus *Pasteurella*, mainly on the basis of bipolar staining or the host species from which the microorganism was isolated (26). When this fashion of naming species after their animal hosts (35) ended, the epithet *septica*, which was proposed by Topley and Wilson in 1929 (64), was adopted for *Pasteurella* in the Anglo-Saxon parts of the world. In 1939, Rosenbusch and Merchant used the epithet *multocida* (53), which had been used first by Kitt in 1893 in the combination "*Bacterium bipolare multocidum*" (32) and by Lehmann and Neumann in 1899 in the name *Bacterium multocidum* (34). Although the epithet *gallicida*, which was used by Burrill in 1883 (5), appears to have priority, *Pasteurella multocida* was proposed to be conserved as the most appropriate name (58).

Until 1932, the genus *Pasteurella* consisted only of the type species, *Pasteurella multocida*. During the next 42 years the genus was expanded to include *Pasteurella haemolytica* by Newsom and Cross (48), *Pasteurella pneumotropica* by Jawetz (27), *Pasteurella gallinarum* by Hall et al. (19), *Pasteurella ureae* by Jones (29), and *Pasteurella aerogenes* by McAllister and Carter (43). Recently, many newly isolated microorganisms have been assigned to the genus *Pasteurella*, including *Pasteurella* "gas" or *Pasteurella* new species 1 (17), the SP group (13), the bovine lymphangitis group (28), a bacterium with the Centers for Disease Control α -numeric designation group HB-5 ("*Pasteurella bettii*"), and *Pasteurella testudinis* (61), as well as some new taxa isolated from poultry, guinea pigs, and calves (1, 2, 35a). With many of these new organisms, however, the difficulties of discriminating between members of the genus *Pasteurella* and members of the genus *Actinobacillus* Brumpt 1910 were significant.

Many investigators have considered the problems of phenotypic differentiation between these two genera. For example, in 1969 Mráz proposed reclassification of *P. haemolytica* as "*Actinobacillus haemolyticus*" because of the phenotypic similarity of this organism to the genus *Actinobacillus* (44). In 1973 Frederiksen suggested that *P. ureae* should be recognized as a species of the genus *Actinobacillus* because of its similarity to this group (12), a proposal that was in accordance with previous statements of Jones (29). In 1978 workers from American Type Culture Collection presented a phenotypic comparison of *Pasteurella* and *Actinobacillus* strains and stated that the two genera could not be separated

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TABLE 1. Strains used in this study

Laboratory no.	Strain ^a	Taxon	Derivation and other information	Reference(s)	G+C content (mol%) ^b
1	NCTC 10322 ^T	<i>P. multocida</i> subsp. <i>multocida</i>	G. R. Carter strain W-9217; Carter serogroup A; Frederiksen biotype 4; porcine, Canada	54	41.6
2	IPDH 108-78	<i>P. multocida</i> subsp. <i>multocida</i>	K.-H. Hinz; chicken, Federal Republic of Germany		43.2
3	SSI P325	<i>P. multocida</i> subsp. <i>multocida</i>	W. Frederiksen strain 7566-64; Frederiksen biotype 2; human	12	42.8
4	SSI P296	<i>P. multocida</i> subsp. <i>multocida</i>	J. E. Smith strain 711; human, dog bite, United Kingdom	55	42.2
5	HIM 709-4	<i>P. multocida</i> subsp. <i>multocida</i>	H. Gerlach strain 1449; ducklings, Federal Republic of Germany		42.3
6	IPDH 630-78	<i>P. multocida</i> subsp. <i>multocida</i>	K.-H. Hinz; duck, Federal Republic of Germany		43.9
7	NCTC 10323	<i>P. multocida</i> subsp. <i>multocida</i>	W. Frederiksen strain SSI P428; J. A. McKiel, strain insein; Frederiksen biotype 5; Carter serogroup 8; bovine, Burma	3, 12	43.0
8	NCTC 8080	<i>P. multocida</i> subsp. <i>multocida</i>	J. E. Smith strain 170; E. D. Hoare strain H; human, United Kingdom	55	42.1
9	NCTC 3195	<i>P. multocida</i> subsp. <i>multocida</i>	H. Schütze strain HS; bovine, United Kingdom		40.8
10	HIM 729-5	<i>P. multocida</i> subsp. <i>multocida</i>	R. C. Meyer strain 7/72; United States		43.5
11	NCTC 10201	<i>P. multocida</i> subsp. <i>multocida</i>	W. Frederiksen strain SSI P424; R. S. Roberts strain A4; Frederiksen biotype 3; Roberts serotype II; avian, United Kingdom	12, 52	41.9
12	CIP A125 ^T	<i>P. multocida</i> subsp. <i>septica</i>	G. Girard strain Souhard; human, cat bite, France		41.5
13	NCTC 11619	<i>P. multocida</i> subsp. <i>septica</i>	Marburg strain 118100/81; human, Federal Republic of Germany		42.5
14	NCTC 11620	<i>P. multocida</i> subsp. <i>septica</i>	H. Gerlach strain 1425; budgerigar, Federal Republic of Germany		42.5
15	HIM 551-1	<i>P. multocida</i> subsp. <i>septica</i>	Marburg strain 142910/76; human, dog bite, Federal Republic of Germany	25	43.5
16	NCTC 10204 ^T	<i>P. multocida</i> subsp. <i>gallicida</i>	W. Frederiksen strain SSI P426; R. S. Roberts strain IV-739; bovine, United Kingdom	52	41.2
17	SSI P697	<i>P. multocida</i> subsp. <i>gallicida</i>	W. Frederiksen; Steigerwalt strain CDC 7987; United States		41.9
18	SSI P808	<i>P. multocida</i> subsp. <i>gallicida</i>	W. Frederiksen; Thorshavn strain FsK. 10752(83)		42.5
19	NCTC 11617 ^T	<i>P. dagmatis</i>	S. D. Henriksen strain 953/60; human, Norway	23	40.0
20	NCTC 11618	<i>P. dagmatis</i>	W. Frederiksen; R. E. Weaver strain C9882; human, dog bite, United States	13	42.0
21	HIM 815-8	<i>P. dagmatis</i>	J. E. Smith strain 151; dog, United Kingdom	56	39.4
22	SSI P497	<i>P. dagmatis</i>	W. Frederiksen; J. Haagsma strain 2/68852; cat, The Netherlands	13, 18	41.5
23	SSI P150	<i>P. dagmatis</i>	W. Frederiksen; human, cat bite, Denmark	13	41.9
24	HIM 661-8	<i>P. dagmatis</i>	J. E. Smith strain 180; dog, United Kingdom	56	38.9
25	ATCC 13361 ^T	<i>P. gallinarum</i>	K. L. Heddlestone strain USDA P-913; chicken, United States	19, 54	43.6
26	ATCC 13360	<i>P. gallinarum</i>	K. L. Heddlestone strain USDA P-982; chicken, United States	19	43.7
27	NCTC 11621 ^T	<i>P. canis</i>	J. E. Smith strain 182; Frederiksen biotype 6; dog, United Kingdom	12, 57, 62	37.8
28	NCTC 11622	<i>P. canis</i>	Marburg strain 40930/67; human, Federal Republic of Germany	25	37.7
29	HIM 712-4	<i>P. canis</i>	Marburg strain 078805-1/81; human, Federal Republic of Germany		39.8
30	HIM 651-5	<i>P. canis</i>	S. D. Henriksen strain 12505/73; Frederiksen biotype 6; dog, Norway	21, 62	39.3
31	HIM 843-5	<i>P. canis</i>	M. Bisgaard strain K267; taxon 13 (Orn ⁺); calf, Denmark	35a	41.9
32	NCTC 11623 ^T	<i>P. stomatis</i>	J. E. Smith strain 166; dog, United Kingdom	56	42.2
33	NCTC 11624	<i>P. stomatis</i>	W. Mannheim strain PE4; cat, Federal Republic of Germany		40.4
34	SSI P294	<i>P. stomatis</i>	J. E. Smith strain 221; Frederiksen biotype 6; dog, United Kingdom	56	43.5
35	HIM 748-5	<i>P. stomatis</i>	J. E. Smith strain 150; dog, United Kingdom	56	41.4
36	NCTC 11413 ^T	<i>P. anatis</i>	M. Bisgaard strain F149; taxon 1; duck, Denmark	1	39.9
37	HIM 745-4	<i>P. anatis</i>	M. Bisgaard strain F279; taxon 1; duck, Denmark	1	42.3

Continued on following page

TABLE 1—Continued

Laboratory no.	Strain ^a	Taxon	Derivation and other information	Reference(s)	G+C content (mol%) ^b
38	SSI P683	<i>Pasteurella</i> species B	V. Janeckova strain Aldova 23193; Frederiksen biotype 6; cat, Czechoslovakia		40.0
39	SSI P809	<i>Pasteurella</i> species B	W. Frederiksen; Odense strain FsK. 11478; human, dog bite		38.9
40	NCTC 1141 ^T	<i>P. langaa</i>	M. Bisgaard strain F73; taxon 4; chicken, Denmark	1	43.9
41	HIM 745-1	<i>P. langaa</i>	M. Bisgaard strain F74; taxon 4; chicken, Denmark	1	45.3
42	ATCC 29546 ^T	<i>P. avium</i>	K.-H. Hinz strain IPDH 2654; chicken, United States	24, 46, 54	44.7
43	IPDH 0002	<i>P. avium</i>	K.-H. Hinz strain TS9; chicken, Federal Republic of Germany	24, 46	44.3
44	HIM 844-2	<i>P. avium</i>	M. Bisgaard strain K 117; taxon 13 (Orn ⁻); calf, Denmark	35a, 46	42.8
45	NCTC 3438 ^T	<i>P. volantium</i>	R. Lovell strain 6; fowl, United Kingdom	24, 46	43.8
46	NCTC 4101	<i>P. volantium</i>	A. Fleming strain 1; human, United Kingdom	46	44.6
47	IPDH 0003	<i>P. volantium</i>	K.-H. Hinz strain TS8; chicken, Federal Republic of Germany	24, 46	44.7
48	ATCC 27883 ^T	<i>P. aerogenes</i>	H. A. McAllister strain P-172-71; swine, United States	43, 54	41.8
49	HIM 612-4/5	<i>P. aerogenes</i>	G. R. Carter strain SS-274-74; swine, United States	13, 43	43.1
50	NCTC 10535	" <i>P. bettii</i> "	D. G. Hollis strain CDC 41-5568; Centers for Disease Control group HB-5; human, United States		38.6
51	NCTC 9380 ^T	<i>P. haemolytica</i>	J. A. Watt strain 1266/56A&B; biotype A; United Kingdom	48, 57	43.6
52	NCTC 10624	<i>P. haemolytica</i>	B. J. Shreeve strain 7H74L; biotype T; serotype 3; lamb, United Kingdom	57	42.6
53	SSI P737	<i>P. haemolytica</i>	W. Frederiksen; Frank, Ames strain 0-353-81; third taxon; sheep, United States	12	43.5
54	SSI P730	<i>P. haemolytica</i>	W. Frederiksen; Frank, Ames strain 0-305-80; "intermedium strain"; sheep, United States		43.9
55	SSI P655	<i>P. haemolytica</i>	W. Frederiksen; fourth taxon; pig, Denmark		41.4
56	NCTC 8141 ^T	<i>P. pneumotropica</i>	E. Jawetz strain M8.19.48; Frederiksen type Jawetz; mouse, United States	27, 54	40.7
57	NCTC 8284	<i>P. pneumotropica</i>	M. T. Parker strain 54818; Frederiksen type Jawetz; mouse, United Kingdom		42.8
58	HIM 640-5/6	<i>P. pneumotropica</i>	O. Mraz strain P.u.2; Frederiksen type Jawetz; mouse, Czechoslovakia	45	41.5
59	ATCC 12555	<i>P. pneumotropica</i>	R. G. Wyllie strain C57; Frederiksen type Heyl; mouse, Australia	16	40.3
60	HIM 769-1	<i>P. testudinis</i>	E. L. Biberstein strain UCD 475-10A; tortoise, United States	61	47.0
61	ATCC 33688 ^T	<i>P. testudinis</i>	E. L. Biberstein strain UCD 90-23-79n; tortoise, United States	61	46.8
62	NCTC 10219 ^T	<i>P. ureae</i>	S. D. Henriksen strain 3520/59; human, Norway	22, 23, 54	41.2
63	NCTC 10220	<i>P. ureae</i>	S. D. Henriksen strain 218/60; human, Norway	22, 23	43.7
64	SSI P602	SP group	Altman strain 7098; human, Israel	13	50.4
65	SSI P603	SP group	W. Frederiksen strain SP1437; guinea pig, Denmark	13	50.5
66	HIM 733-7	SP group	W. Mannheim strain Michel A/76; guinea pig, Federal Republic of Germany	40	52.5
67	ATCC 17911	" <i>P. piscicida</i> "	M. J. Pelczar strain 315; epizootic of white perch, United States	60	39.5
68	NCTC 10699	<i>Pasteurella</i> -like	N. S. Mair strain 5143/70; porcine fetus, United Kingdom		43.4
69	SSI P335	" <i>P. multocida</i> "	W. Frederiksen strain SP5282-64; Frederiksen biotype 1; guinea pig, Denmark		49.3
70	SSI P614	" <i>P. multocida</i> "	S. Namioka serotype 5:A; Frederiksen biotype 6; chicken, Formosa	47	40.9
71	NCTC 10547	Bovine lymphangitis group	M. S. Jayaraman strain I; bovine, India	28	49.7
72	NCTC 9509	<i>Y. pseudotuberculosis</i>	E. Thal strain 105; mink, Denmark	4	50.4

^a ATCC, American Type Culture Collection, Rockville, MD.; HIM, Culture Collection of the Zentrum für Hygiene und Medizinische Mikrobiologie, Marburg, Federal Republic of Germany; IPDH, Institute for Poultry Disease, Hannover, Federal Republic of Germany; NCTC, National Collection of Type Cultures, Central Public Health Laboratory, London, United Kingdom; SSI, W. Frederiksen, Statens Seruminstitut, Copenhagen, Denmark.

^b The values are averages of six to nine assays.

FIG. 1. Two possible dendrograms for OTUs i, j, and k and OTUs i, j, k, and l. See text.

from each other by conventional methods (E. R. Hatt, R. Johnson, and R. L. Gherna, Abstr. Annu. Meet. Am. Soc. Microbiol. 1978, 154, p. 90).

These problems became even more complicated when phenotypic delineation of the genus *Haemophilus* Winslow et al. 1971 was considered, since V-factor dependency was no longer a criterion for separating genera (50).

In an effort to resolve some of these problems, we used deoxyribonucleic acid (DNA)-DNA hybridization to establish genetic relationships within the genus *Pasteurella*, the type genus of the family *Pasteurellaceae* (49; S. Pohl, Ph.D. thesis, Philipps-Universität, Marburg, Federal Republic of Germany, 1979) and separation of this genus from *Actinobacillus* and *Haemophilus*. DNA molecular weight and base composition were considered as additional taxonomic criteria.

In this study we included the recognized species of the three genera (54) and (especially for *P. multocida*), strains of the serogroups established by Carter (7) and the biotypes of Frederiksen (12) and a variety of isolates which represented phenotypic intermediates or possibly new species of the *Pasteurellaceae*.

MATERIALS AND METHODS

Microorganisms. The bacterial strains used in the DNA homology studies and their derivations are listed in Table 1.

Phenotypic characterization. The methods and media used to determine the phenotypic characteristics of the bacterial strains have been described previously (38, 40, 41, 45, 50, 62).

Cultivation techniques and preparation of DNA. Cells were grown aerobically at 35°C in Difco Proteose Peptone medium (68) supplemented with 0.4% (wt/vol) filter-sterilized yeast extract (Oxoid Ltd., London, England) and 0.01 M NaHCO_3 . The cells were harvested in the early stationary phase of growth, tested microscopically and culturally for purity, washed in 1× SSC (0.15 M NaCl plus 0.015 M trisodium citrate) and suspended in 1× SSC containing 0.01 M ethylenediaminetetraacetic acid (disodium salt). High-molecular-weight DNA was isolated by combining the methods of Marmur (41) and Kirby et al. (30), as proposed by De Ley et al. (8).

Characterization of DNA. Thermal denaturation (T_m) mid-points were used to determine the guanine-plus-cytosine (G+C) contents of the DNA preparations (42) (Table 1). The molecular weights of genome DNAs were determined from initial renaturation rates by using the method of Gillis et al. (15). *Escherichia coli* strain Luria B (= NCTC 10537) DNA was used as a reference. DNA preparations were further characterized by determining ultraviolet light spectra, protein contents (3), concentrations of 2-deoxyribose (6), and hyperchromicity.

DNA-DNA hybridization. Initial renaturation rates during homologous or heterologous reassociation were determined by the method of De Ley et al. (8), using a model 250 spectrophotometer (Gilford Instruments GmbH, Düsseldorf, Federal Republic of Germany), a DNA concentration of 80 µg/ml, a salt milieu containing 2× SSC, and a reassociation temperature of 68°C. The reassociation temperature was calculated as proposed by Gillis et al. (15). The reassociation method is supposed to be specific (i.e., to record only true base pairing); the DNA binding values (D values) obtained

FIG. 2. Similarity map of the groups of the genus *Pasteurella* sensu stricto as revealed by principal component analysis. x_1 , x_2 , and x_3 are coordinates of the three-dimensional Euclidean space. Symbols: ●, position of two or more strains; ○, position of one strain. The positions of taxa are indicated by numbers, as follows: 1, *P. multocida* subsp. *multocida*; 2, *P. multocida* subsp. *septica*; 3, *P. multocida* subsp. *gallicida*; 4, *P. dagmatis*; 5, *P. gallinarum*; 6, *P. canis*; 7, *P. stomatis*; 8, *P. anatis*; 9, *Pasteurella* species B; 10, *Pasteurella* species A; 11, *P. langaa*; 12, *P. avium*; 13, *P. volantium*.

TABLE 2. D values obtained with species belonging to the genus *Pasteurella*

Reference strain(s) ^a	DNA binding		Reference strain(s) ^a	DNA binding	
	Strain ^a	D value (%)		Strain ^a	D value (%)
<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>P. multocida</i> subsp. <i>multocida</i> 2	100	<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>P. pneumotropica</i> type Jawetz 56	28
	<i>P. multocida</i> subsp. <i>multocida</i> 3	100		<i>P. multocida</i> biotype 1 strain 69	27
	<i>P. multocida</i> subsp. <i>multocida</i> 4	100		<i>P. pneumotropica</i> type Heyl 59	27
	<i>P. multocida</i> subsp. <i>multocida</i> 5	100	<i>P. multocida</i> subsp. <i>multocida</i> 9	<i>P. pneumotropica</i> type Heyl 59	23
<i>P. multocida</i> subsp. <i>multocida</i> 8	<i>P. multocida</i> subsp. <i>multocida</i> 5	95		" <i>P. bettii</i> " 50	26
<i>P. multocida</i> subsp. <i>multocida</i> 3	<i>P. multocida</i> subsp. <i>multocida</i> 7	100	<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>P. avium</i> 42	22
<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>P. multocida</i> subsp. <i>multocida</i> 7	95		<i>P. langaa</i> 40	20
	<i>P. multocida</i> subsp. <i>multocida</i> 6	97		<i>P. canis</i> 28	17
		97		<i>P. stomatis</i> 33	17
<i>P. multocida</i> subsp. <i>multocida</i> 11	<i>P. multocida</i> subsp. <i>multocida</i> 6	97		<i>P. stomatis</i> 34	16
<i>P. multocida</i> subsp. <i>multocida</i> 5	<i>P. multocida</i> subsp. <i>multocida</i> 8	95		<i>Pasteurella</i> -like SP group strain 64	16
<i>P. multocida</i> subsp. <i>multocida</i> 10	<i>P. multocida</i> subsp. <i>multocida</i> 8	94		<i>P. ureae</i> 62	15
<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>P. multocida</i> subsp. <i>multocida</i> 8	92	<i>P. multocida</i> subsp. <i>multocida</i> 9	<i>P. ureae</i> 62	12
<i>P. multocida</i> subsp. <i>multocida</i> 6	<i>P. multocida</i> subsp. <i>multocida</i> 11	97		<i>P. haemolytica</i> biotype A strain 51	13
<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>P. multocida</i> subsp. <i>multocida</i> 11	84	<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>P. testudinis</i> 60	9
<i>P. multocida</i> subsp. <i>multocida</i> 8	<i>P. multocida</i> subsp. <i>multocida</i> 10	94	<i>P. multocida</i> subsp. <i>multocida</i> 9	<i>P. volantium</i> 45	6
<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>P. multocida</i> subsp. <i>multocida</i> 10	84		<i>Pasteurella</i> -like bovine lymphangitis group strain 71	6
	<i>P. multocida</i> subsp. <i>multocida</i> 9	91	<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>Pasteurella</i> species B strain 38	4
<i>P. multocida</i> subsp. <i>multocida</i> 11	<i>P. multocida</i> subsp. <i>septica</i> 15	82		<i>P. stomatis</i> 35	3
<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>P. multocida</i> subsp. <i>septica</i> 15	78	<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>Pasteurella</i> -like Mair strain 68	1
	<i>P. multocida</i> subsp. <i>septica</i> 12	80		<i>Pasteurella</i> -like Mair strain 68	0
<i>P. multocida</i> subsp. <i>multocida</i> 8	<i>P. multocida</i> subsp. <i>septica</i> 13	77	<i>P. multocida</i> subsp. <i>multocida</i> 9	<i>Pasteurella</i> -like Mair strain 68	0
<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>P. multocida</i> subsp. <i>gallicida</i> 16	77	<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>Y. pseudotuberculosis</i> 72	1
	<i>P. multocida</i> subsp. <i>septica</i> 14	73		<i>P. aerogenes</i> 49	0
<i>P. multocida</i> subsp. <i>multocida</i> 9	<i>P. multocida</i> subsp. <i>septica</i> 14	65	<i>P. multocida</i> subsp. <i>multocida</i> 9	" <i>P. piscicida</i> " 67	0
<i>P. multocida</i> subsp. <i>multocida</i> 5	<i>P. multocida</i> subsp. <i>septica</i> 14	55	<i>P. multocida</i> subsp. <i>septica</i> 12	<i>P. multocida</i> subsp. <i>septica</i> 15	100
<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>P. dagmatis</i> 19	62	<i>P. multocida</i> subsp. <i>septica</i> 15	<i>P. multocida</i> subsp. <i>septica</i> 13	94
	<i>P. dagmatis</i> 20	59	<i>P. multocida</i> subsp. <i>septica</i> 12	<i>P. multocida</i> subsp. <i>septica</i> 14	94
	<i>P. volantium</i> 45	59	<i>P. multocida</i> subsp. <i>septica</i> 13	<i>P. multocida</i> subsp. <i>septica</i> 14	89
	<i>P. volantium</i> 46	43	<i>P. multocida</i> subsp. <i>septica</i> 15	<i>P. multocida</i> subsp. <i>multocida</i> 11	82
	<i>P. anatis</i> 36	54	<i>P. multocida</i> subsp. <i>septica</i> 12	<i>P. multocida</i> subsp. <i>multocida</i> 1	80
<i>P. multocida</i> subsp. <i>multocida</i> 9	<i>P. gallinarum</i> 25	42	<i>P. multocida</i> subsp. <i>septica</i> 15	<i>P. multocida</i> subsp. <i>multocida</i> 1	78
<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>P. canis</i> 29	40	<i>P. multocida</i> subsp. <i>septica</i> 14	<i>P. multocida</i> subsp. <i>multocida</i> 1	73
<i>P. multocida</i> subsp. <i>multocida</i> 5	<i>P. canis</i> 27	33	<i>P. multocida</i> subsp. <i>septica</i> 13	<i>P. multocida</i> subsp. <i>multocida</i> 8	77
<i>P. multocida</i> subsp. <i>multocida</i> 1	<i>P. canis</i> 27	22	<i>P. multocida</i> subsp. <i>septica</i> 12	<i>P. multocida</i> subsp. <i>gallicida</i> 16	67
<i>P. multocida</i> subsp. <i>multocida</i> 3 and 11	<i>P. canis</i> 27	21	<i>P. multocida</i> subsp. <i>septica</i> 14	<i>P. multocida</i> subsp. <i>multocida</i> 9	65
<i>P. multocida</i> subsp. <i>multocida</i> 7	<i>P. canis</i> 27	18		<i>P. multocida</i> subsp. <i>multocida</i> 5	55
<i>P. multocida</i> subsp. <i>multocida</i> 9	<i>P. pneumotropica</i> type Jawetz 57	32	<i>P. multocida</i> subsp. <i>septica</i> 12	<i>P. anatis</i> 36	49
			<i>P. multocida</i> subsp. <i>septica</i> 15	<i>P. multocida</i> biotype 6 strain 70	31

Continued on following page

TABLE 2—Continued

Reference strain(s) ^a	DNA binding		Reference strain(s) ^a	DNA binding	
	Strain ^a	D value (%)		Strain ^a	D value (%)
<i>P. multocida</i> subsp. <i>septica</i> 13	<i>P. langaa</i> 40	25 ^b	<i>P. gallinarum</i> 25	<i>P. avium</i> 42	52 ^b
<i>P. multocida</i> subsp. <i>septica</i> 15	<i>P. stomatis</i> 33	25		<i>P. multocida</i> subsp. <i>multocida</i> 9	42
	<i>P. stomatis</i> 35	13	<i>P. gallinarum</i> 26	<i>P. haemolytica</i> biotype T strain 52	33
	<i>P. dagmatis</i> 24	10	<i>P. gallinarum</i> 25	<i>P. multocida</i> subsp. <i>gallicida</i> 16	30
<i>P. multocida</i> subsp. <i>gallicida</i> 16	<i>P. canis</i> 27	1		<i>P. pneumotropica</i> type Jawetz strain 57	28
	<i>P. multocida</i> subsp. <i>gallicida</i> 17	100		<i>P. pneumotropica</i> type Heyl strain 59	25
	<i>P. multocida</i> subsp. <i>gallicida</i> 18	91		<i>P. ureae</i> 62	21
	<i>P. multocida</i> subsp. <i>multocida</i> 1	77		<i>P. stomatis</i> 33	20
	<i>P. multocida</i> subsp. <i>septica</i> 12	67		<i>P. langaa</i> 40	20 ^b
	<i>Pasteurella</i> species B strain 39	39	<i>P. gallinarum</i> 26	<i>P. haemolytica</i> biotype A strain 51	20
	<i>Pasteurella</i> species B strain 38	38	<i>P. gallinarum</i> 25	<i>P. aerogenes</i> 48	18
	<i>P. gallinarum</i> 25	30		<i>P. anatis</i> 36	13 ^b
<i>P. dagmatis</i> 19	<i>P. dagmatis</i> 21	100		<i>Pasteurella</i> species B strain 38	3
<i>P. dagmatis</i> 22	<i>P. dagmatis</i> 23	100	<i>P. canis</i> 27	<i>P. canis</i> 29	100
<i>P. dagmatis</i> 19	<i>P. dagmatis</i> 23	91	<i>P. canis</i> 30	<i>P. canis</i> 28	100
<i>P. dagmatis</i> 24	<i>P. dagmatis</i> 23	84	<i>P. canis</i> 27	<i>P. canis</i> 28	97
<i>P. dagmatis</i> 20	<i>P. dagmatis</i> 24	100		<i>P. canis</i> 30	99
<i>P. dagmatis</i> 19	<i>P. dagmatis</i> 24	85	<i>P. canis</i> 30	<i>P. canis</i> 31	92
<i>P. dagmatis</i> 23	<i>P. dagmatis</i> 24	84	<i>P. canis</i> 27	<i>P. canis</i> 31	80
<i>P. dagmatis</i> 19	<i>P. dagmatis</i> 20	96	<i>P. canis</i> 31	<i>P. avium</i> 44	69
	<i>P. dagmatis</i> 22	92		<i>Pasteurella</i> species B strain 39	62
	<i>P. gallinarum</i> 25	78	<i>P. canis</i> 27	<i>P. dagmatis</i> 21	62
<i>P. dagmatis</i> 20	<i>P. gallinarum</i> 26	72	<i>P. canis</i> 29	<i>P. dagmatis</i> 19	60
<i>P. dagmatis</i> 19	<i>P. multocida</i> subsp. <i>multocida</i> 1	62	<i>P. canis</i> 27	<i>P. dagmatis</i> 19	43
<i>P. dagmatis</i> 20	<i>P. multocida</i> subsp. <i>multocida</i> 1	59		<i>P. stomatis</i> 35	54
				<i>P. stomatis</i> 33	51
<i>P. dagmatis</i> 21	<i>P. canis</i> 27	62		<i>P. dagmatis</i> 24	44
<i>P. dagmatis</i> 24	<i>P. canis</i> 27	44		<i>P. avium</i> 43	41
<i>P. dagmatis</i> 19	<i>P. canis</i> 27	43	<i>P. canis</i> 29	<i>P. multocida</i> subsp. <i>multocida</i> 1	40
	<i>P. canis</i> 29	60	<i>P. canis</i> 27	<i>P. multocida</i> subsp. <i>multocida</i> 1	22
<i>P. dagmatis</i> 24	<i>P. stomatis</i> 33	59	<i>P. canis</i> 28	<i>P. multocida</i> subsp. <i>multocida</i> 1	18
<i>P. dagmatis</i> 19	<i>P. stomatis</i> 33	40		<i>P. ureae</i> 62	37
<i>P. dagmatis</i> 24	<i>P. stomatis</i> 35	57	<i>P. canis</i> 27	<i>P. ureae</i> 62	31
<i>P. dagmatis</i> 19	<i>P. volantium</i> 45	43	<i>P. canis</i> 28	<i>P. ureae</i> 63	34
<i>P. dagmatis</i> 20	<i>P. volantium</i> 45	25	<i>P. canis</i> 27	<i>P. multocida</i> subsp. <i>multocida</i> 5	33
<i>P. dagmatis</i> 19	<i>Pasteurella</i> species B strain 38	37		<i>P. stomatis</i> 34	23
	<i>P. avium</i> 43	32		<i>P. volantium</i> 45	22
<i>P. dagmatis</i> 24	<i>P. langaa</i> 40	30		<i>P. multocida</i> subsp. <i>multocida</i> 11	21
	<i>P. anatis</i> 36	29		<i>P. multocida</i> subsp. <i>multocida</i> 3	21
	<i>P. multocida</i> biotype 1 strain 69	25		<i>Pasteurella</i> species B strain 38	19
	<i>P. ureae</i> 62	22		<i>P. multocida</i> biotype 6 strain 70	14
<i>P. dagmatis</i> 19	<i>P. ureae</i> 62	3		<i>P. multocida</i> subsp. <i>multocida</i> 9	12
<i>P. dagmatis</i> 24	<i>P. anatis</i> 36	12		<i>P. pneumotropica</i> type Jawetz strain 56	12
	<i>P. multocida</i> subsp. <i>septica</i> 15	10		<i>P. multocida</i> biotype 1 strain 69	10
<i>P. dagmatis</i> 19	<i>P. testudinis</i> 60	6		<i>P. multocida</i> subsp. <i>septica</i> 15	1
	<i>P. pneumotropica</i> type Jawetz strain 56	0		" <i>P. bettii</i> " 50	0
	<i>P. pneumotropica</i> type Heyl strain 59	0	<i>P. stomatis</i> 32	<i>P. stomatis</i> 34	98
	<i>P. aerogenes</i> 48	0		<i>P. stomatis</i> 33	97
	<i>Pasteurella</i> -like SP group strain 64	0	<i>P. stomatis</i> 33	<i>P. stomatis</i> 35	91
	<i>Pasteurella</i> -like SP group strain 65	0	<i>P. stomatis</i> 32	<i>P. avium</i> 44	81
	<i>Y. pseudotuberculosis</i> 72	0	<i>P. stomatis</i> 33	<i>P. avium</i> 42	78
<i>P. gallinarum</i> 25	<i>P. gallinarum</i> 26	90			
	<i>P. dagmatis</i> 19	78			
	<i>P. volantium</i> 45	72			
<i>P. gallinarum</i> 26	<i>P. dagmatis</i> 20	72			
	<i>P. avium</i> 42	61			

Continued on following page

TABLE 2—Continued

Reference strain(s) ^a	DNA binding		Reference strain(s) ^a	DNA binding	
	Strain ^a	D value (%)		Strain ^a	D value (%)
<i>P. stomatis</i> 32	<i>P. avium</i> 43	74		<i>P. gallinarum</i> 25	20 ^b
	<i>Pasteurella</i> species B strain 38	63		<i>P. multocida</i> subsp. <i>multocida</i> 1	20 ^b
<i>P. stomatis</i> 33	<i>P. dagmatis</i> 24	59		<i>P. canis</i> 27	14 ^b
<i>P. stomatis</i> 35	<i>P. dagmatis</i> 24	57		<i>P. haemolytica</i> biotype T strain 52	10 ^b
	<i>P. canis</i> 27	54		<i>P. haemolytica</i> biotype A strain 51	5 ^b
<i>P. stomatis</i> 33	<i>P. canis</i> 27	51		<i>P. avium</i> 42	2 ^b
	<i>P. volantium</i> 45	42		<i>P. ureae</i> 62	0
	<i>P. dagmatis</i> 19	40		<i>P. avium</i> 43	100
	<i>P. anatis</i> 36	38		<i>P. avium</i> 44	88
<i>P. stomatis</i> 35	<i>P. anatis</i> 36	29	<i>P. avium</i> 42	<i>P. stomatis</i> 32	81
<i>P. stomatis</i> 33	<i>P. multocida</i> subsp. <i>septica</i> 15	25	<i>P. avium</i> 44	<i>P. stomatis</i> 32	74
<i>P. stomatis</i> 35	<i>P. multocida</i> subsp. <i>septica</i> 15	13	<i>P. avium</i> 42	<i>P. stomatis</i> 33	78
<i>P. stomatis</i> 34	<i>P. pneumotropica</i> type Jawetz strain 56	22	<i>P. avium</i> 44	<i>P. stomatis</i> 31	69
<i>P. stomatis</i> 33	<i>P. multocida</i> biotype 1 strain 69	20	<i>P. avium</i> 42	<i>P. gallinarum</i> 26	61
	<i>P. gallinarum</i> 25	20		<i>P. volantium</i> 45	60 ^b
	<i>P. multocida</i> subsp. <i>multocida</i> 1	17		<i>P. gallinarum</i> 25	52 ^b
<i>P. stomatis</i> 34	<i>P. multocida</i> subsp. <i>multocida</i> 1	16	<i>P. avium</i> 43	<i>P. volantium</i> 47	44
<i>P. stomatis</i> 35	<i>P. multocida</i> subsp. <i>multocida</i> 1	3		<i>P. canis</i> 27	41
<i>P. stomatis</i> 33	<i>P. multocida</i> biotype 6 strain 70	9	<i>P. avium</i> 42	<i>P. dagmatis</i> 19	32
<i>P. anatis</i> 36	<i>P. anatis</i> 37	94 ^b		<i>Pasteurella</i> species B strain 38	29
	<i>P. multocida</i> subsp. <i>multocida</i> 1	54		<i>P. multocida</i> subsp. <i>multocida</i> 1	22
<i>P. anatis</i> 37	<i>P. langaa</i> 40	51	<i>P. volantium</i> 45	<i>P. anatis</i> 36	15
<i>P. anatis</i> 36	<i>P. langaa</i> 40	36	<i>P. volantium</i> 47	<i>P. langaa</i> 40	2 ^b
	<i>P. multocida</i> subsp. <i>septica</i> 12	49	<i>P. volantium</i> 45	<i>P. volantium</i> 47	90
	<i>P. stomatis</i> 33	38		<i>P. volantium</i> 46	88
<i>P. anatis</i> 37	<i>P. volantium</i> 47	33		<i>P. volantium</i> 46	81
<i>P. anatis</i> 36	<i>P. stomatis</i> 35	29		<i>P. gallinarum</i> 25	72
	<i>P. dagmatis</i> 24	29 ^b		<i>P. gallinarum</i> 26	70
	<i>P. volantium</i> 45	18		<i>P. avium</i> 42	60
	<i>P. avium</i> 42	15	<i>P. volantium</i> 47	<i>P. avium</i> 42	44
	<i>P. gallinarum</i> 25	13 ^b	<i>P. volantium</i> 45	<i>P. multocida</i> subsp. <i>multocida</i> 1	59
	<i>P. dagmatis</i> 19	12	<i>P. volantium</i> 47	<i>P. langaa</i> 40	57
<i>Pasteurella</i> species B strain 38	<i>Pasteurella</i> species B strain 39	87	<i>P. volantium</i> 45	<i>P. langaa</i> 40	49
	<i>P. stomatis</i> 32	63	<i>P. volantium</i> 46	<i>Pasteurella</i> species B strain 39	52
<i>Pasteurella</i> species B strain 39	<i>P. canis</i> 31	62		<i>P. dagmatis</i> 19	43
	<i>P. multocida</i> subsp. <i>gallicida</i> 16	39	<i>P. volantium</i> 45	<i>P. multocida</i> subsp. <i>multocida</i> 9	43
<i>Pasteurella</i> species B strain 38	<i>P. multocida</i> subsp. <i>gallicida</i> 16	38	<i>P. volantium</i> 47	<i>P. stomatis</i> 33	42
	<i>P. dagmatis</i> 19	37	<i>P. volantium</i> 45	<i>P. anatis</i> 37	33
	<i>P. pneumotropica</i> type Heyl strain 62	30	<i>P. volantium</i> 46	<i>P. pneumotropica</i> type Jawetz strain 58	31
	<i>P. avium</i> 42	29	<i>P. volantium</i> 45	<i>P. pneumotropica</i> type Heyl strain 59	29
	<i>P. canis</i> 27	19		<i>P. dagmatis</i> 20	25
	<i>P. multocida</i> subsp. <i>multocida</i> 1	4	<i>P. volantium</i> 46	" <i>P. piscicida</i> " 67	24
	<i>P. gallinarum</i> 25	3	<i>P. volantium</i> 45	" <i>P. piscicida</i> " 67	20
	<i>Y. pseudotuberculosis</i> 72	0	<i>P. volantium</i> 46	<i>P. canis</i> 27	22
<i>P. langaa</i> 40	<i>P. langaa</i> 41	100 ^b	<i>P. volantium</i> 45	<i>Pasteurella</i> -like Mair strain 68	21
	<i>P. volantium</i> 47	57		<i>P. ureae</i> 62	21
	<i>P. anatis</i> 37	51	<i>P. volantium</i> 46	<i>P. anatis</i> 36	18
	<i>P. volantium</i> 45	49 ^b	<i>P. volantium</i> 45	<i>P. pneumotropica</i> type Jawetz strain 57	17
	<i>P. anatis</i> 36	36		<i>P. pneumotropica</i> type Jawetz strain 57	16
	<i>P. dagmatis</i> 19	30 ^b	<i>P. volantium</i> 46	" <i>P. bettii</i> " 50	16
	<i>P. multocida</i> subsp. <i>septica</i> 13	25 ^b	<i>P. volantium</i> 45	" <i>P. bettii</i> " 50	0
				<i>Pasteurella</i> -like Mair strain 68	2
				<i>Pasteurella</i> -like bovine lymphangitis group strain 71	0

^a Laboratory strain numbers (see Table 1).^b Unpublished data from K. Piechulla.

by using this method correspond to the values determined with methods that detect reassociation of radioactively labeled DNA under stringent conditions.

Taxometric evaluation. The numerical methods used in bacterial taxonomy are based on a matrix of distance or similarity coefficients. The construction of the matrix is easy when each operational taxonomic unit (OTU) (59) is characterized by a vector of phenotypic characteristics or by a list of different base sequences, etc. In the case of DNA hybridization, however, each coefficient has to be measured directly. For n OTUs, $n(n-1)/2$ such coefficients would be needed, a quantity that is often too large to be realistic. Therefore, in most cases the distance or similarity matrix is incomplete. This is no handicap when the single-linkage method is used, but excludes other methods, such as the average-linkage method, the Ward method, or principal component analysis. Different methods have been proposed for completion of the matrix, with no one method being entirely satisfactory. Sneath (59) proposed that each pair of OTUs should be compared with a given number of reference strains. However, lack of information at the beginning of this study did not allow the definition of such strains. To carry out a principal component analysis, the similarity matrix was completed by interpolation. The following two methods were used simultaneously, depending on the D values: substitution and maximin interpolation.

(i) **Substitution.** $D_{ij} \geq 90\%$ for OTUs i and j ; if only OTU i is compared with OTU k and not OTU j , then $D_{jk} = D_{ik}$.

(ii) **Maximin interpolation.** If D_{ij} is undetermined, consider an OTU k such that both D_{ik} and D_{jk} are known; then $D_{ij} =$ smaller value of D_{ik} and D_{jk} (min). If there is more than one OTU (OTUs $k, l, \dots$), the greatest of $D_{ik}, D_{il}, \dots$ (max) has been taken.

The substitution method needs no further comments. The justification for the maximin interpolation method follows from Fig. 1, in which two possible dendrograms are shown for OTUs i, j , and k and OTUs i, j, k , and l . The smaller the stretch on the dendrogram from one OTU to another, the higher the similarity between the OTUs. In Fig. 1A, $D_{ij} = D_{ik}$, the smaller of D_{ik} and D_{jk} . In Fig. 1B, where $D_{ij} < D_{ik}$ and D_{il} , the level of similarity is underestimated by this method. The possible error is lessened by using D_{ik} , the greater of D_{ik} and D_{il} . Thus, this method allows the conclusion that $D_{ij} \geq$ the maximal values of D_{ik}, D_{il} , etc. Principal component analysis was carried out by using the Q -technique. Each strain is represented as a point with three coordinates (x_1, x_2 , and x_3) in an Euclidean space (Fig. 2).

RESULTS AND DISCUSSION

DNA reassociation data. The results of the DNA hybridization experiments are summarized in Tables 2 and 3 and Fig. 2.

The genus *Pasteurella* sensu stricto is restricted to organisms that cluster by single linkage above the 50% DNA relatedness level (37). This proposal is in accordance with the principle of nomenclatural stability. If the genus was extended to lower DNA binding levels, the traditional genera and corresponding names (*Actinobacillus*, *Haemophilus*, and *Pasteurella*) could no longer be used (36, 37). On the other hand, well-defined species (Fig. 2) (45, 46) correspond to DNA relatedness clusters that are united at or above a DNA binding level of 85%.

***P. multocida*.** High relatedness values (90 to 100% DNA binding) were observed among the type strain of *P. multocida* (strain 1) and strains 2 through 11 (Table 1).

Additionally, strains belonging to the Carter serogroups (7) were included in this group, as described previously (62). The members of this group exhibited DNA binding levels of about 70% to another *P. multocida* group (namely, strains 12 through 15, which were interrelated at a DNA binding level of more than 90%). This second group could be differentiated from the former group by negative sorbitol fermentation.

A third taxonomic entity, which clustered at a DNA binding level of more than 90%, consisted of *P. multocida* strains which fermented dulcitol and often L-arabinose (strains 16 through 18); this group was related to the two *P. multocida* groups described above at DNA binding levels of 80 and 70%, respectively.

The DNA binding data would allow us to classify the three clusters described above as distinct species. However, this would be rather pointless from the clinical viewpoint. Therefore, we propose that *P. multocida* should be divided into three subspecies which may be useful for epidemiological purposes. The DNA homology group which includes the type strain, the representatives of the Carter serogroups, Frederiksen biotypes 2 to 5, and strain 10, which was used in 16S ribosomal ribonucleic acid studies of procaryotic phylogeny (69; L. B. Zablen, Ph.D. thesis, University of Illinois, Urbana, 1975), becomes *P. multocida* subsp. *multocida*. The cluster consisting of sorbitol-negative strains becomes *P. multocida* subsp. *septica*, and the cluster consisting of dulcitol-positive strains becomes *P. multocida* subsp. *gallicida*. Thus, we preserve the main synonymy of *P. multocida* used in the past: the epithet *septica* is most frequently used in Anglo-Saxon countries, and the epithet *gallicida* is associated with the strains that ferment dulcitol and often arabinose. Rosenbusch and Merchant (53), as well as Dorsey (9) and Heddleston (20), described the fermentation of dulcitol and arabinose as characteristics of *P. multocida* strains isolated from avian sources. Variations in raffinose, lactose, maltose, trehalose, and D-xylose fermentation were of no taxonomic consequence.

Another group in the genus *Pasteurella* is formed by the *P. pneumotropica* type Henriksen-*Pasteurella* "gas"-*Pasteurella* new species 1 group, represented by strains 19 through 24. This group was shown to be related to *P. gallinarum* (strains 25 and 26) at a DNA binding level of 80% and to *P. multocida* at a level of 60%. Based on correspondence between E. O. King and K. P. Carpenter from 1965 (K. P. Carpenter, personal communication), we propose the name *Pasteurella dagmatis* sp. nov. for this new species in the genus *Pasteurella*.

Pasteurella volantium Mutters et al. 1985 (46) (strains 45 through 47) was related to *P. gallinarum* at a DNA binding level of 70% and to *P. dagmatis* at a DNA binding level of 43%.

Biotype 6 of *P. multocida*, represented by strains 27 through 30, exhibited high intragroup DNA relatedness (D value, more than 90%); strain 31, representing Bisgaard taxon 13 (Orn⁺) (35a) was also included in this taxon. This group exhibited D values of 69% to *Pasteurella avium*, 60% to *P. dagmatis*, and between 40 and 20% to *P. multocida*. Strains belonging to this group have also been designated "dog type" strains (12). We propose the name *Pasteurella canis* sp. nov. for this group because it is characteristically isolated from the throats of dogs or from human infections resulting from dog bites. For the needs of clinicians we propose division of this species into the following two biotypes: biotype 1 (indole positive, isolated from dogs and dog bite lesions) and biotype 2 (indole negative, isolated from calves).

TABLE 3. D values obtained with species or groups not affiliated with the genus *Pasteurella*

Reference strain ^a	DNA binding		Reference strain ^a	DNA binding	
	Strain ^a	D value (%)		Strain ^a	D value (%)
<i>P. aerogenes</i> 48	<i>P. aerogenes</i> 49	87	<i>P. pneumotropica</i> 56	<i>P. multocida</i> subsp. <i>multocida</i> 1	28
	<i>Pasteurella</i> -like Mair strain 68	46	<i>P. pneumotropica</i> 58	<i>P. ureae</i> 62	26
	<i>P. pneumotropica</i> type Jawetz strain 56	25	<i>P. pneumotropica</i> 56	<i>P. aerogenes</i> 48	25
	<i>P. gallinarum</i> 25	18		<i>P. stomatis</i> 34	22
<i>P. aerogenes</i> 49	<i>P. multocida</i> subsp. <i>multocida</i> 1	0	<i>P. pneumotropica</i> 57	<i>P. volantium</i> 46	17
<i>P. aerogenes</i> 48	<i>Pasteurella</i> -like SP group strain 64	0	<i>P. pneumotropica</i> 56	<i>P. canis</i> 27	12
	<i>P. dagmatis</i> 19	0	<i>P. pneumotropica</i> 57	<i>Pasteurella</i> -like bovine lymphangitis group strain 71	0
" <i>P. bettii</i> " 50	<i>P. pneumotropica</i> type Jawetz strain 57	29	<i>P. pneumotropica</i> 56	<i>P. dagmatis</i> 19	0
	<i>P. ureae</i> 62	26	<i>P. pneumotropica</i> type Heyl strain 59	<i>P. pneumotropica</i> type Jawetz strain 56	34
	<i>P. multocida</i> subsp. <i>multocida</i> 9	26		<i>P. pneumotropica</i> type Jawetz strain 57	31
	<i>P. pneumotropica</i> type Heyl strain 59	19		<i>Pasteurella</i> species B strain 38	30
	<i>P. volantium</i> 45	16		<i>P. volantium</i> 46	29
	<i>P. haemolytica</i> biotype A strain 51	9		<i>P. multocida</i> subsp. <i>multocida</i> 1	27
	<i>P. volantium</i> 46	0		<i>P. gallinarum</i> 26	25
	<i>P. canis</i> 27	0		<i>P. gallinarum</i> 25	25
<i>P. haemolytica</i> biotype A strain 51	<i>P. haemolytica</i> third taxon strain 53	54		<i>P. multocida</i> subsp. <i>multocida</i> 9	23
	<i>P. testudinis</i> 60	49		<i>P. haemolytica</i> biotype A strain 51	21
	<i>P. ureae</i> 62	45		" <i>P. bettii</i> " 50	19
	<i>P. pneumotropica</i> type Jawetz strain 57	29		<i>Pasteurella</i> -like bovine lymphangitis group strain 71	15
	<i>P. haemolytica</i> intermedium strain 54	29		<i>A. lignieresii</i> 76	15
	<i>Pasteurella</i> -like Mair strain 68	21		<i>P. ureae</i> 62	9
	<i>P. pneumotropica</i> type Heyl strain 59	21		<i>Pasteurella</i> -like Mair strain 68	6
	<i>P. gallinarum</i> 26	20		<i>P. dagmatis</i> 19	0
	<i>P. haemolytica</i> biotype T strain 52	18		" <i>P. piscicida</i> " 67	0
	<i>P. multocida</i> subsp. <i>multocida</i> 9	13	<i>P. testudinis</i> 60	<i>P. testudinis</i> 61	95
	" <i>P. bettii</i> " 50	9		<i>P. haemolytica</i> biotype T strain 52	62
	" <i>P. piscicida</i> " 67	8		<i>P. haemolytica</i> biotype A strain 51	49
	<i>P. langaa</i> 40	5 ^b		<i>P. multocida</i> subsp. <i>multocida</i> 1	9
	<i>Pasteurella</i> -like bovine lymphangitis group strain 71	0		<i>P. dagmatis</i> 19	6
	<i>P. haemolytica</i> fourth taxon strain 55	0	<i>P. ureae</i> 62	<i>P. ureae</i> 63	100
<i>P. haemolytica</i> biotype T strain 52	<i>P. testudinis</i> 60	62		<i>P. haemolytica</i> biotype A strain 51	45
	<i>P. gallinarum</i> 26	33		<i>P. canis</i> 27	37
	<i>P. ureae</i> 62	30		<i>P. canis</i> 28	34
	<i>P. multocida</i> subsp. <i>multocida</i> 9	24	<i>P. ureae</i> 63	<i>P. canis</i> 28	31
	<i>P. haemolytica</i> biotype A strain 51	18	<i>P. ureae</i> 62	<i>P. haemolytica</i> biotype T strain 52	30
	<i>P. langaa</i> 40	10 ^b		" <i>P. bettii</i> " 50	26
	<i>P. haemolytica</i> third taxon strain 53	9		<i>P. pneumotropica</i> type Jawetz strain 61	26
	<i>P. haemolytica</i> fourth taxon strain 55	0		<i>P. dagmatis</i> 24	22
	<i>P. multocida</i> subsp. <i>multocida</i> 1	0		<i>P. gallinarum</i> 25	21
<i>P. pneumotropica</i> type Jawetz strain 56	<i>P. pneumotropica</i> type Jawetz strain 57	93		" <i>P. piscicida</i> " 67	20
	<i>P. pneumotropica</i> type Jawetz strain 58	90		<i>P. volantium</i> 45	15
	<i>P. pneumotropica</i> type Heyl strain 59	34		<i>P. multocida</i> subsp. <i>multocida</i> 1	15
<i>P. pneumotropica</i> 57	<i>P. pneumotropica</i> type Heyl strain 59	31		<i>P. multocida</i> subsp. <i>multocida</i> 9	12
	<i>P. multocida</i> subsp. <i>multocida</i> 9	32		<i>P. pneumotropica</i> type Heyl 59	9
<i>P. pneumotropica</i> 58	<i>P. volantium</i> 45	31		<i>P. pneumotropica</i> type Jawetz strain 57	7
<i>P. pneumotropica</i> 57	<i>P. volantium</i> 45	16		<i>Pasteurella</i> -like Mair strain 68	7
	<i>Pasteurella</i> -like Mair strain 68	30		<i>Pasteurella</i> -like bovine lymphangitis group strain 71	4
	<i>P. haemolytica</i> biotype A strain 51	29		<i>P. dagmatis</i> 19	3
	" <i>P. bettii</i> " 50	29		<i>P. langaa</i> 40	0
	<i>P. gallinarum</i> 25	28		<i>Pasteurella</i> -like SP group strain 66	100
			<i>Pasteurella</i> -like SP group strain 66		
			<i>Pasteurella</i> -like SP group strain 64	<i>Pasteurella</i> -like SP group strain 65	97
				<i>P. multocida</i> subsp. <i>multocida</i> 1	16
				<i>P. aerogenes</i> 48	0
				<i>P. dagmatis</i> 19	0
			<i>Pasteurella</i> -like SP group strain 65	<i>P. dagmatis</i> 19	0

Continued on following page

TABLE 3—Continued

Reference strain ^a	DNA binding	
	Strain ^a	D value (%)
"P. piscicida" 67	<i>P. volantium</i> 45	24
	<i>P. ureae</i> 62	20
	<i>P. volantium</i> 46	20
	<i>P. haemolytica</i> biotype A strain 51	8
	<i>P. pneumotropica</i> type Heyl strain 59	0
<i>Pasteurella</i> -like Mair strain 68	<i>P. multocida</i> subsp. <i>multocida</i> 9	0
	<i>P. aerogenes</i> 48	46
	<i>P. pneumotropica</i> type Jawetz strain 57	30
	<i>P. haemolytica</i> biotype A strain 51	21
	<i>P. volantium</i> 46	21
	<i>P. multocida</i> biotype 1 strain 69	12
	<i>P. ureae</i> 62	7
	<i>P. pneumotropica</i> type Heyl strain 59	6
	<i>P. volantium</i> 45	2
	<i>P. multocida</i> subsp. <i>multocida</i> 1	1
<i>Pasteurella</i> -like bovine lymphangitis group strain 71	<i>Pasteurella</i> -like SP group strain 64	0
	<i>P. multocida</i> subsp. <i>multocida</i> 9	0
	<i>P. pneumotropica</i> type Heyl strain 59	15
	<i>P. multocida</i> subsp. <i>multocida</i> 9	6
	<i>P. testudinis</i> 61	4
	<i>P. volantium</i> 45	0
	<i>P. pneumotropica</i> type Jawetz strain 57	0
	<i>P. haemolytica</i> biotype A strain 51	0

^a Laboratory strain numbers (see Table 1).^b Unpublished data from K. Piechulla.

Another group showing high intragroup DNA homology (more than 90%) is formed by strains 32 through 35. This group is related to *P. dagmatis* at a DNA binding level of 40 to 60%, to *P. canis* at a DNA binding level of 50 to 55%, and to *P. volantium* at a DNA binding level of 42%. With *P. avium* (Hinz and Kunjara) Mutters et al. 1985 (46), represented by strains 42 through 44, D of about 74 to 80% were obtained.

Although this group shows fermentation reaction patterns similar to those of *P. canis*, it can be discriminated by its negative ornithine decarboxylase reaction. The DNA binding data indicate that this group is a species which is closely related to *P. avium*. We propose the name *Pasteurella stomatis* sp. nov. for this group; the normal habitat of these organisms is the throats, gums, and tonsils of mammals.

DNA-DNA hybridization experiments with dulcitol-fermenting strains designated *P. multocida* biotype 6 (strains 38 and 39) indicated levels of DNA homology of 60% with *P. stomatis* and *P. canis* and about 40% with *P. dagmatis* and *P. multocida* subsp. *gallicida*. Despite the small number of strains investigated, these organisms should be tentatively regarded as a distinct species within the genus *Pasteurella* sensu stricto. For the present this species remains unnamed (provisionally called *Pasteurella* species B), since its clinical significance is unknown and a clear separation by computer analysis was not possible on the basis of the present data.

Bisgaard taxa 1 and 4 (1), represented by strains 36 and 37 and strains 40 and 41, respectively, are interrelated at a DNA binding level of 51%. Taxon 1 exhibits 54% DNA homology with *P. multocida*, and taxon 4 exhibits 57% homology with *P. volantium*. Thus, these two taxa, which were isolated

from chickens and ducks, can be regarded as species of *Pasteurella*.

We propose the following names for these organisms: *Pasteurella anatis* sp. nov., for the facultatively pathogenic species represented by taxon 1, and *Pasteurella langaa* sp. nov., for the species consisting of taxon 4.

A description of another new unnamed species of *Pasteurella* consisting of L-arabinose-positive strains (provisionally called *Pasteurella* species A) has been presented previously (46).

Organisms exhibiting less than 50% DNA relatedness to *Pasteurella* sensu stricto. Levels of DNA homology below 40% have been observed between species of the genus *Pasteurella* sensu stricto and representatives of organisms designated *P. aerogenes*, *P. haemolytica*, *P. pneumotropica* types Jawetz and Heyl, *P. ureae*, *P. testudinis*, and "*Pasteurella piscicida*." Between species of *Pasteurella* sensu stricto and members of the bovine lymphangitis group, the SP group, and group HB-5, binding values less than 30% or no measurable DNA binding was observed. DNA-DNA hybridization experiments with *P. multocida* biotype 1 (strain 69) and one biotype 6 strain (strain 70), which differed from other biotype 6 strains by its inability to ferment sucrose, yielded low or no measurable relationships to other *Pasteurella* strains.

A comparison of the species and groups described above with representative members of the *Actinobacillus* group yielded D values for *P. ureae* (strains 62 and 63) compared with *Actinobacillus equuli* NCTC 8529^T (T = type strain) and *Actinobacillus lignieresii* NCTC 4976 of 66 and 53%, respectively. The level of DNA homology between *P. ureae* strain 62 and *P. canis* strain 27 was 40%, and the level of homology between *P. ureae* and the type strain of *P. multocida* (strain 1) was 15%.

P. haemolytica biotype A (strain 51) exhibited levels of DNA homology of 49 and 45% with *P. testudinis* (strain 60) and *P. ureae*, respectively. A level of DNA homology of 62% was observed between *P. testudinis* and *P. haemolytica* biotype T (strain 52). Thus, the two biotypes of *P. haemolytica* are interconnected via *P. testudinis*. The *P. haemolytica* group is more closely related to the genus *Actinobacillus* than to *Pasteurella* sensu stricto. It also includes strain 53, representing the third taxon of *P. haemolytica* (12). So far, the genetic data probably indicate the existence of a new genus-like structure within the family *Pasteurellaceae*, consisting of *P. haemolytica* biotypes A and T, the third taxon, and *P. testudinis*. However, assignment of the "*Actinobacillus salpingitidis*" cluster to this group was not supported by DNA binding studies (K. Piechulla, personal communication).

Recently, *P. pneumotropica* types Jawetz and Heyl have been linked to the *Actinobacillus* group by DNA hybridization via two new species of *Actinobacillus* (R. Mutters and K. Piechulla, unpublished data).

DNA-DNA hybridization experiments with members of *P. aerogenes*, the SP group, group HB-5, the bovine lymphangitis group, "*P. piscicida*," and *Actinobacillus* or *Haemophilus* species did not solve the problems of the taxonomic position of these groups. Only D values of less than 40% have been detected.

Compared with representatives of the genera *Haemophilus* and *Actinobacillus* (*Actinobacillus capsulatus* NCTC 11408^T, *A. equuli* NCTC 8529^T, *A. lignieresii* NCTC 4189^T and NCTC 4976, *Actinobacillus pleuropneumoniae* CCM 5869^T, "*A. salpingitidis*" CCM 5974^T and CCM 5976, "*Actinobacillus seminis*" ATCC 15768^T, *Actinobacillus suis*

CCM 5586^T, *Haemophilus aegyptius* ATCC 11116^T, *Haemophilus aphrophilus* NCTC 5886, *Haemophilus haemoglobinophilus* NCTC 1659^T, *Haemophilus influenzae* NCTC 8143^T and NCTC 4560, *Haemophilus paragallinarum* ATCC 29545^T, *Haemophilus parahaemolyticus* NCTC 8479^T, and *Haemophilus parasuis* NCTC 4557^T) the species of the genus *Pasteurella* sensu stricto showed levels of DNA homology of 40% or less. No measurable DNA binding has been observed among the type species of the three genera (*P. multocida* NCTC 10322^T, *A. lignieresii* NCTC 4189^T, and *H. influenzae* NCTC 8143^T).

A strain of *Yersinia pseudotuberculosis* type III (strain 72) was included in this study because it had been found to give a value of 28% with *P. multocida* under permissive conditions when the hydroxyapatite method was used (4). With the renaturation method, no measurable DNA binding between this *Yersinia* strain and representative strains of *Pasteurella* sensu stricto was detected. Thus, there is no evidence so far for a close connection between the families *Pasteurellaceae* and *Enterobacteriaceae*, as has also been observed by Ursing (67).

Phenotypic features. On the basis of the molecular data presented above, the genus *Pasteurella* sensu stricto can be differentiated from related genera by the features described below. The cells are coccobacillary to rod shaped and 0.3 to 0.4 μm in diameter and appear singly, in pairs, or (less frequently) in short chains. They are not flagellated; endospores are not formed. The gram reaction is negative. The organisms are aerobic to microaerophilic or facultatively anaerobic and contain demethylmenaquinones (always) and ubiquinones (usually) but no menaquinones; glucose catabolism is fermentative. Nitrate is reduced. No growth occurs in Simmons citrate medium. All species are nonhemolytic; catalase is produced by most strains. The DNA base composition ranges from 37.7 to 45.9 mol% G+C; genome molecular weights are between 1.4×10^9 and 1.9×10^9 .

Positive results are always observed for tetramethyl-*p*-phenylenediamine oxidase and alkaline phosphatase; acid is produced within 24 to 48 h from D-glucose, D-galactose, D-fructose, D-mannose, and sucrose.

Negative results are always observed for arginine dihydrolase and lysine decarboxylase; acid is not produced from L-sorbose, L-rhamnose, *m*-inositol, adonitol, or salicin. Starch and esculin are not hydrolyzed.

The DNA binding clusters within the genus, which resemble the species and subspecies of *Pasteurella*, can be differentiated by the characteristics shown in Table 4.

Reclassification of the genus *Pasteurella* Trevisan 1887. Considering the genetic relationships among the organisms investigated, we propose reclassification of the genus *Pasteurella* Trevisan 1887 and its species as shown below.

Genus *Pasteurella* Trevisan 1887. *Pasteurella* (Pas.teu.rel'la. M.L. dim. fem. n. *Pasteurella* named after Louis Pasteur) cells are nonmotile, small, and coccoid to rod shaped, and, depending on the growth stage, they occur singly, in pairs, or short chains. Gram reaction is negative. Not acid fast. Endospores are not formed.

Surface colonies on chocolate agar are round, grayish or yellowish, and nearly 2 mm in diameter after 48 h. Colonies of some species have a rough character and may reach 1 mm in diameter. No hemolysis on sheep blood agar.

Mesophilic; chemoorganotrophic with both oxidative and fermentative types of metabolism. Ubiquinones and demethylmenaquinones are produced; molecular oxygen is used as a terminal electron acceptor but can be replaced by

nitrate and fumarate. Oxidase positive, alkaline phosphatase positive, almost always catalase positive. Most species are V-factor (β -nicotinamide adenine dinucleotide) and X-factor (prothemin or protoporphyrin IX) independent, although V-factor-requiring species and strains do occur.

Members of the genus are always promptly positive for fermentation of D-glucose, D-galactose, D-fructose, D-mannose, and sucrose; acid is not produced from L-sorbose, L-rhamnose, *m*-inositol, or adonitol. No hydrolysis of starch, salicin, or esculin occurs. Arginine dihydrolase, lysine decarboxylase, and liquefaction of gelatin are negative, except for a delayed gelatinase reaction that is observed after more than 14 days of incubation with strains of *P. dagmatis* (13). Fermentation of maltose is mostly combined with fermentation of trehalose. Members of the genus are parasitic in vertebrates, particularly mammals and birds.

The genome DNAs of members of the genus *Pasteurella* contain 37.7 to 45.9 mol% G+C (T_m method). The genome molecular weights range from 1.4×10^9 to 1.9×10^9 .

Type species: *Pasteurella multocida* (Lehmann and Neumann, 1899) Rosenbusch and Merchant 1939.

The proposed species in the genus *Pasteurella* are described below.

***Pasteurella multocida* (Lehmann and Neumann 1899) Rosenbusch and Merchant 1939.** *Pasteurella multocida* (mul.to.ci'da. L.adj. *multus* many; L.adj.suf. *cidus* kill; M.L.fem.adj. *multocida* many killing, referring to pathogenicity for many species of animals) is divided into the following three subspecies: *P. multocida* subsp. *multocida*, *P. multocida* subsp. *septica* (sep'ti.ca. M.L.fem.adj. *septica* poisoning, infecting), and *P. multocida* subsp. *gallicida* (gal.li.ci'da. L.fem.n. *gallina* hen; L.adj.suf. *cida* kill; M.L.adj. *gallicida* hen killing, referring to pathogenicity for poultry).

In addition to the features consistent with all members of the genus, the biochemical reactions described below are common to the three subspecies. Acid is produced from mannitol. Positive ornithine decarboxylase reaction. Acid is produced from trehalose; production of acid from D-xylose differs in different strains. Exceptionally, acid is produced from raffinose, D-lactose, and (exceptionally) maltose. No V-factor requirement. The G+C contents of all subspecies range from 40.8 to 43.9 mol% (T_m method). The molecular weights of genome DNAs range from 1.5×10^9 to 1.9×10^9 . The main characteristics used for differentiation of the three subspecies are fermentation of sorbitol and dulcitol. *P. multocida* subsp. *multocida* strains ferment sorbitol but do not ferment dulcitol; *P. multocida* subsp. *septica* strains exhibit negative reactions for both sorbitol and dulcitol fermentation, whereas the *P. multocida* subsp. *gallicida* strains ferment both sorbitol and dulcitol. Other reactions are shown in Table 4.

Strains of the species are isolated from most mammals, including humans and birds.

Strain NCTC 10322 is the type strain of *P. multocida* subsp. *multocida*. Strain CIP A125 is the type strain of *P. multocida* subsp. *septica*, and strain NCTC 10204 is type strain of *P. multocida* subsp. *gallicida*.

***Pasteurella dagmatis* sp. nov.** *Pasteurella dagmatis* (dag.ma'tis. Gr.fem.gen.n. *dagmatis* from a bite) consists of strains that do not require V-factors. They produce small amounts of gas from D-glucose; positive reactions are obtained for urease, indole, acid production from maltose and, with few exceptions, acid production from trehalose. No acid is produced from D-xylose, L-arabinose, raffinose, mannitol, sorbitol, or dulcitol. Ornithine is not decarboxylated.

TABLE 4. Differential characteristics of the species belonging to *Pasteurella* sensu stricto

Taxon	No. of strains ^a	G+C content (mol%)	NAD requirement ^b	Ornithine	Indole	Urease	Acid produced within 24 to 48 h from:						
							Trehalose	Maltose	D-Xylose	L-Arabinose	Mannitol	Sorbitol	Dulcitol
<i>P. multocida</i> subsp. <i>multocida</i>	26	40.8-43.9	— ^c	+	+	—	d	—	d	—	+	+	—
<i>P. multocida</i> subsp. <i>septica</i>	9	41.5-42.5	—	+	+	—	+	—	+	—	+	—	—
<i>P. multocida</i> subsp. <i>gallicida</i>	6	41.2-42.5	—	+	+	—	—	—	+	d	+	+	+
<i>P. dagmatis</i>	6	38.9-41.5	—	—	+	+	+	+	—	—	—	—	—
<i>P. gallinarum</i>	3	43.6-43.7	—	—	—	—	+	+	—	—	—	—	—
<i>P. canis</i>	5	37.7-39.8	—	+	d	—	d	—	d	—	—	—	—
<i>P. stomatis</i>	6	40.4-43.5	—	—	+	—	+	—	—	—	—	—	—
<i>P. anatis</i>	2	39.9-42.3	—	—	—	—	+	—	+	—	+	—	—
<i>Pasteurella</i> species B	2	38.9-40.0	—	+	+	—	+	+	+	—	—	—	+
<i>Pasteurella</i> species A	4	44.0-45.9	+	—	—	—	+	d	d	+	d	—	—
<i>P. langaa</i>	2	43.9-45.3	—	—	—	—	—	—	—	—	+	—	—
<i>P. avium</i>	3	42.8-44.7	d	—	—	—	+	—	d	—	—	—	—
<i>P. volantium</i>	10	43.2-43.8	+	d	—	—	+	+	d	—	+	d	—

^a Phenotypically identical strains that were not considered for DNA relatedness were included.

^b NAD, Nicotinamide adenine dinucleotide.

^c +, ≥90% of the strains are positive; —, ≥90% of the strains are negative; d, different results observed.

Gelatin may be liquefied after more than 14 days of incubation.

P. dagmatis strains have been isolated from dogs and cats, as well as from human local and systemic infections resulting from animal bites.

The G+C content of the DNA ranges from 38.9 to 41.5 mol% (T_m method); genome molecular weights range from 1.5×10^9 to 1.7×10^9 .

The type strain of *P. dagmatis* is strain NCTC 11617.

***Pasteurella canis* sp. nov.** *Pasteurella canis* (ca'nis. L.gen.n. *canis* of a dog) strains are V-factor independent. The ornithine decarboxylation test is positive. Acid is not produced from L-arabinose, raffinose, D-lactose, maltose, mannitol, sorbitol, or dulcitol. The urease test is negative; variable reactions are obtained for acid production from trehalose and D-xylose. Biotype 1 strains exhibit positive reactions for indole; biotype 2 strains exhibit negative indole formation reactions.

P. canis biotype 1 is found in the oral cavities of dogs and is often isolated from injuries in humans resulting from dog bites. Biotype 2 strains have been isolated from calves. The G+C content of the DNA (T_m method) is 37.7 to 39.8 mol%. The genome molecular weights range from 1.4×10^9 to 1.6×10^9 .

The type strain of *P. canis* is strain NCTC 11621; the reference strain for biotype 2 is strain HIM 843-5.

***Pasteurella stomatis* sp. nov.** *Pasteurella stomatis* (sto.ma'tis. Gr.gen.n. *stomatis* of the throat) strains fulfill the general criteria of the genus *Pasteurella* sensu stricto; in addition, they are V-factor independent, do not decarboxylate ornithine, and give negative urease tests. No acid is produced from L-arabinose, D-xylose, raffinose, D-lactose, maltose, trehalose, mannitol, sorbitol, or dulcitol. Indole and acid are produced from trehalose.

The strains of *P. stomatis* occur in the respiratory tracts of cats and dogs.

The G+C content of the DNA ranges from 40.4 to 43.5 mol% (T_m method). The genome molecular weights range from 1.5×10^9 to 1.6×10^9 .

The type strain is strain NCTC 11623.

***Pasteurella anatis* sp. nov.** *Pasteurella anatis* (a.na'tis.

L.fem.gen.n. *anatis* of a duck) strains have no V-factor requirement. They do not decarboxylate ornithine, do not produce indole, and do not hydrolyze urea. No acid is produced from L-arabinose, maltose, D-lactose, raffinose, sorbitol, or dulcitol; acid is produced from trehalose, D-xylose, and mannitol.

Members of this species have been isolated from the intestinal tracts of ducks.

The G+C content is 39.9 to 42.3 mol% (T_m method). The genome molecular weights range from 1.8×10^9 to 1.9×10^9 .

The type strain of *P. anatis* is strain NCTC 11413.

***Pasteurella langaa* sp. nov.** *Pasteurella langaa* (lan'gaa. L.fem.n. *langaa* referring to Langaa, Denmark) has no V-factor requirement and contains strains which were included in taxon 4 of Bisgaard (1). The members of this species produce acid from mannitol and lactose; tests for ornithine, indole, urease, acid from L-arabinose, D-xylose, raffinose, trehalose, maltose, and sorbitol are negative.

Strains of this species are found in the respiratory tracts of apparently healthy chickens.

The G+C content of the DNA ranges from 43.9 to 45.3 mol%, and the genome molecular weights range from 1.7×10^9 to 1.9×10^9 .

The type strain is strain NCTC 11411.

Unnamed new *Pasteurella* species B should be described when more strains have been studied. We suggest strain SSI P683 as the reference strain for this group.

P. gallinarum corresponds to the original description of Hall et al. (16). However, our data suggest that tests for mannitol, sorbitol, and *m*-inositol fermentation are negative, rather than irregular.

P. avium, *P. volantium*, and an additional new V-factor-dependent species (provisionally called *Pasteurella* species A) have been described previously (46).

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