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Campylobacter mucosalis (Lawson, Leaver, Pettigrew, and Rowland 1981) comb. nov.: Emended Description

R. MARTIN ROOP II,[1] R. M. SMIBERT,[2] JOHN L. JOHNSON,[2] AND NOEL R. KRIEG[1]*

Department of Biology (Microbiology Section)[1] and Department of Anaerobic Microbiology,[2] Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061

Seven strains of *Campylobacter sputorum* subsp. *mucosalis*, reference strains of *Campylobacter fetus*, *Campylobacter jejuni*, *Campylobacter coli*, *Campylobacter laridis*, "*Campylobacter hyointestinalis*," "*Campylobacter fecalis*," *C. sputorum* subsp. *sputorum*, *C. sputorum* subsp. *bubulus*, and *Campylobacter nitrofigilis*, aerotolerant *Campylobacter* sp. strain 02790, and catalase-negative or weakly catalase-positive strain CG-1 were compared with *C. sputorum* subsp. *mucosalis* type strain NCTC 11000 in deoxyribonucleic acid hybridization experiments. Strain NCTC 11000^T (T = type strain) showed a high level of deoxyribonucleic acid homology with all of the *C. sputorum* subsp. *mucosalis* strains tested, but no significant homology with any of the other reference strains used, including *C. sputorum* subsp. *sputorum* and *C. sputorum* subsp. *bubulus* strains. Based on these observations, we propose that *C. sputorum* subsp. *mucosalis* be reclassified as *Campylobacter mucosalis* comb. nov.

In 1974, Lawson and Rowland isolated microaerophilic, gram-negative, curved bacteria from the lesions of porcine intestinal adenomatosis. These organisms resembled *Campylobacter sputorum* in their morphological and phenotypic characteristics and were given the name *Campylobacter sputorum* subsp. *mucosalis* (7, 8). *C. sputorum* subsp. *mucosalis* differs from *C. sputorum* subsp. *sputorum* and *C. sputorum* subsp. *bubulus* in two respects. First, *C. sputorum* subsp. *mucosalis* requires either H_2 or formate as an electron donor for microaerophilic or anaerobic growth (7), whereas *C. sputorum* subsp. *sputorum* and *C. sputorum* subsp. *bubulus* grow under either microaerophilic or anaerobic conditions without H_2 or formate. However, growth of *C. sputorum* subsp. *sputorum* and *C. sputorum* subsp. *bubulus* may be enhanced by these compounds (21). Second, the deoxyribonucleic acid (DNA) base composition reported for *C. sputorum* subsp. *mucosalis* is 34 mol% guanine plus cytosine (G+C) (7), compared with 30 to 32 mol% G+C reported for *C. sputorum* subsp. *sputorum* and *C. sputorum* subsp. *bubulus* (21).

The purpose of this study was to determine the relationship between *C. sputorum* subsp. *mucosalis* and *C. sputorum* subsp. *sputorum*, *C. sputorum* subsp. *bubulus*, and reference strains of other recognized *Campylobacter* species by means of DNA hybridization experiments.

MATERIALS AND METHODS

Organisms. The origins of all of the strains used in this study are shown in Table 1. In all but three cases the type strains were included. In the case of *C. sputorum* subsp. *sputorum*, type strain ER-33 (10) is no longer extant; therefore, strain VPI S-17 was used as the reference strain in this study. This strain fits the original description of the species (10) and has been used by other investigators as a reference strain for *C. sputorum* subsp. *sputorum* (5, 22). In the cases of "*Campylobacter hyointestinalis*" (3) and "*Campylobacter fecalis*" (2) type strains have not been designated, and the strains used were the reference strains suggested by the authors who proposed these names.

Growth conditions. Stock cultures of *C. sputorum* subsp. *mucosalis* and *Campylobacter concisus* were maintained in semisolid brucella medium supplemented with 0.3% fumaric acid and 0.16% agar (semisolid BF medium) and adjusted to pH 7.0 with KOH. Cultures were incubated under an atmosphere containing 6% O_2, 5% CO_2, 15% H_2, and 74% N_2. Stock cultures of other campylobacters were maintained in semisolid brucella medium containing 0.16% agar incubated aerobically. Semisolid brucella medium was supplemented with 1.0% NaCl for growth of *Campylobacter nitrofigilis* (14). All stock cultures except *C. nitrofigilis* and aerotolerant *Campylobacter* sp. strain 02790 stock cultures were incubated at 37°C; *C. nitrofigilis* and aerotolerant *Campylobacter* sp. strain 02790 stock cultures (16) were incubated at 30°C. Stock cultures were transferred weekly and also stored in liquid nitrogen.

For DNA isolation, *C. sputorum* subsp. *mucosalis* strains were inoculated into semisolid BF medium and incubated at 37°C under an atmosphere containing 6% O_2, 5% CO_2, 15% H_2, and 74% N_2. After 48 h, the top 1 to 2 ml of growth from two tubes was used to inoculate a Roux bottle containing a diphasic medium (200 ml of BF medium supplemented with 0.2% sodium formate and solidified with 2.5% agar, overlaid with 50 ml of BF medium broth supplemented with 0.2% sodium formate). These cultures were incubated aerobically at 37°C for 24 to 48 h. The growth from eight Roux bottles was usually sufficient to yield enough DNA for the experiments. Strain CG-1, which was obtained from C. Gebhart and is an unclassified, catalase-negative or weakly catalase-positive strain similar to the strains described by Sandstedt et al. (19), was grown under similar conditions; however, ferrous-bisulfite-pyruvate medium (4) was used in the Roux bottles instead of BF medium supplemented with 0.2% sodium formate. *C. sputorum* strains were grown in Roux bottles containing BF medium as described above, and the growth from two bottles was used to inoculate 1 liter of BF medium broth in a 2-liter Erlenmeyer flask. These cultures were incubated aerobically with shaking at 37°C for 24 h. The growth conditions used for all of the catalase-positive campylobacters except *C. nitrofigilis* have been described previously (18). *C. nitrofigilis* was grown in the same way as the other catalase-positive strains, except that all media were supplemented with 1.0% NaCl (14). All cultures were checked for purity by phase-contrast microscopy prior to harvesting.

* Corresponding author.

TABLE 1. Bacterial strains used in this study

Taxon	Strain	Source[a]	Origin
C. sputorum subsp. *mucosalis*	NCTC 11000^T	Lawson	Porcine
	79-12009	Ward	Porcine
	P-9681C	Hayes	Porcine
	P-10546C	Hayes	Porcine
	P-5007	Hayes	Porcine
	P-11508	Hayes	Porcine
	P-5494	Hayes	Porcine
	P-10742	Hayes	Porcine
C. sputorum subsp. *sputorum*	VPI S-17	Smibert	Human
C. sputorum subsp. *bubulus*	ATCC 33562^T	ATCC	Bovine
"*C. fecalis*"	11363 (= ATCC 33709)[b]	Firehammer	Ovine
C. concisus	ATCC 33237^T	Tanner	Human
C. fetus subsp. *fetus*	ATCC 27374^T	ATCC	Ovine
C. fetus subsp. *venerealis*	ATCC 19438^T	ATCC	Bovine
C. jejuni	ATCC 33560^T	ATCC	Bovine
C. coli	ATCC 33559^T	ATCC	Porcine
C. laridis	NCTC 11352^T	NCTC	Avian
"*C. hyointestinalis*"	80-4577-4 (= ATCC 35217)[c]	Gebhart	Porcine
C. nitrofigilis	ATCC 33309^T	ATCC	*Spartina alterniflora* roots
Catalase-negative or weakly catalase-positive campylobacters	CG-1	Gebhart	Canine
Aerotolerant campylobacters	02790	Neill	Porcine

[a] Lawson, G. H. K. Lawson, Department of Veterinary Pathology, Royal (Dick) School of Veterinary Studies, Midlothian, Scotland; Ward, G. E. Ward, Veterinary Diagnostic Laboratory, University of Minnesota, St. Paul; Hayes, J. Hayes, Purdue University School of Veterinary Medicine, West Lafayette, Ind.; Smibert, R. M. Smibert, Department of Anaerobic Microbiology, Virginia Polytechnic Institute and State University, Blacksburg; ATCC, American Type Culture Collection, Rockville, Md.; Firehammer, B. D. Firehammer, Veterinary Research Laboratory, Montana State University, Bozeman; Tanner, A. C. R. Tanner, Forsyth Dental Center, Boston, Mass.; NCTC, National Collection of Type Cultures, London, England; Gebhart, C. Gebhart, Veterinary Diagnotic Laboratory, University of Minnesota, St. Paul; Neill, S. D. Neill, Veterinary Research Laboratory, Belfast, Ireland.

[b] Suggested type strain (B. D. Firehammer, personal communication).

[c] Suggested type strain (C. Gebhart, personal communication).

DNA isolation, DNA homology experiments, and determination of DNA base composition. DNA was extracted and purified by the hydroxylapatite procedure described by Johnson (6). The S1 nuclease procedure described by Johnson (6) was used for the DNA homology experiments, and the homology experiments were performed under "optimal" conditions (i.e., 25°C below the thermal melting point of the DNA [12]). DNA from *C. sputorum* subsp. *mucosalis* NCTC 11000^T (T = type strain) was labeled in vitro with ^{125}I by using the method of Selin et al. (20).

The thermal melting points of the DNAs from *C. sputorum* subsp. *mucosalis* strains NCTC 11000^T and 79-12009 were determined by using the method described by Johnson (6), and the G+C contents were determined by using the equation of Mandel et al. (11). DNA from *Escherichia coli* strain b, which has a G+C content of 51 mol%, was used as a reference.

Physiological characteristics. The procedures used for determining growth in 1% oxgall, 3.5% NaCl, 1% glycine, and minimal medium, for determining H_2S production in sulfide-indole motility medium, from cysteine (lead acetate strips), and on triple sugar iron agar slants, for determining growth at 25 and 42°C, and for determining susceptibility to nalidixic acid and cephalothin have been described previously (18). Nitrate reduction and nitrite reduction were tested as previously described (18), except that the final concentration of KNO_3 in the medium was 0.7 instead of 1.0%. Deoxyribonuclease activity and the ability to grow on 1.5% NaCl plates were tested as previously described (18), except that the basal medium was replaced with brucella agar supplemented with 0.3% fumaric acid (pH 7.0). In all of the tests mentioned above, cultures were incubated under an atmosphere containing 6% O_2, 5% CO_2, 15% H_2, and 74% N_2.

Catalase activity, oxidase activity, hippurate hydrolysis, and anaerobic growth in 0.1% trimethylamine-*N*-oxide were tested as previously described (18).

RESULTS AND DISCUSSION

All seven strains of *C. sputorum* subsp. *mucosalis* used in this study showed a high level of DNA homology (≥92%) with the type strain of *C. sputorum* subsp. *mucosalis* (strain NCTC 11000) but no significant homology with any of the other reference strains tested, including the reference strain

TABLE 2. Levels of DNA homology of *C. sputorum* subsp. *mucosalis* strains and *Campylobacter* reference strains with *C. sputorum* subsp. *mucosalis* NCTC 11000^T

Source of unlabeled DNA	% Homology with DNA from *C. sputorum* subsp. *mucosalis* NCTC 11000^T
C. sputorum subsp. *mucosalis* NCTC 11000^T	100
P-5007	96
P-5494	96
P-11508	96
P-10546C	95
P-9681C	92
P-10742	92
79-12009	92
C. sputorum subsp. *sputorum* VPI S-17	3
C. sputorum subsp. *bubulus* ATCC 33562^T	5
"*C. fecalis*" 11363	3
C. concisus ATCC 33237^T	9
C. fetus subsp. *fetus* ATCC 27374^T	4
C. fetus subsp. *venerealis* ATCC 19438^T	4
"*C. hyointestinalis*" 80-4577-4	5
C. jejuni ATCC 33560^T	6
C. coli ATCC 33559^T	2
C. laridis NCTC 11352^T	2
C. nitrofigilis ATCC 33309^T	2
Aerotolerant *Campylobacter* sp. strain 02790	2
Catalase-negative or weakly catalase-positive strain CG-1	2

of *C. sputorum* subsp. *sputorum* (strain VPI S-17) and the type strain of *C. sputorum* subsp. *bubulus* (strain ATCC 33562) (Table 2).

The base compositions of the DNAs from *C. sputorum* subsp. *mucosalis* strains 79-12009 and NCTC 11000^T were 38 and 39 mol% G+C, respectively; these values are higher than the value of 34 mol% G+C reported for strain NCTC 11000^T by Lawson et al. (7). The difference may be attributable in part to the use of different equations for calculating the base compositions of the DNAs. The equation of Mandel et al. (11) was used for determining the values given in this paper, whereas the equation of Marmur and Doty (13) was used by Lawson et al. When the G+C values for strains 79-12009 and NCTC 11000^T were recalculated by using the equation of Marmur and Doty, values of 36 and 37 mol% were obtained; these values are still higher than the value reported by Lawson et al. (7). The reason for the discrepancy is not known; however, our results are consistent with the value of 38 mol% G+C obtained for strain NCTC 11000^T by Owen and Leaper (17), using the buoyant density method.

C. sputorum subsp. *mucosalis* strains can be distinguished from all other catalase-negative *Campylobacter* species except *C. concisus* (22) by their requirement for H_2 or formate for microaerophilic growth and H_2 and fumarate or formate and fumarate for anaerobic growth (21). Although *C. concisus* strains are similar to *C. sputorum* subsp. *mucosalis* in their phenotypic characteristics (21, 22), they have only a very low level of DNA homology with *C. sputorum* subsp. *mucosalis* NCTC 11000^T (Table 2). *C. sputorum* subsp. *mucosalis* strains can be distinguished from *C. concisus* strains by their susceptibility to cephalothin, by their ability to grow at 25°C, and by the "dirty yellow" color of their colonies (21). The color is best seen when a colony is picked and smeared on a piece of white paper (9).

Growth in a medium containing 1.5% NaCl and the inability to grow in the presence of 1% glycine were reported by Lawson et al. (7) to be characteristics of *C. sputorum* subsp. *mucosalis*. During the course of the study described in this paper, we found that all eight of the strains tested, including the type strain (strain NCTC 11000), were able to grow in the presence of 1% glycine. We performed this test in a semisolid medium, which is probably the method that is used in most diagnostic laboratories because of its ease of inoculation and easy interpretation of results. Lawson and Rowland (9) inoculated agar plates containing 1% glycine with a velour pad that had been charged with inocula from a blood agar plate; they also used a shorter incubation period (24 to 48 h) than the 4- to 5-day incubation period which we used. In addition, we found that only three of eight *C. sputorum* subsp. *mucosalis* strains used in our study grew on 1.5% NaCl agar plates, and those grew very scantily. This may have been due to differences in the basal media or the methodology used for inoculating the plates. Oxoid blood agar base no. 2 was used as the basal medium by Lawson and Rowland (9), whereas BF medium agar was used in our study. The NaCl agar plates used in our study were inoculated by continuous streaking with a loop needle with inocula from a 24- to 48-h-old semisolid culture, whereas Lawson and Rowland (9) inoculated NaCl agar plates in the same manner as glycine agar plates. We believe that our method is the more sensitive of the two for determining ability to grow in 1.5% NaCl. For instance, growth in 1.5% NaCl is an important differential characteristic for *Campylobacter laridis* (1, 18), and those strains which we have tested grow well when our method is used.

The description of *C. sputorum* subsp. *mucosalis* given in *Bergey's Manual of Systematic Bacteriology* (21) is based on earlier descriptions of this organism (7, 8) and does not reflect the discrepancies with the original description that were found during the course of the present study. The results of our DNA homology experiments (Table 2) indicate that *C. sputorum* subsp. *mucosalis* is a distinct species and is not a subspecies of *C. sputorum*. Therefore, we propose that the name *C. sputorum* subsp. *mucosalis* be changed to *Campylobacter mucosalis* comb. nov., and we provide the emended description given below.

TABLE 3. Phenotypic characteristics of *C. mucosalis*

Characteristic	Reaction of:	
	Strain NCTC 11000^T	Seven other strains
Catalase	−	−[a]
Oxidase	+	+
Nitrate reduction	+	+
Nitrite reduction	−[b]	d[b]
Growth in:		
1% Oxgall	+	+
1.5% NaCl (plates)	−	−
3.5% NaCl	−	−
1% Glycine	+	+
Minimal medium[c]	−	−
Anaerobic growth in 0.1% trimethylamine-*N*-oxide	−	−
H_2S production:		
Sulfide-indole motility medium	+	+
Lead acetate strips	+	+
Triple sugar iron agar	+	+
Growth at:		
25°C	+	+
42°C	+	+
Hippurate hydrolysis	−	−
Deoxyribonuclease activity	−	[−]
Susceptibility to:		
Nalidixic acid (30-μg disk)	+	−
Cephalothin (30-μg disk)	+	+

[a] +, 90 to 100% of the strains are positive; d, 26 to 75% of the strains are positive; [−], 11 to 25% of the strains are positive; −, 0 to 10% of the strains are positive.

[b] Other investigators (7,9) have reported that the majority of the *C. mucosalis* strains that they tested, including strain NCTC 11000^T, reduced nitrite. However, these workers used a different basal medium (nitrate broth supplemented with 5% inactivated horse serum) than the medium used in the study reported here (brucella broth).

[c] See reference 18.

Description of *Campylobacter mucosalis* (Lawson, Leaver, Pettigrew, and Rowland 1981) comb. nov. The following description of *Campylobacter mucosalis* (mu. co' sal. is. L. n. *mucosus* mucus; L. gen. n. *mucosalis* of mucus, pertaining to mucus) is based upon descriptions given by Lawson et al. (7, 9) and Smibert (21) and upon observations made during the course of this study. The cells are short, irregularly curved, and gram negative and may appear as spiral forms 0.25 to 0.3 μm in diameter and 1 to 3 μm long. Motile by means of a single polar flagellum. Coccoid bodies and filamentous forms may be seen in older cultures. Colonies are 1.5 mm in diameter, circular, and raised with flat surfaces. The colonies have a dirty yellow color that is best seen by smearing a colony on a piece of white paper (9). Requires either hydrogen or formate as an electron donor for growth. Grows under microaerophilic conditions (6% O_2, 5%

CO_2, 15% H_2, 74% N_2) where O_2 serves as the electron acceptor or anaerobically with fumarate as the terminal electron acceptor. Contains appreciable amounts of lauric acid (C_{12}) in its cellular fatty acids (15). Other phenotypic characteristics of type strain NCTC 11000 and seven other strains are listed in Table 3.

Isolated from the intestinal mucosa of pigs with porcine intestinal adenomatosis, necrotic enteritis, regional ileitis, and proliferative hemorrhagic enteropathy; also isolated from the oral cavities of pigs.

The G+C content of the DNA of type strain NCTC 11000 is 39 mol%, as calculated by the equation of Mandel et al. (11). The thermal melting point of the DNA is 84.3°C in 1× SSC buffer (0.15 M NaCl plus 0.015 M sodium citrate, pH 7.0).

C. mucosalis NCTC 11000^T shows less than 9% DNA homology with reference strains of *C. sputorum* subsp. *sputorum*, *C. sputorum* subsp. *bubulus*, *C. concisus*, *Campylobacter fetus* subsp. *fetus*, *C. fetus* subsp. *venerealis*, *Campylobacter jejuni*, *Campylobacter coli*, *C. laridis*, *C. nitrofigilis*, "*C. fecalis*," and "*C. hyointestinalis*," catalase-negative or weakly catalase-positive strain CG-1, and aerotolerant *Campylobacter* sp. strain 02790 (Table 2).

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