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Description of *Campylobacter laridis*, a New Species Comprising the Nalidixic Acid Resistant Thermophilic *Campylobacter* (NARTC) Group

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Abstract. Ten strains of the nalidixic acid-resistant thermophilic *Campylobacter* (NARTC) group, of which 2 were isolated from human feces, were compared with 12 reference strains representing various species of *Campylobacter*. The NARTC strains were a homogeneous group with respect to their cell morphology and 28 physiological and biochemical characters. All were microaerophilic, motile (amphitrichate), gram-negative, curved, S-shaped or helical rods, and representative strains had mean DNA base compositions of 31 to 32 mol % G+C. Distinctive features of the 10 strains were resistance to nalidixic acid and anaerobic growth in the presence of trimethylamine N-oxide hydrochloride (TMAO). The latter feature may account for the common occurrence of NARTC strains in the fecal contents of seagulls. DNA-DNA hybridizations indicated high (≥76%) base sequence relatedness within the group and low (≤15%) relatedness to other species of *Campylobacter*. The 10 strains were classified in the genus *Campylobacter* but they could not be assigned to any previously defined species. Therefore, a new species, with the name *Campylobacter laridis*, is proposed for these 10 strains; the type strain is NCTC 11352.

Resistance to nalidixic acid, which selectively inhibits DNA synthesis in gram-negative bacteria, is a feature of *Campylobacter fetus*, the type species of the genus *Campylobacter*. In contrast, *C. jejuni* and *C. coli*, the clinically important members of the genus that cause acute enterocolitis, are sensitive to this agent [22]. These latter organisms are also distinguished from other *Campylobacter* species by their high optimum growth temperature, a feature first described by King, who referred to this group as "related vibrios" [10]. They grow optimally at about 43°C but do not grow at 25°C.

In 1980, Skirrow and Benjamin [19] described a group of 42 *Campylobacter* isolates that resembled *C. jejuni* and *C. coli* in their high growth temperature requirements but differed in several other ways, notably that they were resistant to nalidixic acid. The first isolation was made in 1976 from the feces of a symptomless 6-year-old boy, but most strains were obtained later from wild seagulls examined during the course of a study of birds overwintering at inland sites (Worcestershire and Warwickshire Wintering Gull Project). Although we have identified similar strains from a variety of animals since then, gulls of the genus *Larus* are the only hosts in which they have been found frequently (about 25% of apparently healthy gulls) [19]. We know of only four instances of their isolation from people and in no case could these bacteria clearly be associated with disease. Phenotypically these strains appeared to constitute a distinct species, but in the absence of supportive DNA hybridization data, Skirrow and Benjamin [19] simply referred to them as "nalidixic acid-resistant thermophilic *Campylobacter* (NARTC). These data, with a full description of a representative collection of NARTC strains including guanine-plus-cytosine (G+C) contents of the deoxyribonucleic acids (DNA), are now presented. The evidence confirms that the group constitutes a new species for which the name *C. laridis* is proposed.

Materials and Methods

Bacterial strains. The origins and strain designations of the 10 strains of *C. laridis* studied in this investigation and the 12 *Campylobacter* reference strains used for comparison are listed in Table 1. The reference strains were obtained from the Nation-

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Table 1. Strains of *Campylobacter* studied.

Name	Strain numbers[a] this study	other	Source of isolation
C. laridis	NCTC 11352[b]	WRI 3034/77	herring gull *(Larus argentatus)*, cloacal swab
	NCTC 11457	WRI 921/79, A20/81	dog, feces
	NCTC 11458	WRI 175/82, A80/82	child, feces
	A21/81	WRI 1094/79	healthy Rhesus monkey
	A22/81	WRI 229/80	water, park lake
	A23/81	WRI 268/80	fur seal with enteritis, feces
	A24/81	WRI 366/80	cow, feces
	A25/81	WRI 399/80	duck, feces
	A27/81	WRI 462/80	foal with diarrhea, feces
	A79/82	WRI 169/82	child, feces
C. fetus subsp. *fetus*	NCTC 10842[b]	CIP 5396 (ATCC 27374)	sheep fetus, brain
C. fetus subsp. *venerealis*	NCTC 10354[b]	ATCC 19438	heifer, vaginal mucus
C. coli	NCTC 11366[b]	CIP 7080	pig, feces
C. jejuni biotype 1	NCTC 11351[b]	CIP 702	bovine, feces
	NCTC 11168	WRI 5636/77	human, feces
	NCTC 11349	CIP 7086	human, blood
C. jejuni biotype 2	NCTC 11392	WRI 852/79	human, feces
C. sputorum subsp. *mucosalis*	NCTC 11000[b]		pig, small intestine
	NCTC 11001		pig, intestinal mucosa
C. sputorum subsp. *bubulus*	NCTC 11367[b]		bull, sperm
"C. fecalis"	NCTC 11415	C-32 Harvey	sheep, feces
	NCTC 11416	C-33 Harvey	sheep, feces

[a] NCTC, National Collection of Type Cultures, London; A, laboratory reference of strains received for identification at NCTC; WRI, laboratory reference for strains received at Worcester Royal Infirmary.
[b] Type strain.

al Collection of Type Cultures (NCTC), London. The name "*C. fecalis*" appears in quotation marks to indicate that the name is not on the Approved Lists of Bacterial Names [17].

Media. The following media were used: nutrient agar (NA) (Oxoid BA Base No. 2 CM271); FBP agar (columbia agar [Oxoid CM331 containing FBP supplement ($FeSO_4 \cdot 7H_2O$, sodium metabisulphite, and sodium pyruvate, each at a concentration of 0.5 g/l)]); yeast extract nutrient agar (YNA) (NA containing 1 g/l yeast extract [Difco]); blood agar (BA) (NA or columbia agar containing 5% defibrinated horse blood); VPT agar (columbia agar containing vancomycin 10 mg/l, polymyxin B 2500 IU/l, trimethoprim 5 mg/l, and lysed defibrinated horse blood 50 ml/l); nutrient broth (NB) (Oxoid CM67); yeast-extract nutrient broth (YNB) (NB containing 1 g/l yeast extract [Difco] and 2g/l New Zealand agar); and FBP broth (YNB containing FBP supplement).

Cultural methods. Unless otherwise stated, cultures were incubated at 37°C under microaerobic conditions (about 7% oxygen) attained by incubating in anaerobic jars (without the catalyst) from which two-thirds of the air had been withdrawn (500 mm Hg below atmospheric pressure) and replaced with a 10–15% carbon dioxide: 85–90% hydrogen mixture. Strains were propagated on BA and stored in liquid nitrogen or freeze-dried for long-term preservation. All cultures were checked for purity before being tested. Unless otherwise stated the inocula used in the following tests were prepared by suspending growth from an overnight BA culture in NB to an absorbance at 540 nm of at least 2 units. Solid media were inoculated with a swab dipped in the suspension, and fluid media were inoculated with about 0.1 ml of the suspension.

Morphological examination. Colonial and microscopical morphology were recorded from 48-h cultures on BA; tests for swarming growth and rapid coccal transformation were performed by the methods of Karmali et al. [9]. Smears were stained with 2% carbol fuchsin for 5 min. The presence of flagella and their arrangement was examined with an electron microscope; selected strains were grown overnight in peptone water, stained with 1% (w/v) phosphotungstic acid, and examined at a magnification of 10,000. Motility was tested by the hanging-drop method on cultures grown overnight at 37°C in NB.

Bacteriological tests. Cytochrome oxidase activity was determined by streaking growth from a 48-h NA culture on a filter paper moistened with a drop of 1% (w/v) tetramethyl-*p*-phenylenediamine dihydrochloride and examining for the development of the deep purple color within 10 sec. Catalase activity was

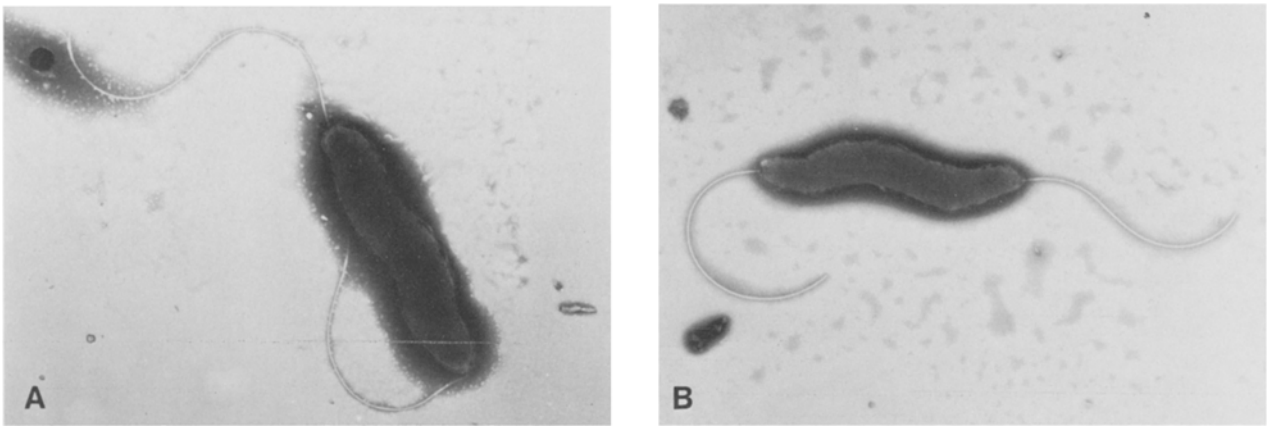

Fig. 1. Electron micrographs of *Campylobacter laridis* NCTC 11352, type strain (A); NCTC 11457 (B). Magnification × 16,500.

determined by adding 3% hydrogen peroxide to a 48-h NA culture and examining for the formation of gas bubbles. Oxidation or fermentation of glucose was determined by the method of Hugh and Leifson [8]. Nitrate reduction was determined by the method of Cook [4]. H_2S production was determined in three test systems: 1) growth in NB for 48 h using a paper strip containing lead acetate as indicator; 2) growth in triple sugar iron (TSI) agar (Oxoid CM277) for 7 days (stab inoculation and incubation in closed tube); and 3) heavy inoculation of FBP broth from overnight growth on BA [18]. (This test is liable to fail if the oxygen concentration of the overnight BA culture is allowed to rise above 7%.) In each of these tests the presence of blackening caused by the formation of lead or iron sulfides was recorded as positive. Indole production was determined by adding 0.5 ml Kovacs' reagent [5] to a 48-h culture in NB, shaking, and examining for the development of a red color in the reagent layer. Susceptibility to nalidixic acid (30 μg), cephalothin (30 μg), and metronidazole (5 μg) was determined by disc diffusion tests on FBP agar incubated for 48 h; the absence of a clear zone of inhibition was recorded as resistant. Tolerance to sodium chloride (1.5% and 3.5%), glycine (1%), and 2,3,5-triphenyltetrazolium chloride (TTC) (0.4 g/l and 1.0 g/l) were determined by culturing for 48 h on YNA containing the stated concentrations of each compound. TTC tolerance was also tested by a previously described strip diffusion method [19]. Tests for growth at 25.0°C, 30.5°C, 37.0°C, 43.0°C, and 45.5°C and reduction of sodium selenite were performed as previously described [19]. Growth anaerobically in the presence of sodium fumarate (0.2%) and in the presence of trimethylamine N-oxide hydrochloride (TMAO) (0.1%) were determined by inoculating bottles of YNB supplemented with the relevant compound. The medium was incubated and examined periodically up to 7 days for growth throughout the medium in addition to growth just below the surface [16]. The test for hydrolysis of sodium hippurate was performed as previously described [18].

Extraction of DNA and determination of G+C contents. The bacterial cells from the blood agar slants were collected in 0.5 M sucrose, and the DNA was isolated and purified as described previously [12,14], except that the Sepharose 4B column was equilibrated with 0.0168 M NaCl. The DNA base composition (mol % G+C) was estimated from the thermal denaturation temperature (T*m*) as described previously [15] except the T*m* was determined in 0.33 × SSC buffer. The base composition was calculated and expressed relative to *Escherichia coli* NCTC 10537 (52 mol % G+C) using the equation: mol % G+C = 52.0 + (2.24 T*m* − 82.9).

DNA hybridization. The nick translation method used to label DNA from NCTC 11352 was described elsewhere [12]. The DNA mixtures were incubated at 63°C for 20 h in 0.42M sodium chloride and assayed for hybridization by the S1 endonuclease method as described previously [12].

Results

Morphology. The 10 strains of the new species were microaerophilic, slender, gram-negative rods. Bacterial cells on average were 1.7–2.4 μm in length by 0.3 μm in width, straight, curved, S-shaped or helical, with rounded ends (see Fig. 1). A single flagellum was attached at each end of the cell. The wavelength and amplitude of the spirals were similar to those of *C. jejuni*, that is, of the "short" category of Karmali et al. [9]. All strains underwent rapid coccal transformation on exposure to air [9]; this feature was more pronounced than we have seen in any other *Campylobacter* species. All strains showed rapid darting motility with the bacteria spinning around their long axes. Colonies were 1–1.5 mm in diameter, low convex, smooth, translucent, and entire; swarming was absent on normally dried media but some strains, including the type strain, swarmed on very moist media.

Bacteriological tests. The results of other cultural and biochemical tests are listed in Tables 2 and 3. Table 2 lists the characters in which all strains were positive, and Table 3 lists the characters in which all strains were negative. The only tests in which

Table 2. Characters for which all 10 strains of *C. laridis* were positive.

Oxidase production
Catalase production
Growth at: 30.5°C, 37.0°C, 43.0°C, 45.5°C
Reduction of nitrate to nitrite
Reduction of sodium selenite
H_2S production in:
Nutrient broth with lead acetate paper as indicator
Iron/metabisulphite medium (FBP broth)
Growth on VPT agar
Resistance to:
Nalidixic acid
Cephalothin
Metronidazole
Tolerance to:
1.5% NaCl (agar)
1.0% glycine
Anaerobic growth in presence of TMAO

Table 3. Characters for which all 10 strains of *C. laridis* were negative.

Growth in air
Anaerobic growth in unsupplemented media
Growth at 25.0° C
Oxidation or fermentation of glucose
Indole production
H_2S production in TSI medium
Hippurate hydrolysis
Tolerance to:
TTC 1.0 g/l
3.5% sodium chloride

strains varied were anaerobic growth in the presence of fumarate (8 of 10 strains positive) and tolerance to TTC 0.4 g/l (6 strains no growth; 4 strains slight growth).

G+C contents of *C. laridis* DNA. Table 4 lists the G+C contents of the DNA from phenotypically representative strains of the new species. The values were between 31.2 and 32.5 mol % with a mean and standard deviation of 31.7 ± 0.7 mol %.

DNA-DNA hybridization. Labeled DNA from NCTC 11352 hybridized at high levels (≥ 76%) with DNA from 8 other *C. laridis* strains as shown in Table 4. The average hybridization within *C. laridis* was 82% with a standard deviation of ± 6%. The new species was 15% related to *C. fetus* subsp. *fetus*, but had lower levels of hybridization with *C. jejuni* and *C. coli* (mean 9 ± 1%) and with *C. fetus* subsp. *venerealis*, *C. sputorum*, and "*C. fecalis*" (mean 4 ± 3%). The DNA results on these species are illustrated in Fig. 2.

Discussion

The results presented indicate that the 10 strains of gram-negative, microaerophilic bacteria, for which the name *Campylobacter laridis* is here proposed, constitute a homogeneous taxon. This new species corresponds to the definition of the genus *Campylobacter* given by Véron and Chatelain [22] in that it contains bacteria that are gram-negative, motile, amphitrichate, microaerophilic, and have DNA with G+C contents of 31 to 33 mol %.

The phenotypic characters by which *C. laridis* can be distinguished from other species of *Campylobacter* are shown in Table 5, which is compiled from published data as well as from our results. The most conspicious test difference between *C. laridis* and the other thermophilic campylobacters, namely *C. coli* and *C. jejuni*, is nalidixic acid resistance. However, the fact that resistance to this drug has recently been found in occasional strains of *C. jejuni* (strains that have also shown resistance to other antimicrobial agents) suggests that this property may be transferable and therefore not altogether reliable for identification purposes. On the other hand, this does not hold true for enterobacteria in which nalidixic acid resistance is neither common nor transferable [3,7]. While there is doubt on this point, the classification of *C. laridis* should rest on characters other than nalidixic acid resistance and on the characters of its DNA.

It is evident from Table 5 that the phenotypic characters of *C. laridis* are closest to those of *C. coli*, although some characters are shared with *C. jejuni* and *C. fetus* subsp. *fetus*. Apart from resistance to nalidixic acid, the characters that most consistently distinguish *C. laridis* from *C. coli* are rapid coccal transformation on exposure to air; sensitivity to TTC; tolerance to 1.5% NaCl; production of H_2S in iron/metabisulphite medium; the ability to grow anaerobically in the presence of TMAO; and the presence of only trace amounts or absence of 19:0Δ cellular fatty acid. Because we have not found any other *Campylobacter* capable of anaerobic growth in the presence of TMAO, this appears to be a unique feature of the new species. It has been suggested (R. W. A. Park, personal communication) that the ability to use the oxygen in TMAO may facilitate the growth of organisms in the gut of animals that eat marine fish, in which the compound is commonly present as a product of urinary excretion. Since marine fish form part of the

Table 4. DNA base compositions and DNA-DNA hybridization of *C. laridis*.

Source of unlabeled DNA	G+C content (mol %)	% relative hybridization with labeled DNA from *C. laridis* NCTC 11352
C. laridis NCTC 11352[a]	32.5 [14]	100 (homologous)
NCTC 11457	31.4	90 ± 7[b]
A21/81		72 ± 2
A22/81		81 ± 9
A23/81		87 ± 2
A24/81		81 ± 6
A25/81		85 ± 5
A27/81		78 ± 2
A79/82	31.2	76 ± 2
C. jejuni biotype 1 NCTC 11168	31.6 [14]	7 ± 1 (15 [12])
NCTC 11349	32.7 [12]	9 ± 2 (22 [12])
NCTC 11351[a]	31.6 [14]	10
C. jejuni biotype 2 NCTC 11392	32.3 [14]	8 ± 0 (26 [12])
C. coli NCTC 11366[a]	32.3 [14]	10 (13 [14])
C. fetus subsp. *fetus* NCTC 10842[a]	36.3 [14]	15
C. fetus subsp. *venerealis* NCTC 10354	36.3 [14]	6
C. sputorum subsp. *mucosalis* NCTC 11000[a]	37.8 [14]	2
NCTC 11001		2
C. sputorum subsp. *bubulus* NCTC 11367[a]	32.3 [14]	<1
"*C. fecalis*" NCTC 11415		8
NCTC 11416		4

[a] Type strain.
[b] The relative hybridization values represent the average of duplicate determinations at TOR (63°C). All values are corrected for self-reassociation of the label (about 6%). Reproducibility of absolute hybridization estimate was ≤9% (average 6%).

diet of sea gulls, this may account for the high frequency of isolation of *C. laridis* from their intestinal contents.

The thermophilic species, namely *C. coli, C. jejuni,* and *C. laridis,* constitute a homogeneous group within *Campylobacter* with respect to their DNA base compositions with values between 29.1 and 34.1 mol % and a mean and standard deviation of 32.0 ± 1.0 % (n = 34) [12,14]. They are quite distinct from *C. fetus* strains with G+C contents of about 35 mol %. However, the results presented in this study and in previous investigations in our laboratory using different labeled DNA probes show that low levels of DNA base sequence similarity exist between *C. laridis* and other thermophilic campylobacters [12,14]. The mean reciprocal hybridizations between *C. laridis* and *C. jejuni,* although low (8% and 22%; this study and [12]), were significantly different and indicated the two species probably have slightly different genome sizes. By contrast, the reciprocal hybridizations between *C. laridis* and *C. coli* agreed closely (10% and 13%; this study and [12]), suggesting the two species have similar genome sizes. In a recent DNA hybridization study of thermophilic campylobacters, Belland and Trust [1] found significant levels (32% and 48%

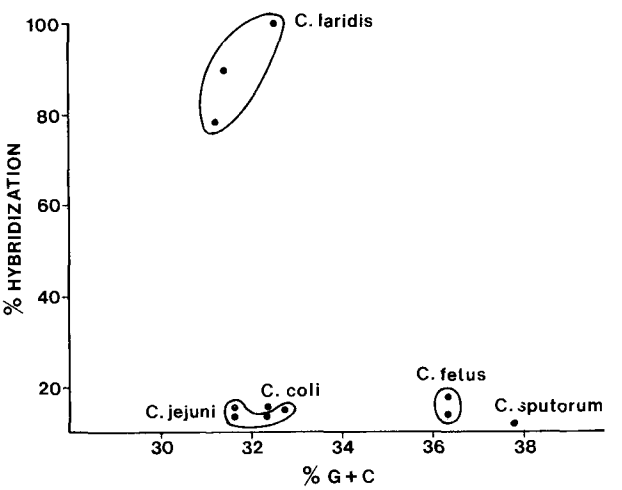

Fig. 2. DNA-DNA hybridization relative to ^{3}H-labeled DNA from *C. laridis* NCTC 11352.

at 70°C, and 86% and 92% at 55°C reassociation temperatures) of relatedness between two reference strains of *C. jejuni* and a strain of the NARTC group. Sufficient sequence divergence was detected to prove that the NARTC strain was not identical to *C. jejuni,* but it was concluded that it should be placed in that species until more strains had been

Table 5. Characters useful for distinguishing strains of *C. laridis* from other species of catalase-positive *Campylobacter*.[a]

Character	*C. laridis*	*C. coli*	*C. jejuni* biotype 1	*C. jejuni* biotype 2	*C. fetus* subsp. *fetus*	*C. fetus* subsp. *venerealis*
Morphology:						
Wavelength of spirals[b]	short	short	short	short	medium	long
Rapid coccal transformation	+	±	+	+	−	−
Flagellar arrangement	A	A	A	A	M	M
Swarming on moist agar	d	d	+	+	−	−
Growth at:						
25.0°C	−	−	−	−	+	+
30.5°C	+	d	−	−	+	+
43.0°C	+	+	+	+	−	−
45.5°C	+	d	d	d	−	−
Hippurate hydrolysis	−	−	+	+	−	−
Susceptibility to:						
Nalidixic acid (30 μg disc)	R	S	S	S	R	R
Cephalothin (30 μg disc)	R	R	R	R	S	S
Metronidazole (5 μg disc)	R	d	d	d	R	R
Tolerance to:						
TTC 1.0 g/l	−	+	−	d	−	−
TTC 0.4 g/l	d	+	±	+	−	−
NaCl 1.5% (agar)	+	−	−	−	+	−
Glycine 1.0%	+	+	+	+	+	−
H_2S production in:						
Nutrient broth with lead acetate strip	+	+	+	+	±	−
Iron/metabisulphite medium	+	−	−	+	−	−
Anaerobic growth in the presence of:						
Fumarate (2 g/l)	d	−	−	−	+	+
TMAO (1 g/l)	+	−	−	−	−	−
Presence of 19:0Δ fatty acid[c]	−	+	+	+	−	−
Mol % G+C ± standard deviation	31.7 ± 0.7	32.9 ± 0.8	31.6 ± 0.6	31.5 ± 0.9	35.4 ± 0.9	35.2 ± 0.9

[a] Symbols: +, 85–100% strains positive; −, 0–15% strains positive; ±, 85–100% strains weak positive; d, 16–84% strains positive (or sensitive); A, predominantly amphitrichate; M, predominantly monotrichate; R, resistant; S, sensitive.
[b] Categorization according to Karmali et al. [9].
[c] This character was scored as positive if the fatty acid was detected at a mean concentration of ≥5% of the total fatty acid concentration.

investigated. Now that this has been done, it is clear that the NARTC group (*C. laridis*) is distinct from *C. jejuni*. For *C. coli* and *C. fetus*, Belland and Trust [1] observed levels of relatedness to the NARTC group that were similar to the values reported in the present study.

Analysis of cellular fatty acids provides further evidence that the NARTC group warrants recognition as a new species. In a study that included most of the strains now placed in *C. laridis*, Leaper and Owen [11] found that eight NARTC strains contained small amounts (average 2.9%) of a 19-cyclopropane acid (19:0Δ), which was also present in small but significant amounts (7.8%) in both *C. coli* and *C. jejuni*, but not in *C. fetus* subsp. *fetus*. Blaser et al. [2] found the presence of this acid a valuable means of identifying *C. coli* and *C. jejuni*, although it is apparently not present in all strains of *C. coli* [13]. More recently, Curtis [6] reported that the 19-cyclopropane acid was absent from his two NARTC strains, and his numerical taxonomic analysis of the fatty acid profiles of 11 groups of campylobacters supported the view that the NARTC group should be classified as a separate species occupying a position intermediate between *C. coli*/*C. jejuni* and *C. fetus*.

It is concluded from the present study that *C. laridis* is a distinct species within the genus *Campylobacter* and that it is more similar in conventional bacteriological characters to *C. coli* than to *C.*

jejuni or any other species. Results on *C. sputorum* and *C. concisus,* a species isolated from human gingival crevices [20], were not included in this study because they are catalase negative and are unlikely to be confused with *C. laridis*. However, DNA of the new species and DNA of *C. sputorum* subsp. *mucosalis* (there is currently no extant type strain of *C. sputorum* subsp. *sputorum*) were examined by hybridization and negligible relatedness was detected.

Description of C. laridis. (la·ri'dis, Gr. noun *laros* seabird; gen. sing. *laridis* of a seabird). Gram-negative, non-spore forming rods, 1.7–2.4 μm in length and 0.3 μm in width (at 48 h), curved, S-shaped or helical, with rounded ends. Wavelength and amplitude of spirals similar to *C. jejuni,* that is, the "short" category of Karmali et al. [9]. Rapid transformation to large coccal forms in cultures exposed to air. Rapid darting motility (organisms spin around long axes) in hanging-drop preparations of broth cultures. Single flagellum at each pole (amphitrichate). Colonies 1 to 1.5 mm diameter, convex, translucent, and entire or semi-effuse (at 48 h); some strains swarm on very moist agar.

Microaerophilic, but grows anaerobically in the presence of trimethylamine N-oxide hydrochloride. No growth at 25.0°C but grows at 30.5 and 45.5°C.

Oxidase and catalase produced. Glucose not fermented and does not support growth. Nitrates reduced. Hydrogen sulfide produced in nutrient broth with lead acetate paper as indicator, and in iron/metabisulfite medium (FBP broth), but not in triple sugar iron medium. Indole not produced. Hippurate not hydrolysed to glycine.

Resistant to nalidixic acid, cephalothin, metronidazole, trimethoprim, vancomycin, and polymyxin B.

Sensitive to 2,3,5-triphenyltetrazolium chloride 1.0 g/l; most strains sensitive to 0.4 g/l.

Tolerant to 1% glycine and 1.5% NaCl (agar medium).

The G+C content of the DNA is 31 to 32 mol % (thermal denaturation and buoyant density).

Found in the intestinal contents of gulls of the genus *Larus* and occasionally other animals and humans.

Pathogenicity is unknown.

Description of the type strain. The type strain (NCTC 11352) has the characters given above except it shows slight growth in the presence of 0.4 g/l TTC. It grows anaerobically in the presence of fumarate. The G+C content of the DNA is 32.6 mol %. Found in the cloacal swab of a herring gull (*Larus argentatus*).

Two additional strains of *C. laridis* have been deposited in the National Collection of Type Cultures: NCTC 11457 (= WRI 921/79) and NCTC 11458 (= WRI 175/82).

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