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Comprehensive Ribotyping Scheme for Heat-Stable Serotypes of *Campylobacter jejuni*

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Strains from diverse sources belonging to all 47 heat-stable Penner serotypes of *Campylobacter jejuni* were examined for polymorphism around the 16S rRNA genes. Penner serotype reference strains and a group of nonserotypeable isolates were included in the study. Complete typeability was obtained; 30 distinct *Pst*I and 42 *Hae*III polymorphisms were found. Three bands were detected in almost all strains with these enzymes, confirming that three copies of the 16S rRNA gene are typical for *C. jejuni*. By combination of the two enzyme polymorphisms, 77 16S ribotypes were defined among the 261 strains analyzed. With two exceptions, no specific association was observed between these ribotypes and heat-stable serotypes. Nine serotypes were homogeneous with respect to the 16S ribotype. Most nonserotypeable strains belonged to ribotypes defined elsewhere in the study. The 16S ribotypes of *C. jejuni* described here were not found in strains of *Campylobacter coli*, and vice versa.

The thermotolerant microaerophilic bacterium *Campylobacter jejuni* is the most common agent of human gastroenteritis in developed countries. Most infections are sporadic and are contracted from a variety of zoonotic and environmental sources (17, 21). There are two principal serotyping schemes for the thermotolerant campylobacters; they are based, respectively, on the O (heat-stable [HS]) antigens and the heat-labile (HL) antigens (9, 15). The former method distinguishes 47 HS serotypes of *C. jejuni* and 18 HS serotypes of the related species *Campylobacter coli* by an indirect hemagglutination technique. The latter method defines 108 HL serotypes among thermotolerant campylobacters by a slide agglutination technique with absorbed antisera. Single serotypes in either scheme sometimes correspond to multiple ones in the other. A slightly greater number of isolates are typeable in the HS scheme than in the HL scheme (13). Two main shortcomings of *Campylobacter* serotyping are the transience of expression of some antigens and the occurrence of nontypeable isolates (14).

rRNA polymorphisms in genomic DNA, or ribotypes (6), have been examined in *C. jejuni* with general-purpose probes consisting of 16S plus 23S rRNA and intergenic regions (3, 11). With a PCR-generated intragenic probe, polymorphism around the 16S rRNA gene has proven useful for molecular epidemiological studies of enteropathogenic bacteria, including large numbers of strains of *Salmonella typhimurium* and *Campylobacter upsaliensis* (18, 19) and of three individual HS serotypes of *C. jejuni* (5, 12). In the present study we investigated the diversity and distribution of 16S ribotypes among all 47 HS serotypes of *C. jejuni*, i.e., within the species as a whole.

MATERIALS AND METHODS

Bacterial strains and serotyping. Forty-seven reference strains for the HS serotyping scheme and 214 *C. jejuni* isolates from human, poultry, bovine, ovine, canine, feline, and environmental sources were included in the study. The latter were isolated between 1989 and 1994 in 16 different laboratories collaborating to supply strains for a large-scale study of typing methods for campylobacters. Except for rarely occurring serotypes (HS22, HS32, HS40, HS41, HS52, HS58, HS60, HS62, HS64, and HS65), four strains of each serotype and its reference strain were analyzed. For the rare serotypes, the reference strain and one or two isolates were analyzed. A group of 15 nonserotypeable isolates was also analyzed. Strains were cultivated and identified to species level as previously described (5, 12). They were serotyped according to the HS antigen scheme of Penner and Hennessy (15) by using avian (chicken) erythrocytes (4), and a panel of 47 O antisera was provided by A. Lastovica (Red Cross War Memorial Children's Hospital, Cape Town, South Africa).

DNA preparation, hybridization, and PCR. The preparation of genomic DNA from *C. jejuni* and genomic Southern blot hybridization were performed as previously described (19). Oligonucleotide primers were from Pharmacia Biosystems; the forward and reverse primers and PCR conditions used to amplify a 1,500-bp fragment from the 16S (*rrn*) gene of *C. jejuni* NCTC 11168 were those previously described (18, 19).

RESULTS

16S rRNA gene polymorphisms. Restriction fragment length polymorphisms around the 16S rRNA genes of 214 clinical isolates and the 47 Penner reference strains, belonging to 47 HS serotypes of *C. jejuni*, were examined. All strains could be typed by this method.

The sizes of *Pst*I bands varied from 5.9 to ~30 kbp (Fig. 1). Thirty distinct 16S ribotypes were obtained with this enzyme. The most common *Pst*I (P) type in the study, P4, contained 74 of 261 strains, belonging to 20 HS serotypes with a global distribution (United Kingdom, Gambia, Spain, Tunisia, Pakistan, Bangladesh, Thailand, and Australia). The next most common P type, P5, contained 40 of 261 strains and was found in 14 HS serotypes but was restricted to isolates from the United Kingdom. Three P ribotypes (P16, P1, and P12) contained over 20 strains each distributed among eight or nine serotypes. Nineteen P ribotypes contained only one or two strains. Five of these 19 ribotypes contained the sole example of a rarely occurring HS serotype.

The sizes of *Hae*III bands varied from 1.0 to ~20.0 kbp (Fig. 2), and 42 distinct 16S ribotypes were obtained with this enzyme. Two *Hae*III (H) types, H1 and H5, contained 47 strains each, and both had a global distribution. There was a more widespread distribution of the 261 strains among H ribotypes than among P ribotypes: 8 H ribotypes contained 10 or more strains, and 13 H ribotypes contained 5 or more strains. Ten of the 16 H types which contained a single strain belonged to HS serotypes uncommon in our studies, and many of these were serotype reference strains.

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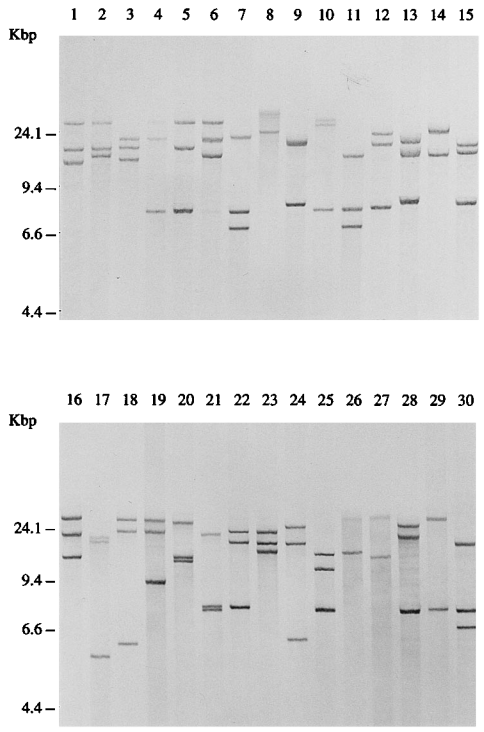

FIG. 1. *Pst*I ribotypes of *C. jejuni*. Genomic Southern blots were probed with a PCR-amplified 1,500-bp probe internal to the 16S rRNA gene of NCTC 11168. The 30 P ribotypes are shown. Lanes 1 to 30, types P1 to P30, respectively. Types P1 to P10 were as described in a report of a large-scale study of *C. jejuni* serotypes HS1 and HS4 (12).

Combined 16S ribotypes. The *Pst*I and *Hae*III polymorphisms were used to designate 77 combined 16S ribotypes, whose compositions are shown in Table 1 (for example, the 20 of 261 strains which were P1 H1 were designated Cj-R1, and so forth). The largest group of strains belonged to Cj-R11, a ribotype containing 33 strains with a global distribution and 14 HS serotypes.

There were 46 combined ribotypes for which there was only one example found within the set. Fourteen of those ribotypes belonged in this study to Penner reference strains (HS10, HS12, HS21, HS29, HS31, HS35, HS40, HS41, HS43, HS44, HS52, HS53, HS58, and HS63). There were 15 nonserotypeable strains, but no specific combined ribotypes were associated with these as a group. Rather, many of these strains had combined ribotypes characteristic of common HS serotypes; for example, three nontypeable strains were Cj-R1, a ribotype found for seven HS serotypes.

No specific association between the combined 16S ribotypes and the majority of HS serotypes was observed. Certain ribotypes (Cj-R1, Cj-R11, Cj-R31, Cj-R73, and Cj-R25) were more prevalent than others, reflecting the fact that they occurred widely across the species. All of these ribotypes were also distributed among strains originating from different countries and continents, which is indicative of a global distribution. Conversely, there were nine unique ribotypes, which were unusual in the United Kingdom and belonged to isolates from patients returning from foreign travel (e.g., Cj-R28 from India or Cj-R62 from Thailand).

Strains with the same combined ribotype occurred in cases of human enteritis and in diverse animal hosts. For example, ribotype Cj-R11 occurred in HS5 strains from humans, poultry, and sheep and in other serotypes isolated from a variety of sources (e.g., HS18, HS31, or HS37 from humans, HS8 or HS37 from poultry, and HS10 or HS18 from dogs). There was no evidence that virulence, assayed indirectly by virtue of an outcome as human enteritis, was more prevalent in any particular ribotype or serotype.

The 16S ribotypes of reference strains for the most prevalent Lior serotypes of *C. jejuni* (14) occur among those described in Table 1. These Lior reference strains, their corresponding Penner serotypes and their 16S ribotypes were as follows: NCTC 12104, HL1/HS4 and Cj-R8; NCTC 12106, HL2/HS1 and Cj-R56; NCTC 11168, HL4/HS2 and Cj-R1; NCTC 12563, HL5/HS23 and Cj-R39; NCTC 12564, HL6/HS6, 7, 27 and Cj-R31; NCTC 12105, HL7/HS50 and Cj-R5; NCTC 12565,

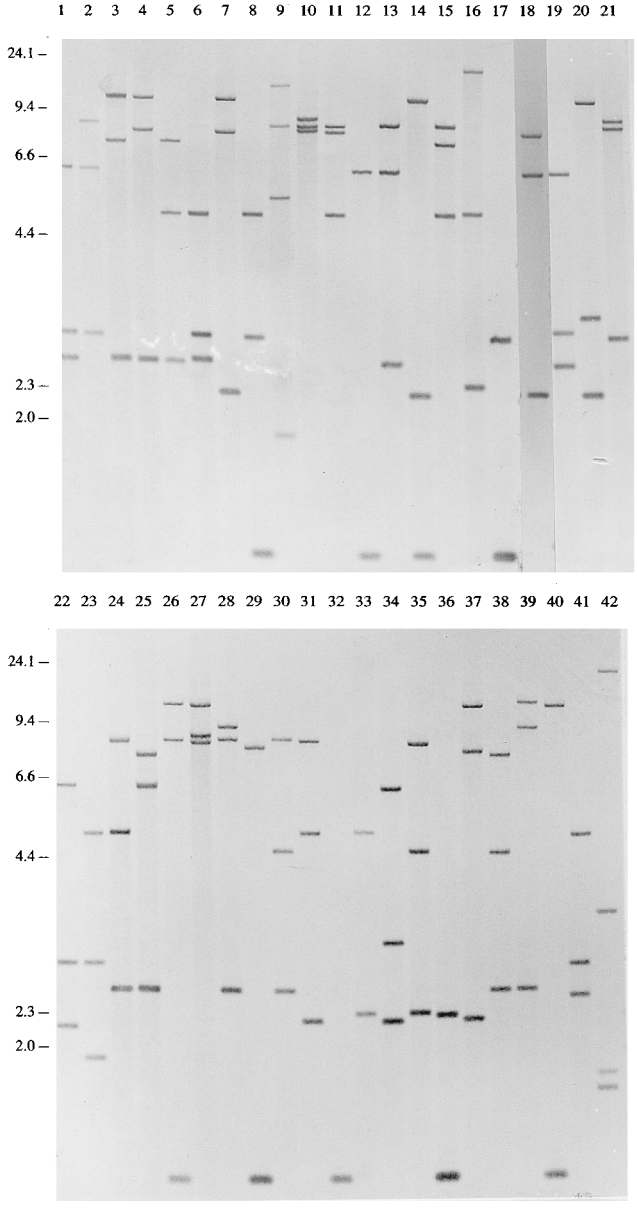

FIG. 2. *Hae*III ribotypes of *C. jejuni*. Genomic Southern blots probed as described for Fig. 1. Lanes 1 to 42, types H1 to H42, respectively. Types H1 to H9 were as described in a report of a large-scale study of *C. jejuni* serotypes HS1 and HS4 (12). Numbers on the left are molecular sizes in kilobase pairs.

TABLE 1. Compositions and serotype distributions of 16S ribotypes of *C. jejuni*

P (*Pst*I) type	H (*Hae*III) type	Combined type	Found in HS serotype(s):	Designated reference strain
P1	H1	Cj-R1	HS1, HS2, HS8, HS10, HS17, HS57, HS63, NT[a]	NCTC 12500
	H2	Cj-R2	HS1	A1034/92
P2	H1	Cj-R3	HS1, HS2, HS44, HS8	NCTC 12507
P3	H1	Cj-R4	HS1	C591/93
P2	H3	Cj-R5	HS65, HS4	NCTC 12558
P4	H1	Cj-R6	HS4, HS8, HS10, HS15, HS17, HS44	NCTC 12513
P1	H3	Cj-R7	HS4	C296/93
P5	H1	Cj-R8	HS2, HS4	C4/92
	H4	Cj-R9	HS6, 7, 27, HS12, HS53	NCTC 12506
P6	H1	Cj-R10	HS4, HS8, HS17, HS44	NCTC 12561
P4	H5	Cj-R11	HS2, HS5, HS6, 7, 27, HS8, HS9, HS10, HS11, HS15, HS18, HS31, HS33, HS37, HS44, NT	NCTC 12504
	H6	Cj-R12	HS17, HS18, HS53	NCTC 12515
P7	H7	Cj-R13	HS4	C758/93
P8	H1	Cj-R14	HS4	C589/93
P9	H8	Cj-R15	HS15, HS45	C371/94
P10	H9	Cj-R16	HS4	NCTC 12548
P2	H13	Cj-R17	HS31, NT	C535/94
	H25	Cj-R18	HS4	C1142/93
P4	H11	Cj-R19	HS23	NCTC 11351
	H15	Cj-R20	HS11	C1128/93
	H25	Cj-R21	HS10	NCTC 12509
	H19	Cj-R22	HS4	C524/94
	H23	Cj-R23	HS4, NT	C1137/93
	H24	Cj-R24	HS37	C540/93
	H18	Cj-R25	HS9, HS38, HS53	NCTC 12508
	H26	Cj-R26	HS12	A1064/92
	H38	Cj-R27	HS37	C51/93
	H41	Cj-R28	HS9	C410/94
P5	H5	Cj-R29	HS3	C521/93
	H6	Cj-R30	HS31	NCTC 12523
	H7	Cj-R31	HS6, 7, 27, HS15, HS33, HS37, HS42, HS60	NCTC 12505
	H26	Cj-R32	HS12	NCTC 12511
	H27	Cj-R33	HS21	NCTC 12518
	H31	Cj-R34	HS55	NCTC 12546
P6	H5	Cj-R35	HS6, 7, 27, HS62	NCTC 12555
	H11	Cj-R36	HS23	A1047/92
P7	H24	Cj-R37	HS58	C1151/93
P9	H29	Cj-R38	HS32, HS36	NCTC 12524
P11	H10	Cj-R39	HS19	NCTC 12517
	H13	Cj-R40	HS41	NCTC 12542
	H21	Cj-R41	HS19	C68/92
	H28	Cj-R42	NT[a]	C356/93
P12	H12	Cj-R43	HS19, NT	C1145/93
	H14	Cj-R44	HS21, HS29, HS57	NCTC 12552
	H20	Cj-R45	HS21, HS42, HS45	NCTC 12544
	H34	Cj-R46	HS58	NCTC 12553
	H37	Cj-R47	HS21	C437/93
	H40	Cj-R48	HS57	C845/93
P13	H4	Cj-R49	HS53	C798/93
	H5	Cj-R50	HS37	C952/93
	H17	Cj-R51	HS1	C586/94
P14	H1	Cj-R52	HS2	C258/94
	H36	Cj-R53	HS53	NCTC 12560
P15	H1	Cj-R54	NT	C662/94
P16	H5	Cj-R55	HS2, HS3, HS31, NT	NCTC 12502
	H6	Cj-R56	HS31	C791/94
	H11	Cj-R57	HS8, HS17, HS22, HS23, HS35, NT	NCTC 12519
P17	H22	Cj-R58	HS6, 7, 27	C1133/93
P18	H32	Cj-R59	HS10, HS33	C355/93
P19	H16	Cj-R60	HS1	A1031/92
P20	H35	Cj-R61	HS4, HS64	NCTC 12557
P21	H6	Cj-R62	HS5	C245/94
P22	H12	Cj-R63	HS23	C169/93
	H14	Cj-R64	HS57	C761/93
P23	H14	Cj-R65	HS57	C824/94
P24	H42	Cj-R66	HS52	C1015/93
P25	H39	Cj-R67	HS41	C768/94

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TABLE 1—*Continued*

P (*Pst*I) type	H (*Hae*III) type	Combined type	Found in HS serotype(s):	Designated reference strain
P26	H1	Cj-R68	HS44	NCTC 12549
	H33	Cj-R69	HS63	NCTC 12556
P27	H11	Cj-R70	HS35	NCTC 12538
P28	H6	Cj-R71	HS2	C40/92
P29	H6	Cj-R72	HS53	C209/92
P30	H10	Cj-R73	HS23, HS29, HS36	C174/92
	H21	Cj-R74	HS36	C118/93
	H28	Cj-R75	HS29	NCTC 12522
	H30	Cj-R76	HS40	NCTC 12541
	H31	Cj-R77	HS52	NCTC 12545

[a] NT, nonserotypeable group.

HL9/HS5 and Cj-R11; and NCTC 12566, HL10/HS1 and Cj-R3.

DISCUSSION

The choice of enzymes for this study was made on the basis of our previous experience that they yielded simplified ribotyping data which were discriminatory within serotypes HS1 and HS4 of *C. jejuni* (12). Data from genomic Southern blots made with *Pst*I or *Hae*III also directly reflect the 16S rRNA gene copy number, since the sequence of this gene from the type strain *C. jejuni* NCTC 11351 (GenBank number L04315) contains no sites for these enzymes.

Twenty-three of the 30 P types clearly consisted of three well-separated *Pst*I fragments. Most of the seven remaining types exhibited comigrating bands (e.g., the two bands at 25 kbp of type P27 [Fig. 1, lane 27]) which could be resolved under different electrophoresis conditions (data not shown). It is significant that none of the P ribotypes detected in this study occurred in a parallel study of *C. coli* strains carried out in our laboratory (20). This is consistent with the known DNA homology differences between the two species (16) and with their separation by multilocus enzyme electrophoresis (2). Since these two major agents of human campylobacter infection are not readily separated by phenotype (16) and since the highly homologous sequence of the 16S rRNA gene has so far precluded the development of a differential PCR, 16S ribotyping may provide a convenient way to distinguish between them.

Of the 42 H types, 33 consisted of three well-separated *Hae*III fragments. Six H types consisted of two bands, and in most such cases this would be explained by comigration of bands (e.g., two bands of 1 kbp in types H12 and H17 [Fig. 2, lanes 12 and 17]). Two H types consisted of four *Hae*III fragments. If the number of *Hae*III bands was other than three, the number of corresponding *Pst*I bands was usually three, and vice versa. There were two reference strains for which only two bands were found with either enzyme, but conclusions about gene copy number variation were not drawn, since the upper *Pst*I band was large enough to contain two gene copies. We conclude that the copy number of the gene across the species as a whole is three, in agreement with results from a single strain (7).

The proportion of *C. jejuni* isolates which are nontypeable (and hence indistinguishable) by serotyping can exceed 20% (8), and this phenomenon is a principal reason to develop molecular genotyping of campylobacters (1). Only two nonserotypeable strains had unique ribotypes. The capacity of a test to provide an unambiguous result for each isolate examined is called typeability. Nontypeable isolates are those which produce a null or ambiguous result (10). The present study indicates that 16S ribotyping can resolve the epidemiological uncertainty associated with nonserotypeable isolates of *C. jejuni.*

A number of Penner reference strains exhibited ribotypes which were not typical of contemporary United Kingdom isolates. Establishment of 16S ribotyping as a routine epidemiological tool will therefore require its own set of reference strains, as described in Table 1. A fundamentally important feature of any typing method is its discriminatory power (10). The discriminatory power of the scheme could be increased by adding other enzyme digestions to further subdivide the combined ribotypes described.

The great majority of human infections with *C. jejuni* occur sporadically, while outbreaks are apparently rare (21). In practice, a combination of subtyping methods is required to characterize *Campylobacter* outbreaks, and when ribotyping has been used, its results are congruent with other typing data such as phage typing or pulsed-field gel electrophoresis macrorestriction profiles (5, 11, 12, 20). We have elsewhere characterized outbreak-associated strains by a combination of 16S ribotype and HS serotype. For example, two HS4 strains (191/92 and 193/92 in this study) of ribotype Cj-R5 were the causative agent of a milk-borne outbreak, while HS1 strains (series A622/89 to A628/89 in this study) of ribotype Cj-R1 (12) caused a water-borne outbreak (11). Two other strains in this study (162/92 and 174/92) were representative isolates from another milk-associated outbreak caused by HS17 strains of ribotype Cj-R10 and HS23 strains of ribotype Cj-R73.

The purpose of the present study was to provide a comprehensive 16S ribotyping scheme for all Penner HS serotypes of *C. jejuni*, i.e., for the species as a whole. Previously published ribotyping studies have not approached comprehensive coverage of the species or its serotyping scheme(s). The further inclusion of Lior HL serotypes would create a "gold standard" for typing *C. jejuni*, but this must await further study of an equivalent large number of strains of the Lior HL serotypes corresponding to *C. jejuni* (the Lior scheme crosses species and includes *C. coli* and *Campylobacter lari*). We have, however, established that there is excellent congruence, in that serotype reference strains of the two schemes share the same 16S ribotype. For example, the HL4 reference strain NCTC 11168 is an HS2 strain and has ribotype Cj-R1, that of the HS2 reference strain. Similarly, the HL9 reference strain NCTC 12565, which is an HS5 strain, has ribotype Cj-R11, that of the HS5 reference strain. Thus, 16S ribotyping as described here has the potential to integrate both existing serotyping schemes.

Other studies in our laboratory (20) have indicated that 16S ribotyping of *C. coli* has a coherent hierarchical relationship to flagellin gene polymorphism and to pulsed-field gel macro-

restriction profiles of the genome. Thus, the 16S ribotyping scheme described here may be used directly for subspecific differentiation of *C. jejuni* or as a framework for other methods of molecular subtyping of this most important agent of human enteric disease.

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