Campylobacter hyointestinalis subsp. *lawsonii* subsp. nov., Isolated from the Porcine Stomach, and an Emended Description of *Campylobacter hyointestinalis*

STEPHEN L. W. ON,^{1*} BUCHARDT BLOCH,² BARRY HOLMES,³ BART HOSTE,⁴
AND PETER VANDAMME^{4,5}

Danish Veterinary Laboratory, DK-1790 Copenhagen V,¹ and Department of Veterinary Microbiology, Royal Veterinary and Agricultural University, DK-1870 Frederiksberg C,² Denmark; National Collection of Type Cultures, Central Public Health Laboratory, London NW9 5HT, United Kingdom³; and Laboratorium voor Microbiologie, University of Ghent, B-9000 Ghent,⁴ and Department of Medical Microbiology, University of Antwerp, B-2610 Antwerp,⁵ Belgium

The taxonomic relationships of seven isolates obtained from porcine stomachs (the “CHY” group), which resembled (but were distinct from) the type strain and other reference strains of *Campylobacter hyointestinalis*, were examined by using phenotypic and genomic methods. The phenotypic characteristics and ultrastructure of the new organisms were characteristic of *Campylobacter* species, although they could be distinguished from all previously described taxa. A numerical analysis of 38 phenotypic characters revealed that the new isolates formed a distinct group at a similarity level of 90.1% and could be clearly distinguished from reference strains representing 20 related taxa, principally species and subspecies belonging to the genera *Campylobacter*, *Arcobacter*, and *Helicobacter*. DNA-DNA hybridization studies revealed that the porcine stomach strains were genomically homogeneous (levels of relatedness, 84 to 90%), although the levels of DNA homology with type and reference strains of *C. hyointestinalis* were relatively high (56 to 71%). Differences in the DNA base compositions of the CHY group and *C. hyointestinalis* strains were also observed. Our data indicate that the new porcine isolates should be considered members of a subspecies of *C. hyointestinalis*, for which we propose the name *Campylobacter hyointestinalis* subsp. *lawsonii* subsp. nov. The type strain is strain CHY 5 (= LMG 14432 = NCTC 12901 = CCUG 34538). The description of *C. hyointestinalis* is emended accordingly, and a description of *Campylobacter hyointestinalis* subsp. *hyointestinalis* subsp. nov. is given.

The taxonomy of the genus *Campylobacter* has been significantly revised since the genus was proposed in 1963, when it included only two species (35). At this time, the genus comprises 15 species (including four taxa formerly classified as members of the genus *Wolinella* [9, 38, 39] or the genus *Bacteroides* [38]) and four subspecies (42). The species *Campylobacter hyoilei* has been described recently (1). Furthermore, *Bacteroides ureolyticus* and an unnamed free-living organism (20) are closely phylogenetically related to the genus *Campylobacter* phylogenetically as determined by rRNA-DNA homology (45) and 16S rRNA sequence similarity (6) analyses. However, several taxa previously described as campylobacters have now been reassigned to the genus *Arcobacter* (45, 48) or *Helicobacter* (15, 45). Both the genus *Campylobacter* and the genus *Arcobacter* are included in the family *Campylobacteraceae* (44). All of these bacteria represent a distinct phylogenetic lineage which is referred to as rRNA superfamily VI (45) or the epsilon division of the class *Proteobacteria* (36).

Campylobacters are important agents of principally gastrointestinal disorders in both humans and animals (33). In a study of the distribution of *Campylobacter* species in swine with enteric disease (particularly swine with proliferative enteritis), Gebhart et al. (13) isolated 19 strains of a phenotypically distinct taxon which they named *Campylobacter hyointestinalis*. Members of this species have subsequently been isolated from cases of enteritis in humans (7, 11, 23), cattle (41), deer (16), and hamsters (12), although the pathogenic potential of *C. hyointestinalis* has not been determined. The antigenic proper-

ties (10), cellular fatty acid composition (18), isoprenoid quinone content (24), DNA base composition, levels of DNA homology (12, 41), levels of rRNA-DNA hybridization (45), and 16S rRNA sequence data (6, 50) determined for *C. hyointestinalis* support the original generic assignment made by Gebhart et al. (12, 13).

A recent study of the use of numerical analysis of whole-cell electrophoretic protein profiles for identifying and typing *C. hyointestinalis* (28) indicated that seven isolates obtained from porcine stomachs were somewhat distinct, although they were closely related to the majority of the other *C. hyointestinalis* strains studied. These isolates were originally identified as “*C. hyointestinalis*-like” and were referred to as the “CHY” group strains. Phenotypic differences between the CHY group and *C. hyointestinalis* strains were observed (28), although detailed descriptions of the biochemical profiles were not given.

Because of the agreement between protein profile data and DNA-DNA hybridization data (19, 46), we investigated the taxonomic status of the CHY group isolates in more detail by using phenotypic and genomic methods. In this paper we propose a new subspecies, *Campylobacter hyointestinalis* subsp. *lawsonii*, for these strains; strain CHY 5 (= LMG 14432 = NCTC 12901) is the type strain of this taxon. The description of *C. hyointestinalis* is revised accordingly below.

MATERIALS AND METHODS

Bacterial strains. A total of 60 bacterial strains were studied (Table 1). These strains included the seven CHY group isolates, as well as 16 *C. hyointestinalis* strains, 18 *Campylobacter fetus* strains, and 19 type or reference strains of related taxa.

Culture media and growth conditions. For the phenotypic characterization study, the strains were grown on 5% (vol/vol) horse blood agar for 3 days under optimal atmospheric and growth conditions, as described previously (29, 31). For electron microscopy and DNA extraction, strains were grown for 2 days at 37°C

* Corresponding author. Mailing address: Danish Veterinary Laboratory, Bülowsvej 27, DK-1790 Copenhagen V, Denmark. Phone: 45 35 30 01 00. Fax: 45 35 30 01 20.

TABLE 1. Strains used

Organism ^a	Strain ^b	Additional information	Clinical and geographical origin (if known) ^c
<i>Campylobacter</i> species and subspecies			
<i>C. hyointestinalis</i> subsp. <i>lawsonii</i>	CHY 5 ^T (= LMG 14432 ^T = NCTC 12901 ^T = CCUG 34538 ^T)	Electrophoretype 17 ^d	Porcine stomach, United Kingdom
<i>C. hyointestinalis</i> subsp. <i>lawsonii</i>	CHY 6 (= LMG 14433 = CCUG 34541)	Electrophoretype 7 ^d	Porcine stomach, United Kingdom
<i>C. hyointestinalis</i> subsp. <i>lawsonii</i>	CHY 7 (= LMG 14434 = CCUG 34542)	Electrophoretype 7 ^d	Porcine stomach, United Kingdom
<i>C. hyointestinalis</i> subsp. <i>lawsonii</i>	CHY 8 (= LMG 14435 = CCUG 34543)	Electrophoretype 2 ^d	Porcine stomach, United Kingdom
<i>C. hyointestinalis</i> subsp. <i>lawsonii</i>	CHY 9 (= LMG 14436 = CCUG 34544)	Electrophoretype 2 ^d	Porcine stomach, United Kingdom
<i>C. hyointestinalis</i> subsp. <i>lawsonii</i>	CHY 3 (= CCUG 34539)	Electrophoretype 2 ^d	Porcine stomach, United Kingdom
<i>C. hyointestinalis</i> subsp. <i>lawsonii</i>	CHY 4 (= CCUG 34540)	Electrophoretype 2 ^d	Porcine stomach, United Kingdom
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	NCTC 11608 ^T (= LMG 7817 ^T)	Electrophoretype 1 ^d	Porcine intestine, PE, Minnesota
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	NCTC 11562	Electrophoretype 3 ^d	Porcine intestine, NC, Scotland
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	NCTC 11563	Electrophoretype 12 ^d	Porcine intestine, PE, Minnesota
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	NCTC 11609 (= CCUG 14170)	Electrophoretype 1 ^d	Porcine intestine, PE, Minnesota
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	NCTC 11610	Electrophoretype 1 ^d	Porcine intestine, PE, Minnesota
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	CCUG 14170 (= NCTC 11609)	Electrophoretype 1 ^d	Porcine intestine, PE, Minnesota
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	CCUG 14915	Electrophoretype 1 ^d	Porcine intestine, ileitis, Uppsala, Sweden
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	CCUG 14916	Electrophoretype 11 ^d	Bovine diarrhea, Uppsala, Sweden
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	CCUG 20704	Electrophoretype 15 ^d	Bovine feces, Preston, United Kingdom
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	CCUG 20822	Electrophoretype 10 ^e	Human feces, United States
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	CCUG 24570	Electrophoretype 1 ^d	Unknown
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	CCUG 23200 (= NCTC 11609)		Porcine intestine, PE, Minnesota
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	CCUG 24177 (= LMG 8464)		Porcine, Canada
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	CCUG 24179 (= LMG 8632)		Bovine feces, Canada
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	LMG 8464	Electrophoretype 7 ^e	Porcine, Canada
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	LMG 8632	Electrophoretype 5 ^e	Bovine feces, Canada
<i>C. coli</i>	NCTC 11366 ^T	Penner serotype 4	Porcine feces, Brussels, Belgium
<i>C. concisus</i>	NCTC 11485 ^T		Human gingival sulcus, Boston, Mass.
<i>C. curvus</i>	NCTC 11649 ^T		Human alveolar abscess, Virginia
<i>C. fetus</i> subsp. <i>fetus</i>	NCTC 10842 ^T		Ovine fetus brain, Paris, France
<i>C. fetus</i> subsp. <i>fetus</i>	NCTC 5850	Biotype b	Ovine contagious abortion, Cambridge, United Kingdom
<i>C. fetus</i> subsp. <i>fetus</i>	CCUG 7473		Human blood, Paris, France
<i>C. fetus</i> subsp. <i>fetus</i>	CCUG 11286		Human blood, Paris, France
<i>C. fetus</i> subsp. <i>fetus</i>	CCUG 17693		Bovine fetus, France
<i>C. fetus</i> subsp. <i>fetus</i>	CCUG 17694		Bovine genitalia, Belgium
<i>C. fetus</i> subsp. <i>fetus</i>	CCUG 17695A		Ovine feces
<i>C. fetus</i> subsp. <i>fetus</i>	UA 778		Ovine, United Kingdom
<i>C. fetus</i> subsp. <i>venerealis</i>	NCTC 10354 ^T		Bovine vaginal mucus, Reading, United Kingdom
<i>C. fetus</i> subsp. <i>venerealis</i>	CCUG 7477		Unknown
<i>C. fetus</i> subsp. <i>venerealis</i>	CCUG 11287	Biotype intermedius	Human blood, Paris, France
<i>C. fetus</i> subsp. <i>venerealis</i>	CCUG 11288	Biotype intermedius	Human blood, Paris, France
<i>C. fetus</i> subsp. <i>venerealis</i>	UA 790	Biotype intermedius	Bovine, Victoria, Australia
<i>C. fetus</i> subsp. <i>venerealis</i>	UA 791	Biotype intermedius	Bovine, Victoria, Australia
<i>C. fetus</i> subsp. <i>venerealis</i>	UA 813	Biotype intermedius	Bovine, Victoria, Australia
<i>C. fetus</i> subsp. <i>venerealis</i>	UA 814	Biotype intermedius	Bovine, Victoria, Australia
<i>C. fetus</i> subsp. <i>venerealis</i>	ADRI 812	Biotype intermedius	Bovine, Victoria, Australia
<i>C. fetus</i> subsp. <i>venerealis</i>	ADRI 813	Biotype intermedius	Bovine, Victoria, Australia
<i>C. gracilis</i>	NCTC 12738 ^T		Human periodontitis, Boston, Mass.
<i>C. helveticus</i>	NCTC 12470 ^T		Feline feces, Berne, Switzerland
<i>C. jejuni</i> subsp. <i>doylei</i>	NCTC 11951 ^T		Human infantile diarrhea, Adelaide, Australia
<i>C. jejuni</i> subsp. <i>jejuni</i>	NCTC 11351 ^T	Penner serotype 23	Bovine feces, Brussels, Belgium
<i>C. lari</i>	NCTC 11352 ^T		Herring gull cloacal swab, United Kingdom

Continued on following page

TABLE 1—Continued

Organism ^a	Strain ^b	Additional information	Clinical and geographical origin (if known) ^c
<i>C. mucosalis</i>	NCTC 11000 ^T	Serotype A	Porcine small intestine, PIA, Edinburgh, United Kingdom
<i>C. rectus</i>	NCTC 11489 ^T		Human periodontal pocket, Boston, Mass.
<i>C. showae</i>	CCUG 30254 ^T		Human gingival crevice, Showa, Japan
<i>C. sputorum</i>	NCTC 11528 ^T	Biovar sputorum	Human oral cavity, United States
<i>C. sputorum</i>	NCTC 11367	Biovar bubulus	Bovine semen, Brussels, Belgium
<i>C. sputorum</i>	NCTC 11415	Biovar fecalis	Ovine feces, Los Angeles, Calif.
<i>Campylobacter</i> sp. (unnamed free-living group)	CCUG 13942		Anaerobic sludge, The Netherlands
<i>C. upsaliensis</i>	NCTC 11541 ^T		Canine feces, Malmo, Sweden
Related species			
<i>Arcobacter nitrofigilis</i>	CCUG 15893 ^T		Roots of <i>Spartina alterniflora</i> , Canada
[<i>Bacteroides</i>] <i>ureolyticus</i>	NCTC 10941 ^T		Human amniotic fluid, Edmonton, Canada
<i>Helicobacter pylori</i>	NCTC 11637 ^T		Human gastric antrum gastritis, Australia

^a Brackets indicate that a species is generically misnamed and is considered a species incertae sedis (43).

^b ADRI, Animal Disease Research Institute, Nepean, Canada; CCUG, Culture Collection of the University of Göteborg, Göteborg, Sweden; CHY, *C. hyointestinalis*-like strain; LMG, Laboratorium voor Microbiologie, Ghent, Belgium; NCTC, National Collection of Type Cultures, London, England; UA, University of Alberta, Edmonton, Alberta, Canada.

^c PE, proliferative enteritis; NC, necrotizing colitis; PIA, porcine intestinal adenomatosis.

^d Electrophoretype of *C. hyointestinalis* as defined in reference 28.

^e Electrophoretype of *C. hyointestinalis* as defined in reference 47.

on 5% calf blood agar (electron microscopy) or for 2 to 3 days on Mueller-Hinton agar (catalog no. CM337; Oxoid, Ltd., Basingstoke, United Kingdom) containing 5% horse blood (DNA extraction) under microaerobic conditions as previously described (31, 45).

Phenotypic characterization. A total of 39 phenotypic characteristics were determined for 58 of the strains listed in Table 1. Isolates LMG 8464 and LMG 8632 were not examined since duplicate cultures of these strains (CCUG 24177 and CCUG 24179, respectively) were included in the study. Tests were performed by using the recommended media and methods described previously (17, 26, 29–32). However, the medium containing cephalothin (32 mg/liter) was prepared by using filter-sterilized solutions prepared with the native antibiotic (obtained from Sigma Chemical Co., Ltd., Poole, England). Hydrogen sulfide production in triple sugar iron medium was recorded as copious (blackening of >60% of the butt), trace (blackening of <60% of the butt or at the butt-slope interface only), or negative. Additional tests were performed as follows. Media containing 1.5 and 2.0% bile were prepared by using the protocol described previously for medium containing 1.0% bile (30) except that the proportions were altered accordingly. Medium containing crystal violet (0.0005%; Sigma) was prepared by aseptically adding an autoclaved (115°C, 10 min) aqueous solution containing the appropriate amount of test substance to sterile, molten nutrient agar base. Medium containing sodium fluoride (0.05%; Sigma) was prepared similarly, except that blood agar was used as the basal medium. All growth test preparations were inoculated and incubated as recommended previously (30, 31). The following were determined only for the members of the CHY group: bacterial cell morphology was determined by using the Hucker modification of the Gram stain method (3); the ability to oxidize or ferment carbohydrates was determined by using the medium of Hugh and Leifson (3); and motility was determined by using an aqueous suspension of a 3-day-old culture examined with a light microscope. All tests were performed on two separate occasions by using freshly prepared media, and the quality of each medium was tested by using appropriate control strains (27).

Numerical analysis of phenotypic tests. Previously described procedures were used to perform a numerical analysis of the phenotypic test results (25). Briefly, the simple matching coefficient was used to calculate levels of similarity between strains, and a dendrogram which reflected these levels of similarity was constructed. Strains were clustered by the unweighted pair group with mathematical average method.

Electron microscopy. Cells were suspended in distilled water, and an equal volume of a 4% formaldehyde solution was added. A small drop was negatively stained with 1% uranyl acetate on a carbon-coated Formvar grid and then made hydrophilic by glow discharge and examined with a model JEM 100B electron microscope.

Preparation of high-molecular-weight DNA. High-molecular-weight native DNA was prepared as described previously (48).

DNA base compositions. All of the guanine-plus-cytosine (G+C) values were

determined by the thermal denaturation method and were calculated as described by De Ley (4).

DNA-DNA hybridization experiments. Levels of DNA-DNA binding, expressed as percentages, were determined spectrophotometrically by the initial renaturation rate method of De Ley et al. (5). Each value given below was the average of the values from at least two hybridization experiments. DNA binding values of 30% or less do not represent significant levels of DNA homology. The total DNA concentration used was 39 µg/ml, and the optimal renaturation temperature in 2× SSC (sodium saline citrate; 1× SSC is 0.15 M NaCl plus 0.015 M sodium citrate, pH 7) was 64.6°C.

RESULTS

Phenotypic characterization. As expected, the CHY group isolates and the type and reference strains of *C. hyointestinalis* were similar. Nonetheless, these taxa could be distinguished on the basis of tolerance to 1.5% bile; a number of other useful discriminatory features were also found (Table 2). All of the *C. hyointestinalis* strains could be clearly differentiated from closely related taxa (Table 2). The phenotype of the CHY group strains is described in detail below.

Numerical analysis. Only those phenotypic characters that were determined for each strain were used in the numerical analysis. The anaerobic growth data were not included since the results obtained for *C. hyointestinalis* were inconsistent with previous data (7, 41) and we felt that they were overtly prejudicial. An examination of the dendrogram produced (Fig. 1) revealed that 19 phena were formed at a level of similarity of 85%. One of these phena comprised the seven CHY group isolates, while strains of *C. hyointestinalis*, *Campylobacter fetus* subsp. *fetus*, *Campylobacter fetus* subsp. *venerealis*, and *Campylobacter sputorum* were also found in discrete clusters. A total of 12 phena contained single strains that were included in the study as reference organisms. One of the two remaining phena contained the type strains of the enteric catalase-negative species *Campylobacter helveticus* and *Campylobacter upsaliensis*, and the other contained the type strains of the enteropatho-

TABLE 2. Characteristics that differentiate *C. hyointestinalis* subsp. *lawsonii* subsp. nov. from other campylobacteria^a

Organism	Hydrolysis of:			Growth at:		Tolerance to:				G+C content (mol%)
	Catalase	Hippurate	Indoxyl acetate	25°C	42°C	1.5% Bile	2% Bile ^c	1.0% Glycine	0.1% Potassium permanganate	
<i>C. hyointestinalis</i> subsp. <i>lawsonii</i>	+ ^b	—	—	—	+	—	—	(—)	—	31–33
CHY 5 ^T (= LMG 14432 ^T)	+	—	—	—	+	—	—	+	—	32
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	+	—	—	(—)	+	+	(+)	+	(+)	35–36
NCTC 11608 ^T (= LMG 7817 ^T)	+	—	—	—	+	+	+	+	+	35
<i>C. coli</i>	+	—	+	—	+	+	(+)	(+)	+	30–33
<i>C. concisus</i>	—	—	—	—	(+)	(—)	(—)	(—)	(—)	37–41
<i>C. curvus</i>	—	(—)	V	—	V	—	—	+	(+)	45–46
<i>C. fetus</i> subsp. <i>fetus</i>	+	—	—	+	(+)	+	+	+	+	33–35
<i>C. fetus</i> subsp. <i>venerealis</i>	(+)	—	—	(+)	—	+	(+)	(—)	(—)	33–34
<i>C. gracilis</i>	(—)	—	(+)	—	(+)	—	—	+	+	44–46
<i>C. helveticus</i>	—	—	+	—	+	+	V	V	—	34
<i>C. jejuni</i> subsp. <i>doylei</i>	(+)	+	+	—	—	+	—	(—)	(+)	30–31
<i>C. jejuni</i> subsp. <i>jejuni</i>	+	+	+	—	+	+	(+)	(+)	+	30–33
<i>C. lari</i>	+	—	(—)	—	+	+	+	+	(—)	30–32
<i>C. mucosalis</i>	—	—	—	—	+	(+)	(+)	V	—	36–38
<i>C. rectus</i>	(—)	—	+	—	(—)	—	—	+	—	45–46
<i>C. showae</i>	+	—	V	—	V	—	—	V	—	44–46
<i>C. sputorum</i>	V	—	—	—	(+)	V	V	+	—	29–32
<i>Campylobacter</i> sp. strain CCUG 13942	—	—	+	+	—	—	—	—	+	41–42
<i>C. upsaliensis</i>	—	—	+	—	(+)	+	+	+	V	32–36
<i>A. nitrofigilis</i>	+	—	+	+	—	—	—	—	+	28–29
[<i>B.</i>] <i>ureolyticus</i>	(—)	—	(—)	—	V	—	—	+	(—)	28–30
<i>H. pylori</i>	+	—	(—)	—	(—)	—	—	—	—	36–38

^a Phenotypic data for *C. hyointestinalis* and *C. fetus* were determined in this study. The data for the other taxa are from reference 26 and were determined with the same methods. Values for DNA base compositions are from this study (*C. hyointestinalis*), from references 44 and 45, and from the original descriptions of the taxa.

^b +, all strains are positive; —, all strains are negative; (+), 70 to 90% of the strains are positive; (—), 7 to 33% of the strains are positive; V, 44 to 66% of the strains are positive.

^c The type strain of *C. hyointestinalis* subsp. *hyointestinalis* does not give a consistent result in this test.

genic species *Campylobacter coli* and *Campylobacter jejuni* subsp. *jejuni*.

Electron microscope examination of whole cells. The ultrastructures of strains CHY 5^T (T = type strain), CHY 6, and CHY 9 were examined, and we observed only minor differences among these isolates. Most cells were slightly curved (Fig. 2a), although others were more spiral (Fig. 2b). A single, unsheathed, polar flagellum was common, but a few cells exhibited a biflagellated, monopolar arrangement (Fig. 2a). Both monoflagellated and biflagellated cells were observed in the same culture of strain CHY 6.

DNA base compositions. The G+C ratios were determined for four CHY group strains and three reference strains (including the type strain) of *C. hyointestinalis* (Table 3). The values obtained for the CHY group strains ranged from 31 to 33 mol% (mean, 32 mol%), while the values obtained for *C. hyointestinalis* strains ranged from 34 to 35 mol% (mean, 34 mol%).

DNA-DNA hybridization. A number of representative strains belonging to the CHY group and *C. hyointestinalis* were used for DNA homology studies. Strains assigned to the same taxon exhibited DNA binding values ranging from 84 to 90% (CHY group isolates) and from 80 to 96% (*C. hyointestinalis* strains) (Table 3). The levels of DNA relatedness between members of these two taxa were significantly lower, ranging from 56 to 71% under the stringent conditions used.

DISCUSSION

Our data suggest that seven strains (the CHY group) which were related to (but distinct from) *C. hyointestinalis* as determined by a numerical analysis of the whole-cell protein pat-

terns (28) should be considered members of a subspecies of *C. hyointestinalis*. We propose the name *C. hyointestinalis* subsp. *lawsonii* for the CHY group, and an emended description of the species is given below.

Differentiation of campylobacters and related taxa with phenotypic tests is often considered difficult (14, 22) because of the biochemical inertness of these organisms. While the results of only one test (tolerance to 1.5% bile) clearly distinguished the CHY group from *C. hyointestinalis*, several tests provided good discrimination when their results were combined (Table 2), which may explain the differentiation of these taxa in the numerical analysis described in this paper (Fig. 1). Our phenotypic data were obtained by using standardized test methods, the reproducibility of which has been evaluated previously (30–32). Our results (the results of only one test, growth on potato starch, were not found to be completely reproducible for members of the CHY group) further demonstrate the reliability of the protocols which we used. However, caution must be exercised when workers use test methods that differ from those used in this study for differentiating *C. hyointestinalis* isolates from members of the CHY group, since phenotypic test results for campylobacteria may vary significantly between laboratories when different methods are used (30–32).

Since *C. fetus* exhibits considerable phenotypic (12, 13, 23), antigenic (10), genomic (11, 12, 46), and phylogenetic (6, 45, 50) similarity to *C. hyointestinalis*, we included a number of strains (principally identified by genomic methods [34, 49]) of *C. fetus* subsp. *fetus* and *C. fetus* subsp. *venerealis* in the phenotypic analysis to confirm that the CHY group and these taxa are distinct. These three taxa could be clearly distinguished from each other and from other campylobacteria (Table 2 and Fig. 1). Since we performed this study, a new species (*C.*

FIG. 1. Dendrogram based on the results of a cluster analysis of phenotypic data for the strains examined. The numbers on the horizontal axis indicate the levels of similarity as determined by the simple matching coefficient and unweighted pair group average linkage clustering. Phenotypes were formed at a level of similarity of 85%.

hyoilei) has been isolated from porcine intestines and described (1). However, this taxon does not exhibit a significant level of DNA homology to *C. hyointestinalis* and is phenotypically and genotypically most similar to *C. coli* (1). These data strongly suggest that the CHY group and *C. hyoilei* are distinct taxa.

Our observations regarding the different flagellar arrangements of certain CHY group strains are significant for two reasons. It has been suggested that the number of flagella which may be observed in *Campylobacter* species should not be considered an essential taxonomic criterion for this genus (43). Our results support this view, since both mono- and biflagellated cells (of the same general shape and size) were observed in the same culture of strain CHY 6. Therefore, it is reasonable to assume that aflagellate (43) and multiflagellate (8) taxa may belong to the same genus. It is also clear that genetic

change in campylobacters may occur as a result of spontaneous mutation, as well as mechanisms such as natural and plasmid-borne transformation (40). Such changes may help explain the considerable phylogenetic diversity which has been observed in members of the genus *Campylobacter* and related organisms (45).

The DNA base composition values which we determined for three reference strains (including the type strain) of *C. hyointestinalis* were comparable to the values published previously (12, 41). However, the CHY group strains which we examined had lower G+C contents, suggesting that the genomes of these taxa differ. This was confirmed by the DNA homology data (Table 3), which indicated that the CHY group is a well-defined taxon that is affiliated with, but distinct from, *C. hyointestinalis*. These data, in conjunction with the phenotypic data

FIG. 2. Electron micrographs of cells of two *C. hyointestinalis* subsp. *lawsonii* strains showing the range of morphologic variation. Note the slight curvature and biflagellate arrangement of the strain CHY 6 cell (a) and the spiral morphology of the monoflagellate strain CHY 9 cell (b). Bars = 1 μ m.

(this study) and whole-cell protein profile data (28), clearly show that the CHY group is a subspecies of *C. hyointestinalis*, for which we propose the name *C. hyointestinalis* subsp. *lawsonii*. The inclusion of the CHY group isolates in *C. hyointes-*

tinalis justifies emendation of the specific description, as has been done previously for *C. fetus* (49).

Emended description of *Campylobacter hyointestinalis* Gebhart, Edmonds, Ward, Kurtz, and Brenner 1985. Cells are

TABLE 3. DNA base compositions and DNA-DNA hybridization results for *C. hyointestinalis* strains

Taxon	Strain ^a	G+C content (mol%)	% DNA-DNA homology with ^b :						
			LMG 7817 ^T	LMG 8464	LMG 8632	CHY 5 ^T	CHY 6	CHY 7	CHY 8
<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	LMG 7817 ^T	35	100						
	LMG 8464	34	96 $\pm$ 6 ^c	100					
	LMG 8632	34	80 $\pm$ 3		100				
<i>C. hyointestinalis</i> subsp. <i>lawsonii</i>	CHY 5 ^T	32	71 $\pm$ 4			100			
	CHY 6	33				90 $\pm$ 6	100		
	CHY 7	31					88 $\pm$ 4	100	
	CHY 8	33			56 $\pm$ 1	84 $\pm$ 3	90 $\pm$ 1		100

^a LMG, Culture Collection of the Laboratorium voor Mikrobiologie, University of Ghent, Ghent, Belgium; CHY, *C. hyointestinalis*-like strain.

^b Levels of binding were determined in at least two hybridization experiments for each comparison.

^c Mean $\pm$ standard deviation.

non-spore-forming, gram-negative rods (0.2 to 0.5 μm wide and 1.2 to 2.5 μm long) which are curved or loosely helical. Motile by means of a single, unsheathed, polar flagellum. Some cells possess two polar flagella (12; this study). Glucose is not fermented or oxidized. Optimal growth occurs under microaerobic (ca. 5% O_2) conditions; some strains may grow anaerobically (7, 41; this study). No growth occurs in air. The inclusion of blood in the culture medium enhances but is not essential for growth. After 48 h of growth on 5% blood agar at 37°C, colonies are circular, convex, and pinpoint to 2.0 mm in diameter. A greenish color, accompanied by alpha-hemolytic activity, may be apparent in cultures of some strains. All strains grow at 42°C. Oxidase and catalase are produced. Selenite and nitrate are reduced. Hydrolysis of hippurate, indoxyl acetate, and urea does not occur. Hydrogen sulfide is usually produced in triple sugar iron medium. Strains grow in the presence of 1% bile and 0.032% methyl orange; some strains exhibit tolerance to 1.5 and 2.0% bile. Not tolerant to NaCl (>2.0%). All strains are resistant to nalidixic acid (32 mg/liter); most strains are susceptible to cephalothin (32 mg/liter).

Isolated from the intestines and stomachs of pigs, hamster intestines, and the feces of cattle, deer, and humans. Associated with enteritic disorders, but pathogenicity is not known.

The type strain is strain 80-4577-4 (= LMG 7817 = NCTC 11608 = CCUG 14169 = ATCC 35217), which was isolated from the intestine of a pig with proliferative enteritis in Minnesota in 1980. The G+C content of the DNA of this strain is 35 mol% (this study) or 36 mol% (10).

Description of *Campylobacter hyointestinalis* subsp. *hyointestinalis* subsp. nov. *Campylobacter hyointestinalis* subsp. *hyointestinalis* subsp. nov. (hy.o.in.tes' tin.al.is. Gr. n. hyos, hog; M. L. adj. intestinalis, pertaining to the intestines; M. L. gen. n. *hyointestinalis*, pertaining to a hog's intestine). Grows in the presence of 1.0 and 1.5% bile (most strains tolerate 2.0% bile). Other characteristics are the same as the characteristics for the species given above and previously (12).

The DNA base composition ranges from 34 mol% (this study) to 36 mol% (12; this study). Isolated from the intestines of pigs and hamsters, the stomachs of pigs, and cattle, deer, and human feces. May be associated with porcine proliferative enteritis and diarrhea in animals and humans. Pathogenicity is not known.

The type strain is strain 80-4577-4; the characteristics of this strain are described above.

Description of *Campylobacter hyointestinalis* subsp. *lawsonii* subsp. nov. *Campylobacter hyointestinalis* subsp. *lawsonii* subsp. nov. (law. son'ni.i. M.L. gen. n. *lawsonii*, of Lawson, in honor of Gordon H. K. Lawson, a bacteriologist at Edinburgh University whose studies on enteric disease in pigs led to the delineation of *Campylobacter mucosalis* and the unculturable bacterium Ileal symbiont intracellularis). The cells of the seven isolates studied are gram-negative, slightly curved rods or spirals (0.2 μm wide and 1.4 to 2.0 μm long) as determined by light microscopy. Motile in wet preparations by means of one or two polar flagella. Colonies after 3 days of microaerobic growth on 5% calf blood agar are pinpoint to 1 mm in diameter, round, smooth, and slightly raised. All strains produce oxidase, catalase, and hydrogen sulfide in triple sugar iron agar; most (six of seven) strains give strong reactions in triple sugar iron agar under the conditions which we used. Both nitrate and selenite are reduced. All strains grow at 37 and 42°C on 5% blood agar under microaerobic conditions and grow weakly at 37°C anaerobically. All strains grow on unsupplemented nutrient agar and on *Campylobacter* charcoal-deoxycholate (i.e., unsupplemented "Preston" base) medium.

All strains grow in the presence of 1% bile, 0.032% methyl orange, and 32 mg of nalidixic acid per liter.

Not able to hydrolyze hippurate, indoxyl acetate, and urea. Triphenyltetrazolium chloride is not reduced. Does not grow at room temperature (18 to 22°C), at 25°C, or under aerobic conditions on unsupplemented 5% blood agar. Does not grow on media containing 1.5 or 2.0% bile, 2.0, 3.5, or 4.0% NaCl, 0.1% potassium permanganate, 0.05% sodium fluoride, or 0.04% triphenyltetrazolium chloride. Pitting of agar media does not occur. All isolates are asaccharolytic.

Of the seven strains tested, CHY 8 and CHY 9 are alpha-hemolytic and the growth is a greenish color. CHY 6 produces alkaline phosphatase. Tolerance to 1% glycine medium is exhibited by CHY 5^T and CHY 9, while CHY 3, CHY 4, CHY 6, and CHY 7 are tolerant to 0.0005% crystal violet. Although all strains initially grew on potato starch medium, CHY 3 and CHY 7 gave negative results when they were retested.

The DNA base composition ranges from 31 to 33 mol%. So far, strains have been isolated only from the stomachs of pigs. Pathogenicity is not known.

The type strain is strain CHY 5 (= LMG 14432 = NCTC 12901 = CCUG 34538); its characteristics are the same as the characteristics given in the description above, and the G+C content of its DNA is 32 mol%.

The phenotypic (7, 13; this study), antigenic (2), protein electrophoretic (28, 46, 47), genomic (2, 12), and phylogenetic (6, 50) diversity of *C. hyointestinalis* strains, especially the bovine and porcine strains, has been described previously. The presence of this species in stomach tissue is a more recent finding (28) and is significant since organisms such as *Helicobacter pylori* are more commonly associated with the colonization of this region (33). Although no pathological data were available for the strains of *C. hyointestinalis* subsp. *lawsonii* that we studied, cases of human gastritis associated with infection with another campylobacter (*Campylobacter jejuni* subsp. *doylei*) have been recorded (37). Additional studies will be required to establish the significance and prevalence of these campylobacters in animal stomachs. However, the data indicate that the presence of spiral organisms in gastric tissue does not always indicate infection with *H. pylori* or similar helicobacters.

The lack of standardization in phenotypic testing makes it difficult to determine if strains of *C. hyointestinalis* subsp. *lawsonii* have been isolated previously. Certain pig strains defined as *C. hyointestinalis* (12, 21) failed to grow in 1% glycine medium, a trait common to most (five of seven) of our isolates. Ursing et al. (41) described five strains isolated from cattle and pigs which they felt were distinct from *C. hyointestinalis*. However, two of these strains (CCUG 14915 and CCUG 14916) exhibited close affinity to the type strain of *C. hyointestinalis* when numerical analyses of protein profiles (28, 46, 47) and phenotypic tests (this study) were performed. Gebhart et al. (12) described two porcine strains of *C. hyointestinalis* which exhibited relatively low DNA binding values (<63%) with the type strain. However, one of these strains (81-13037) closely resembled the type strain of *C. hyointestinalis* when numerical analyses of protein profiles were performed (28, 46, 47). Despite these conflicting data, *C. hyointestinalis* is clearly an ecologically, phenotypically, and genomically diverse species, and the delineation of further subspecific taxa remains a distinct possibility.

ACKNOWLEDGMENTS

We thank E. Falsen (University of Göteborg, Göteborg, Sweden), D. E. Taylor (University of Alberta, Edmonton, Alberta, Canada), and M. M. Garcia (Animal Disease Research Institute, Canada) for kindly

providing strains and K. Möller and P. Astrup for secretarial assistance.

P.V. is indebted to the National Fund for Scientific Research (Belgium) for a position as a senior research assistant.

REFERENCES

- Alderton, M. R., V. Korolik, P. J. Coloe, F. E. Dewhirst, and B. J. Paster. 1995. *Campylobacter hyoilei* sp. nov., associated with porcine proliferative enteritis. *Int. J. Syst. Bacteriol.* **45**:61–66.
- Bryner, J. H., and I. V. Wesley. 1987. Analysis of *Campylobacter hyointestinalis* isolates by antigenic and genomic relationships, p. 101. In *Abstracts of the Annual Meeting of the American Society for Microbiology 1987*. American Society for Microbiology, Washington, D.C.
- Cowan, S. T. 1974. *Cowan & Steel's manual for the identification of medical bacteria*, 2nd ed. Cambridge University Press, London.
- De Ley, J. 1970. Reexamination of the association between melting point, buoyant density, and chemical base composition of deoxyribonucleic acid. *J. Bacteriol.* **101**:738–754.
- De Ley, J., H. Cattoir, and A. Reynaerts. 1970. The quantitative measurement of DNA hybridization from renaturation rates. *Eur. J. Biochem.* **12**: 133–142.
- Dewhirst, F. E., B. J. Paster, G. J. Fraser, and I. Olsen. 1992. Phylogeny of 9 major groups of eubacteria based on 16S rRNA sequence comparisons, p. 6. In *Proceedings of the Conference on Taxonomy and Automated Identification of Bacteria*. Czechoslovak Society for Microbiology, Prague, Czech Republic.
- Edmonds, P., C. M. Patton, P. M. Griffin, T. J. Barrett, G. P. Schmid, C. N. Baker, M. A. Lambert, and D. J. Brenner. 1987. *Campylobacter hyointestinalis* associated with human gastrointestinal disease in the United States. *J. Clin. Microbiol.* **25**:685–691.
- Etoh, Y., F. E. Dewhirst, B. J. Paster, A. Yamamoto, and N. Goto. 1993. *Campylobacter showae* sp. nov., isolated from the human oral cavity. *Int. J. Syst. Bacteriol.* **43**:631–639.
- Etoh, Y., M. Takahashi, and A. Yamamoto. 1988. *Wolinella curva* subsp. *intermedius* subsp. nov.: isolated from human gingival crevice. *J. Showa Univ. Dent. Soc.* **8**:349–354.
- Falsen, E., L. Nehls, and A. Börjesson. 1988. Immunotyping campylobacters. Taxonomic implications, p. 56–59. In B. Kaijser and E. Falsen (ed.), *Campylobacter IV*. Proceedings of the Fourth International Workshop on *Campylobacter* Infections. University of Göteborg, Göteborg, Sweden.
- Fennell, C. L., A. M. Rompalo, P. A. Totten, K. L. Bruch, B. M. Flores, and W. E. Stamm. 1986. Isolation of "*Campylobacter hyointestinalis*" from a human. *J. Clin. Microbiol.* **24**:146–148.
- Gebhart, C. J., P. Edmonds, G. E. Ward, H. J. Kurtz, and D. J. Brenner. 1985. "*Campylobacter hyointestinalis*" sp. nov.: a new species of *Campylobacter* found in the intestines of pigs and other animals. *J. Clin. Microbiol.* **21**:715–720.
- Gebhart, C. J., G. E. Ward, K. Chang, and H. J. Kurtz. 1983. *Campylobacter hyointestinalis* (new species) isolated from swine with lesions of proliferative enteritis. *Am. J. Vet. Res.* **44**:361–367.
- Gebhart, C. J., G. E. Ward, and P. Murtaugh. 1989. Species-specific cloned DNA probes for the identification of *Campylobacter hyointestinalis*. *J. Clin. Microbiol.* **27**:2717–2723.
- Goodwin, C. S., J. A. Armstrong, T. Chilvers, M. Peters, M. D. Collins, L. Sly, W. McConnell, and W. E. S. Harper. 1989. Transfer of *Campylobacter pylori* and *Campylobacter mustelae* to *Helicobacter* gen. nov. as *Helicobacter pylori* comb. nov. and *Helicobacter mustelae* comb. nov., respectively. *Int. J. Syst. Bacteriol.* **39**:397–405.
- Hill, B. D., R. J. Thomas, and A. R. Mackenzie. 1987. *Campylobacter hyointestinalis*-associated enteritis in Moluccan rusa deer. *J. Comp. Pathol.* **97**: 687–694.
- Holmes, B., S. L. W. On, M. Ganner, and M. Costas. 1992. Some new applications of probabilistic identification, p. 6–9. In *Proceedings of the Conference on Taxonomy and Automated Identification of Bacteria*. Czechoslovak Society for Microbiology, Prague, Czech Republic.
- Hudson, M. J., P. Bhavsar, and R. Wait. 1988. Chemotaxonomy of the campylobacters, p. 34–36. In B. Kaijser and E. Falsen (ed.), *Campylobacter IV*. Proceedings of the Fourth International Workshop on *Campylobacter* Infections. University of Göteborg, Göteborg, Sweden.
- Kerstens, K., and J. De Ley. 1980. Classification and identification of bacteria by electrophoresis of their proteins. *Soc. Appl. Bacteriol. Symp. Ser.* **8**:273–297.
- Laanbroek, H. J., W. Kingma, and H. Veldkamp. 1977. Isolation of an aspartate-fermenting, free-living *Campylobacter* species. *FEMS Microbiol. Lett.* **1**:99–102.
- Lambert, M., J. M. W. Jones, and S. A. Lister. 1984. Isolation of *Campylobacter hyointestinalis* from pigs in the United Kingdom. *Vet. Rec.* **115**:128–129.
- Lastovica, A., E. Le Roux, R. Warren, and H. Klump. 1993. Clinical isolates of *Campylobacter mucosalis*. *J. Clin. Microbiol.* **31**:2835–2836. (Letter.)
- Minet, J., B. Grosbois, and F. Megraud. 1988. *Campylobacter hyointestinalis*: an opportunistic enteropathogen? *J. Clin. Microbiol.* **26**:2659–2660.
- Moss, C. W., M. A. Lambert-Fair, M. A. Nicholson, and G. O. Guerrant. 1990. Isoprenoid quinones of *Campylobacter cryaerophila*, *C. cinaedi*, *C. fennelliae*, *C. hyointestinalis*, *C. pylori*, and "*C. upsaliensis*." *J. Clin. Microbiol.* **28**:395–397.
- On, S. L. W. 1994. Confirmation of human *Campylobacter concisus* isolates misidentified as *Campylobacter mucosalis* and suggestions for improved differentiation between the two species. *J. Clin. Microbiol.* **32**:2305–2306.
- On, S. L. W. 1994. Ph.D. thesis. The Open University, London, England.
- On, S. L. W. Unpublished data.
- On, S. L. W., M. Costas, and B. Holmes. 1993. Identification and intra-species heterogeneity of *Campylobacter hyointestinalis* using numerical analysis of one-dimensional SDS-PAGE protein profiles. *Syst. Appl. Microbiol.* **16**:37–46.
- On, S. L. W., M. Costas, and B. Holmes. 1994. Classification and identification of *Campylobacter sputorum* using numerical analyses of phenotypic tests and of one-dimensional electrophoretic protein profiles. *Syst. Appl. Microbiol.* **17**:543–553.
- On, S. L. W., and B. Holmes. 1991. Effect of inoculum size on the phenotypic characterization of *Campylobacter* species. *J. Clin. Microbiol.* **29**:923–926.
- On, S. L. W., and B. Holmes. 1991. Reproducibility of tolerance tests that are useful in the identification of campylobacteria. *J. Clin. Microbiol.* **29**:1785–1788.
- On, S. L. W., and B. Holmes. 1992. Assessment of enzyme detection tests useful in identification of campylobacteria. *J. Clin. Microbiol.* **30**:746–749.
- Penner, J. L. 1988. The genus *Campylobacter*: a decade of progress. *Clin. Microbiol. Rev.* **1**:157–172.
- Salama, S. M., M. M. Garcia, and D. E. Taylor. 1992. Differentiation of the subspecies of *Campylobacter fetus* by genomic sizing. *Int. J. Syst. Bacteriol.* **42**:446–450.
- Sebald, M., and M. Véron. 1963. Teneur en bases de l'ADN et classification des vibrios. *Ann. Inst. Pasteur* **105**:897–910.
- Stackebrandt, E. 1992. Unifying phylogeny and phenotypic diversity, p. 19–46. In A. Balows, H. G. Trüper, M. Dworkin, W. Harder, and K. H. Schleifer (ed.), *The prokaryotes*, 2nd ed. Springer-Verlag, New York.
- Steele, T. W., and R. J. Owen. 1988. *Campylobacter jejuni* subsp. *doylei* subsp. nov., a subspecies of nitrate-negative campylobacters isolated from human clinical specimens. *Int. J. Syst. Bacteriol.* **38**:316–318.
- Tanner, A. C. R., S. Badger, C.-H. Lai, M. A. Listgarten, R. A. Visconti, and S. S. Socransky. 1981. *Wolinella* gen. nov., *Wolinella succinogenes* (*Vibrio succinogenes* Wolin et al.) comb. nov., and description of *Bacteroides gracilis* sp. nov., *Wolinella recta* sp. nov., *Campylobacter concisus* sp. nov., and *Eikenella corrodens*, all from humans with periodontal disease. *Int. J. Syst. Bacteriol.* **31**:432–445.
- Tanner, A. C. R., M. A. Listgarten, and J. L. Ebersole. 1984. *Wolinella curva* sp. nov.: "*Vibrio succinogenes*" of human origin. *Int. J. Syst. Bacteriol.* **34**: 275–282.
- Taylor, D. E. 1992. Genetics of *Campylobacter* and *Helicobacter*. *Annu. Rev. Microbiol.* **46**:35–64.
- Ursing, J., K. Sandstedt, and E. Hansson. 1984. Genetic and phenotypic characteristics of a new group of *Campylobacter* isolated from pigs and cattle. *Acta Pathol. Microbiol. Immunol. Scand. Sect. B Microbiol.* **91**:71–72.
- Ursing, J. B., H. Lior, and R. J. Owen. 1994. Proposal of minimal standards for describing new species of the family *Campylobacteraceae*. *Int. J. Syst. Bacteriol.* **44**:842–845.
- Vandamme, P., M. I. Daneshvar, F. E. Dewhirst, B. J. Paster, K. Kersters, H. Goossens, and C. W. Moss. 1995. Chemotaxonomic analyses of *Bacteroides gracilis* and *Bacteroides ureolyticus* and reclassification of *B. gracilis* as *Campylobacter gracilis* comb. nov. *Int. J. Syst. Bacteriol.* **45**:145–152.
- Vandamme, P., and J. De Ley. 1991. Proposal for a new family, *Campylobacteraceae*. *Int. J. Syst. Bacteriol.* **41**:451–455.
- Vandamme, P., E. Falsen, R. Rossau, B. Hoste, P. Segers, R. Tytgat, and J. De Ley. 1991. Revision of *Campylobacter*, *Helicobacter*, and *Wolinella* taxonomy: emendation of generic descriptions and proposal of *Arcobacter* gen. nov. *Int. J. Syst. Bacteriol.* **41**:88–103.
- Vandamme, P., B. Pot, E. Falsen, K. Kersters, and J. De Ley. 1990. Intra- and interspecific relationships of veterinary campylobacters revealed by numerical analysis of electrophoretic protein profiles and DNA:DNA hybridizations. *Syst. Appl. Microbiol.* **13**:295–303.
- Vandamme, P., B. Pot, and K. Kersters. 1991. Differentiation of campylobacters and *Campylobacter*-like organisms by numerical analysis of one-dimensional electrophoretic protein patterns. *Syst. Appl. Microbiol.* **14**:57–66.
- Vandamme, P., M. Vancanneyt, B. Pot, L. Mels, B. Hoste, D. Dewettinck, L. Vlaes, C. Van Den Borre, R. Higgins, J. Hommez, K. Kersters, J.-P. Butzler, and H. Goossens. 1992. Polyphasic taxonomic study of the emended genus *Arcobacter* with *Arcobacter butzleri* comb. nov. and *Arcobacter skirrowii* sp. nov., an aerotolerant bacterium isolated from veterinary specimens. *Int. J. Syst. Bacteriol.* **42**:344–356.
- Véron, M., and R. Chatelain. 1973. Taxonomic study of the genus *Campylobacter* Sebald and Véron and designation of the neotype strain for the type species, *Campylobacter fetus* (Smith and Taylor) Sebald and Véron. *Int. J. Syst. Bacteriol.* **23**:122–134.
- Wesley, I. V., R. D. Wesley, M. Cardella, F. E. Dewhirst, and B. J. Paster. 1991. Oligodeoxynucleotide probes for *Campylobacter fetus* and *Campylobacter hyointestinalis* based on 16S rRNA sequences. *J. Clin. Microbiol.* **29**:1812–1817.