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Identification of *Proteus penneri* sp. nov., Formerly Known As *Proteus vulgaris* Indole Negative or As *Proteus vulgaris* Biogroup 1

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The name *Proteus penneri* sp. nov. is proposed for a group of organisms previously called *Proteus vulgaris* indole negative or *P. vulgaris* biogroup 1. All of these strains were salicin negative, esculin negative, and chloramphenicol resistant (zone size, <14 mm). DNA relatedness studies indicated that when DNA from *P. penneri* strain 1808-73 was labeled and tested against unlabeled DNA from 13 other *P penneri* strains, a highly related group was formed (88 to 99% relatedness at 60°C and 67 to 99% relatedness at 75°C). Strain 1808-73 (ATCC 33519) is proposed as the type strain of *P. penneri*. In this study, two distinct groups of indole-positive *P. vulgaris* strains were also apparent. The first group (defined as *P. vulgaris* biogroup 2) was indole positive, salicin positive, and esculin positive, and the second group (defined as *P. vulgaris* biogroup 3) was indole positive, salicin negative, and esculin negative. The current type strain of *P. vulgaris* (ATCC 13315) belongs to biogroup 3. The DNA from *P. penneri* strains was not highly related to labeled DNA from the type strain of *P. vulgaris* (14 to 30% relatedness at 75°C) or from *P. vulgaris* strain PR 1 (ATCC 29905), which belongs to biogroup 2 (27 to 33% relatedness at 75°C). Strains of biogroup 2 were sensitive to chloramphenicol (zone size, >19mm), and 10 of these strains formed a highly related group by DNA hybridization when DNA from PR 1 was labeled (64 to 100% relatedness at 60°C and 70 to 100% relatedness at 75°C), but they were not highly relatedness to the type strain of *P. vulgaris* (51 to 68% relatedness at 60°C and 14 to 44% relatedness at 75°C). Further DNA relatedness studies are needed on strains of biogroup 3 before a definitive taxonomic proposal can be made for these two indole-positive biogroups.

Until recently, the most popular classification of the genus *Proteus* contained four species, *P. vulgaris* (the type species for the genus), *P. mirabilis, P. morganii*, and *P. rettgeri*. These species are phenotypically similar in a number of respects, but many workers have indicated that this may be a superficial similarity which does not reflect relatedness in an evolutionary or phylogenetic sense. The DNA-DNA hybridization studies of Brenner et al. (3) clarified these conflicting phenotypic data. *P. morganii* was moved to the genus *Morganella* because of its low relatedness to the swarming *Proteus* species, *P. vulgaris* and *P. mirabilis*. Similarly, *P. rettgeri* was moved to the genus *Providencia* because of a closer relatedness, to *Providencia stuartii* and *Providencia alcalifaciens* in both phenotype and DNA hybridization. The final proposal was to limit the genus *Proteus* to the three species which were closely related by DNA hybridization, *P. vulgaris, P. mirabilis*, and *P. myxofaciens* (which has never been isolated from a human clinical specimen).

P. vulgaris is a well-known species that was thought to be homogeneous, although there were some reports of phenotypic variation. The DNA hybridization study of Brenner and coworkers (3) in 1978, however, showed *P. vulgaris* to be a heterogeneous species. The recommendation at that time was that all strains be maintained as *P. vulgaris* until a definitive recommendation could be made. We (F. W. Hickman, A. G. Steigerwalt, J. J. Farmer III, and D. J. Brenner, Abstr. Annu. Meet. Am. Soc. Microbiol. 1981, C298, p. 312) studied the DNA hybridization groups of *P. vulgaris* and found that one group was indole negative (indole$^-$), salicin negative (salicin$^-$), and esculin negative (esculin$^-$) and had small zones (14 mm or less) around chloramphenicol disks. We indicated that this group probably represented a new species of *Proteus* but because this publication

was only an abstract, we did not give the species a scientific name, we referred to it instead as *P. vulgaris* biogroup 1. In addition to the indole$^-$ group, two distinct indole-positive (indole$^+$) groups have now become apparent. One group is indole$^+$, salicin positive (salicin$^+$), and esculin positive (esculin$^+$), and one is indole$^+$, salicin$^-$, and esculin$^-$. Others had also noted indole$^-$ strains and strain-to-strain variation with salicin fermentation and esculin hydrolysis. As early as 1968, Suter et al. (14) reported that 6 of their 18 strains of *P. vulgaris* were indole$^-$ and that 6 of 18 were salicin$^-$ (it was not stated whether these were the same six strains). Ewing and Davis (7) found that 98% of 66 *P. vulgaris* strains were indole$^+$, 67% were salicin$^+$, and 62% were esculin$^+$ in 7 days. McKell and Jones (11) found that 96% of 25 *P. vulgaris* strains were indole$^+$, 44% were salicin$^+$, and 48% were esculin$^+$. The purpose of the present study was to further characterize those strains now identified as *P. vulgaris*. In this paper we formally propose the species named *Proteus penneri* for the organism previously called *P. vulgaris* biogroup 1, and we define the indole$^+$, salicin$^+$, esculin$^+$ strains as biogroup 2 and the indole$^+$, salicin$^-$, esculin$^-$ strains as biogroup 3.

TABLE 1. *List of Proteus penneri strains used in this study.*

Strain no.	Clinical source	Location of sender
3960-66	?	Michigan
1655-67	Blood	Maryland
4910-67	Urine	Kansas
3266-68	?	Puerto Rico
4732-68	Stool	Texas
0606-69	?	Louisiana
1071-69	Stool	Missouri
0645-72	Urine	Missouri
0931-72	Urine	Georgia
4647-72	?	Georgia
73-015410	Urine	North Carolina
1808-73 (ATCC 33519)[a]	Urine	Alaska
0541-74	Urine	New Jersey
2518-74	Bronchial exudate	Georgia
2963-74	Stool	Maryland
0465-75	Urine	Arizona
1410-75	Urine	New Jersey
2900-77	Stool	Wisconsin
0572-78	Abdominal wound	New York
0766-80	Urine	North Carolina

[a]Type strain for the species.

MATERIALS AND METHODS

Nomenclature. All names used appear in the *Approved Lists of Bacterial Names* (13). The classification of the *Proteus* groups used in this paper was described in detail by Brenner and co-workers (3). Within the species *P. vulgaris*, we define three groups. *P. penneri* (type strain, CDC 1808-73 [ATCC 33519]) is coined for *P. vulgaris* biogroup 1 strains which are indole$^-$, salicin$^-$, and esculin$^-$ and have small zones (less than 14 mm) around chloramphenicol disks. *P. vulgaris* biogroup 2 is defined as strains which are indole$^+$, salicin$^+$, and esculin$^+$. *P. vulgaris* biogroup 3 is defined as strains which are indole$^+$, salicin$^-$, and esculin$^-$. Most strains of *P. vulgaris* isolated from clinical specimens are biogroup 2 or 3. The nomenclatural type strain for *P. vulgaris* is ATCC 13315, which is indole$^+$, salicin$^-$, and esculin$^-$ (biogroup 3).

Bacterial strains. A total of 20 strains which were eventually identified as *P. penneri* strains were studied (Table 1), as were 10 strains of biogroup 2 and the type strain of *P. vulgaris* (ATCC 13315), which is in biogroup 3. Late in the study, 20 strains of *P. vulgaris* biogroup 3 were obtained from John L. Penner, Toronto, Canada. They were tested for phenotype and antimicrobial susceptibility but not DNA hybridization. All of the strains were maintained on Trypticase soy agar (BBL Microbiology Systems, Cockeysville, Md.) at room temperature (18 to 28°C), and all incubations were at 36 ± 1°C unless otherwise noted.

Media and biochemical testing. Whenever possible, dehydrated media from commercial sources were used. The methods used for biochemical testing were those discussed by Hickman and co-workers (8, 9) and are basically those of Edwards and Ewing (6). Blood agar refers to Trypticase soy agar plus 5% defibrinated sheep blood (BBL). Blood agar plates were used to detect swarming. The test for indole production was done in peptone water with Kovacs reagent (6). All negative strains were tested in heart infusion broth with Erhlich-Boehme reagent after xylene extraction (10).

Antibiotic susceptibility tests. Antimicrobial susceptibility was determined by both agar diffusion and broth dilution. Antibiograms were done by the disk method of Bauer et al. (1). The following antibiotic disks were used: ampicillin, 10 μg; carbenicillin, 100 μg; cephalothin, 30 μg; chloramphenicol, 30 μg; colistin, 10 μg; gentamicin, 10 μg; kanamycin, 30 μg; nalidixic acid, 30 μg; penicillin 10 U; streptomycin, 10 μg; sulfadiazine, 250 μg; and tetracycline, 30 μg (see Table 3).

Sensititre plates (APO 2 for gram-negative organisms; GIBCO Diagnostics, Lawrence, Mass.) were used for determining minimal inhibitory concentrations of antibiotics according to the instructions of the manufacturer. A 4- to 6-h culture in brain heart infusion broth was diluted 1:10,000 in Mueller-Hinton broth (GIBCO) to a final concentration of about 10^5 cells (colony forming units) per ml. Then, 50 μl of this dilution was delivered to each well in the Sensititre plates. The plates were incubated and read after 24 h. The following antibiotic concentrations were used: amikacin, 0.25 to 32 μg/ml; ampicillin, 0.25 to 32 μg/ml; carbenicillin, 4 to 512 μg/ml; cephalothin, 1 to 128 μg/ml; chloramphenicol, 0.5 to 64 μg/ml; gentamicin, 0.12 to 16 μg/ml; kanamycin, 0.5 to 64 μg/ml; tetracycline, 0.25 to 32 μg/ml; and tobramycin, 0.12 to 16 μg/ml.

DNA hybridization. DNA relatedness was determined for the 20 *P. penneri* strains, the 10 strains of *P. vulgaris* biogroup 2, and the type strain of *P. vulgaris*

(ATCC 13315). Unlabeled DNA was isolated and purified by methods previously described (2, 3). DNA from *P. penneri* strains 1808-73, the type strain of *P. vulgaris*, and biogroup 2 strain PR 1 was labeled in vitro with ^{32}P by nick translation, essentially by the methods of Rigby et al. (12) and according to the instructions furnished with a commercial nick translation reagent kit (catalog no. 8160; Bethesda Research Laboratories, Inc., Rockville, Md.). The relatedness of labeled DNA from these three strains to unlabeled DNA from all of the strains was determined on hydroxyapatite by the methods of Brenner et al. (3). Strains with a percentage of hybridization of 70% (or more) at 60°C or of 50% (or more) at 75°C are usually considered as belonging to the same species (3).

G+C content of DNA. The percentage of guanine plus cytosine (G+C) in DNA from the type strain of *P. penneri* (strain 1808-73) was calculated from the values for the midpoint of thermal denaturation. These values were determined by the method described by De Ley (5), and the G+C ratio was calculated according to the method of Colwell and Mandel (4).

RESULTS

Biochemical tests. The biochemical reactions of the 20 *P. penneri* strains are listed in Table 2 along with the reactions of the type strain. All of the strains were indole$^-$, salicin$^-$, and esculin$^-$ at 48 h. Strain 931-72 was weakly salicin$^+$ at 7 days. Only 40% of the strains were H_2S positive at 7 days and only 65% swarmed on blood agar. Otherwise, the reactions were typical of those that would be expected for *P. vulgaris* (7).

Antibiotic susceptibility tests. The results of the antibiograms are given in Table 3. All of the *P. penneri* strains were completely resistant (no zone of inhibition) to ampicillin, cephalothin, colistin, and penicillin; the average zone size around the chloramphenicol disk was 10 mm. The zone size around chloramphenicol averaged 27 mm for the biogroup 2 strains and 18 mm for 23 *P. mirabilis* strains previously tested. Biogroup 3 strains have not been fully tested; therefore, data for this group are not included here. The minimal inhibitory concentrations of the nine antibiotics tested for the 20 *P. penneri* strains are given in Table 4. These results confirmed that these *P. penneri* strains were resistant to chloramphenicol (minimal inhibitory concentrations of 32 to 64 μg/ml).

DNA hybridization. The results obtained when DNA from *P. penneri* strain 1808-73 was labeled and tested against unlabeled DNA from 13 other *P. penneri* strains are given in Table 5. A highly related group was formed (88 to 99% relatedness at 60°C and 67 to 96% relatedness at 75°C). The percentage of divergence in related sequences was 0.1 to 0.5. The relatedness of unlabeled DNA from the 14 *P. penneri* strains to labeled DNA from the type strain of *P. vulgaris* and biogroup 2 strain PR 1 is given in Table 6. At 75°C, these two strains were not related to the *P.*

TABLE 2. *Biochemical reactions of 20 P. penneri strains and the type strain.*

Test	Cumulative % positive at time:			Reaction for type strain ATCC 33519
	1d	2d	7d	
Indole	[a]	0		–[b]
Methyl red		100		+
Voges-Proskauer		0		–
Citrate (Simmons)	0	0	23	–
H_2S on TSI	10	10	10	–
H_2S on PIA	10	25	40	$+^{7}$
Urea	100	100	100	+
Phenylalanine	100			+
L-Lysine (Møller's)	0	0	0	–
L-Arginine (Møller's)	0	0	0	–
L-Ornithine (Møller's)	0	0	0	–
Motility	85	85	85	–
Gelatin (22°C)	20	50	75	$+^{2}$
KCN-growth in	95	95	100	+
Malonate	0	0	10	–
D-Glucose Acid	100	100	100	+
Gas	40	45	45	–
Acid from:				
Adonitol	0	0	0	–
L-Arabinose	0	0	0	–
D-Arabitol	0	0	0	–
Cellobiose	0	0	0	–
Dulcitol	0	0	0	–
Erythritol	0	0	0	–
D-Galactose	95	95	100	+
Glycerol	20	55	95	$+^{2}$
i-Inositol	0	0	0	–
Lactose	0	0	0	–
Maltose	100	100	100	+
D-Mannitol	0	0	0	–
D-Mannose	0	0	0	–
Melibiose	0	0	0	–
α-CH_3-glucoside	60	80	100	$+^{2}$
Raffinose	0	0	0	–
L-Rhamnose	0	0	0	–
Salicin	0	0	5	–
D-Sorbitol	0	0	0	–
Sucrose	100	100	100	+
Trehalose	10	55	95	$+^{2}$
D-Xylose	95	100	100	$+^{2}$
Esculin	0	0	0	–
Mucate	0	0	0	–
Tartrate (Jordan)	50	85	95	$+^{2}$
Acetate	0	5	15	–
Lipase (Corn oil)	45	45	50	–
DNase 25°C	0	25	85	$+^{4}$
36°C	20	45	85	$+^{4}$
$NO_3^- \rightarrow NO_2^-$	90			+
Oxidase	0			–
ONPG	0	0	0	–
Citrate (Christensen)	0	0	0	–
Red slant on LIA	50	75	75	–
Tyrosine clearing	100	100	100	+
Swarming on Blood Agar	65	65	65	–

[a] A blank space indicates not determined.

[b] Symbols: –, negative at end of appropriate incubation period or 7 d; +, positive at 24 h or at time of test. Superscript gives the day the reaction became positive.

TABLE 3. *Susceptibility of 20 P. penneri strains by agar diffusion.*

Antibiotic	Zone diameter (mm):		
	Range	Mean	Standard deviation
Ampicillin	6	6	0
Carbenicillin	6-19	13	4.7
Cephalothin	6	6	0
Chloramphenicol	6-14	10	2.1
Colistin	6	6	0
Gentamicin	21-27	23	1.9
Kanamycin	14-28	22	3.4
Nalidixic acid	11-24	20	4.3
Penicillin	6	6	0
Streptomycin	6-23	15	4.9
Sulfadiazine	6-22	14	5.1
Tetracycline	7-25	20	3.7

penneri strains at the species level. Strains of biogroup 2 formed a highly related group by DNA hybridization when DNA from strain PR 1 was labeled (64 to 100% relatedness at 60°C and 70 to 100% relatedness at 75°C), but they were not highly related to the type strain of *P. vulgaris* (51 to 68% relatedness at 60°C and 14 to 44% relatedness at 75°C).

G+C ratio. The midpoint of thermal denaturation for DNA from *P. penneri* strain 1808-73 ranged from 84.8 to 85.2°C (mean, 85.0°C). The G+C content was 38 mol%.

DISCUSSION

The results of the DNA relatedness studies indicated that the strains that had been previously designated *P. vulgaris* biogroup 1 should be elevated to the species level within the genus *Proteus*. The genetic data correlate with phenotypic differences between the new group and *P. vulgaris*. Presumably, the phenotypic and genetic differences reflect evolutionary divergence.

TABLE 4. *Minimal inhibitory concentrations of nine antibiotics for 13 strains of P. penneri.*

Antibiotic	Minimal inhibitory concentration (μg/ml):	
	Range	Mode
Amikacin	0.5-8	2
Ampicillin	>32	>32
Carbenicillin	8-512	32
Cephalothin	>128	>128
Chloramphenicol	32-64	64
Gentamicin	0.5-2	0.5
Kanamycin	1-8	2
Tetracycline	1-8	2
Tobramycin	0.25-2	0.5

TABLE 5. *DNA relatedness of 14 P. penneri strains.*

Source of unlabeled DNA	% Relatedness to labeled DNA of *P. penneri* ATCC 33519		
	60°C	%D[a]	75°C
1808-73	100	0.0	100
3960-66	88	[b]	80
1655-67	90	0.5	67
4732-68	99		96
0606-69	95		90
1071-69	98		89
0645-72	97	0.4	97
0931-72	98		84
4647-72	92		83
73-015410	94	0.1	94
2518-74	96		90
1410-75	94		88
0572-78	88		83
0766-80	94		89

[a] %D = percentage of divergence (3).

[b] A blank space indicates not determined.

Low relatedness by DNA hybridization and phenotypic differences have been our main criteria for proposing new species. *Proteus penneri* sp. nov. is proposed as the name for this group, formerly known as *P. vulgaris* biogroup 1. The species name is treated as a neo (modern) Latin genitive noun, *penneri*, meaning "of Penner," and is coined to honor John L. Penner, a Canadian microbiologist who has made many contributions to studies of the three genera in the tribe *Proteeae*.

A description of the species follows. *P. penneri* has the general characteristics of the genus *Proteus*, which are as follows: positive tests for urea hydrolysis, phenylalanine deaminase, gelatin hydrolysis, H_2S production, and tyrosine clearing; swarming on blood agar; a negative test for D-mannose fermentation; and resistance to colistin. The following tests are positive for most *P. penneri* strains: methyl red; motility; growth in the presence of KCN; and fermentation of D-

TABLE 6. *DNA relatedness of 14 P. penneri strains to the type strain of P. vulgaris (ATCC 13315) and to P. vulgaris strain PR 1.*

Source of labeled DNA	% Relatedness at:	
	60°C	75°C
ATCC 13315 (Indole$^+$ salicin$^-$ esculin$^-$)	46-62	14-30
PR 1 (Indole$^+$ salicin$^+$ esculin$^+$)	49-70	27-33

TABLE 7. *Proposed classification of the genus Proteus including the tests useful for differentiating the species and biogroups.*

Test or description	Species and biogroups:				
	P. vulgaris				
	Biogroup 2	Biogroup 3	*P. penneri*	*P. mirabilis*	*P. myxofaciens*[a]
Indole production	+[b]	+	–	–	–
Ornithine decarboxylase	–	–	–	+	–
Maltose fermentation	+	+	+	–	+
Salicin fermentation	+	–	–	–	–
D-Xylose fermentation	+	+	+	+	–
Esculin hydrolysis	+	–	–	–	–
Occurs in human clinical specimens	+	+	+	+	–
Occurs as pathogen of gypsy moth larvae	–	–	–	–	+

[a]Reactions of only one strain.

[b]All results are at 36 ±1°C and 48 h incubation; + = 90% or more positive; – = 0-10% positive.

galactose, maltose, sucrose, and D-xylose. The following tests are negative for all or most *P. penneri* strains: indole production; Voges-Proskauer; lysine and ornithine decarboxylase (Møllers); arginine dihydrolase (Møllers); malonate utilization; fermentation of adonitol, L-arabinose, D-arabitol, cellobiose, dulcitol, erythritol, *i*-(*myo*)-inositol, lactose, melibiose, raffinose, L-rhamnose, salicin, D-sorbitol, and mucate; esculin hydrolysis; and acetate utilization. The proposed type strain is CDC 1808-73 (ATCC 33519). The G+C content of this strain is 38 mol%. A more detailed description of the new species is given in Tables 2, 3, and 4.

The *P. penneri* strains were resistant to chloramphenicol by both agar diffusion and broth dilution methods. We suspect that this resistance is intrinsic rather than plasmid-mediated because some of our strains were isolated in the 1960s and have been stored over a long period of time, yet all of them have remained resistant. The biogroup 2 strains were all sensitive to chloramphenicol; however, preliminary data on biogroup 3 suggest that it may contain both sensitive and resistant strains. von Graevenitz and Nourbakhsh (15) reported that 14% of 66 indole$^+$ strains of *P. vulgaris* were resistant to chloramphenicol. Perhaps these strains belong in biogroup 3.

It now appears that the indole reaction, along with the reactions for salicin and esculin, separate what was previously known as *P. vulgaris* into three groups. In this study we have shown that the indole$^-$, salicin$^-$, esculin$^-$, chloramphenicol-resistant group is a separate species. Our study and a previous study (3) indicate that the biogroup 2 strains also represent a separate species. Biogroup 3 is currently the group that should be designated *P. vulgaris* since the type strain belongs to this group. We are currently collecting strains in this group so that a full study can be conducted. This study must be completed before a logical classification can be proposed for biogroups 2 and 3, which are still classified as *P. vulgaris*. Table 7 gives a summary of our current classification of the genus *Proteus* and the tests that are useful for differentiation.

The clinical significance of *P. penneri* is unknown. There was one blood isolate, but no other clinical information was available for this strain. Perhaps this report will stimulate others to look for this organism and help define its ecology and role in human disease. Clinical laboratories should suspect *P. penneri* for a *Proteus* strain that is indole$^-$ and has a small zone around chloramphenicol but otherwise resembles *P. vulgaris*. Salicin$^-$, esculin$^-$, ornithine decarboxylase negative, and maltose positive reactions would differentiate it from *P. vulgaris* and *P. mirabilis*.

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