Classification of the *Flavobacterium-Cytophaga* Complex on the Basis of Respiratory Quinones and Fumarate Respiration

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Respiratory quinones and the ability to use fumarate as a terminal electron acceptor in anaerobic respiration were investigated in 49 bacterial strains representing a variety of conventional *Flavobacterium* or *Cytophaga* species. The organisms examined were subdivided into two categories according to their quinones. (i) Ubiquinones are used by the neotype strain of *Flavobacterium aquatile* and by cultures representing *F. acidificum*, *F. capsulatum*, *F. devorans*, *F. halmephilum*, and some unnamed *Flavobacterium* species. (ii) Menaquinones are produced by both typical *Cytophaga* strains and many so-called *Flavobacterium* or "*Flavobacterium/Cytophaga*" cultures. Several members of category ii exhibited low to medium reduced nicotinamide adenine dinucleotide-fumarate reductase activities when grown in un-aerated complex media supplemented with fumarate. In addition, with *F. meningosepticum*, "group IIb" organisms, and a strain of *F. odoratum*, the yields of oxygen-limited growth were markedly increased by fumarate, indicating an energetic use of fumarate respiration. On the basis of these findings, restriction of the genus *Flavobacterium* to "low-guanine-plus-cytosine" organisms containing ubiquinones and resembling *F. aquatile* is proposed. The incorporation of some former "flavobacteria" into a natural group of organisms containing menaquinones and placement in the vicinity of the *C. hutchinsonii* guanine-plus-cytosine ratio are discussed.

The traditional genus *Flavobacterium* Bergey et al. consists of miscellaneous chemoorganotrophic bacteria that produce yellowish pigments. These organisms have proved to be highly heterogeneous regarding Gram reaction, type of motility, a variety of metabolic features, and, more recently, the base composition of their deoxyribonucleic acids (25). There appears to be general agreement that any attempt to reclassify these organisms would also have to consider the taxonomy of related groups, especially *Cytophaga*. This field has been termed the "*Flavobacterium-Cytophaga* complex" (15, 20).

The present study was initiated by the observation that *Flavobacterium meningosepticum* uses menaquinone in aerobic and anaerobic respiration, whereas *F. aquatile* contains ubiquinone as the sole respiratory quinone (E. Callies, unpublished data). Since, as a rule, quinone patterns define well-established groups of chemoorganotrophic bacteria (9, 19), the taxonomic implications of this finding had to be considered. Therefore, the investigation was extended to a number of collection cultures representing several more-or-less recognized *Flavobacterium* or *Cytophaga* species. The data presented here show that quinones and quinone-mediated respiratory functions are very promising tools in defining natural groups of organisms contained in the *Flavobacterium-Cytophaga* complex.

MATERIALS AND METHODS

Microorganisms. The bacterial strains investigated are listed in Table 1. They were recovered from the lyophilic state by using appropriate media and conditions. Cloned subcultures were reidentified by a set of tests sufficient to rule out contamination and confusion, and propagated in mass cultures by using the media and growth conditions shown in Table 1.

Media. The following complex media were used and were supplemented with 50 mM fumarate (disodium fumarate, sterilized by filtration; Fluka, Buchs, Switzerland) where indicated: (a) proteose peptone medium (26); (b) medium (a) supplemented with 0.25% (wt/vol) D-(+)-glucose (sterilized separately by heat in aqueous solution; E. Merck, Darmstadt, Germany); (c) medium (a) modified for the minerals sodium chloride (0.8 M) and magnesium sulfate (8 mM) (Merck chemicals); (d) medium (a) with 0.5 M sodium chloride; (e) Trypticase soy broth (Baltimore Biological Laboratory, Cockeysville, Md.); (f) medium (e) with sodium chloride (final concentration, 2.65 M); (g) NCMB seawater medium (12); (h) tryptone-yeast extract-glucose medium according to McDermott et al. (14); (i) American Type Culture Collection medium 65; (k) medium (a) with sodium chloride (final concentration, 2 M) and supplemented with 0.2 M potassium nitrate (25); (l) Dubos salts solution (12) supplemented with 5.0% (wt/vol) D-(+)-glucose. Although, before heat sterilization, some of the medium constituents contained varying amounts of lipoquinones, appropriate controls ensured that the results could not be affected by exogenous quinones (16).

Cultivation. "Aerobic" cultures were grown in

Fernbach flasks (no. 20511; Schott & Gen., Mainz, Germany) containing 250 ml of medium and aerated vigorously with a rotatory shaker (model G-25; New Brunswick Scientific Co., New Brunswick, N.J.). Oxygen-limited cultures were grown statically in Fernbach flasks filled up to the neck (ca. 2,000 ml of medium). Late-exponential- or early-stationary-phase cells were harvested at $10,000 \times g$, 0 to 4°C, and washed twice in 0.1 M tris(hydroxymethyl)aminomethane-hydrochloride buffer, pH 7.2.

Disintegration of the cells, determination of protein, assay of NADH oxidase and of NADH-fumarate reductase, and extraction and determination of quinones. Cells were disintegrated, protein was determined, reduced β -nicotinamide adenine dinucleotide (NADH) oxidase and NADH-fumarate reductase were assayed, and quinones were assayed and determined as described previously (9, 19).

Estimation of the effect of fumarate on growth densities in oxygen-limited cultures. Two 13-mm-wide culture tubes containing 10 ml of medium with or without added fumarate received small inocula from a preculture or suspension of the organism to be tested and were incubated statically at the individual growth temperature (see Table 1). Visual readings of the relative turbidities were done after 12, 18 to 24, and 48 h, taking into consideration the possibility of a prolonged lag period with the cultures containing fumarate. For photometric recording, clear calibrated tubes were used, a tube that contained uninoculated medium serving as a blank.

RESULTS

Effect of fumarate on oxygen-limited growth. In unaerated tube cultures, most of the organisms studied grew poorly; among the organisms able to reach moderate growth densities in oxygen-limited cultures, *Flavobacterium meningosepticum*, the phenotypically related group IIb organisms, and *F. odoratum* (ATCC 4651) were unique in showing markedly increased growth responses after addition of fumarate to the complex medium. Essentially the same results were obtained with strictly anaerobic culture conditions. Therefore, quinone contents and electron transport activities of cells grown with oxygen or fumarate as an electron acceptor could be compared only in a minority of the strains investigated (see Table 1).

Quinones. The organisms representing *Flavobacterium* or *Cytophaga* species were found to contain either ubiquinones, between 0.3 and 2.2 $\mu\text{mol/g}$ of cell protein (category i; Table 1A), or menaquinones, from 0.5 to about 5 $\mu\text{mol/g}$ of cell protein (category ii; Table 1B), the amount of quinone produced by a given strain varying with culture conditions. Category i consists of several *Flavobacterium* species including the neotype strain of *F. aquatile*. Category ii contains the strains attributed to the genus *Cytophaga*, including the suggested working type of *C. hutchinsonii*, but also many so-called *Flavo-*

bacterium cultures and, among them, those representing the *F. meningosepticum* group (i.e., serovars A to F and E. O. Kings group IIb).

Electron transport activities. NADH oxidase, at greatly varying activities, was present in all strains examined. Electron transport from NADH to fumarate, however, occurred only in some of the organisms containing menaquinones, namely, the *F. meningosepticum* group and the strains of *C. hutchinsonii*, *C. johnsonae*, *F. odoratum*, *F. tirrenicum*, and *F. uliginosum* examined. Thus, category ii is subdivided into two physiological groups capable, or not capable, of utilizing fumarate as a terminal acceptor in anaerobic electron transport.

DISCUSSION

If natural groups of chemoorganotrophic bacteria are characterized by their respiratory quinones, the data presented lead to the conclusion that the genus *Flavobacterium* should be restricted to organisms producing ubiquinones as the sole respiratory quinones and that the genus *Cytophaga* should comprise only organisms containing menaquinones. On the other hand, neither category i nor category ii is a homogeneous group of organisms, the base composition of their deoxyribonucleic acids ranging from below 30% to about 70% guanine plus cytosine (G+C). It is likely that a homogeneous group can be detected among the nonfermentative, oxidase-negative, low-G+C organisms containing ubiquinone and resembling *F. aquatile* (genus *Flavobacterium sensu strictiori*). Considering phenotypical characters and G+C ratios, however, each of the other named species listed in Table 1A appears to represent a particular taxonomic group distinct from *Flavobacterium sensu strictiori*. Category ii remains heterogeneous even after the gram-positive organisms (*F. arborescens*, *F. esteroaromaticum*, *F. flavescens*, and *F. suaveolens*; Table 1B) are removed. Since a natural *Cytophaga* group (genus *Cytophaga sensu strictiori*) has to be restricted to a narrow range of G+C ratios (4) situated in the vicinity of that of *C. hutchinsonii*, its relationship to the *F. meningosepticum* group (20) should be investigated, and the fate of both low-G+C and high-G+C strains outside this G+C range (cf. Table 1B) remains open. Undoubtedly, the usefulness of the respiratory quinones as taxonomic criteria should be verified by investigating the deoxyribonucleic acid relatedness between selected members of the *Flavobacterium-Cytophaga* complex.

The data presented are in accordance with earlier reports on the quinones of *Flavobacterium* strain O147 (7). The oxidase-positive *Flavobacterium* strains of Denis et al. (6), contain-

TABLE 1. *Respiratory quinones, NADH oxidase, and NADH-fumarate reductase activities of some Flavobacterium and Cytophaga strains grown in complex media with oxygen or fumarate as the terminal electron acceptor (late-exponential-phase cells)*^a

Organism ^b	G+C content of DNA (mol%)	Medium ^c and incubation temp (°C) used for mass cultivation	Stimulation of oxygen-limited growth by fumarate	Growth density ^d (g [dry wt]/liter)	Quinones (μmol/g of cell protein)	Electron transport (μmol of NADH oxidized per g of protein per min) to:	
						Oxygen	Fumarate
(A) Organisms containing ubiquinones							
<i>Flavobacterium aquatile</i> , E. W. Taylor F 36 (ATCC 11947)	32.0 (25) ^e	i, 25	—	(1) 0.04 (2, 3) NG	0.35	9.4	0.0
<i>F. halmeophilum</i> , B. Elazari-Volcani (ATCC 19717)	49.7 (UD)	k, 30	—	(1) 0.70 (2, 3) NG	1.56	9.4	0.0
<i>F. acidificum</i> , E. A. Steinhäus (ATCC 8366)	52.7 (UD)	a, 30	—	(1) 2.00 (2) 0.03 (3) 0.02	0.57 0.45 0.35	112.6 64.6 21.5	0.0 0.0 0.0
<i>F. capsulatum</i> , E. Leifson 28 (ATCC 14666)	63.0 (20)	a, 30	—	(1) 1.70 (2, 3) NG	1.20	4.4	0.0
<i>F. devorans</i> , N. Porges (ATCC 10829)	69.0 (25) 67.7 (UD)	a, 30	—	(1) 1.40 (2, 3) NG	0.81	57.5	0.0
<i>Flavobacterium</i> sp., L. S. Suter K4 (ATCC 13945)	NT	a, 30	—	(1) 2.65 (2) 0.09 (3) 0.09	1.72 2.15 0.35	50.9 3.2 4.2	0.0 0.0 0.0
<i>Flavobacterium</i> sp., Marburg 19757/70 (HIM 377-1)	NT	a, 30	—	(1) 2.50 (2, 3) NG	0.21	30.8	0.0
<i>Flavobacterium</i> sp., Marburg 91100/74 (HIM 484-7)	NT	a, 30	—	(1) 0.76 (2, 3) NG	0.57	4.1	0.0
<i>Flavobacterium</i> sp., Marburg 91098/74 (HIM 484-8)	NT	a, 30	—	(1) 1.00 (2, 3) NG	0.59	30.0	0.0
(B) Organisms containing menaquinones							
<i>F. breve</i> , Ajinomoto Co., Inc. S-15 (ATCC 14234)	26.0 (25) 33.7 (22)	a, 30	—	(1) 2.10 (2, 3) NG	4.76	1.4	0.9
<i>F. uliginosum</i> , C. E. ZoBell 553 (ATCC 14397)	32.0 (25)	g, 30	—	(1) 0.95 (2, 3) NG	3.21	5.1	5.6
<i>F. pectinovorum</i> , M. J. Dorey, 81 (ATCC 19366)	32.9 (20) 34.2 (23) 34.9 (22) 35.5 (UD)	a, 30	—	(1) 2.50 (2, 3) NG	1.74	1.3	0.0
<i>Cytophaga johnsonae</i> , C. B. van Niel, MYX. 1.1.1. (ATCC 17061)	33-35 (13) 33.0 (14)	a, 30	—	(1) 2.70 (2) 0.03 (3) 0.02	1.82 2.98 0.56	16.5 5.1 2.6	0.0 12.7 0.0
<i>Flavobacterium</i> sp., Hoffmann-La Roche & Co. AG. O147 (R 1519)	33.9 (UD)	h, 20	—	(1) 0.48 (2) 0.01	2.11 2.00	26.7 2.7	0.0 0.0
<i>F. tirrenicum</i> , A. Grein (ATCC 15997)	34.4 (UD)	a, 30	—	(1) 0.33 (2) 0.01 (3) 0.01	0.90 1.28 1.09	69.6 351.1 9.9	17.8 8.8 6.7
<i>Flavobacterium/Cytophaga</i> sp., (5) (NCMB 251)	35.6 (5, 18)	f, 24	—	(1) 0.17 (2, 3) NG	3.40	6.4	0.0
<i>Flavobacterium/Cytophaga</i> sp., (5) (NCMB 275)	35.8 (5, 18)	a, 24	—	(1) 0.17 (2, 3) NG	1.04	9.2	0.7
<i>Flavobacterium/Cytophaga</i> sp., (5) (NCMB 289)	35.8 (5) 35.5 (UD)	c, 24	—	(1) 0.95 (2, 3) NG	1.80	3.1	6.0
<i>Flavobacterium/Cytophaga</i> sp., (5) (NCMB 264)	36.6 (5, 18)	c, 24	—	(1) 1.40 (2, 3) NG	2.49	15.5	0.0

TABLE 1—Continued

Organism ^b	G+C content of DNA (mol%)	Medium ^c and incubation temp (°C) used for mass cultivation	Stimulation of oxygen-limited growth by fumarate	Growth density ^d (g [dry wt]/liter)	Quinones (μmol/g of cell protein)	Electron transport (μmol of NADH oxidized per g of protein per min) to:	
						Oxygen	Fumarate
<i>F. odoratum</i> , M. Stutzer (ATCC 4651)	36.7 (22)	a, 30	++	(1) 1.20 (2) 0.42 (3) 0.16	1.83 2.01 1.22	31.2 78.8 29.6	22.0 95.5 15.1
<i>F. meningosepticum</i> , serovar A, E. O. King (NCTC 10016)	35.5 (24) 37.6 (21) 38.3 (18, 20) 38.4 (UD)	a, 30	++	(1) 2.70 (2) 0.57 (3) 0.01	2.73 4.50 1.58	16.9 22.6 6.4	50.5 279.4 12.8
<i>F. meningosepticum</i> , serovar B, R. E. Weaver (NCTC 10585)	36.4 (20) 36.8 (21) 50.0 (24)	a, 30	++	(1) 1.10 (2) 0.06	2.80 2.44	2.8 8.9	4.0 14.0
<i>F. meningosepticum</i> , serovar C, R. E. Weaver (NCTC 10586)	36.4 (20) 37.2 (21) 37.5 (24)	a, 30	++	(1) 1.11 (2) 0.04	3.37 2.23	3.4 13.2	10.4 42.8
<i>F. meningosepticum</i> , serovar D, S. N. Arseculeratne (NCTC 10587)	36.8 (21) 38.0 (24)	a, 30	++	(1) 0.92 (2) 0.03	2.11 2.06	1.3 3.9	3.5 11.8
<i>F. meningosepticum</i> , serovar E, L. Allen (NCTC 10588)	36.1 (21) 39.0 (24)	a, 30	++	(1) 1.10 (2) 0.05	1.80 1.62	1.7 10.5	2.1 0.0
<i>F. meningosepticum</i> , serovar F, A. Blevins (NCTC 10589)	31.6 (24) 37.0 (21)	a, 30	++	(1) 1.00 (2) 0.05	1.97 2.45	17.0 13.8	5.0 14.4
<i>Flavobacterium</i> sp., group IIb (21) (NCTC 10795)	38.5 (21)	a, 30	++	(1) 2.50 (2) 0.11	1.20 2.43	13.0 13.6	18.7 8.4
<i>Flavobacterium</i> sp., group IIb (21) (NCTC 10796)	39.4 (22)	a, 30	++	(1) 2.10 (2) 0.19	1.45 1.35	19.1 20.7	46.2 42.5
<i>Flavobacterium</i> sp., group IIb (21) (NCTC 10797)	36.1 (22)	a, 30	+	(1) 1.74 (2) 0.01	0.77 0.88	13.1 13.6	14.6 6.9
<i>Flavobacterium</i> sp., group IIb, Marburg 5388/69 (HIM 326-8)	NT	a, 30	+	(1) 1.70 (2) 0.23	1.40 NT	2.0 7.0	0.4 5.6
<i>Flavobacterium</i> sp., group IIb, Marburg 153421/71 (HIM 418-5)	NT	a, 30	++	(1) 1.41 (2) 0.19	2.18 3.03	15.2 3.1	21.8 7.1
<i>Flavobacterium</i> sp., group IIb, Marburg 141230/73 (HIM 496-4)	NT	a, 30	+	(1) 2.53 (2) 0.18	2.12 NT	9.3 5.6	2.3 4.9
<i>Flavobacterium</i> sp., group IIb, Marburg 190568/73 (HIM 464-2)	NT	a, 30	+	(1) 2.30 (2) 0.23	4.11 1.40	8.3 8.2	4.4 3.3
<i>Flavobacterium</i> sp., group IIb, Marburg 14135/74 (HIM 494-3)	NT	a, 30	++	(1) 2.65 (2) 0.16	4.76 7.51	15.3 15.0	14.3 5.5
<i>Flavobacterium</i> sp., group IIb, Marburg 54552/74 (HIM 482-9)	NT	a, 30	+	(1) 2.13 (2) 0.15	3.05 NT	5.2 2.7	1.3 1.4
<i>Flavobacterium</i> sp., group IIb, Marburg 123496/74 (HIM 488-5)	NT	a, 30	(Flocculent)	(1) 1.70 (2) 0.02	2.47 2.74	5.3 7.9	4.6 5.6
<i>C. marinoflava</i> , R. Spencer (ATCC 19326)	37.0 (3)	c, 30	—	(1) 0.93 (2, 3) NG	1.61	2.8	1.6
<i>C. hutchinsonii</i> , R. Y. Stanier, 9-37 (NCIB 9469)	39.0 (14)	1, 25	—	(1) 0.42 (2, 3) NG	0.81	8.5	15.0
<i>C. fermentans</i> , H. Veldkamp (ATCC 19072)	41.2 (14)	a, 30	—	(1) 0.29 (2) 0.02 (3) 0.02	0.66 0.91 0.89	7.1 4.1 8.8	0.0 0.0 0.0
<i>Flavobacterium/Cytophaga</i> sp., (5) (NCMB 249)	40.6 (5)	a, 24	—	(1) 0.05 (2, 3) NG	0.79	5.1	0.9

TABLE 1—*Continued*

Organism ^b	G+C content of DNA (mol%)	Medium ^c and incubation temp (°C) used for mass cultivation	Stimulation of oxygen-limited growth by fumarate	Growth density ^d (g [dry wt]/liter)	Quinones (μmol/g of cell protein)	Electron transport (μmol of NADH oxidized per g of protein per min) to:	
						Oxygen	Fumarate
<i>C. aurantiaca</i> , H. Bortels (ATCC 12208)	42.0 (14)	a, 30	—	(1) 2.53 (2, 3) NG	1.00	16.5	0.0
<i>F. heparinum</i> , E. K. Korn (NIH) (ATCC 13125)	42.2 (20) 44.7 (22) 45.0 (UD) 45.6 (23)	a, 30	—	(1) 0.76 (2, 3) NG	1.15	NT	NT
<i>F. ferrugineum</i> , Julia M. Coffey 3576 (ATCC 13524)	42.6 (25)	a, 30	—	(1) 0.27 (2, 3) NG	0.65	1.4	1.0
<i>Flavobacterium/Cytophaga</i> sp., (5) (NCMB 244)	62.9 (5, 18)	b, 24	—	(1) 1.55 (2, 3) NG	1.33	1.6	0.0
<i>Flavobacterium/Cytophaga</i> sp., (5) (NCMB 259)	63.7 (5, 18)	b, 24	—	(1) 2.30 (2, 3) NG	0.91	45.6	0.0
<i>F. esteroaromaticum</i> , C. P. Hegarty (ATCC 8091)	69.0 (25)	a, 30	—	(1) 2.54 (2, 3) NG	0.93	8.5	0.0
<i>F. arborescens</i> , A. Stewart (ATCC 4358)	71.0 (25)	a, 30	—	(1) 0.24 (2, 3) NG	0.50	2.4	0.0
<i>F. flavescens</i> , C. Darling 72 (ATCC 8315)	71.0 (25)	a, 30	—	(1) 1.41 (2, 3) NG	0.94	4.0	0.0
<i>F. suaveolens</i> , M. Levine 1045 (1) (ATCC 958)	70.0 (25)	a, 30	—	(1) 2.50	1.23	10.1	0.0

^a Abbreviations: ATCC, American Type Culture Collection, Rockville, Md.; HIM, culture collection of the Hygiene-Institut der Philipps-Universität Marburg, Germany; NCIB, National Collection of Industrial Bacteria, Torry Research Station, Aberdeen, Scotland; NCMB, National Collection of Marine Bacteria, Torry Research Station, Aberdeen, Scotland; NCTC, National Collection of Type Cultures, Public Health Laboratory, London, England; R, Culture Collection of the Hoffmann-La Roche & Co. AG, Basel, Switzerland. DNA, deoxyribonucleic acid; NG, no growth; NT, not tested; UD, unpublished data of E. Callies.

^b Strain designations, according to the culture collection catalogues, most recent editions, or personal communications (HIM, R, respectively).

^c For compositions of media, see Materials and Methods.

^d 1, Oxygen; 2, fumarate; 3, no added acceptor.

^e Reference.

ing Q-8, Q-9, or Q-indeterminate (Q represents ubiquinone), are probably different from *F. aquatile*, which is oxidase negative, the length of the isoprenoid side chains of the quinones not being considered in the present communication. Some organisms considered to be related to *Cytophaga*, like the flexibacters and myxobacters, contain menaquinones (10; E. Callies, unpublished data). However, other organisms thought to be more or less closely related to *Cytophaga*, such as *Beggiatoa* and *Vitreoscilla*, contain only ubiquinones when cultivated under conditions similar to those used in the present study (Callies, unpublished data); the *Beggiatoa* culture investigated by Carr and co-workers (2) produced naphthoquinones in addition to ubiquinone.

The growth stimulation by fumarate in unaerated proteose peptone cultures observed with organisms of the *F. meningosepticum* group deserves attention in diagnostic bacteriology, since this phenomenon indicates the presence of

naphthoquinone-mediated anaerobic electron transport. Anaerobic fumarate respiration is also characteristic of the *Enterobacteriaceae*, the *Actinobacillus*, *Haemophilus*, and *Pasteurella* groups, and some *Bacteroidaceae* (9; unpublished data). The NADH-fumarate reductase system of *F. meningosepticum* involves *b*-type cytochromes and menaquinone and is membrane bound (E. Callies, manuscript in preparation), thus resembling that of *Proteus rettgeri* (11). The NADH-fumarate reductase activities reported do not necessarily account for the extent of anaerobic electron transport, since other donors that may be used, such as formate or hydrogen, were not taken into consideration. The presence of presumably membrane-bound NADH-fumarate reductases in some *Flavobacterium* and *Cytophaga* strains lacking the growth response to fumarate in anaerobic complex media cannot be discussed here in detail. Regarding the similarity of *F. acidificum* and *Erwinia herbicola* (20), the absence of NADH-

fumarate reductase in the former (ATCC 8366; Table 1A) should be noted, since *E. herbicola* is able to produce a highly active, quinone-free, soluble NADH-fumarate reductase system (W. Mannheim and co-workers, unpublished data).

REPRINT REQUESTS

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