Some Features of *Campylobacter sputorum* subsp. *mucosalis* subsp. nov., nom. rev. and Their Taxonomic Significance

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We studied strains of "*Campylobacter sputorum* subsp. *mucosalis*" isolated from intestinal adenomatosis from several sources. Our results supported the contention that this organism should be regarded as a distinct subspecies of *Campylobacter sputorum*. However, since the name of this organism was not included on the Approved Lists of Bacterial Names, we propose it as a revived name (i.e., *Campylobacter sputorum* subsp. *mucosalis* subsp. nov., nom. rev.). The type strain is FS253/72 (= NCTC 11000). The guanine-plus-cytosine content of the deoxyribonucleic acid of this organism supports its inclusion within the genus *Campylobacter*, but in its hydrogen dependence this organism shows clear similarities to the human oral vibrios and to *Vibrio succinogenes*. However, "*C. sputorum* subsp. *mucosalis*" possesses an unusual type *c* cytochrome, and in this way it appears to differ from *V. succinogenes*. It may be differentiated readily from other members of the species *C. sputorum* by salt and glycine tolerance tests or by serological techniques.

At one time, the microaerophilic vibrios and the aerobic glucose-fermenting vibrios were included in a single genus, *Vibrio*. Later, these two groups of organisms were separated, and the microaerophilic organisms were placed in a different genus, *Campylobacter* (1). Broadly, this latter genus was divided into two main groups, the catalase-positive organisms associated with animal and human diseases and a single catalase-negative species, *Campylobacter sputorum*; within the species *C. sputorum* two subspecies were recognized, *C. sputorum* subsp. *sputorum* from the human gingival margin and *C. sputorum* subsp. *bubulus*, a commensal from the bovine genital tract. Often catalase-negative, microaerophilic vibrio can be recovered in very large numbers from the lesions of porcine intestinal adenomatosis. This organism shares many features with the two named subspecies of *C. sputorum* but can be distinguished from them, and on this basis the name "*Campylobacter sputorum* subsp. *mucosalis*" was proposed by Lawson and Rowland (5). This organism may have a particular relevance to the lesions of adenomatosis, as an intracellular vibrio-shaped bacterium has been observed lying free in the apical cytoplasm of intestinal cells in lesions of this disease (13).

The initial descriptions of "*C. sputorum* subsp. *mucosalis*" were based on relatively few strains, and therefore it was desirable to study more strains in order to define the taxon better and more fully. Although validly published (7), the

name "*C. sputorum* subsp. *mucosalis*" did not appear on the Approved Lists of Bacterial Names (14), and therefore it has no standing in nomenclature. (Names in quotation marks are not on the Approved Lists.) In this paper we provide a more comprehensive description of this organism and revive the name *C. sputorum* subsp. *mucosalis*, thereby giving it standing in nomenclature.

MATERIALS AND METHODS

Bacterial strains. The *C. sputorum* strains which we studied included some previously described strains (6, 7) and some recently isolated strains. We isolated the majority of the "*C. sputorum* subsp. *mucosalis*" strains from cases of intestinal adenomatosis. We also studied strains from similar pathological material from the sources listed in Table 1.

Characterization tests and serology. The tests used for hydrogen sulfide and catalase production, nitrate and nitrite reduction, and growth in the presence of glycine, sodium chloride, and deoxycholate have been described previously (6, 7). Antisera were obtained from rabbits, and agglutination tests were carried out with serovar (serotype) A strain 1, serovar B strain 23, and an additional strain (strain 41), designated serovar C; these tests were performed by previously described methods (5).

Tests for growth in gaseous environments. The hydrogen microaerophilic atmosphere used (5) contained 77% hydrogen, 10% nitrogen, 3% oxygen, and 10% CO₂. An additional gaseous environment used was prepared in a similar way except that nitrogen replaced the hydrogen; this atmosphere contained 87% nitrogen, 3% oxygen, and 10% CO₂. Replicate plates

TABLE 1. Sources and characteristics of catalase-negative *Campylobacter* strains recovered from pigs

Strain no. ^a	Laboratory no.	NCTC no. ^b	Origin	Source	Nitrite reduction	H ₂ S production ^c	Growth in 1% glycine	Growth in 1.5% NaCl	Growth in 2.5% NaCl	Agglutination with antisera against ^d		
										Serovar A (strain 1)	Serovar B (strain 23)	Serovar C (strain 41)
1	FS253/72	NCTC 11000	PIA ^e	Lawson et al. ^f	+	+	-	+	-	+	-	-
2	FS302/72	NCTC 11001	PIA	Lawson et al.	+	+	-	+	-	+	-	-
3	FS252/72		PIA	Lawson et al.	+	+	-	+	-	+	-	ND ^g
4	FS124/73		PIA	Lawson et al.	+	+	-	+	-	+	-	-
5	FS614/73		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
6	FS1181/73		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
7	FS5/74		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
8	FS60/74		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
9	FS101/74		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
10	FS182/74		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
11	FS489/74		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
12	FS604/74		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
13	FS632/74		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
14	FS777/74		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
15	FS106/75		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
16	FS273/75		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
17	FS722/75		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
18	FS792/75		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
19	FS801/75		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
20	FS944/75		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
21	FS273/76		PIA	Lawson et al.	+	+	-	+	-	+	-	ND
22	FS1080/76		PIA	Lawson et al.	+	+	-	+	-	+	-	-
23	FS982/76		PIA	Lawson et al.	+	+	-	+	-	+	-	-
24	FS140/76-220		PIA	Gunnarson ^h	+	+	-	+	-	+	-	-
25	FS140/76-235		PIA	Gunnarson	+	+	-	+	-	+	-	-
26	FS728/77		PIA	Love ⁱ	+	+	-	+	-	+	-	-
27	FS644/77-8983		PIA	Kurtz ^j	+	+	-	+	-	+	-	ND
28	FS644/77-7169		PIA	Kurtz	+	+	-	+	-	+	-	ND
29	FS509/76		PIA	V.I. Centre, Leeds ^k	+	+	-	+	-	+	-	ND
30	FS1382/75		PIA	V.I. Centre, Cambridge ^l	+	+	-	+	-	+	-	ND
31	FS207/75-A		Mouth	Lawson et al.	+	+	-	+	-	+	-	ND
32	FS207/75-B		Mouth	Lawson et al.	+	+	-	+	-	+	-	ND
33	FS207/75-C		Mouth	Lawson et al.	+	+	-	+	-	+	-	ND
34	FS1189/74		Mouth	Lawson et al.	-	+	-	+	-	+	-	ND
35	FS179/75		Mouth	Lawson et al.	-	-	-	+	-	+	-	ND
36	FS59/75-4		Mouth	Lawson et al.	+	+	-	+	-	+	-	ND
37	FS106/75		Mouth	Lawson et al.	+	+	-	+	-	+	-	ND
38	FS20/74		Feces	Lawson et al.	+	+	+	+	-	+	-	ND
39	FS9/74		Feces	Lawson et al.	+	+	+	+	-	+	-	ND

Crawley, England) on ice. Cell lysates were examined either immediately after being held at 5°C or after freezing at -50°C. A stock *Pseudomonas aeruginosa* strain was used to obtain cytochrome preparations for comparison.

Investigation of constituent cytochromes. A total of 14 ml of sonic extract was centrifuged at 150,000 × *g* for 2 h. The resulting pellet was suspended in 2 ml of water, and both this suspension and the supernatant were used for cytochrome characterizations.

A Unicam SP1800 spectrophotometer was used to determine the absorption characteristics of the cytochromes or their derivatives (pyridine ferrochromes). Difference spectra (dithionite reduced minus ferricyanide oxidized and CO reduced minus reduced) were obtained for samples prepared by standard procedures.

Investigation of respiratory substrates. The possible sources of reducing equivalents for strain 1 were identified in two ways. Either the ability of the substrate to reduce endogenous cytochrome was determined spectrophotometrically with the Unicam SP1800 spectrophotometer, or oxygen utilization was followed by using an oxygen electrode. To study the reduction of cytochromes, sonic extracts were equilibrated with hydrogen (for estimating reduction with hydrogen) or nitrogen (for all other possible reductants).

RESULTS

Examination of strains. A total of 43 strains of catalase-negative vibrios isolated from adenomatosis or related conditions or recovered from pigs over a period of 6 years were included in this study. All of the strains examined reduced nitrate and failed to grow in the presence of deoxycholate; other characteristics of the strains are given in Table 1. The strains which we isolated were recovered from material obtained from eight separate pig farms, and these strains plus the strains isolated from other areas of the United Kingdom and from four continents should constitute a fair representation of the taxon.

The characteristics of the strains isolated from adenomatosis conformed to the descriptions published previously for "*C. sputorum* subsp. *mucosalis*." A few strains showed slight growth in some tests with 1% glycine or 0.2% deoxycholate; this growth was always minimal compared with the growth obtained with control media lacking these substances. Occasionally, recently isolated strains failed to reduce nitrite over the period of the test; this feature rarely persisted on repeated tests. Identical organisms and other similar but distinct catalase-negative vibrios could be recovered from the mouths, feces, and alimentary tracts of pigs.

Two and possibly three distinct serogroups of organisms appeared to be involved in the aden-

omatosis complex; these were the commonly occurring types which reacted with antisera prepared against strain 1 serovar A organisms and the types which reacted with strain 23 or 41 antisera (serovars B and C, respectively). Confirmation that serovar C strains are involved in adenomatosis has yet to be obtained, as a serovar C strain was isolated from only the feces of a clinical case.

DNA base composition. The DNA base composition of strain 1 was 33.9 mol% guanine plus cytosine, as calculated from the thermal denaturation temperature of 83.2°C. In Table 2 these results are compared with the results obtained by other workers for members of the genus *Campylobacter* and related organisms.

Growth in nitrogen and hydrogen. Table 3 summarizes the growth of *Campylobacter* strains in the hydrogen and nitrogen microaerophilic atmospheres. *Campylobacter fetus* subsp. *fetus* strain FS461/73 grew normally in both the nitrogen and hydrogen atmospheres, whereas all of the *C. sputorum* strains grew well only in the hydrogen-rich atmosphere. There appeared to be small differences between the amount of growth produced by the "*C. sputorum* subsp. *mucosalis*" strains and the amount of growth produced by the human and pig oral strains

TABLE 2. Base compositions of DNAs of *Campylobacter* strains and *V. succinogenes*

Organism(s)	Guanine-plus-cytosine content (mol%)	Reference
<i>C. fetus</i> subsp. <i>fetus</i>	34.4	16
<i>C. fetus</i> subsp. <i>venerealis</i>	34.4	16
<i>C. sputorum</i> subsp. <i>bubulus</i>	30.1	16
Catalase-positive human oral strains	49.3	15
Catalase-negative human oral strains	48.2	15
<i>V. succinogenes</i>	49.0	4
" <i>C. sputorum</i> subsp. <i>mucosalis</i> " FS253/72 (=NCTC 11000)	33.9	

TABLE 3. Growth of *Campylobacter* species in hydrogen and nitrogen microaerophilic atmospheres

Organism	No. of strains tested	Growth in: ^a	
		H ₂	N ₂
<i>C. fetus</i> subsp. <i>fetus</i>	1	+++	+++
<i>C. sputorum</i> subsp. <i>sputorum</i>	3	+++	- or ±
<i>C. sputorum</i> subsp. <i>mucosalis</i>			
Serovar A	14	+++	+ or -
Serovar B	1	+++	+
Porcine mouth strain (catalase negative; not serovar A or B)	1	+++	-

^a -, No growth discernible; ±, occasional, small colonies; +, some small colonies; +++, normal colony development.

tested. The latter strains produced little or no growth, whereas the former frequently yielded very small colonies which did not enlarge during reincubation; visualization of these fine colonies depended to some extent on the method of inoculation, and imprints in the agar surface obscured their presence. There seemed to be no evidence for any difference in the behavior between old stock cultures and recent isolates of "*C. sputorum* subsp. *mucosalis*."

Nature of cytochromes. Preliminary spectrophotometric studies of "*C. sputorum* subsp. *mucosalis*" showed that it contained relatively large quantities of a type *c* cytochrome. Figure 1 shows dithionite-reduced minus ferricyanide-oxidized difference spectrum of a sonicated cell suspension. This figure shows α and β absorption peaks at 553 and 524 nm, respectively. After centrifugation of this sonic extract at $150,000 \times g$ for 2 h, we determined the distribution of heme C and protoheme IX in the supernatant and pellet (Table 4). Heme C, the major heme detected, was found in both the pellet and the supernatant. The combined heme C content was 123 nmol/1.12 g (wet weight) of cells; if present in one monoheme cytochrome, this content would represent $>100 \mu\text{mol}$ of cytochrome per kg (wet weight).

Reduced minus oxidized difference spectra of

FIG. 1. Difference spectra of a "*C. sputorum* subsp. *mucosalis*" cell sonic extract. The cell sonic extract was prepared at a concentration of 80 mg (wet weight) of cells per ml. Line A shows the base line established with the cell sonic extract in both reference and sample cuvettes. Line B shows the results when the reference solution was oxidized with potassium ferricyanide and the sample solution was reduced with sodium dithionite.

both the suspended pellet and the supernatant also showed the presence of the type *c* cytochrome α absorption band at 553 nm. Figure 2 shows absolute spectra of the supernatant. Ascorbate (2 mM) was not effective in reducing the type *c* cytochrome, which suggests that the midpoint oxidation reduction potential had a negative value; i.e., it was comparatively low for a type *c* cytochrome.

The reduced minus oxidized difference spectrum of a sonicated cell suspension (Fig. 1) also showed a weak, broad band at 620 nm. Carbon monoxide reduced minus reduced difference spectra showed a small but definite peak at 630 nm. These results suggested that a type *d* cytochrome may have been present. However, we

TABLE 4. Distribution of heme after centrifugation of cell sonic extract^a

Heme	Amt (nmol) in:	
	Pellet	Supernatant
Heme C	42	81
Protoheme IX	6	

^a A total of 14 ml of a suspension containing 80 mg (wet weight) of cells per ml was sonicated and centrifuged at $150,000 \times g$ for 2 h. Protoheme IX in the suspended pellet and protoheme IX in the supernatant were extracted into 1% HCl in acetone, and their amounts were determined as pyridine ferrohemochrome (maximum, 557 nm). Heme C is not extracted into acid-acetone, and the amount of heme C was also determined as pyridine ferrohemochrome (maximum, 550 nm).

FIG. 2. Absolute spectra of "*C. sputorum* subsp. *mucosalis*" cytochrome c_{553} . A cell sonic extract (80 mg [wet weight] of cells per ml) was centrifuged at $150,000 \times g$ for 2 h. The dithionite-reduced (line R) and ferricyanide-oxidized (line O) spectra were recorded by using the clear supernatant.

were not able to detect any type *d* heme in acid-acetone extracts.

Respiratory substrates. The endogenous cytochrome *c*₅₅₃ of "*C. sputorum* subsp. *mucosalis*" (1) was reduced rapidly when cell suspensions or sonic extracts were supplied with either hydrogen or formate. Lactate, succinate, and reduced nicotinamide adenine dinucleotide gave slight reductions, and methanol, formaldehyde, malate, glutamate, and serine were inactive. On exposure to air, the hydrogen- or formate-reduced cytochrome was reoxidized rapidly, and this reoxidation was not affected by cyanide up to a concentration of 3 mM.

In the oxygen utilization experiments with the oxygen electrode, sonic extracts and cell suspensions gave similar results, and once again the same substrates (hydrogen, formate and, to a small extent, reduced nicotinamide adenine dinucleotide and succinate) favored the utilization of oxygen. This reaction was insensitive to cyanide (0.4 mM). Glutamate, lactate, malate, glycerol, glucose, glucose 6-phosphate, and glycerol phosphate were inactive as respiratory substrates.

Growth in the presence of sodium formate. Plates containing sodium formate in a nitrogen atmosphere supported the growth of 13 of 14 strains of "*C. sputorum* subsp. *mucosalis*" serovars A and B at a level comparable to the level obtained with the same basal media in a hydrogen atmosphere. However, one strain (strain 27) grew only poorly under formate-nitrogen conditions.

Fluid media. "*C. sputorum* subsp. *mucosalis*" grows poorly in most conventional fluid media and requires a hydrogen microaerophilic atmosphere in addition to an agar slant with a broth overlay to provide satisfactory fluid phase growth. Our results suggested a solution to this problem, and we obtained satisfactory growth of the six strains tested (strains 1, 2, 4, 26, 27, and 28) in a fluid medium containing 2.5 g of sodium chloride, 7.5 g of proteose peptone (type L46; Oxoid) 1.25 g of liver digest (type L27; Oxoid) 2.5 g of yeast extract (Difco Laboratories), 1.25 g of sodium formate, and distilled water to 500 ml. The ingredients were dissolved by heating the preparation to 56°C; the solution was then cooled, and the pH was adjusted to 7.4 with 1.0 N NaOH. Containers filled with 5 ml of this medium were autoclaved at 15 lb/in² for 15 min with the caps loose; after autoclaving, the caps were tightened while they were hot, and when the medium was cool, 0.1 ml of inactivated rabbit serum (Wellcome Research Laboratories) was added to each 5 ml of medium. Such media could be inoculated and incubated without any special atmospheric precautions.

DISCUSSION

An examination of "*C. sputorum* subsp. *mucosalis*" strains derived from a variety of sources indicated that this taxon is homogeneous and that strain FS253/72 (=NCTC 11000) is representative of this group. The taxonomic positions of the other biochemically and serologically distinct catalase-negative vibrios isolated from pigs are less certain. We are in favor of retaining the name "*C. sputorum* subsp. *mucosalis*" for those organisms that can be demonstrated within the cells of adenomatosis lesions and for bacteria that cannot be distinguished from these organisms. Consequently, we propose that the name *Campylobacter sputorum* subsp. *mucosalis* be revived for the same organism with which the name was associated when it was published originally by Lawson et al. (5, 7). The type strain is FS253/72 (=NCTC 11000). The separation of *C. sputorum* subsp. *mucosalis* from *C. sputorum* subsp. *sputorum* and *C. sputorum* subsp. *bubulus* can be achieved in the laboratory in most instances relatively easily by salt or glycine tolerance tests or by serological means (7). *C. sputorum* subsp. *bubulus* is glycine and salt tolerant, and *C. sputorum* subsp. *sputorum* is glycine tolerant, whereas "*C. sputorum* subsp. *mucosalis*" does not grow in 1% glycine but does grow in salt concentrations similar to those in which *C. sputorum* subsp. *sputorum* grows. Serological cross-reactions among these subspecies have not been reported.

The taxonomic positions of the human oral vibrios and of *V. succinogenes* are uncertain. The guanine-plus-cytosine contents of the DNAs of the oral vibrios and of *V. succinogenes* are between 48 and 50 mol% (15, 17); this should exclude them from the genus *Campylobacter*, in which guanine-plus-cytosine contents are between 30 and 35 mol% (1). The guanine-plus-cytosine contents of strains of oral vibrios originally identified as *C. sputorum* subsp. *sputorum* (9) have not been determined.

During its phase of intracellular parasitism, *C. sputorum* subsp. *mucosalis* is thought to multiply primarily within cells. Ultrastructural studies of the parasitized mucosa fail to show a bacterial population outside and adjacent to the infected cells, and profiles of dividing bacteria can be seen within the cell cytoplasm (6). Presumably, the energy necessary for such bacterial multiplication is derived from the host cells, and an understanding of this relationship may indicate how the bacteria influence a parasitized cell. It is believed that hydrogen is produced within the alimentary tract in humans at levels which are detectable in breath. The increase in respiratory hydrogen levels after eating indicates

that the lower ileum may be the site of origin of this gas (2). At the moment, whether hydrogen acts as an important electron donor during the intracellular growth of *C. sputorum* subsp. *mucosalis* is highly speculative. *C. sputorum* subsp. *mucosalis* can become established in the oral cavity, a site at which hydrogen is likely to be considerably less abundant, except possibly in microclimates. This organism also becomes established in gnotobiotic piglets monocontaminated only by members of the genus *Bacillus* and can survive in the presence of tissue culture systems in which hydrogen enrichment of the gaseous phase is not used. Both nitrate and nitrite are reduced by *C. sputorum* subsp. *mucosalis*, and in this way this organism seems to be similar to *V. succinogenes*, which can grow in a medium in which formate and nitrate are the sole energy sources.

Cytochrome *c*₅₅₃ has been identified as the major cytochrome of *C. sputorum* subsp. *mucosalis*. The reducibility of this cytochrome by formate suggests that it may act in an electron transport chain concerned with formate oxidation that is similar to the chain present in other organisms (8). However, in *E. coli* and *V. succinogenes* the electron acceptor for formate dehydrogenase is a type *b* cytochrome rather than a type *c* cytochrome (3), and indeed rather few low-spin type *c* cytochromes are known that have redox potentials comparable to those found in type *b* cytochromes (12). The best-characterized low-spin, low-potential, type *c* cytochrome is cytochrome *c*₃ of the sulfate-reducing bacteria. However, *C. sputorum* subsp. *mucosalis* cytochrome *c*₅₅₃ is spectroscopically distinct from these cytochromes in that it has a relatively low sorbet reduced/sorbet oxidized spectroscopic ratio and no indication of a weak shoulder to the short wavelength side of the sorbet reduced peak (Fig. 2).

A further comparison of the *C. sputorum* subsp. *mucosalis* cytochrome with other type *c* cytochromes (such as the low-potential cytochrome *c*₅₅₃ found in some sulfate-reducing bacteria) would be premature and must await the purification of this cytochrome.

REPRINT REQUESTS

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