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Biochemical and Genetic Characteristics of Atypical *Campylobacter fetus* subsp. *fetus* Strains Isolated from Humans in the United States

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During a 2-year period, 14 biochemically atypical *Campylobacter fetus* subsp. *fetus*-like strains were received by the *Campylobacter* Reference Laboratory at the Centers for Disease Control. Sources of the isolates were blood, nine strains; stools, two strains; amniotic fluid, one strain; and abscesses, two strains. Atypical phenotypic characteristics exhibited by one or more strains were growth at 42°C, 10 strains; no H_2S by lead acetate paper, 3 strains; resistance to a 30-μg cephalothin disk, 2 strains; and nonmotility, 1 strain. By DNA-DNA hybridization, all 14 isolates and the type strain of *C. fetus* subsp. *fetus* (ATCC 27374) were 94 to 100% related in reassociation reactions at 50°C, with 0.0 to 0.5% divergence, and were 86 to 100% related in reassociation reactions at 65°C. Thus, all of these atypical strains were *C. fetus* subsp. *fetus*. MICs of 11 antimicrobial agents for these 14 strains were variable. All strains were susceptible to chloramphenicol, erythromycin, gentamicin, and tetracycline, and most were susceptible to ampicillin, clindamycin, and penicillin. Eleven strains were resistant to cephalothin (MIC ≥ 16 μg/ml), nine were resistant to rifampin (MIC ≥ 8 μg/ml), and all were resistant to nalidixic acid (MIC > 32 μg/ml) and vancomycin (MIC > 32 μg/ml). One can expect to see biochemical variability in *C. fetus* subsp. *fetus* strains and to encounter such strains from a variety of human sources, the most important of which appears to be blood.

The genus *Campylobacter* (24) contains gram-negative, slender, spirally curved rods that require a microaerophilic or anaerobic environment for growth. These bacteria have a respiratory type of metabolism. They do not ferment or oxidize carbohydrates, but obtain energy from amino acids or tricarboxylic acid cycle intermediates. Thus, very few biochemical tests are useful for differentiating *Campylobacter* species. One differential character is growth response at temperatures between 25 and 43°C. The species that grow at 42 to 43°C are commonly referred to as thermophilic (1, 15, 26) or thermotolerant (31) campylobacters. These terms are used interchangeably in the literature. *C. jejuni*, *C. coli*, and *C. laridis* grow at 35 to 37°C and 42 to 43°C, but not at 25°C. These species, especially *C. jejuni*, are important pathogens because they cause gastrointestinal disease in humans (2, 23, 24). In contrast, most strains of *C. fetus* subsp. *fetus* grow well at 25°C and at 35 to 37°C, but usually not at 42 to 43°C (23–25). *C. fetus* subsp. *fetus* is generally recognized as an opportunist species that causes abortion in cattle and sheep and systemic diseases in humans, but recent studies provide evidence that these bacteria may also cause human gastrointestinal disorders (7, 11, 19; B. S. Klein, personal communication) and human abortion or premature labor with septicemia in neonates (6).

We have received in the *Campylobacter* Reference Laboratory at the Centers for Disease Control 14 strains resembling *C. fetus* subsp. *fetus* but having atypical phenotypic characteristics that make them difficult to identify. Reactions considered to be atypical when compared with those for the type strain of *C. fetus* subsp. *fetus* were growth at 42°C, 10 strains; no H_2S with lead acetate paper, 3 strains; resistance to cephalothin, 2 strains; and nonmotility, 1 strain. These strains were all isolated from human clinical specimens. In this report we present data to biochemically and genetically characterize these strains as *C. fetus* subsp. *fetus*.

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MATERIALS AND METHODS

***C. fetus* subsp. *fetus* strains.** The 14 strains used in this study were isolated from multiple clinical sources, but most were from extraintestinal sources, usually blood (Table 1). One of the strains was associated with a patient with diarrheal disease, two were associated with patients with both intestinal and extraintestinal disease, nine were associated with patients with only extraintestinal disease, and for two strains (one patient) the disease was not known. All strains were received at the Centers for Disease Control in 1982 and 1983. They were from 11 different U.S. states, Washington, D. C., and Chile.

Biochemical characterization. All strains were incubated in an atmosphere of about 5% oxygen, 10% carbon dioxide, and 85% nitrogen for 48 h at 36°C on heart infusion agar containing 5% defibrinated rabbit blood (HIA-RB). The inoculum for biochemical tests was growth harvested from the HIA-RB plates, suspended in heart infusion broth, and adjusted to a McFarland no. 1 standard turbidity.

Biochemical test results were read after the *Campylobacter* strains were incubated for 3 days, unless specified otherwise. Temperature tolerance at 25, 36, and 42°C was tested on HIA-RB plates by making a single streak with a loopful of suspension across the plates. Naladixic acid and cephalothin disks (30 μg) were placed on each end of the streak of inoculum on the 36°C plate to test for susceptibility to these antibiotics (12). The isolate was considered susceptible if there was any zone of inhibition. The oxidase test was performed by spreading a loopful of 24- or 72-h growth on an area of filter paper moistened with a drop of oxidase reagent (14). Development of purple within 10 s was read as positive. For the catalase test, 2 or 3 drops of 3% H_2O_2 was added to 24- or 72-h growth of the strains on an HIA slant. The appearance of bubbles was considered positive, and the intensity of the reaction was recorded as 1+ through 4+. Strains were tested for growth in an aerobic atmosphere at 36°C on HIA. Nitrate reduction was tested in nitrate broth

TABLE 1. Description of bacterial strains

CDC strain no.[a]	Year received	Geographical source	Clinical source	Disease
D52	1982	Alabama	Groin abscess	Postsurgical abscess
D223	1982	West Virginia	Amniotic fluid	Postabortion infection
D231	1982	Idaho	Blood and exudate	Hemiparesis and aphasia
D233	1983	Indiana	Stool	Cystic fibrosis and diarrhea
D381	1983	Mississippi	Blood	Fever of unknown origin
D383[b]	1983	Georgia	Blood	Unknown
D384[b]	1983	Georgia	Stool	Unknown
D402	1983	Connecticut	Blood	Surgical fever
D406	1983	Chile	Blood	Sepsis
D411	1983	Texas	Blood	Immune deficiency disease
D412	1983	Virginia	Blood	Diarrhea, vomiting, abdominal pain, fever
D417	1983	Wisconsin	Blood	Fever, chills, endocarditis
D443	1983	Washington, D.C.	Blood and cerebrospinal fluid	Sepsis, encephalitis, fever, myalgia
D1104	1983	Oregon	Ankle abscess	Cellulitis and diarrhea

[a] CDC, Centers for Disease Control.
[b] These two isolates were from the same patient but are phenotypically different.

prepared with heart infusion broth (Difco Laboratories, Inc., Detroit, Mich.) basal medium (32). Production of H_2S was tested in triple sugar iron agar slants and also with a lead acetate strip over brucella albimi broth (GIBCO Laboratories, Grand Island, N.Y.) which contained 0.16% agar and 0.02% cysteine hydrochloride. Strains were tested for growth in brucella albimi semisolid medium (0.16% agar containing either 1% glycine or 3.5% NaCl). The ability of the cells to metabolize glucose by oxidation or fermentation was tested in oxidation-fermentation medium for nonfermenting gram-negative bacilli (32) and in fermentation-carbohydrate base containing 1% glucose (32). A rapid hippurate hydrolysis test was used and is described elsewhere (16). Strains were examined microscopically by dark-field illumination for cellular morphology and motility and also by flagellum stain (13) for location and number of flagella.

Antimicrobial susceptibility. The strains were tested for susceptibility to 11 antimicrobial agents by a broth microdilution MIC procedure (29) with incubation at 35 to 37°C in an atmosphere of 5% oxygen, 10% carbon dioxide, and 85% nitrogen for 48 h.

DNA hybridization. To obtain large yields of cells, each strain was subcultured to 20 to 25 HIA-RB plates (150 by 15 mm) and incubated for 24 h at 35 to 37°C in an atmosphere of 5% oxygen, 10% carbon dioxide, and 85% nitrogen. Cells were harvested and lysed, and the DNA was extracted, purified, and tested for relatedness by a previously described hydroxyapatite method (5). DNA from one clinical isolate (D406) was labeled in vitro with $^{32}PO_4$ by using commercial nick translation reagents (Bethesda Research Laboratories, Inc., Gaithersburg, Md.) and tested for relatedness to unlabeled DNA from the same strain (homologous reaction) and to unlabeled DNA from each of the other clinical isolates and the type or reference strains (heterologous reactions). Since DNAs from *Campylobacter* species have a low moles percent guanine plus cytosine (18), reassociation reactions were done at 50°C (optimal) and 65°C (stringent). DNA relatedness was expressed as the relative binding ratio (RBR): RBR = (percent heterologous DNA bound to hydroxyapatite/percent homologous DNA bound to hydroxyapatite) × 100. Divergence is the amount of unpaired bases within related DNA sequences and was calculated on the assumption that each decrease of 1°C in the thermal stability of a heterologous DNA duplex, compared with that of the homologous DNA duplex, is caused by approximately 1% of unpaired bases (3, 5). Divergence was calculated to the nearest 0.5%. Labeled DNA was incubated in the absence of unlabeled DNA to serve as a control for nonspecific binding of DNA to hydroxyapatite in each experiment. The control value was subtracted before relatedness was calculated. Each relative binding ratio is the mean of two separate experiments.

RESULTS

Phenotypic characteristics. Results of differential tests with type strains of various *Campylobacter* species and the 14 test strains are shown in Table 2. All clinical strains were microaerophilic, gram-negative, curved or spiral rods that grew at 25 and 36°C, and phenotypically most strains closely resembled *C. fetus* subsp. *fetus*. This subspecies differs from *C. fetus* subsp. *venerealis* by its tolerance to 1% glycine. Reactions of the 14 test strains that differed from those considered typical for *C. fetus* subsp. *fetus* were growth at 42°C, 10 strains; no H_2S with lead acetate paper, 3 strains; resistance to cephalothin, 2 strains; and nonmotility, one strain. The two strains from different sites in the same patient differed in that one was resistant to cephalothin. On the basis of the key phenotypic criteria (i.e., catalase positivity, growth at 25°C, no H_2S in triple sugar iron agar, and tolerance to 1% glycine), all 14 strains were closest to *C. fetus* subsp. *fetus*, even though the reactions of each of the isolates deviated in one or more tests from the reactions of the *C. fetus* subsp. *fetus* type strain.

DNA hybridization. DNA relatedness values for the 14 clinical strains and for representative *Campylobacter* type and reference strains are shown in Table 3. Labeled DNA from the clinical strain D406 was 94 to 100% related to all clinical strains in reassociation reactions at 50°C, with 0.0 to 0.5% divergence, and was 86 to 100% related in reassociation reactions at 65°C, a stringent temperature at which only closely related *Campylobacter* DNA sequences can reassociate. Labeled DNA from strain D406 was 94% related to the type strain of *C. fetus* subsp. *fetus* ATCC 27374 at 50°C and 100% related at 65°C, and was 6 to 12% related to type and reference strains of other *Campylobacter* species in reactions at 50°C. Thus, all 14 atypical strains are *C. fetus* subsp. *fetus*.

Antimicrobial susceptibility. The MICs for the 14 strains of

TABLE 2. Phenotypic characteristics of *Campylobacter* species

Strain	Growth conditions: Atmosphere: Aerobic	Atmosphere: 5% Oxygen	Atmosphere: Anaerobic[b]	Temp (°C): 25	Temp (°C): 35	Temp (°C): 42	Biochemicals[a]: Catalase production	Nitrate reaction	Test for H_2S on: Oxidase	Test for H_2S on: TSI	Tolerance to: Pb-Ac	Tolerance to: 1% Glycine	Tolerance to: 3.5% NaCl	Nalidixic acid	Cephalothin	Hippurate hydrolysis	Motility	Gram reaction	Glucose O/F
C. jejuni NCTC 11351	−	+	−	−	+	+	+	+	+	−	+	+	−	S	R	+	+	−	−/−
C. coli NCTC 11366	−	+	−	−	+	+	+	+	+	−	+	+	−	S	R	−	+	−	−/−
C. laridis NCTC 11352	−	+	−	−	+	+	+	+	+	−	+	+	−	R	R	−	+	−	−/−
C. fetus subsp. *fetus* ATCC 27374	−	+	+(w)[c]	+	+	+[d]	+	+	+	−	+	+	−	R	S	−	+	−	−/−
C. fetus subsp. *venerealis* ATCC 19438[e]	−	+	+	+	+	−	+	+	+	−	+(w)	−	−	R	S	−	+	−	−/−
"*C. fecalis*" NCTC 11415	−	+(w)	+(w)	+	+	+	+	+	+	+	+	+	+	R	S	−		−	−/−
C. sputorum subsp. *mucosalis* NCTC 11000[b]	−	−	+	+	+	+	−	+	+	+	+	−	−	S	S	−	+	−	−/−
"*C. hyointestinalis*" ATCC 35217[f]	−	+	+	+(w)	+	+	+	+	+	+	+	+	−	R	S	−	+	−	−/−
D52	−	+	+(w)	+	+	−	+	+	+	−	+(w)	+	−	R	R	−	+	−	−/−
D223	−	+	+(w)	+	+	−	+	+	+	−	+(w)	+	−	R	S	−	+	−	−/−
D231	−	+	+(w)	+	+	+	+	+	+	−	+(w)	+	−	R	S	−	+	−	−/−
D233	−	+	+(w)	+	+	+	+	+	+	−	+(w)	+	−	R	S	−	+	−	−/−
D381	−	+	+(w)	+	+	+	+	+	−	−	−	+	−	R	S	−	+	−	−/−
D383	−	+	+(w)	+	+	−	+	+	+	−	−	+	−	R	R	−	+	−	−/−
D384	−	+	+(w)	+	+	−	+	+	+	−	−	+	−	R	S	−	+	−	−/−
D402	−	+	+(w)	+	+	+	+	+	+	−	+(w)	+	−	R	S	−	−[g]	−	−/−
D406	−	+	+(w)	+	+	+	+	+	+	−	+(w)	+	−	R	S	−	+	−	−/−
D411	−	+	+(w)	+	+	+	+	+	+	−	+(w)	+	−	R	S	−	+	−	−/−
D412	−	+	+(w)	+	+	+	+	+	+	−	+(w)	+	−	R	S	−	+	−	−/−
D417	−	+	+(w)	+	+	+	+	+	+	−	+(w)	+	−	R	S	−	+	−	−/−
D443	−	+	+(w)	+	+	+	+	+	+	−	+(w)	+	−	R	S	−	+	−	−/−
D1104	−	+	+(w)	+	+	+	+	+	+	−	+(w)	+	−	R	S	−	+	−	−/−

[a] Abbreviations: TSI, triple sugar iron agar; PB-Ac, lead acetate; O/F, oxidation/fermentation; S, susceptible; R, resistant.
[b] Incubated anaerobically in a GasPak jar.
[c] w, Weak reaction or poor growth.
[d] Under the conditions used in this study, this strain grows at 42°C.
[e] From reference 24.
[f] From reference 8.
[g] Nonmotile, no flagella.

C. fetus subsp. *fetus* are summarized in Table 4. All strains were susceptible to chloramphenicol, erythromycin, gentamicin, and tetracycline. Most strains were susceptible to ampicillin, clindamycin, and penicillin. However, these strains exhibited a high degree of resistance to the other antimicrobial agents. Eleven strains were resistant to cephalothin (MIC $\geq$ 16 μg/ml), nine were resistant to rifampin (MIC $\geq$ 8 μg/ml), and all were resistant to nalidixic acid (MIC > 32 μg/ml) and vancomycin (MIC > 32 μg/ml).

DISCUSSION

The 14 strains were primarily from extraintestinal sources, and most were probably opportunistic pathogens. Blood was the most common clinical source, but some strains were associated with diarrheal disease. Although all of the strains differed from the type strain of *C. fetus* subsp. *fetus* in one or more tests, they could be identified phenotypically. Of the extraintestinal *Campylobacter* infections reported (9, 22, 30), the clinical source of the strain was most often blood, and most cases were attributed to *C. fetus* subsp. *fetus*.

The clinical isolates of *C. fetus* subsp. *fetus* used in this study are phenotypically more similar to *C. fetus* subsp. *venerealis* (24) and "*Campylobacter hyointestinalis*" (8) than to other microaerophilic, catalase- and oxidase-positive campylobacters. Although *C. fetus* subsp. *fetus* and *C. fetus* subsp. *venerealis* cannot be differentiated genetically (10, 18; H. Kodaka, L. C. Hagler, and D. J. Brenner, unpublished data), they are separable on the basis of their glycine reaction (positive for *C. fetus* subsp. *fetus* and negative for *C. fetus* subsp. *venerealis*). Because very few biochemical tests are useful for differentiating *Campylobacter* species, and because phenotypic characteristics reflect the expression of genes from only a small portion of the DNA of an organism, we identified these atypical *C. fetus* subsp. *fetus* strains by DNA-DNA hybridization, which is a measure of shared nucleotide sequences throughout the entire bacterial genome (3–5). On the basis of DNA relatedness, strains of the same species are 70% or more related in reactions at an optimal reassociation temperature, with less than 6% divergence in related sequences, and are 55% or more related in reactions at the stringent reassociation temperature (3–5).

By applying these criteria, we demonstrated conclusively that all 14 of the clinical isolates are strains of *C. fetus* (Table 3).

Some strains of *C. fetus* subsp. *fetus* are known to grow at both 25°C and 42 to 43°C, but this capability is considered to be atypical when compared with the type strain (24). Although growth at 25°C appear to be a consistent differential characteristic, reports of variability in the ability of *C. fetus* subsp. *fetus* to grow at 42 to 43°C are increasing (7, 11, 19, 21, 25). Ten of the 14 strains included in this study grew at 42 to 43°C and were reported as thermotolerant *C. fetus* subsp. *fetus*. Only a few reports have implicated thermotolerant strains of *C. fetus* subsp. *fetus* as etiological agents of human disease, and rarely have such strains been isolated from patient stool specimens (7, 11, 19). In each of those studies, *C. fetus* subsp. *fetus* was recovered from stools by using a cephalothin-free medium. Recently, thermotolerant *C. fetus* subsp. *fetus*, in addition to *C. jejuni*, was isolated from stools of patients after the consumption of raw milk in a common-source outbreak of *Campylobacter* gastroenteritis in Wisconsin (B. S. Klein, personal communication). Such strains have also been isolated from stools of homosexual males (7) and from stools of patients in sporadic cases of gastrointestinal diseases (11).

These *C. fetus* subsp. *fetus* strains were all resistant to nalidixic acid and vancomycin. None were resistant to erythromycin, the drug of choice for treating human infections caused by *Campylobacter* species (24), and none were resistant to tetracycline. Plasmid-mediated resistance to tetracycline has been detected in clinical strains of *C. jejuni*, and such plasmids were demonstrated to be transmissible to the type strain of *C. fetus* subsp. *fetus* (27). Although 11 of the strains studied were resistant to cephalothin (Table 4), these MICs should not be compared with susceptibility data shown in Table 2, which was obtained by using the cephalothin-impregnated disk. The disk method of susceptibility testing is extremely valuable as an identification aid for differentiating *C. jejuni* from *C. fetus* subsp. *fetus* (12) but is not reliable for detecting drug resistance in campylobacters (20).

Our data show that *C. fetus* subsp. *fetus* strains are biochemically variable. Strains atypical in reactions for growth at 42°C, no H_2S with lead acetate paper, and resistance to cephalothin were shown to be genetically typical *C. fetus*. The definition of *C. fetus* must therefore be expanded to include variability in susceptibility to the 30-μg cephalothin disk.

TABLE 3. DNA relatedness of 14 atypical clinical strains of *C. fetus* subsp. *fetus* to respresentative *Capylobacter* type and reference strains[a]

Source of unlabeled DNA	Relatedness to $^{32}PO_4$-labeled DNA from strain D406		
	RBR, 50°C	% D	RBR, 65°C
Clinical strains			
D406	100	0.0	100
D233	100	0.5	88
D384[b]	100	0.5	86
D402	100	0.5	96
D412	100	0.5	90
D381	99	0.0	100
D223	99	0.0	97
D417	98	0.0	94
D411	98	0.5	92
D231	97	0.0	100
D52	97	0.5	94
D443	95	0.5	100
D383[b]	95	0.0	88
D1104	94	0.5	94
Type and reference strains			
C. fetus supsp. *fetus* ATCC 27374	94	1.0	100
"*C. hyointestinalis*" ATCC 35217[c]	30	8.0	14
"*C. fecalis*" NCTC 11415	12		
C jejuni NCTC 11351	10		
C. laridis NCTC 11352	10		
C. sputorum subsp. *mucosalis* NCTC 11000	10		
C. coli NCTC 11366	6		

[a] Abbreviations: RBR, relative binding ratio; D, divergence; ATCC, American Type Culture Collection, Rockville, Md.; NCTC, National Collection of Type Cultures, Colindale, London, England.
[b] Strains from different sites in the same patient.
[c] Data are from reference 8 in reactions with $^{32}PO_4$-labeled DNA from "*C. hyointestinalis*" and *C. fetus* subsp. *fetus* ATCC 27374.

TABLE 4. Susceptibility patterns for clinical isolates of *C. fetus* subsp. *fetus*

Antimicrobial agent	No. of isolates with MIC (μg/ml) of:								MIC (μg/ml)[a] breakpoint for resistant isolates
	≤0.25	≤0.5	1	2	4	≥8	≥16	>32	
Ampicillin		1		2	10		1		>16
Cephalothin			1			2	11		>16
Chloramphenicol				1	7	6			>16
Clindamycin			6	7	1				>4
Erythromycin			9	5					>4
Gentamicin	13	1							>8
Nalidixic acid								14	>16
Penicillin		1			2	8	3		>16
Rifampin				5		9			>4[b]
Vancomycin								14	>16
Tetracycline	2	8		4					>8

[a] From reference 17.
[b] From reference 28.

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