Taxonomic Significance of Respiratory Quinones and Fumarate Respiration in *Actinobacillus* and *Pasteurella*

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The lipoquinones and associated respiratory functions of 34 cultures representing 17 bacterial species hitherto assigned to the genus *Actinobacillus* or *Pasteurella* were investigated. Strains representing recognized *Actinobacillus* or *Pasteurella* species regularly contained desmethylmenaquinones and were capable of anaerobic electron transport with fumarate as a terminal acceptor when grown in oxygen-limited cultures. On aeration, the majority of the strains produced ubiquinones in addition to desmethylmenaquinones, with inter- and intraspecific variations. The use of lipoquinone patterns and features indicating fumarate respiration, such as stimulation of oxygen-limited growth by fumarate, in the classification and identification of *Actinobacillus*, *Pasteurella*, and phenotypically similar organisms is discussed.

In the 8th edition of *Bergey's Manual*, four species of the genus *Pasteurella* Trevisan and two species of the genus *Actinobacillus* Brumpt are recognized, and, furthermore, some species incertae sedis are listed (7, 10). Several species of *Pasteurella* and *Actinobacillus* described more recently are waiting for recognition or rejection. On the basis of phenotypical data, both circumscription of the two traditional genera and their classification below the generic level are at present difficult to assess. Moreover, *Pasteurella* and *Actinobacillus* are closely related at least to some members of the conventional genus *Haemophilus* (10). Thus, additional classifying features of the organisms in question are desired.

After a preliminary study on the composition of the respiratory chain system of some *Actinobacillus* and *Pasteurella* strains (R. Zabel, M.D. thesis, Philipps University, Marburg/Lahn, Germany, 1974), we felt that the respiratory quinones are not only indicative of basic physiological properties of these organisms, but may be also useful tools in group and species characterization. This communication will present evidence for the taxonomic significance of quinone patterns and of the fumarate respiration pathway mediated by desmethylmenaquinone (DMK) in the organisms investigated.

MATERIALS AND METHODS

Microorganisms. The organisms investigated are listed in Table 1. Vegetative cultures were kept for short periods (up to 1 week) at 4°C on chocolate agar; freeze-dried stocks were maintained in evacuated ampoules at room temperature in the dark. Before use, the strains were purified by repeated subcultivation of single colonies and reidentified by examination of

micromorphology, Gram reaction, and appropriate biochemical characters.

Media and cultivation. Chocolate agar (5% [vol/vol] defibrinated sheep blood in tryptic soy agar [Difco Laboratories, Detroit, Mich.] heated to 80°C for 20 min before pouring) was used for maintenance and purity checks. Proteose peptone medium (14) with proteose peptone no. 3 (Difco) was used throughout for mass cultivation; the peptone lots used were known to contain less than 10^{-10} mol of both benzo- and naphthoquinones per g of dry weight (R. Holländer and W. Mannheim, unpublished data). Disodium fumarate (Fluka AG., Buchs, Switzerland; sterilized by filtration) was supplemented to a final concentration of 50 mM where indicated. "Aerobic" cells were grown by shaking 250-ml batches in Fernbach flasks (no. 20511, Schott & Gen., Mainz, Germany), using a rotary shaker (model G-25, New Brunswick Scientific Co., New Brunswick, N.J.), the shaking frequency depending on the sensitivity of the cultivated organism to aeration. "Oxygen-limited" cells were harvested from Fernbach flasks filled to the neck (about 2,000 ml of medium) and incubated statically. Incubation temperature was 37°C except for *P. piscicida*, which was grown at 25°C. Late-exponential-phase cells were sedimented at $12,000 \times g$, 0 to 4°C, and washed twice with 0.1 M tris(hydroxymethyl)aminomethane-hydrochloride buffer, pH 7.2.

Determination of protein. Protein was determined, after sonic disintegration of the cells, by a modified biuret method (12).

Determination of NADH oxidase and NADH-fumarate reductase activities. Oxidation of reduced β -nicotinamide adenine dinucleotide, disodium salt (NADH; E. Merck, Darmstadt, Germany) in sonic cell homogenates buffered with phosphate (50 mM, pH 7.2) at 25°C was determined by recording the decrease in absorbancy at 366 nm. Whereas NADH oxidase was tested under aerobic conditions, NADH-fumarate reductase activity was determined in the same cuvette after addition of fumarate (final concentration, 10 mM) in the presence of excess NADH,

when NADH oxidase had become oxygen limited (5). Freshly harvested bacteria that had been kept at 0°C (but not frozen) before testing were used.

Extraction and determination of quinones. To determine the quinone contents, sonic cell homogenates containing 5 to 10 mg of bacterial protein and no added phosphates (A. Kröger, personal communication) were used. After oxidation with H₂O₂, the quinones were extracted into light petroleum (bp, 40 to 60°C) and characterized by their difference spectra (reduced minus oxidized KBH₄, recorded at 230 to 305 nm) in ethanolic solution buffered with acetate, pH 5.4 (2, 6). Known extinction coefficients of ubiquinone (Q) and menaquinone (MK) (6) and of DMK (13) were used. Q, present in small amounts together with naphthoquinones, was partly purified by preparative thin-layer chromatography (2). MK, present in low concentrations together with Q, was detected by recording difference spectra of completely reduced minus partly reduced states of the quinone mixture, the high-potential quinone (Q) being far more rapidly reduced than the low-potential quinone (MK). The individual amounts of Q and MK contained in the mixture were calculated from the difference spectrum "completely reduced minus oxidized" (6).

RESULTS

Quinone patterns. As shown by the data summarized in Table 1, the organisms investigated contained one or two different quinones in amounts varying, with strains and culture conditions, from about 0.2 to about 5 µmol/g of cell protein. Qualitatively, the organisms listed in the table were heterogeneous regarding the quinones synthesized, although they appeared to be homogeneous at the species level with the exception of *A. equuli*. Typical *Actinobacillus* and *Pasteurella* organisms invariably contain DMK, and the majority of them are able to form Q in addition to DMK (category i; Table 1A); a second category (ii; Table 1B) of *Actinobacillus* and *Pasteurella* organisms, namely, *A. actinomycetem-comitans*, *A. suis*, *P. bettii*, and *P. pneumotropica* produces DMK as the only quinone.

Two species deviating phenotypically from *Pasteurella* and *Actinobacillus* in many other respects, and included here for comparison, lack DMK: Jayaraman's (8) organisms of the bovine lymphangitis group contain Q and, under anaerobic growth conditions, MK in relatively small amounts (category iii; Table 1C). The so-called *Actinobacillus actinoides* (ATCC 15900), a gram-positive organism apparently related to the *Actinomycetales*, produced MK as the sole quinone (category iv; Table 1D).

Quinone function. Furthermore, the data of Table 1 strongly suggest that the functional roles of DMK and Q with *Actinobacillus* and *Pasteurella* are similar to those observed for members of the genus *Haemophilus* (2; R. Holländer,

Ph.D. thesis, Philipps University, Marburg/Lahn, Germany, 1976; see also R. Holländer, FEBS Lett. 72:98-100, 1976). The presence of an anaerobic electron transport system containing DMK and leading to fumarate as the terminal electron acceptor in true *Actinobacillus* and *Pasteurella* strains (categories i and ii) is indicated by the following observations. The DMK contents of the cells were greater in anaerobic cultures and, even more pronouncedly, after addition of fumarate to the growth medium. *Actinobacillus* and *Pasteurella* strains containing DMK exhibited increased NADH-fumarate reductase activities when cultivated in the absence of oxygen and, more markedly, after addition of fumarate to the growth medium. Finally, the growth yields of oxygen-limited cultures were greater in the presence of fumarate, indicating an energetic use of fumarate respiration.

In *Actinobacillus* and *Pasteurella* strains containing two quinones (category i), Q participates in aerobic respiration, as suggested by the increase in the Q/DMK ratio during aerobic cultivation. The cell yields of aerated cultures were markedly increased compared with those of oxygen-limited cultures supplemented with the low-potential acceptor fumarate, even with organisms lacking Q (category ii). This suggests that both DMK and Q participate in the electron transport from NADH to oxygen, as has been shown in *Haemophilus influenzae* by extraction-reincorporation experiments (Holländer, Ph.D. thesis). However, some of the organisms containing DMK as the sole quinone were more or less microaerophilic when grown in hemin-free media, yielding only moderate growth upon aeration.

No growth stimulation by fumarate was observed in oxygen-limited cultures of the organisms of categories iii and iv (Table 1C and D), and the presence of enzymes involved in fumarate respiration with these organisms is doubtful.

DISCUSSION

Since the redox potential and possible respiratory functions of a given quinone depend on the nature of its core, the information readily obtained by ultraviolet difference spectra (reduced minus oxidized) of lipid extracts appears to be most useful in the physiostaxonomy of chemoorganotrophic bacteria. The length of the isoprenoid side chains of respiratory quinones, although less attractive from the physiological point of view, may be an additional classifying criterion but was not considered here. The results presented allow a more thorough understanding of the metabolic versatility of the *Actinobacillus* and *Pasteurella* organisms as a group capable of using, in addition to glycolysis,

TABLE 1. Growth densities, respiratory quinones, and electron transport from NADH to oxygen, or fumarate, of some *Actinobacillus* and *Pasteurella* strains grown in proteose peptone medium with oxygen or fumarate as the electron acceptor (late-exponential-phase cultures)^a

Organism	Electron acceptor during growth ^b	Growth density (mg [dry wt]/ml) ^c	Quinones (μmol/g of protein)		Q/Naq. ^d	μmol of NADH/g of protein per min	
			Q	DMK or MK, respectively		NADH oxidase	NADH-fumarate reductase
(A) Organisms containing Q and DMK							
<i>Actinobacillus equuli</i>							
W. C. Miller	1	0.21	0.43	0.39	1.1	51.7	21.4
PM 30/53 (D108)	2	0.14	NT	NT	— ^e	NT	NT
(NCTC 8529)	3	0.20	0.05	0.85	0.06	NT	NT
<i>A. lignieresii</i>							
P. H. Martin	1	0.24	0.64	0.01	64	90.9	32.8
CM-2	2	0.04	NT	NT	—	NT	NT
(NCTC 4976)	3	0.14	0.01	0.67	0.01	49.5	64.6
<i>A. lignieresii</i>							
L. Thompson 1	1	0.25	0.23	0.37	0.6	6.2	13.4
(NCTC 4189)	2	0.05	0.10	0.65	0.1	NT	NT
	3	0.11	0.12	0.94	0.1	11.1	29.4
<i>A. seminis</i>							
G. C. Simmons	1	0.08	0.34	0.10	3.4	5.4	2.2
K 3844-C	2	0.03	NT	NT	—	NT	NT
(ATCC 15768)	3	0.08	0.23	0.75	0.3	55.0	27.4
<i>Pasteurella gallinarum</i>							
K. L. Heddleston	1	0.21	0.62	0.07	8.9	45.6	10.0
P 892	2	0.09	0.13	0.50	0.3	30.8	40.5
(ATCC 13360)	3	0.14	0.18	0.44	0.4	103.7	134.7
<i>P. haemolytica</i> , biovar A							
B. J. Shreeve	1	0.33	0.49	0.19	2.6	90.7	10.1
S-5R	2	0.07	NT	NT	—	NT	NT
(NCTC 10610)	3	0.11	0.31	1.05	0.3	161.6	109.9
<i>P. haemolytica</i> , biovar T							
B. J. Shreeve	1	0.26	0.83	0.26	3.2	154.6	90.9
7H74L	2	0.08	NT	NT	—	NT	NT
(NCTC 10624)	3	0.10	0.42	1.41	0.3	253.6	218.3
<i>P. haemolytica</i>							
S. D. Henriksen	1	0.19	0.41	0.52	0.8	240.3	76.0
T 185	2	0.06	NT	NT	—	NT	NT
(NCTC 10218)	3	0.13	0.03	1.31	0.02	306.8	194.4
<i>P. haemolytica</i>							
J. A. Watt	1	0.64	0.79	0.46	1.7	NT	NT
1266/56 A&B	2	0.07	NT	NT	—	NT	NT
(NCTC 9380)	3	0.11	0.48	0.52	0.9	NT	NT
<i>P. mastitidis</i>							
E. A. Tunnicliff	1	0.20	0.90	0.47	1.9	71.4	35.5
B-31 (4540)	2	0.05	0.13	0.91	0.1	35.4	26.6
(ATCC 10898)	3	0.12	0.19	1.20	0.2	81.1	52.4
<i>P. multocida</i>							
H. Schütze HS	1	0.34	1.21	0.53	2.3	257.6	96.3
(NCTC 3195)	2	0.05	NT	NT	—	NT	NT
	3	0.08	0.12	0.68	0.2	221.1	112.5
<i>P. multocida</i> , Carter's serovar A							
G. R. Carter	1	1.05	0.32	0.16	2.0	NT	NT
T 4967 porcine	2	0.06	0.34	1.14	0.3	NT	NT
(HIM 449-1)	3	0.12	0.28	1.25	0.2	NT	NT
<i>P. multocida</i> , Carter's serovar B							
G. R. Carter	1	0.39	1.46	0.59	2.5	276.4	113.1
1305-1 buffalo	2	0.06	NT	NT	—	NT	NT
(HIM 302-3)	3	0.08	0.27	0.75	0.4	169.2	158.7
<i>P. multocida</i> , Carter's serovar C							
G. R. Carter	1	0.85	NT	NT	—	NT	NT
211 deer	2	0.09	1.12	1.39	0.8	275.3	157.4
(HIM 302-4)	3	0.21	0.18	1.31	0.1	256.9	162.2
<i>P. multocida</i> , Carter's serovar D							
G. R. Carter	1	0.95	1.55	0.39	4.0	NT	NT
93 bovine	2	0.05	NT	NT	—	NT	NT
(HIM 147-3)	3	0.09	0.26	0.49	0.5	NT	NT

TABLE 1—Continued

Organism	Electron acceptor during growth ^b	Growth density (mg [dry wt]/ml) ^c	Quinones (μmol/g of protein)		Q/Naq. ^d	μmol of NADH/g of protein per min	
			Q	DMK or MK, respectively		NADH oxidase	NADH-fumarate reductase
<i>P. piscicida</i> ^f							
M. J. Pelczar	1	0.28	0.89	0.12	7.3	82.6	29.3
315	2	0.12	0.34	0.67	0.5	34.5	77.8
(ATCC 17911)	3	0.14	0.25	0.72	0.3	43.7	115.0
<i>P. ureae</i>							
S. D. Henriksen	1	0.06	0.49	0.25	1.9	19.8	2.7
3520/59	2	0.04	0.37	1.14	0.3	15.6	6.7
(ATCC 25976)	3	0.05	1.15	1.27	0.9	63.5	15.5
<i>P. ureae</i>							
S. D. Henriksen	1	0.05	NT	NT	—	NT	NT
218/60	2	0.04	0.85	0.31	2.7	0.9	0.7
(NCTC 10220)	3	0.04	0.17	0.16	1.1	3.6	3.6
<i>Pasteurella</i> sp.							
N. S. Mair	1	0.33	0.43	0.12	3.6	12.2	3.4
5143/70	2	0.05	0.09	0.17	0.5	14.0	14.8
(NCTC 10699)	3	0.13	0.02	0.40	0.05	51.0	83.3
<i>Pasteurella</i> sp. ^g							
W. Mannheim	1	0.53	0.83	0.22	3.8	528.5	71.8
A/1a rat	2	0.14	NT	NT	—	NT	NT
(NCTC 11051)	3	0.21	0.01	0.66	0.02	51.5	48.2
(B) Organisms containing DMK as the sole respiratory quinone							
<i>A. actinomycetem-comitans</i>							
P. Holm	1	0.04		0.18		7.7	3.9
120/48-49 (3)	2	0.03		NT		NT	NT
(NCTC 9709)	3	0.07		0.35		12.2	9.5
<i>A. actinomycetem-comitans</i>							
P. Holm	1	0.12		0.05		6.3	0.7
277/49-50	2	0.02		NT		NT	NT
(NCTC 9710)	3	0.12		0.74		4.1	2.0
<i>A. equuli</i>							
A. L. Sheather	1	0.12		0.54		42.0	64.7
Foal	2	0.14		NT		NT	NT
(NCTC 3365)	3	0.39		1.32		140.3	163.0
<i>Actinobacillus</i> sp.							
R. F. Ross	1	0.14		0.48		236.8	170.0
192	2	0.07		1.05		NT	NT
(NCTC 10801)	3	0.13		1.39		273.0	456.6
<i>Actinobacillus</i> sp.							
R. F. Ross	1	0.15		1.48		139.2	59.1
63	2	0.08		NT		NT	NT
(ATCC 27073)	3	0.21		2.36		133.9	173.0
<i>P. bettii</i>							
D. G. Hollis	1	0.14		0.49		11.9	2.7
CDC 41-5568	2	0.12		2.15		118.7	144.7
(NCTC 10535)	3	0.14		1.72		42.0	32.3
<i>P. pneumotropica</i>							
E. Jawetz	1	0.51		0.61		88.5	19.8
M 8.19.48	2	0.22		0.89		NT	NT
(NCTC 8141)	3	0.19		1.01		102.7	93.2
<i>P. pneumotropica</i>							
M. T. Parker	1	0.18		0.13		105.9	68.5
54818	2	0.06		0.60		NT	NT
(NCTC 8284)	3	0.17		0.18		87.2	40.2
<i>P. pneumotropica</i>							
R. G. Wyllie	1	0.13		0.62		55.5	37.4
C 57	2	0.03		0.27		NT	NT
(ATCC 12555)	3	0.08		5.45		34.2	8.1
<i>P. pneumotropica</i>							
F. E. Andre	1	0.15		1.50		63.1	20.9
(NCTC 10603)	2	0.13		1.10		NT	NT
	3	0.18		1.95		100.3	80.4

TABLE 1—Continued

Organism	Electron acceptor during growth ^b	Growth density (mg [dry wt]/ml) ^c	Quinones (μmol/g of protein)		Q/Naq. ^d	μmol of NADH/g of protein per min	
			Q	DMK or MK, respectively		NADH oxidase	NADH-fumarate reductase
(C) Organisms containing Q and MK							
<i>Pasteurella</i> sp., BL group							
M. S. Jayaraman	1	0.25	0.56	0.00	—	98.8	0.0
I	2	0.02	NT	NT	—	NT	NT
(NCTC 10547)	3	0.03	0.99	0.00	—	25.0	1.6
	3 + NADH ^e	0.03	0.22	0.09	2.4	71.3	0.0
<i>Pasteurella</i> sp., BL group							
M. S. Jayaraman	1	0.18	0.43	0.00	—	93.7	0.0
III	2	0.05	0.45	0.02	22.5	7.5	1.7
(NCTC 10549)	3	0.03	0.45	0.18	2.5	6.0	0.5
<i>Pasteurella</i> sp., BL group							
M. S. Jayaraman	1	0.19	0.94	0.00	—	100.0	0.0
VII	3	0.02	0.58	0.08	7.3	18.9	1.4
(NCTC 10553)	3	0.01	0.51	0.17	2.9	5.7	0.0
(D) Organisms containing MK as the sole respiratory quinone							
<i>Actinobacillus actinoides</i>							
BUCSAV 61.1	2	0.29		0.28		NT	NT
(USSR RIA 644)	3	0.02		0.14		NT	NT
(ATC 15900)							

^a For references regarding the individual strains investigated see the culture collection catalogs (1, 8). Abbreviations: ATCC, American Type culture collection, Rockville, Md.; HIM, culture collection of the Hygiene-Institut der Universität Marburg/Lahn, Germany; Naq., naphthoquinone (i.e., in the present context, MK or DMK, respectively); NCTC, National Collection of Type Cultures, London, England; NT, not tested.

^b 1, Oxygen; 2, oxygen limited; 3, fumarate.

^c Bacterial dry weight, 80°C, 48 h.

^d —, Not applicable.

^e In (A) and (B), Naq. = DMK; in (C) and (D), Naq. = MK.

^f Specific epithet proposed by Janssen and Surgalla (3).

^g See Schulz et al. (9).

^h Medium 3 supplemented with 8×10^{-5} M NADH.

both aerobic respiration and DMK-mediated fumarate respiration as energy-yielding pathways.

The presence of both Q and DMK in the respiratory chain system has been found to be characteristic of typical *Pasteurella* and *Actinobacillus* species, whereas the presence of DMK alone is most characteristic of representative *Haemophilus* species (2), although some members of *Actinobacillus* and *Pasteurella* do not form Q, and some *Haemophilus* strains contain Q in addition to DMK. Therefore, an attempt to reclassify these organisms on the basis of quinone patterns would lead to the rearrangement of the taxonomic entities constituting the three traditional genera into two interrelated groups, namely, *Haemophilus* containing DMK as the sole respiratory quinone and *Pasteurella* plus *Actinobacillus* containing DMK and Q (Table 2). However, this concept has to await confirmation, or modification, by molecular data, in particular the deoxyribonucleic acid relationships between the numerous phenotypical groups of organisms of the three genera in question.

At present, the quinone patterns appear to be useful in defining the *Actinobacillus*, *Haemophilus*, and *Pasteurella* group as a whole and probably also in species characterization (Table 2). DMK and DMK-mediated fumarate respiration have been found in all recognized *Actinobacillus*, *Haemophilus*, and *Pasteurella* species examined so far, the only exception being *H. parainfluenzae* Pitman 429, an organism producing an unusual naphthoquinone but capable of reactivating fumarate respiration on incorporation of exogenous DMK (Holländer, Ph.D. thesis).

In diagnostic bacteriology, examination of the growth-stimulating effect of fumarate on oxygen-limited tube cultures may be helpful in differentiation of nonmotile, nonsporulating, chemoorganotrophic, fastidious, small coccobacillary or rod-shaped gram-negative bacteria. For example, the lack of DMK and of growth stimulation by fumarate differentiates the organisms of the bovine lymphangitis group from *Pasteurella*; similarly, small gram-negative and fermentative rods such as *Cardiobacterium*

TABLE 2. Classification of conventional, and some more recently proposed, *Actinobacillus*, *Haemophilus*, and *Pasteurella* species according to their quinones and respiratory capabilities

Quinone(s) formed in proteose peptone medium	Terminal electron acceptors used	Species
DMK	O ₂ , NO ₃ ⁻ , fumarate	<i>A. actinomycetem-comitans</i> , <i>A. equuli</i> (in part), <i>A. suis</i> <i>H. aegyptius</i> , <i>H. agni</i> , <i>H. aphrophilus</i> , <i>H. ducreyi</i> , <i>H. influenzae</i> , <i>H. parainfluenzae</i> (in part), <i>H. paraphrophilus</i> , <i>H. parahaemolyticus</i> , <i>H. somnus</i> ^a <i>P. bettii</i> , <i>P. pneumotropica</i>
DMK + Q	O ₂ , NO ₃ ⁻ , fumarate	<i>A. equuli</i> (in part), <i>A. lignieresii</i> , <i>A. seminis</i> <i>H. haemoglobinophilus</i> , <i>H. paragallinarum</i> , <i>H. parainfluenzae</i> (in part), <i>H. parasuis</i> ^a <i>P. gallinarum</i> , <i>P. haemolytica</i> (biovars A and T), <i>P. mastitidis</i> , <i>P. multocida</i> , <i>P. ureae</i> , and two unnamed <i>Pasteurella</i> species ^b
DMK + Q	O ₂ , fumarate	<i>P. piscicida</i>
Q	O ₂ , NO ₃ ⁻	<i>H. piscium</i> ^a
Q	O ₂	<i>H. vaginalis</i> ^a
Q + MK	O ₂	Organism of bovine lymphangitis
MK	O ₂	<i>A. actinoides</i>

^a Data from Holländer and Mannheim (2) and from Holländer (Ph.D. thesis).^b Those represented by strains NCTC 10699 and NCTC 11051 (9).

hominis and *Moraxella kingii* that form Q as the sole respiratory quinone, as well as *Gemella haemolysans* and *Streptobacillus moniliformis* that do not form quinones (at least in the micromolar order of magnitude), may be separated from *Actinobacillus*, *Haemophilus*, or *Pasteurella* by their quinone patterns and absence of fumarate respiration (unpublished data). On the other hand, the data presented do not contribute to the arguments eliminating *P. piscicida* (4), or *P. bettii*, an organism that produces gas from glucose, from the *Pasteurella* group. Among the gram-negative bacteria, however, DMK is not restricted to *Actinobacillus*, *Haemophilus*, and *Pasteurella* since it is also a respiratory quinone of some, if not all, *Vibrionaceae* (unpublished data), whereas the respiratory naphthoquinone of the *Enterobacteriaceae*, including *Yersinia*, appears to be predominantly MK (6; R. Jediss, M.D. thesis, Philipps University, Marburg/Lahn, Germany, 1973; unpublished data).

REPRINT REQUESTS

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LITERATURE CITED

1. American Type Culture Collection. 1974. Catalogue of strains, 11th ed. American Type Culture Collection, Rockville, Md.
2. Holländer, R., and W. Mannheim. 1975. Characterization of hemophilic and related bacteria by their respiratory quinones and cytochromes. *Int. J. Syst. Bacteriol.* 25:102-107.
3. Janssen, W. A., and M. J. Surgalla. 1968. Morphology, physiology, and serology of a *Pasteurella* species pathogenic for white perch (*Roccus americanus*). *J. Bacteriol.* 96:1606-1610.
4. Koike, Y., A. Kuwahara, and H. Fujiwara. 1975. Characterization of "*Pasteurella*" *piscicida* isolated from white perch and cultivated yellowtail. *Jpn. J. Microbiol.* 19:241-247.
5. Kröger, A., and V. Dadak. 1969. On the role of quinones in bacterial electron transport. The respiratory chain system of *Bacillus megaterium*. *Eur. J. Biochem.* 11:328-340.
6. Kröger, A., V. Dadak, M. Klingenberg, and F. Diemer. 1971. On the role of quinones in bacterial electron transport. Differential roles of ubiquinone and menaquinone in *Proteus rettgeri*. *Eur. J. Biochem.* 21:322-333.
7. Philipps, J. E. 1974. Genus *Actinobacillus* Brumpt 1910, 849, p. 373-374. In R. E. Buchanan and N. E. Gibbons (ed.), *Bergey's manual of determinative bacteriology*, 8th ed. The Williams & Wilkins Co., Baltimore.
8. Public Health Laboratory Service Board. 1972. Catalogue of the National Collection of Type Cultures. Her Majesty's Stationery Office, London.
9. Schulz, S., S. Pohl, and W. Mannheim. 1977. Mischinfektion von Albinoratten durch *Pasteurella pneumotropica* und eine neue pneumotrope *Pasteurella* species. *Zentralbl. Veterinärmed. Reihe.* 24:476-485.
10. Smith, J. E. 1974. Genus *Pasteurella* Trevisan 1887, 94 nom. cons., opin. 13, *Jud. Comm.* 1954, 153, p. 370. In R. E. Buchanan and N. E. Gibbons (ed.), *Bergey's manual of determinative bacteriology*, 8th ed. The Williams & Wilkins Co., Baltimore.
11. Sneath, P. H. A., and R. Johnson. 1973. Numerical

- taxonomy of *Haemophilus* and related bacteria. Int. J. Syst. Bacteriol. **23**:405-418.
12. Szarskowska, L., and M. Klingenberg. 1963. On the role of ubiquinone in mitochondria. Spectrophotometric and chemical measurements of its redox reaction. Biochem. Z. **338**:647-697.
13. White, D. C. 1965. The function of 2-demethyl vitamin K₂ in the electron transport system of *Haemophilus parainfluenzae*. J. Biol. Chem. **240**:1387-1394.
14. White, D. C., and L. Smith. 1962. Hematin enzymes of *Haemophilus parainfluenzae*. J. Biol. Chem. **237**:1332-1336.