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"*Campylobacter hyointestinalis*" sp. nov.: a New Species of *Campylobacter* Found in the Intestines of Pigs and Other Animals†

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The name "*Campylobacter hyointestinalis*" sp. nov. is proposed for a *Campylobacter* species that was isolated from the intestines of pigs with proliferative enteritis. "*C. hyointestinalis*" is also found in the feces of cattle and has been isolated from the intestine of a hamster. "*C. hyointestinalis*" is distinguished from previously described catalase-positive *Campylobacter* species by colony morphology, ability to produce H_2S in triple sugar iron agar, ability to grow anaerobically in 0.1% trimethylamine *N*-oxide hydrochloride, resistance to nalidixic acid, susceptibility to cephalothin and metronidazole, and hydrogenase activity. Sixteen "*C. hyointestinalis*" strains were highly related (≥76%) by DNA-DNA hybridization (hydroxyapatite method, 50 and 65°C). Other *Campylobacter* species were ≤30% related to "*C. hyointestinalis*." The type strain of "*C. hyointestinalis*" is designated 80-4577-4 (=ATCC 35217), and its DNA has a guanine-plus-cytosine content of 36 mol%.

The genus *Campylobacter* was named in 1963 by Sebald and Véron (21) to accomodate a group of bacteria previously classified as *Vibrio* species. Bacteria included in this genus are gram-negative, slender, curved or spiral cells, are motile by a single polar flagellum, grow microaerophilically or anaerobically, do not ferment carbohydrates, and have a guanine-plus-cytosine (G+C) content of 28 to 38 mol% (22, 26). Certain *Campylobacter* species are recognized pathogens in domestic animals and humans (2, 22, 26).

In 1983, strains of a new species, "*Campylobacter hyointestinalis*," isolated from pigs with proliferative enteritis, were described biochemically (9). These bacteria were catalase positive, H_2S positive in triple sugar iron (TSI) agar, glycine tolerant, intolerant of 3.0% sodium chloride, susceptible to cephalothin, and resistant to nalidixic acid. The initial description of "*C. hyointestinalis*" was not validly published and was based on relatively few phenotypic characteristics. DNA relatedness studies were not done, the new species was not formally described or proposed, and a type strain was not designated. It therefore has no standing in nomenclature. In this paper we present an extension and refinement of the original description.

"*C. hyointestinalis*" was particularly interesting because it was consistently isolated from the intestines of pigs with proliferative enteritis but not from pigs with other enteritis diseases (9). Swine proliferative enteritis is a disease complex characterized by the proliferation of intestinal epithelial cells with resultant thickening of the wall of the intestine, primarily the ileum. Chang et al. (5), using an indirect fluorescent-antibody technique, demonstrated that "*C. hyointestinalis*" and *C. sputorum* subsp. *mucosalis* were present in large numbers within the enterocytes of these proliferative lesions.

Since the first report of "*C. hyointestinalis*" isolated from pigs with proliferative enteritis, phenotypically similar bacteria have been isolated from cattle feces (18, 24, 27; D. Werner, unpublished data) and from the intestine of a hamster with enteritis (C. J. Gebhart, unpublished data). On the bases of phenotypic and DNA relatedness data we now confirm that the pig, cattle, and hamster isolates are the same species, which is described and formally proposed as "*Campylobacter hyointestinalis*" sp. nov.

MATERIALS AND METHODS

Bacterial strains. The 16 "*C. hyointestinalis*" strains used in this study and their sources are listed in Table 1. We isolated the porcine and hamster strains by previously described methods (9). Bovine strains were supplied by other investigators. All "*C. hyointestinalis*" strains were stored at −70°C in defibrinated sheep blood. Strains were cultured on

TABLE 1. Designations and sources of "*C. hyointestinalis*" strains

"*C. hyointestinalis*" strain	Origin[a]	Source
80-4577-4^{T}[b] (=ATCC 35217^{T})	CVM, UM	Pig intestine[c]
81-13037	CVM, UM	Pig intestine[c]
124/73-1	Lawson	Pig intestine[c]
Wisc 699	CVM, UM	Pig intestine[c]
81-14151-1	CVM, UM	Pig intestine[c]
80-9806	CVM, UM	Pig intestine[c]
P9681-81	CVM, UM	Pig intestine[c]
81-6107	CVM, UM	Pig intestine[c]
83-12908	CVM, UM	Pig intestine[c]
83-5557	CVM, UM	Pig intestine[c]
82-9593	CVM, UM	Pig intestine[c]
20,085	Firehammer	Pig intestine[c]
20,048	Firehammer	Bovine feces
20,049	Firehammer	Bovine feces
8705	Werner	Bovine feces
WT1	CVM, UM	Hamster intestine[c]

[a] CVM, UM, College of Veterinary Medicine, University of Minnesota, St. Paul; Lawson, G. H. K. Lawson, Department of Veterinary Pathology, University of Edinburgh Veterinary Field Station, Midlothian, Scotland; Firehammer, B. D. Firehammer, Department of Veterinary Science, Montana State University, Bozeman; and Werner, D. Werner, National Animal Disease Center, Ames, Iowa.

[b] University of Minnesota control strain number.

[c] The animal had proliferative enteritis; the etiological agent has not been proven.

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TABLE 2. DNA relatedness of "*C. hyointestinalis*" strains

Source of unlabeled DNA	RBR at 50°C [a,b]	%D[a]	RBR at 65°C[a,c]
"*C. hyointestinalis*"			
80-4577-4^T (=ATCC 35217)	100	0.0	100
81-14151-1	100		84
Wisc 699	100		89
83-12908	100		92
WT1	99	0.5	96
82-9593	99		96
20,085	99		87
80-9806	97		86
20,048	96	0.5	86
81-6107	95		85
P9681-81	94	0.0	87
8705	92	0.5	84
124/73-1	91	0.5	88
20,049	88		80
81-13037	76	0.5	63
83-5557	76	5.0	59
Campylobacter type and reference strains:			
C. fetus subsp. *fetus* ATCC 27374	30	8.0	14
C. sputorum subsp. *bubulus* NCTC 11367	16		
C. sputorum subsp. *mucosalis* NCTC 11000	10		
"*C. fecalis*" NCTC 11415	4		
C. laridis NCTC 11352	3		
C. coli NCTC 11366	2		
C. jejuni NCTC 11351	2		

[a] Tested against $^{32}PO_4$-labeled DNA from "*C. hyointestinalis*" 80-4577-4^T (=ATCC 35217).
[b] The control value ranged from 0.7 to 2.9.
[c] The control value ranged from 1.2 to 2.6.

Mueller-Hinton agar (Difco Laboratories, Detroit, Mich.) containing 5% defibrinated sheep blood in a microaerophilic environment at 37°C. A microaerophilic atmosphere was produced by using an evacuation replacement system (GasPak 150; BBL Microbiology Systems, Cockeysville, Md.) with no catalyst. The air was evacuated twice to 400 mm of Hg (ca. 53.33 kPa), and the jar was refilled each time with a gas mixture of 10% carbon dioxide–10% hydrogen–80% nitrogen. For phenotypic tests, the frozen cultures were thawed, subcultured once, and checked for purity by microscopic examination of Gram-stained cells and for characteristic motility by phase-contrast microscopy of wet mounts.

Tests for phenotypic characteristics. Test procedures were as previously described (9) with the following variations. Test inocula were prepared by suspending growth from a 24-h culture into Mueller-Hinton broth to a density of a McFarland no. 1 standard. Unless otherwise noted, all plated media were incubated in a microaerophilic atmosphere. Strains were also tested for anaerobic growth on Mueller-Hinton agar in an atmosphere generated by GasPak H_2-CO_2 generator envelopes (BBL) in GasPak jars (BBL) with the catalyst in place. Hydrogenase activity was tested by the procedure of Goodman and Hoffman (11). The ability to grow anaerobically in 0.1% trimethylamine *N*-oxide hydrochloride (TMAO) was tested by a modification (20) of the technique described by Benjamin et al. (1). A multiple-inoculum replicator (Cathra International, Inc., St. Paul, Minn.) was used to inoculate tests for tolerance of 2,3,5-triphenyltetrazolium chloride (TTC), growth in the presence of 1.5, 2.0, and 3.0% sodium chloride, growth in 1.0% glycine, temperature tolerance, and susceptibility to metronidazole (Sigma Chemical Co., St. Louis, Mo.). Susceptibility to metronidazole was determined by incorporating 5 μg of metronidazole per ml into Mueller-Hinton agar. After 48 h, the plates yielding no growth or a barely perceptible haze were considered positive. Antimicrobial MICs were determined as previously described (10).

TABLE 3. Phenotypic characteristics of "*C. hyointestinalis*"

Characteristic	Reaction of strain 80-4577-4^T (=ATCC 35217^T)[a]	% of strains positive (n = 15)	Strain(s) that gave the less common result
Oxidase	+	100	
Catalase	+	100	
Yellow pigment	+	87	20,085 and 8705
Motility	+	100	
Swarming on moist agar	−	0	
Rapid coccal transformation	−	0	
H_2S production:			
In TSI agar	+	100	
With lead acetate indicator	+	100	
Growth:			
25°C	+[b]	60[b]	81-13037, 124/73-1, 80-9806, 20,048, 20,049 and 81-14151-1
30.5°C	+	100	
43°C	+	93	20,085
1.5% NaCl	−	20	81-6107, 20,048, and 20,049
2.0% NaCl	−	0	
3.0% NaCl	−	0	
1.0% Glycine	+	100	
0.04% TTC	−	7	81-13037
Anaerobically in 0.1% TMAO	+	100	
Nitrate reduction	+	100	
Nitrite reduction	−	0	
Susceptibility to:			
Nalidixic acid	−	0	
Cephalothin	+	100	
Metronidazole	+	93	124/73-1
Sodium hippurate hydrolysis	−	0	
Hydrogenase activity	+	87	20,048 and 20,049
Gelatin liquefaction	−	0	
Urease	−	0	

[a] +, Positive; −, negative.
[b] These strains were only weakly positive.

TABLE 4. Susceptibility patterns of "*C. hyointestinalis*" strains to selected antimicrobial agents[a]

Susceptibility pattern and antimicrobial agent	MIC range[b]
Susceptible	
Metronidazole	0.5–1.0
Dimetridazole	0.25–1.0
Furazolidone	≤0.125–0.25
Nitrofurantoin	1.0–2.0
Carbadox	≤0.125
Penicillin	8.0–32.0
Ampicillin	0.25–0.5
Carbenicillin	1.0–32.0
Chloramphenicol	2.0–16.0
Cephaloridine	0.5–2.0
Cephalosporin C	0.5
Amikacin	2.0–8.0
Gentamicin	1.0–2.0
Variable	
Clindamycin	1.0–≥128
Tetracycline	4.0–≥128
Erythromycin	4.0–≥128
Kanamycin	4.0–≥128
Neomycin	4.0–≥128
Resistant	
Virginiamycin	≥128
Bacitracin	≥128
Colistin	≥128
Polymyxin B	64–≥128
Sulfathiazole	≥128
Tylosin	≥128
Streptomycin	≥128
Vancomycin	≥128
Nalidixic acid	≥128
Trimethoprim	64–≥128
Cyclohexamide	≥128

[a] Data are from reference 10 and are based on 10 porcine "*C. hyointestinalis*" isolates from the College of Veterinary Medicine, University of Minnesota, St. Paul.

[b] All MIC ranges are in micrograms per milliliter, except for those of penicillin, bacitracin, colistin, and tylosin, which are in units per milliliter.

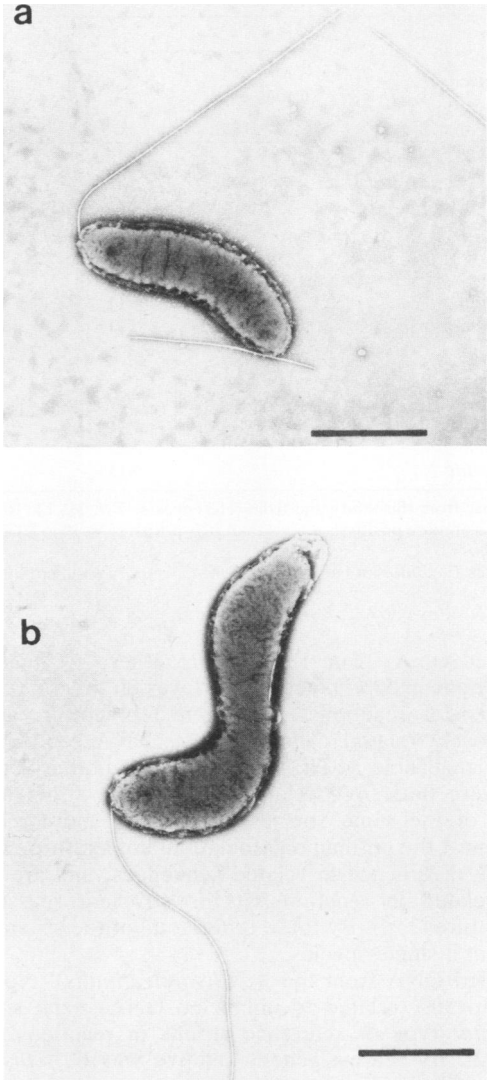

FIG. 1. Electron micrographs of two strains of "*C. hyointestinalis*" showing single polar flagella. (a) Strain 80-4577-4^T; (b) strain 81-14151-1. Bar, 1 nm.

Colony and microscopic morphologies were recorded for 48-h cultures on Mueller-Hinton agar. Tests for swarming growth and rapid coccal transformation were performed by the method of Karmali et al. (13). The presence and arrangement of flagella was determined with selected strains grown on Mueller-Hinton agar for 18 h. The cells were emulsified in sterile water, negatively stained with 3% phosphotungstic acid, and examined with a transmission electron microscope.

Tests for DNA relatedness. For DNA hybridization studies, we harvested cells from Mueller-Hinton agar plates after 48 h of incubation. The cells were lysed, and the DNA was extracted, purified, and tested for relatedness by a previously described hydroxyapatite technique (4). G+C determinations were performed by procedures described by De Ley (6). DNA from the type strain of "*C. hyointestinalis*," 80-4577-4 (=ATCC 35217), was labeled with $^{32}PO_4$ and tested for relatedness to unlabeled DNA from the same strain (homologous reaction), to unlabeled DNAs from each of the other "*C. hyointestinalis*" isolates, and to unlabeled DNAs from type or reference strains of other *Campylobacter* species (heterologous reactions). Because DNAs from *Campylobacter* species have a low G+C content (19), the hybridization reactions were carried out at 50°C, an optimal reassociation criterion, and at 65°C, a stringent reassociation criterion (4). DNA relatedness was expressed as the relative binding ratio (RBR): RBR = (percent heterologous DNA bound to hydroxyapatite/percent homologous DNA bound to hydroxyapatite) × 100. *D* is the amount of divergence, i.e., unpaired bases in DNA sequences held in common by two bacteria. *D* was calculated on the assumption that each decrease of 1°C in the thermal stability of a heterologous DNA duplex, compared with that of a homologous DNA duplex, is caused by ca. 1% unpaired bases (3, 4). *D* was calculated to the nearest 0.5%. Labeled DNA incubated in the absence of unlabeled DNA served as a control for nonspecific binding of DNA to hydroxyapatite in each experiment. The control value was subtracted before relatedness was calculated. Each RBR value is the mean of two separate experiments.

RESULTS AND DISCUSSION

Labeled DNA from the type strain of "*C. hyointestinalis*," 80-4577-4 (=ATCC 35217), was 88 to 100% related to

TABLE 5. Characteristics differentiating "*C. hyointestinalis*" from other *Campylobacter* species[a]

Species	Characteristics of strains[b]							
	Catalase	Flagellar arrangement	H_2S production in TSI agar	Growth:				
				25°C	43°C	3.0% NaCl	1.0% Glycine	0.04% TTC
"*C. hyointestinalis*"	+	M	+	V[w]	+	−	+	−
C. fetus subsp. *fetus*	+	M	−	+	V	−	+	−
C. fetus subsp. *venerealis*	+	M	−	+	−	−	−	−
"*C. fecalis*"	+	ND	+	−	+	+	+	−
C. laridis	+	A	−	−	+	−	+	V
C. nitrofigilis	+	ND	ND	+	−	+	−	−
Campylobacter-like organisms	+	ND	−	−	V	−	+	+
C. coli	+	A	−	−	+	−	+	+
C. jejuni biotype I	+	A	−	−	+	−	+	+[w]
C. jejuni biotype II	+	A	+	−	+	−	+	+[w]
C. concisus	−	ND	+	−	−	−	−	ND
C. sputorum[c]	−	ND	+	V	V	V	V	ND

[a] Data are from this study and from references 1, 7–9, 11, 12, 16, 17, 22, 23, and 27.

[b] +, 85% or more positive; −, less than 10% positive; V, 10 to 80% positive; [w], weakly positive; ND, no results found or test not done; M, monotrichous; A, amphitrichous.

[c] Includes *C. sputorum* subsp. *sputorum*, *C. sputorum* subsp. *bubulus*, and *C. sputorum* subsp. *mucosalis*.

unlabeled DNAs from 13 of the 15 other "*C. hyointestinalis*" strains in 50°C reactions and was 80 to 96% related to them in 65°C reactions, a stringent temperature at which only closely related *Campylobacter* DNA sequences can reassociate (Table 2). The two exceptions, both isolates from pigs, were both 76% related to the type strain at 50°C. Strains of the same species are 70% or more related in reactions at the optimal reassociation temperature, with less than 6% divergence in related sequences, and are 55% or more related in reactions at the stringent reassociation temperature (3, 4). By these criteria, all of the strains tested belong in a single species.

Labeled DNA from the "*C. hyointestinalis*" type strain was 2 to 30% related to unlabeled DNAs from six *Campylobacter* type or reference strains in reactions at 50°C (Table 2). Its nearest genetic relative was *C. fetus* subsp. *fetus*.

The phenotypic characteristics of "*C. hyointestinalis*" are shown in Table 3. "*C. hyointestinalis*" strains most resembled *C. fetus* subsp. *fetus* strains; however, these species could be distinguished by several biochemical tests. Roop et al. (20) also found that "*C. hyointestinalis*" showed closer genotypic and phenotypic relationships to *C. fetus* subsp. *fetus* than to any other catalase-positive *Campylobacter* species. Characteristics that most consistently distinguished "*C. hyointestinalis*" from other catalase-positive species were colony pigment, susceptibility to nalidixic acid, cephalothin, and TTC, anaerobic growth in TMAO, and hydrogenase activity. In our study, TTC tolerance proved to be a reliable characteristic for differentiating "*C. hyointestinalis*" from *C. coli*. Temperature tolerance results were variable with "*C. hyointestinalis*" and were dependent on the inoculum size, the age of the culture, and the medium used; they were thus unreliable for identifying "*C. hyointestinalis*" isolates. Most strains of "*C. hyointestinalis*" grew at 43°C, but none showed as heavy growth at this temperature as did *C. coli* or *C. jejuni* strains. Many strains (60%) of "*C. hyointestinalis*" grew at 25°C, but growth was barely perceptible at this temperature. The production of H_2S in TSI agar by "*C. hyointestinalis*" was a reliable characteristic only when fresh medium and a carefully controlled microaerophilic atmosphere containing hydrogen were used. Hydrogen sulfide production was noted most often on the slant and rarely in the stab of TSI agar.

The ranges of MICs for "*C. hyointestinalis*" isolates are summarized in Table 4.

Campylobacter strains phenotypically similar to "*C. hyointestinalis*" have been reported previously. In 1975, Lawson et al. (15) noted differences between pig isolates classified as *C. coli*. These organisms were classified as *C. coli* types I, II, and III. Type I, represented by strain 124/73-1 in this study, is phenotypically and genetically similar to "*C. hyointestinalis*." Walder et al. (27) reported on a group of eight nalidixic acid-resistant, sodium hippurate-negative, thermotolerant campylobacters of porcine and bovine origin that resembled "*C. hyointestinalis*." Ursing et al. (24, 25) subsequently showed that these strains constituted a genetically homogeneous and distinct group. Except for its ability to grow weakly at 25°C, "*C. hyointestinalis*" is phenotypically similar to these organisms. Lambert et al. (14) reported the isolation of "*C. hyointestinalis*" from 40 pigs in the United Kingdom, often in association with other potential enteric pathogens.

"*C. hyointestinalis*" is the organism most frequently isolated from pigs with proliferative enteritis (9). Proliferative enteritis in hamsters is a disease similar to swine proliferative enteritis, and thus it is interesting that one "*C. hyointestinalis*" isolate in this study was obtained from a hamster with enteritis. The bovine strains in this study were isolated from the feces of healthy calves; however, Ursing et al. (24) reported the isolation of phenotypically similar strains from the feces of cattle with chronic diarrhea.

We propose the name "*Campylobacter hyointestinalis*" sp. nov. (hy.o.in.tes'.tin.al.is., Gk. n. *hys*, *hyos*, a hog; M. L. adj. *intestinalis*, pertaining to the intestines; M. L. gen. n., of a hog's intestine; therefore, *Campylobacter hyointestinalis*, the *Campylobacter* of a hog's intestine).

Description of "*Campylobacter hyointestinalis*" sp. nov. The phenotypic characteristics of "*C. hyointestinalis*" fit the definition of the genus *Campylobacter* (26). Cells of "*C. hyointestinalis*" are gram-negative, oxidase-positive, nonsporeforming, nonencapsulated, curved rods with character-

TABLE 5.—*Continued*

Anaerobically in 0.1% TMAO	Nitrite reduction	Susceptibility to: Nalidixic acid (30-μg disk)	Cephalothin (30-μg disk)	Metronidazole (5 μg)	Sodium hippurate hydrolysis	Hydrogenase activity	G+C content (mol%)
+	−	−	+	+	−	+	36
−	−	−	+	−	−	−	33–36
−	−	−	+	−	−	−	33–36
+	+	−	+	ND	ND	ND	37
+	ND	−	−	−	−	ND	28
ND	ND	+	+	ND	−	ND	28.3
−	ND	+	V	ND	−	ND	ND
−	−	+	−	V	−	+	32–34
−	−	+	−	V	+	+	31–32
−	−	+	−	V	+	ND	31–32
−	+	−	ND	+	−	ND	34–38
ND	+	V	+	+	ND	ND	29–34

istic darting motility due to a single polar flagellum, as seen by electron microscopy (Fig. 1). A few cells containing two flagella at one pole were observed. The cells are microaerophilic to anaerobic and do not use glucose either fermentatively or oxidatively. They do not hydrolyze gelatin or urea, and they have no lipase activity.

Colonies of "*C. hyointestinalis*" are circular, convex, slightly mucoid, and 1.5 to 2.0 mm in diameter after 48 h of incubation. Colonies scraped from plates appear yellow and do not swarm on moist medium. The organisms are long, loosely spiraled, and ca. 0.35 to 0.55 μm wide, and they do not tend to become coccoid. Filamentous forms are seen in old cultures.

All strains produced positive results in the following tests: catalase, anaerobic growth in the presence of 0.1% TMAO, growth in 1% glycine, growth at 30.5°C, H_2S production (TSI and lead acetate), susceptibility to cephalothin, reduction of nitrate to nitrite, and oxidase. All strains produced negative results in the following tests: growth in 2.0 and 3.0% sodium chloride, hippurate hydrolysis, reduction of nitrites, susceptibility to nalidixic acid, gelatin liquefaction, and urease. Most strains grew at 25 and 43°C, were susceptible to 0.04% TTC and to metronidazole, and had hydrogenase activity. Growth of and H_2S production by "*C. hyointestinalis*" were enhanced by hydrogen. A further description of "*C. hyointestinalis*," including MICs of antibiotics, is found in the text and tables above.

Strains were isolated from the intestines of pigs with proliferative enteritis in Minnesota, Montana, Wisconsin, Iowa, and Scotland. They were also isolated from bovine feces and a hamster intestine. The type strain of "*C. hyointestinalis*" is 80-4577-4 (=ATCC 35217), which was isolated from the intestine of a weaned pig with lesions of proliferative enteritis in Minnesota in 1980. The G+C content of its DNA is 36 mol%. Its biochemical characteristics are those shown in Table 3.

Characteristics by which "*C. hyointestinalis*" can be distinguished from other *Campylobacter* species are shown in Table 5. "*C. hyointestinalis*" can be differentiated from *C. sputorum* subsp. *sputorum*, *C. sputorum* subsp. *bubulus*, *C. sputorum* subsp. *mucosalis*, and *C. concisus* by its catalase production and intolerance of 1.5% sodium chloride and from *C. coli* and *C. jejuni* by its susceptibility to TTC and nalidixic acid, its resistance to cephalothin, its inability to undergo rapid coccal transformation, and its inability to swarm on moist agar. It differs from *Campylobacter*-like organisms (7) by its ability to produce H_2S in TSI agar, its susceptibility to TTC, its ability to grow anaerobically in 0.1% TMAO, and its resistance to nalidixic acid and from *C. nitrofigilis* (17) by its failure to grow in media containing 2.0 or 3.0% sodium chloride, its tolerance of 1.0% glycine, and its resistance to nalidixic acid. "*C. hyointestinalis*" differs from *C. laridis* (1) by its flagellar arrangement, its failure to readily develop coccal forms and to tolerate 2.0% sodium chloride, and its susceptibility to cephalothin and metronidazole. The inability of "*C. hyointestinalis*" to grow in media containing 3.0% sodium chloride distinguishes it from "*C. fecalis*" (8). In addition, "*C. hyointestinalis*" produces moderate amounts of H_2S only on the slant of TSI agar, whereas "*C. fecalis*" produces heavy amounts of H_2S throughout the agar. The production of H_2S in TSI agar, susceptibility to metronidazole, anaerobic growth in 0.1% TMAO, and hydrogenase activity differentiate "*C. hyointestinalis*" from *C. fetus* subsp. *venerealis* and *C. fetus* subsp. *fetus*, its nearest phenotypic relatives.

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