

## Class V. *Epsilonproteobacteria* class. nov.

GEORGE M. GARRITY, JULIA A. BELL AND TIMOTHY LILBURN

*Ep.si.lon.pro.te.o.bac.te'ri.a.* Gr. n. *epsilon* name of fifth letter of Greek alphabet; Gr. n. *Proteus* ocean god able to change shape; Gr. n. *bakterion* a small rod; M.L. fem. pl. n. *Epsilonproteobacteria* the class of bacteria having 16S rRNA gene sequences related to those of the members of the order *Campylobacteriales*.

The class *Epsilonproteobacteria* was circumscribed for this volume on the basis of phylogenetic analysis of 16S rRNA sequences; the

class contains the order *Campylobacteriales*.  
Type order: **Campylobacteriales** ord. nov.

### Order I. *Campylobacteriales* ord. nov.

GEORGE M. GARRITY, JULIA A. BELL AND TIMOTHY LILBURN

*Cam.py.lo.bac.ter.a'les.* M.L. masc. n. *Campylobacter* type genus of the order; *-ales* ending to denote order; M.L. fem. n. *Campylobacteriales* the *Campylobacter* order.

The order *Campylobacteriales* was circumscribed for this volume on the basis of phylogenetic analysis of 16S rRNA sequences; the order contains the families *Campylobacteraceae*, *Helicobacteraceae*, and "*Nautiliaceae*".

Actively growing cells generally curved or spiral-shaped, except for *Thiovulum*. Metabolically and ecologically diverse; in-

cludes human and animal pathogens. *Nautilia* and *Caminibacter* are anaerobic marine thermophiles.

Type genus: **Campylobacter** Sebald and Véron 1963, 907 emend. Vandamme, Falsen, Rossau, Hoste, Segers, Tytgat and De Ley 1991a, 98.

### Family I. *Campylobacteraceae* Vandamme and De Ley 1991, 453<sup>VP</sup>

PETER VANDAMME, FLOYD E. DEWHIRST, BRUCE J. PASTER AND STEPHEN L.W. ON

*Cam.py.lo.bac.ter.a'ce.ae.* M.L. masc. n. *Campylobacter* type genus of the family; suff. *-aceae* denoting family; M.L. masc. pl. n. *Campylobacteraceae*, the *Campylobacter* family.

Curved, S-shaped, or **spiral rods** that are 0.2–0.8 × 0.5–5 µm. Gram negative. Nonsporeforming. Cells in old cultures may form spherical or coccoid bodies. Mostly motile with a **characteristic corkscrew-like motion** by means of a single, **polar, unsheathed flagellum** at one or both ends of the cell.

**Microaerophilic**, with a respiratory type of metabolism. Some taxa grow also under aerobic or anaerobic conditions. Optimal temperature is 30–37°C. **Chemooorganotrophs. Carbohydrates are neither fermented nor oxidized.** Fumarate is reduced to succinate. Colonies are usually nonpigmented. Serum or blood enhances growth but is not necessary. **Energy is obtained from amino acids or tricarboxylic acid cycle intermediates, not carbohydrates.** Mostly oxidase positive. Methyl red and Voges–Proskauer negative, and no production of indole. Most species reduce nitrate and do not hydrolyze hippurate.

Menaquinones are the only respiratory quinones detected, with menaquinone-6 (three different structural types) and menaquinone-5 as major components. Internal transcribed spacers or intervening sequences occur in the 16S or 23S ribosomal RNA genes of strains of several species. Most species occur in man or animals, or both, primarily in the reproductive organs, intestinal tract, and oral cavity. Some species are considered true pathogens and are a significant cause of diarrheal disease; some species are associated with periodontal disease.

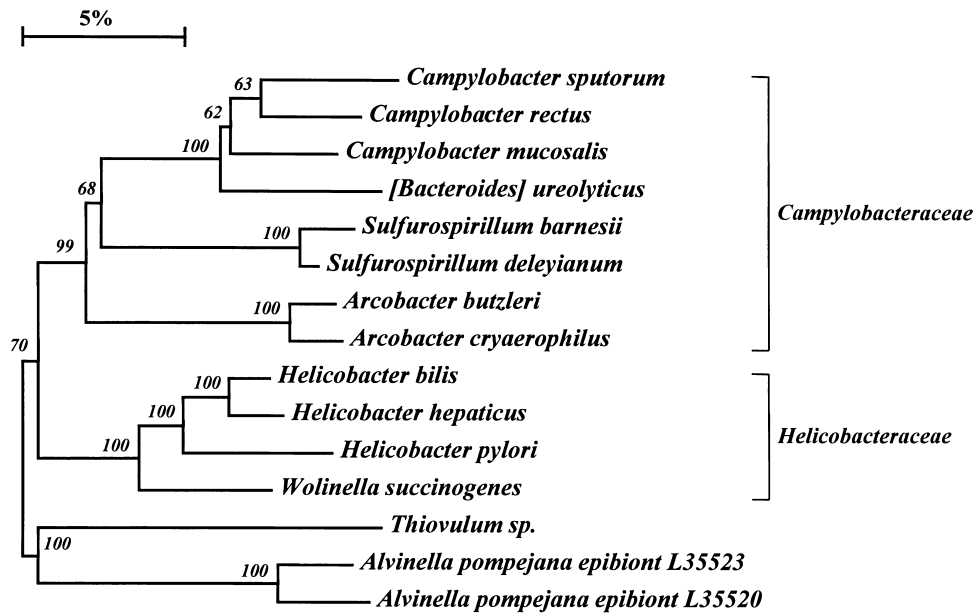
The mol% G + C of the DNA is: 27–47.

Type genus: **Campylobacter** Sebald and Véron 1963, 907 emend. Vandamme, Falsen, Rossau, Hoste, Segers, Tytgat and De Ley 1991a, 98.

#### FURTHER DESCRIPTIVE INFORMATION

The family *Campylobacteraceae* comprises the genera *Campylobacter*, *Arcobacter*, and *Sulfurospirillum*, and the generically misclassified species *Bacteroides ureolyticus* (Fig. BXII.ε.1). As described below, *B. ureolyticus* phylogenetically belongs to this family and shares most of its characteristics with other members of this family. It resembles *Campylobacter* species in its respiratory quinone content, its DNA base ratio, and most of its phenotypic characteristics but differs from campylobacters in its fatty acid composition and its proteolytic metabolism. *B. ureolyticus* was not formally reclassified pending the isolation and thorough taxonomic characterization of additional *B. ureolyticus*-like bacteria, and is thus considered species *incertae sedis*.

The delineation of this bacterial family was primarily based on phylogenetic criteria and is not supported by biochemical, chemotaxonomic, or ultrastructural characteristics. The genera *Helicobacter* and *Wolinella* are the closest phylogenetic neighbors of members of the *Campylobacteraceae*. Genus level identification is primarily achieved via the identification of strains to the species level.



**FIGURE BXII.e.1.** Phylogeny of the family *Campylobacteraceae*. The family *Campylobacteraceae* forms a coherent phylogenetic group in the *Epsilonproteobacteria* that is comprised of members of the genera *Campylobacter*, the misclassified *Bacteroides ureolyticus*, *Arcobacter*, and *Sulfurospirillum*. Bar = 5% difference in 16S rDNA nucleotide sequences. The Neighbor-Joining method was used for tree construction. One hundred bootstrap trees were generated, and bootstrap confidence levels (shown as percentages above the nodes) were determined.

#### Key to the genera of the family Campylobacteraceae

1. The mol% G + C content of the DNA is 29–47. Optimal growth is between 30 and 37°C, in microaerobic to anaerobic conditions. Menaquinone-6 and a methyl-substituted menaquinone-6 are the major respiratory quinones. No hydrolysis of casein or gelatin. Most strains do not hydrolyze urea. Isolated primarily from the reproductive organs, intestinal tract, and oral cavity of humans and animals. Internal transcribed spacers or intervening sequences occur in 16S and 23S rRNA genes of a variety of species.

##### Genus *Campylobacter*

2. The mol% G + C content of the DNA is 27–31. Optimal growth between 15 and 30°C, in microaerobic to aerobic conditions. Menaquinone-6 and a second menaquinone-6, the detailed structure of which has not been determined, are the major respiratory quinones. No hydrolysis of casein or gelatin. Most strains do not hydrolyze urea. Isolated primarily from the reproductive organs and intestinal tract of man and animals. Internal transcribed spacers or intervening sequences have not been reported.

##### Genus *Arcobacter*

3. The mol% G + C content of the DNA is 32–42. Optimal growth between 20 and 37°C, in microaerobic to anaerobic conditions. Menaquinone-6 and a methyl-substituted menaquinone-6 are the major respiratory quinones. Utilization of sulfur as electron acceptor. Free-living, found in freshwater and marine environments. Internal transcribed spacers or intervening sequences have not been reported.

##### Genus *Sulfurospirillum*

4. The mol% G + C content of the DNA is 28–30. Optimal growth between 30 and 42°C, in microaerobic to anaerobic conditions. Menaquinone-6 and a methyl-substituted menaquinone-6 are the major respiratory quinones. Hydrolysis of casein, gelatin, and urea. Isolated primarily from superficial ulcers, soft-tissue infections, the urogenital tract, and oral cavity of humans.

##### *Species incertae sedis Bacteroides ureolyticus*

*Genus I. Campylobacter* Sebald and Véron 1963, 907,<sup>AL</sup> emend. Vandamme, Falsen, Rossau, Hoste, Segers, Tytgat and De Ley 1991a, 98

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*Cam.py'lo.bac.ter.* Gr. adj. *campylo* curved; Gr. n. *bacter* rod; M.L. masc. n. *Campylobacter* a curved rod.

Cells of most species are **slender, spirally curved rods**, 0.2–0.8 × 0.5–5 µm; cells of some species are predominantly curved or straight rods. The rods may have one or more spirals and can be as long as 8 µm. They also appear S-shaped and gull-winged when two cells form short chains. Nonsporeforming. Cells in old cultures may form spherical or coccoid bodies. Cells have a multilaminar polar membrane at both ends of the cell that is located under the cytoplasmic membrane. Gram negative. Cells of most species are motile with a characteristic **corkscrewlike motion** by means of a single polar **unsheathed flagellum** at one or both ends of the cell. The flagella may be 2–3 times the length of the cells. Cells of other species are nonmotile (*Campylobacter gracilis*) or have multiple flagella (*Campylobacter showae*). Occasionally differences in the number of flagella shown by cells in a single culture are seen (*Campylobacter hyointestinalis*).

**Microaerophilic, with a respiratory type of metabolism.** Several species require anaerobiosis for optimal growth and grow only microaerobically in the presence of fumarate with formate or hydrogen. Require an oxygen concentration between 3% and 15% and a CO<sub>2</sub> concentration of 35%. Growth at 35–37°C, not at 4°C. **Chemoorganotrophs. Carbohydrates are neither fermented nor oxidized.** No acid or neutral end products produced. Serum or blood enhances, but is not required for, growth. **Energy is obtained from amino acids or tricarboxylic acid cycle intermediates, not carbohydrates.** Gelatin, casein, starch, and tyrosine are not hydrolyzed. Methyl red and Voges–Proskauer negative. **Oxidase activity** is present in all species except *C. gracilis* and sporadic isolates of *Campylobacter concisus* and *C. showae*. **Arylsulfatase activity is reported in some species**, but no lipase or lecithinase activity. Most species **reduce nitrate**. Pigments are not produced. Most species are pathogenic for man and animals. **Found in the reproductive organs, intestinal tract, and oral cavity of humans and animals.**

**Internal transcribed spacers** or intervening sequences (IVS) were first reported in rRNA genes of *Campylobacter* strains by Van Camp et al. (1993). Intervening sequences were present in the 16S rRNA genes of all *C. sputorum* strains (Van Camp et al., 1993; On et al., 1998) and some *C. hyointestinalis* subsp. *lawsonii* strains (Harrington and On, 1999) were examined. The IVS occurs in a 7-base stem-loop that is centered at position 210 (*E. coli* numbering). The length of the IVS replacing the 7-base stem-loop is 240 bases. Dewhirst and Paster (unpublished) have found IVS's in the type strain of *C. curvus* (147 bases), a different IVS in a *C. curvus*-like strain (SU C10; 208 bases), and in a *C. rectus*-like strain (CCUG 19168, 196 bases). Linton et al. (1994a) reported on the presence of an IVS (152 bases) in the 16S rRNA genes of some *C. helveticus* strains. 23S rRNA genes of all *C. fetus* strains examined (Van Camp et al., 1993), and the 23S rRNA genes of some of the *C. jejuni* and *C. upsaliensis* strains examined (Van Camp et al., 1993) have IVS elements. Hurtado and Owen (1997a) reported on intervening sequences in 23S rRNA genes of strains of *C. jejuni* (both subspecies), *C. coli*, *C. helveticus*, *C. fetus*, *C. sputorum*, and *C. upsaliensis*.

The mol% G + C of the DNA is: 29–47.

**Type species: *Campylobacter fetus*** (Smith and Taylor 1919) Sebald and Véron 1963, 907 (*Vibrio fetus* Smith and Taylor 1919, 301).

#### FURTHER DESCRIPTIVE INFORMATION

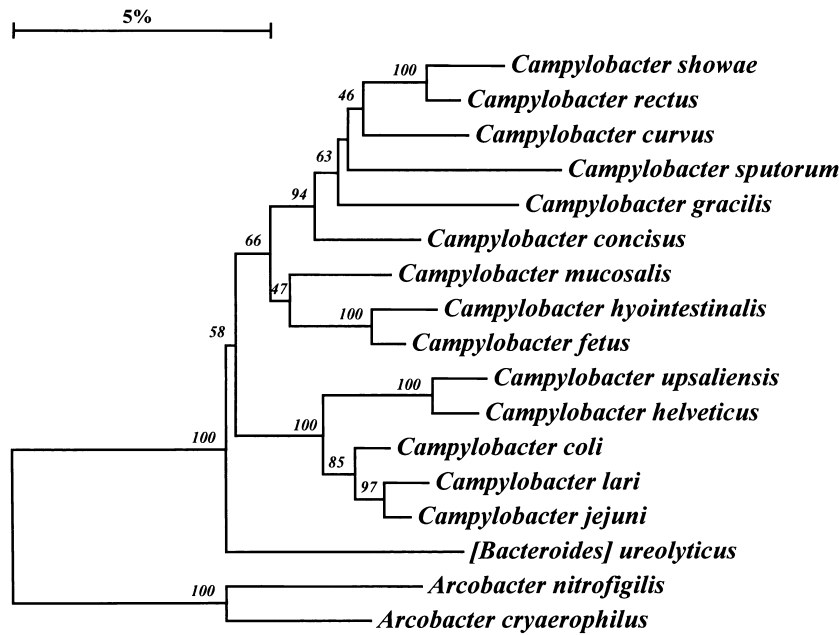
The genera *Campylobacter*, *Arcobacter*, *Sulfurospirillum*, and the generically misclassified species *Bacteroides ureolyticus*, constitute the family *Campylobacteraceae* and belong to the *Epsilonproteobacteria*. Within the genus *Campylobacter*, the group of the thermophilic (or more accurately, thermotolerant) campylobacters (*C. jejuni*, *C. coli*, *C. lari*, *C. upsaliensis*, and *C. helveticus*) forms a distinct subcluster (Fig. BXII.ε.2). *C. fetus* and *C. hyointestinalis* are also close relatives, while the remaining species form a loose assemblage of predominantly hydrogen-requiring organisms. Low but significant DNA–DNA hybridization values (which vary with the hybridization techniques used) have been reported between (i) *C. fetus* and *C. hyointestinalis*; (ii) *C. jejuni* and *C. coli* (reviewed by Vandamme and Goossens, 1992); (iii) *C. upsaliensis* and *C. helveticus* (Stanley et al., 1992); and (iv) *C. showae* and *C. rectus* (Etoh et al., 1993); the level of DNA–DNA hybridization toward and between all other species were reported as not substantial.

*Campylobacter* cells are typically helically curved and have a very characteristic corkscrew-like darting type of motility, which is observed with phase contrast or darkfield microscopy. The growth medium becomes alkaline (pH 8.5–9.0), and coccoid forms occur under these unfavorable conditions. The coccoid forms are considered by many to be degenerative forms rather than a dormant stage of the organism and are difficult to detect using PCR methods. Increase of viable numbers of aged coccoid cultures is attributed to multiplication of residual viable cells (Hazeleger et al., 1994; Bovill and Mackey, 1997).

The outer cell membrane is double-layered, loosely fitted over the cell wall and has a wavy morphology. The cytoplasmic membrane is thickened at the polar region. This polar membrane can be seen at both ends of the cell and a similar structure has been reported in other bacteria (Smibert, 1978). In contrast, *C. rectus* exhibits a distinct cell wall structure in which the outer membrane is covered with a distinctive array of hexagonally packed macromolecular subunits (Lai et al., 1981).

*Campylobacter* species have a respiratory metabolism. *C. fetus* oxidizes citrate, *cis*-aconitate, isocitrate, α-ketoglutarate, succinate, fumarate, malate, and oxaloacetate. A complete tricarboxylic acid (TCA) cycle has been demonstrated. There is no oxidation or fermentation of carbohydrates. Energy for *C. fetus* is obtained from TCA intermediates and from amino acids such as glutamate and aspartate that can be deaminated to TCA intermediates. Mendz et al. (1997) reported on the role of pyruvate in the energy and biosynthesis metabolism of *Campylobacter* species. The important role of pyruvate was illustrated by the variety of products formed using pyruvate as the sole substrate and by the existence of anaplerotic sequences and anabolic pathways that employ pyruvate.

All campylobacters grow under microaerobic conditions. Several species (*C. concisus*, *C. curvus*, *C. rectus*, *C. mucosalis*, *C. showae*, *C. gracilis*, and, partly, *C. hyointestinalis*) require hydrogen or formate as an electron donor for microaerobic growth and some species grow preferentially under anaerobic conditions (Han et al., 1991). Hydrogen stimulates growth of the majority of species when inoculated on common agar bases. Cytochromes *b*, *c*, and carbon monoxide-binding cytochrome *c* have all been reported



**FIGURE BXII.e.2.** Phylogeny of *Campylobacter* species. The phylogenetic relationships of the named species of the genus *Campylobacter* and the misclassified *Bacteroides ureolyticus* are shown above. Bar = 5% difference in 16S rDNA nucleotide sequences. The Neighbor-Joining method was used for tree construction. One hundred bootstrap trees were generated, and bootstrap confidence levels (shown as percentages above the nodes) were determined.

in *Campylobacter* species, but not types *a* and *d*; the presence of cytochrome *o*, is controversial (Goodhew et al., 1988; Han et al., 1992). Many species also have catalase activity.

Menaquinone-6 (2-methyl-3-farnesyl-farnesyl-1,4-naphthoquinone) and a methyl-substituted menaquinone-6 (2, [5 or 8]-dimethyl-3-farnesyl-farnesyl-1,4-naphthoquinone) have been reported as major respiratory quinones in *Campylobacter* species (Moss et al., 1984, 1990b; Vandamme et al., 1995a).

Plasmids have been described in a variety of species including *C. jejuni*, *C. coli*, *C. upsaliensis*, *C. mucosalis*, *C. hyointestinalis*, and *C. fetus* (Taylor et al., 1981; Boosinger et al., 1990; Goossens et al., 1990a; Varga, 1991; Waterman et al., 1993). Tetracycline and kanamycin resistance were shown to be plasmid-mediated and transferable (Taylor et al., 1981; Cabrita et al., 1992; Velazquez et al., 1995).

Several serological typing systems have been developed but are focused primarily on *C. jejuni* and *C. coli* (reviewed by Patton and Wachsmuth, 1992). In addition, bacteriophage typing, biotyping, plasmid profiling, and a variety of DNA based typing methods such as pulsed field gel electrophoresis of large genomic fragments, ribotyping, and PCR based genomic fingerprinting, have all been used in epidemiological studies (Griffiths and Park, 1990; Mazurier et al., 1992; Patton and Wachsmuth, 1992; Owen et al., 1993).

Thermophilic campylobacters cause gastroenteritis in humans. In particular, *C. jejuni* is known worldwide as a major enteropathogen causing as much enteric disease in man as *Salmonella* and *Shigella*. *C. jejuni* infects people of all ages. It is more frequently diagnosed in children than adults and the seasonal incidence shows it to be higher in the summer and fall than in winter or spring (Butzler and Skirrow, 1979). The organism is found in the intestinal tract of a wide variety of animals. Enteric infection in animals has been reported. Transmission is most likely oral or fecal-oral. *Campylobacter* enteritis is a foodborne disease with meat, milk, and water as most important vehicles.

Other members of the thermophilic species group are *C. coli*, *C. lari*, and *C. upsaliensis*, all of which are known to cause enteritis in humans and to be carried in the intestinal tract of a variety of animals, in particular pigs, pets (cats and dogs), and poultry. Varying isolation rates—which may be due to genuine differences in prevalence, to inappropriate isolation or identification procedures, or to any combination of these factors—have been reported. *C. jejuni* infection is a known antecedent of Guillain-Barré syndrome and is associated with axonal degeneration, slow recovery, and severe residual disability (Rees et al., 1995b; Jacobs et al., 1996; Nachamkin et al., 1998). *C. rectus* and other oral species are associated with periodontal disease in humans, and may cause infections in other parts of the body. *C. fetus* and *C. hyointestinalis* are primarily important in veterinary medicine, causing sporadic abortion in cattle and abortion in sheep (*C. fetus* subsp. *fetus*), abortion and reproductive problems in cattle (*C. fetus* subsp. *venerealis*), and enteric disease in pigs (*C. hyointestinalis*). *C. fetus* subsp. *fetus* also causes bacteremia in humans. Thus far, *C. mucosalis* and *C. helveticus* are the only species not isolated from human infections.

The pathogenicity mechanisms by which campylobacters cause gastroenteritis are unclear, and a good animal model is not available. As with other enteropathogens, motility, chemotaxis, adherence, invasion, and toxin production have been recognized as virulence properties (Ketley, 1997). Flagella, lipopolysaccharides, outer membrane proteins, and a carbohydrate moiety may act as adhesins. An enterotoxin immunologically related to cholera toxin, a heat-labile trypsin-sensitive cytotoxin, a cytotoxin active on Vero and HeLa cells, a cytolethal distending toxin, a shiga-like toxin, a hemolytic toxin, and a hepatotoxin have all been documented. Their role in disease remains unclear (Griffiths and Park, 1990; Ketley, 1995, 1997; Wassenaar, 1997).

*C. jejuni* and *C. coli* are susceptible to a variety of antimicrobial agents including macrolides, fluoroquinolones, aminoglycosides, chloramphenicol, and tetracycline (Nachamkin, 1995). Eryth-

romycin is the drug of choice for treating *C. jejuni* gastrointestinal infections, with ciprofloxacin as an alternative. However, considerable percentages of *C. coli* strains are resistant to erythromycin and emergence of fluoroquinolone resistance has been reported.

#### ENRICHMENT AND ISOLATION PROCEDURES

Isolation of *Campylobacter* species can be accomplished by two methods. The first involves filtration of the cells through membrane filters with a pore size of 0.45, 0.65, or 0.8  $\mu\text{m}$  using a nonselective agar medium or broth medium. *Campylobacter* cells are small and highly motile and can penetrate the filter. All agar plates or broth cultures must be incubated in a microaerobic atmosphere preferably containing both  $\text{CO}_2$  and  $\text{H}_2$ . Commercial products are available for establishing microaerobic environments. Microaerobic atmospheres without hydrogen will not allow growth of some *Campylobacter* species on commonly used agar bases.

The second method for isolating campylobacters is the use of selective agar media. A variety of different selective media has been described, some using blood agar, others a blood-free agar base as basal medium (Goossens et al., 1989; Griffiths and Park, 1990; Aspinall et al., 1993; Corry et al., 1995). However, none of these selective supplements supports growth of all of the *Campylobacter* species. Selective media reported to be suitable for the isolation of all thermophilic campylobacters including *C. upsaliensis* were reported by Burnens and Nicolet (1992) and Aspinall et al. (1996).

Incubation of inoculated media at 42–43°C will increase selectivity by the elimination or inhibition of many, but not all, other intestinal organisms and is particularly useful for the isolation of the thermotolerant campylobacters. It will, however, inhibit growth of some other *Campylobacter* species.

There is no gold standard for the routine isolation of all *Campylobacter* species. Simultaneous application of a microaerobic atmosphere containing hydrogen with a filtration method and a selective base is methodologically the optimal solution. However, *C. jejuni* and *C. coli*, the predominant species in human infection, can be readily grown in a microaerobic atmosphere on selective media without the necessity of using hydrogen. In order to evaluate the presence of other, less common species, appropriate culture conditions need to be applied.

#### MAINTENANCE PROCEDURES

Stock cultures of *Campylobacter* species can be maintained under microaerobic conditions by weekly transfer onto common blood agar bases. Addition of blood to media may increase survival. Cultures may be stored for many years by lyophilization, freezing at 80°C, or in liquid nitrogen. Cryoprotective agents such as 10% glycerol or DMSO should be added to cultures before freezing, and heavy cell concentrations should be used.

#### DIFFERENTIATION OF THE GENUS *CAMPYLOBACTER* FROM OTHER GENERA

Classical biochemical differentiation of the genus *Campylobacter* from related genera such as *Arcobacter* and *Helicobacter* is primarily achieved via the identification of the individual species. However, in general, campylobacters can be differentiated from arcobacters by the lower optimal growth temperatures (25–30°C compared to 30–42°C) and the aerotolerance of arcobacters. Analysis of respiratory quinones enables a clear differentiation of *Campylobacter* strains from *Arcobacter* or *Helicobacter* strains but is of limited value in a routine diagnostic laboratory.

#### TAXONOMIC COMMENTS

Since the creation of *Campylobacter* as a genus in 1963, a variety of Gram-negative, microaerobic to anaerobic, asaccharolytic, and oxidase-positive bacteria have been included in the genus. Phylogenetic work based on ribosomal RNA gene sequence analysis or hybridization experiments revealed within this ill-defined genus the presence of three independent subdivisions, each of which were subsequently given separate genus rank (Lau et al., 1987; Paster and Dewhirst, 1988; Thompson et al., 1988; Goodwin et al., 1989a; Vandamme et al., 1991a). The name *Campylobacter* was preserved for the lineage containing *C. fetus*, the type species. The genus *Arcobacter* was proposed to accommodate *C. nitrofigilis* and *C. cryaerophilus* and, later, *C. butzleri*, while the genus *Helicobacter* was proposed for *C. pylori* and *C. mustelae*, and, subsequently, *C. cinaedi* and *C. fennelliae*. In addition, several so-called free-living campylobacters (Laanbroek et al., 1977; Wolfe and Pfennig, 1977) were found to constitute a separate fourth branch and were later classified into the genus *Sulfurospirillum* (Schumacher et al., 1992). Since the 1991 revision of its taxonomy and nomenclature, the classification of the genus *Campylobacter* is primarily phylogeny based. It should be emphasized that this phylogeny-driven taxonomy unified species with extremely different cellular morphologies and a range in DNA base ratio that exceeds that of most well-defined genera. Although the present classification has been generally accepted, these anomalies remain unexplained.

There are taxonomic problems at the species and infraspecific level. The name *C. sputorum* subsp. *mucosalis* was validly published but subsequent DNA–DNA hybridization and 16S rRNA gene sequence analysis demonstrated that the more recent classification of this organism as a separate species, *C. mucosalis*, is correct (Roop et al., 1985a; Thompson et al., 1988). Also, although the names *C. sputorum* subsp. *sputorum* and *C. sputorum* subsp. *bubulus* have standing in nomenclature, recent taxonomic analyses demonstrated that it is more appropriate to abandon this subspecies classification and to consider both taxa as a single biovar: *C. sputorum* biovar *sputorum*. The organism previously known as “*Campylobacter fecalis*”, and a newly described taxon, represent two additional biovars of *C. sputorum* (biovar *faecalis* and biovar *paraureolyticus*, respectively) (On et al., 1998).

Another problem concerns the taxonomic position of phenotypically unusual thermophilic campylobacters referred to as nalidixic acid-sensitive campylobacters, urease-positive thermophilic campylobacters, and others (Endtz et al., 1997). One dimensional whole-cell protein electrophoresis (Owen et al., 1988; Vandamme et al., 1991b), rRNA gene sequence analysis (Alderton et al., 1995), and semiquantitative DNA–DNA hybridization (Mégraud et al., 1988) indicated that these taxa are closely related to, or belong to, *C. lari*, and these strains have been referred to as *C. lari* variants. Quantitative DNA–DNA hybridization experiments between *C. lari* and a reference strain of the urease-positive thermophilic *Campylobacter* group proved that it indeed belonged to *C. lari* (Vandamme et al., 1997c). Subsequent work reported by Endtz et al. (1997) described a striking heterogeneity among and within the different groups of *C. lari* variants. The exact relationships between genuine *C. lari* strains and the various biochemical variants and protein electrophoretic subtypes should be explored further by means of DNA–DNA hybridization experiments.

In addition, the separation of *C. jejuni* subsp. *jejuni* and *C. coli* remains an important taxonomic problem. These taxa are re-

markably similar by virtue of their overall phenotype and genotype and are often found in the same ecologic and pathologic niches. The most reliable and commonly used test is the hippurate hydrolysis test done according to the method of Hwang and Ederer (1975) as described by Harvey (1980), in which *C. coli* is negative. However, some strains of *C. jejuni* subsp. *jejuni* also give a negative result. Additional useful tests are hydrogen sulfide production in triple sugar iron agar and growth on a minimal medium (On et al., 1996). In contrast with *C. jejuni* subsp. *jejuni*, *C. coli* usually utilizes propionate when a commercial identification system (API Campy, bioMérieux, France) is used (Occhialini et al., 1996). Growth in 8% glucose and brilliant green media are not reliable traits for species identification (Skirrow and Benjamin, 1980). The complexity of this taxonomic area has been emphasized by data showing that strains first described as *C. hyoilei* (associated with porcine proliferative enteritis) are, in fact, *C. coli* (Vandamme et al., 1997c), despite a higher 16S rRNA gene sequence similarity to *C. jejuni* (Alderton et al., 1995). Moreover, the description of strains that closely resemble *C. coli*, yet are genotypically more divergent from the type strain (60% DNA–DNA relatedness) (Morris et al., 1985) than is usual, further emphasizes the problems associated with the taxonomy of the “thermotolerant campylobacters”. There is a need for better genotypic and phenotypic markers to further investigate relationships among members of this group. Further studies are required to evaluate the taxonomic (and indeed clinical) significance of both genomically divergent *C. coli*-like strains (Morris et al., 1985), and pig isolates that may be referred to as a “*hyoilei*” variant of *C. coli* (Vandamme et al., 1997c).

#### DIFFERENTIATION OF THE SPECIES OF THE GENUS *CAMPYLOBACTER*

Biochemical characteristics useful in distinguishing the various species of the genus *Campylobacter* are listed in Table BXII.ε.1. Additional descriptive characteristics are given in Table BXII.ε.2.

A variety of different methods has been applied for the identification of *Campylobacter* species; these methods have been recently reviewed by On (1996). Several authors studied the suitability of cellular fatty acid analysis for the differentiation and identification of campylobacters (reviewed by Vandamme and Goossens, 1992). Gas–liquid chromatography groups of *Campylobacter* species were defined by Lambert et al. (1987) and Goodwin et al. (1989b). Several of these gas–liquid chromatography groups consisted of more than one species, and several species have strains in different GLC groups. Additional phenotypic tests were often required for identification to the species level.

DNA probe- and PCR-based identification assays have been described for *C. fetus* (Ezaki et al., 1988; Chevrier et al., 1989;

The organisms listed in the “Other Organisms” section in the first edition of *Bergey’s Manual of Systematic Bacteriology* have all been formally classified. “*Campylobacter fecalis*” is a distinct biovar of *C. sputorum*. The nitrogen-fixing organisms from salt marsh plants (McClung and Patriquin, 1980) and the aerotolerant campylobacters (Neill et al., 1985) are now classified as *Arcobacter* species (Vandamme et al., 1991a). “*Spirillum* 5175” and the free-living organism described by Laanbroek et al. (1977) are classified in the genus *Sulfurospirillum* (Schumacher et al., 1992).

#### ACKNOWLEDGMENTS

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Wesley et al., 1991; Bastyns et al., 1994; Blom et al., 1995; Eaglesome et al., 1995; Hum et al., 1997); *C. hyointestinalis* (Chevrier et al., 1989; Gebhart et al., 1989; Wesley et al., 1991; Bastyns et al., 1994); *C. mucosalis* (Gebhart et al., 1989; Bastyns et al., 1994); *C. concisus* (Bastyns et al., 1995b); *C. sputorum* (Bastyns et al., 1994); *C. jejuni* (Stucki et al. 1995; Occhialini et al., 1996; Day et al., 1997; Gonzalez et al., 1997a; Linton et al., 1997; Vandamme et al., 1997c; van Doorn et al., 1997); *C. coli* (Gonzalez et al., 1997a; Linton et al., 1997; Vandamme et al., 1997c; van Doorn et al., 1997); *C. lari* (Linton et al. 1996; Oyarzabal et al., 1997; van Doorn et al., 1997); *C. upsaliensis* (Lawson et al., 1997; van Doorn et al., 1997); and *C. helveticus* (Stanley et al., 1992; Lawson et al., 1997). Broad-spectrum molecular identification schemata based on restriction fragment analysis of PCR amplicons derived from 16S (Cardarelli-Leite et al., 1996) and 23S (Hurtado and Owen, 1997a) rRNA genes have also been described.

#### List of species of the genus *Campylobacter*

1. ***Campylobacter fetus*** (Smith and Taylor 1919) Sebald and Véron 1963, 907<sup>AL</sup> (*Vibrio fetus* Smith and Taylor 1919, 301.) *fetus*. L. masc. n. *fetus* fruit; L. gen. masc. n. *fetus* of a fetus.

Slender curved rods that are 0.2–0.3 × 1.5–5 μm. They appear comma-, S-, and gull-shaped. The ends of the cells are pointed. Loosely wound spiral filaments up to 8 μm long appear in old cultures. Spherical or coccoid forms are also found in old cultures especially when grown on agar plates.

Very actively motile with a characteristic darting and corkscrewlike motion. Motility and rotation of the cells are

so rapid the curvature of the cells may be overlooked. Best observed with a phase-contrast microscope.

Several types of colonies are found on agar on primary isolation (Bryner et al., 1962). Smooth colonies, the most frequently found, are small, 0.5 mm in diameter, round, slightly raised, smooth, colorless, and slightly translucent. “Cut-glass” colonies are 1 mm in diameter, round, raised, translucent, and granular with reflecting facets. Rough colonies are rare and similar to smooth colonies with the exception of being granular and more opaque. Mucoid colonies are similar to smooth and cut-glass colonies but are

TABLE BXII.ε.1. Differential characters for *Campylobacter* spp. and *Bacteroides ureolyticus*<sup>a</sup>

Characteristic	<i>C. fetus</i> subsp. <i>fetus</i>	<i>C. fetus</i> subsp. <i>venerialis</i>	<i>C. coli</i>	<i>C. concisus</i>	<i>C. curvus</i>	<i>C. gracilis</i>	<i>C. helveticus</i>	<i>C. hominis</i>	<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	<i>C. hyointestinalis</i> subsp. <i>lawsonii</i>	<i>C. jejuni</i> subsp. <i>jejuni</i>	<i>C. jejuni</i> subsp. <i>doylei</i>	<i>C. lamienae</i>	<i>C. lari</i>	<i>C. mucosalis</i>	<i>C. rectus</i>	<i>C. showae</i>	<i>C. sputorum</i>	<i>C. upsaliensis</i>	<i>B. ureolyticus</i>
Catalase	+	M	+	-	-	F	-	-	+	+	+	M	+	+	-	F	+	V	-	F
Urease	-	-	-	-	-	-	-	-	-	-	-	-	-	V	-	-	-	V	-	+
Indoxyl acetate hydrolysis	-	-	+	-	M	M	+	-	-	-	+	+	-	-	-	+	-	-	+	-
Hippurate hydrolysis	-	-	-	-	F	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-
Nitrate reduction	+	M	+	F	+	M	+	-	+	+	+	-	+	+	-	+	+	+	+	+
Selenite reduction	M	-	+	F	-	-	-	-	+	+	+	-	+	+	-	+	+	+	+	-
H <sub>2</sub> S/TSI	-	-	F <sup>b</sup>	- <sup>b</sup>	F	-	-	-	M <sup>b</sup>	M <sup>c</sup>	-	-	-	-	+	-	F	+	-	-
25°C	+	M	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
42°C	M	-	+	M	M	M	+	F	+	+	+	-	+	+	+	F	F	+	M	M
1% glycine	+	-	+	F	+	+	F	+	+	F	M	F	-	+	F	+	F	+	+	+

<sup>a</sup>Symbols: +, 95–100% strains positive; -, 0–11% strains positive; V, test result varies between defined infrasubspecific taxa (see text for details); F, 14–50% strains positive; M, 60–93% strains positive. All data are based on reactions obtained by using recommended, standardized procedures (On and Holmes 1991, 1992, 1995).

<sup>b</sup>Trace quantities.

<sup>c</sup>Copious quantities.

TABLE BXII.ε.2. Additional diagnostic tests for *Campylobacter* spp. and *Bacteroides ureolyticus*<sup>a</sup>

Characteristic	<i>C. fetus</i> subsp. <i>fetus</i>	<i>C. fetus</i> subsp. <i>venerialis</i>	<i>C. coli</i>	<i>C. concisus</i>	<i>C. curvus</i>	<i>C. gracilis</i>	<i>C. helveticus</i>	<i>C. hominis</i>	<i>C. hyointestinalis</i> subsp. <i>hyointestinalis</i>	<i>C. hyointestinalis</i> subsp. <i>lawsonii</i>	<i>C. jejuni</i> subsp. <i>jejuni</i>	<i>C. jejuni</i> subsp. <i>doylei</i>	<i>C. lamienae</i>	<i>C. lari</i>	<i>C. mucosalis</i>	<i>C. rectus</i>	<i>C. showae</i>	<i>C. sputorum</i>	<i>C. upsaliensis</i>	<i>B. ureolyticus</i>
Oxidase	+	+	+	M	+	-	+	+	+	+	+	+	+	+	+	+	F	+	+	+
2.0% NaCl	-	-	-	F	F	F	-	M	-	-	-	-	-	M	M	M	+	+	-	+
2.0% ox-bile	+	M	M	F	-	-	F	F	+	-	M	-	-	+	M	-	-	I	+	-
Growth on minimal medium	F	M	+	-	M	F	-	-	M	M	-	-	-	-	-	-	F	I	-	F
Nalidixic acid	+	M	-	M	+	M	-	M	+	+	-	-	+	V	M	M	-	M	-	-
Metronidazole	M	F	+	F	-	-	F	-	-	I	M	F	+	+	M	-	+	F	M	-
Sodium fluoride	M	M	+	M	-	M	-	+	M	-	+	-	I	+	-	-	+	M	-	+
KMnO <sub>4</sub>	+	F	+	-	M	+	-	-	F	-	+	M	-	F	-	-	-	-	-	-
0.02% safranin	+	M	+	F	+	+	-	-	+	+	+	-	F	+	+	-	-	I	+	F

<sup>a</sup>Symbols: +, 95–100% strains positive; -, 0–11% strains positive; V, test result varies between defined infrasubspecific taxa (see text for details); F, 14–50% strains positive; M, 60–93% strains positive; I, irreproducible. All data are based on reactions obtained by using recommended, standardized procedures (On and Holmes 1991, 1992, 1995).

viscid. On primary isolation, colonies sometimes occur as a thin veil of confluent growth that is translucent and a very light gray or tan color. Colonies on blood agar are nonhemolytic, round, 1 mm in diameter, smooth, raised, convex, and grayish white in appearance. Strains will grow on media containing 1.0–1.5% ox-bile and at 30°C, but not on media containing 0.04% triphenyl-tetrazolium chloride.

Most strains are tolerant to 0.032% methyl orange and 0.1% sodium deoxycholate.

Although the two subspecies of *C. fetus* are associated with distinct diseases in animals, their differentiation is not straightforward. Classical biochemical tests useful for the differentiation of these taxa are tolerance to glycine and the ability to produce hydrogen sulfide. Whole-cell protein

electrophoresis does not separate the two taxa (Vandamme et al., 1991b). Salama et al. (1992a) reported the genomes of *C. fetus* subsp. *fetus* strains to be smaller (1.1 Mb) than those of *C. fetus* subsp. *venerealis* strains (1.3–1.5 MB). General differences between the *Sma*I-based macrorestriction profiles of the two subspecies have also been noted (Hum et al., 1997). A PCR-based assay designed for species and subspecies identification was 98% specific (Hum et al., 1997).

Erythromycin, ampicillin, or third-generation cephalosporins are usually effective against *C. fetus* infections (Neuzil et al., 1994). Aminoglycosides, ampicillin, and chloramphenicol have been successfully used to treat central nervous system or other serious infections caused by *C. fetus*.

*The mol% G + C of the DNA is:* 32–36 ( $T_m$ ).

*Type strain:* CIP 5396, ATCC 27324, CCUG 6823, DSM 5361, LMG 6442, NCTC 10842.

*GenBank accession number (16S rRNA):* LO4314, M65012.

- a. ***Campylobacter fetus* subsp. *fetus*** Véron and Chatelain 1973, 126<sup>AL</sup> (*Vibrio fetus* biovar intestinalis Florent 1959, 955; *Vibrio foetusovis* Buxton 1929, 47; *Campylobacter fetus* subsp. *intestinalis* Smibert 1974, 209.)

Morphology and characteristics as for species except as noted. Intermediate-sized spirals with an average wavelength of 1.8  $\mu$ m and an average amplitude of 0.55  $\mu$ m (Karmali et al., 1981a). Several types of colonies are found on agar on primary isolation (Bryner et al., 1962). Smooth colonies are 1 mm in diameter, colorless to slightly cream colored. Rough colonies are small, round, finely granular, opaque and white to cream or tan colored. They are 1–2 mm in diameter. “Cut-glass” colonies do not develop in primary cultures. Smooth colonies incubated for 6–8 days become mucoid. Upon subculture, smooth cut-glass and rough cut-glass colonies appear, as well as smooth colonies. On primary isolation, colonies are frequently low, flat, grayish to tan colored, and translucent with an irregular edge. They spread along the direction of the streak and coalesce. They may also form a thin veil of confluent growth on agar plates. Colonies on blood agar are nonhemolytic, round, 1–2 mm in diameter, smooth, convex, and grayish white or light tan colored. Grow on media containing 0.05% safranin and 64 mg/l cefoperazone.

Pathogenic. Cause of abortion in sheep and sporadic abortion in cattle, as well as a cause of human blood and, occasionally, gastrointestinal infections. Transmitted orally. Isolated from the placentas and stomach content of fetuses from aborted sheep and cattle and from the blood, intestinal content, and bile of infected ewes and cattle. Isolated from blood, spinal fluid, aborted fetuses, and abscesses from most parts of the body of humans. This organism will grow in the intestinal tract and gallbladder of man and animals (Bryner et al., 1964).

*The mol% G + C of the DNA is:* 33–36 ( $T_m$ ).

*Type strain:* CIP 5396, ATCC 27324, CCUG 6823, DSM 5361, LMG 6442, NCTC 10842.

*GenBank accession number (16S rRNA):* LO4314, M65012.

- b. ***Campylobacter fetus* subsp. *venerealis*** (Florent 1959) Véron and Chatelain 1973, 126<sup>AL</sup> (*Vibrio fetus* biovar vene-

realis Florent 1959, 955; *Campylobacter fetus* subsp. *fetus* Smibert 1974, 209.)

*ve.né' re.al.is.* L. *venereus* from Venus goddess of love; L. adj. *venereal* L. gen. n. *venerealis* of Venus, goddess of love.

Morphology and characteristics are for species except as noted. Large spirals with an average wavelength of 2.43  $\mu$ m and an average amplitude of 0.73  $\mu$ m (Karmali et al., 1981a). Approximately 67% and 7% of strains will grow on 0.05% safranin- and 64 mg/l cefoperazone-containing media (On et al., 1996), respectively.

Pathogenic. A cause of abortion and infertility in cattle. Transmitted venereally. Found in the vaginal mucus of infected cows, the semen and prepuce of bulls, and in the placenta and tissues of aborted bovine fetuses. Pathogenic for cattle, guinea pigs, hamsters, and embryonated chicken eggs. Rarely isolated from human blood. Not pathogenic for rabbits, mice, or rats when injected intraperitoneally. Will not multiply in the intestinal tract of man and animals (Bryner et al., 1964).

*The mol% G + C of the DNA is:* 33–36 ( $T_m$ ).

*Type strain:* CIP 68.29, ATCC 19483, CCUG 538, LMG 6443, NCTC 10354.

*GenBank accession number (16S rRNA):* L14633, M65011.

2. ***Campylobacter coli*** (Doyle 1948) Véron and Chatain 1973, 127<sup>AL</sup> (*Vibrio coli* Doyle 1948, 50; *Campylobacter hyoilei* Alderton, Korolik, Coloe, Dewhirst and Paster 1995, 65.) *co'li.* Gr. n. *colon* large intestine, colon; M.L. gen. n. *coli* of the colon.

Small, tightly coiled spiral, S-shaped or curved cells, 0.2–0.3  $\times$  1.5–5.0  $\mu$ m that transform rapidly to coccoid forms with age, or exposure to toxic concentrations of oxygen (Ng et al., 1985; Moran and Upton, 1987). Colonies are round, 1–2 mm in diameter, raised, convex, smooth, and glistening. On moist media, colonies are flat, grayish, and spread in the direction of the streak. Most, but not all strains are nonhemolytic. As with *C. jejuni*, the hemolytic activity (where noted) is usually cell-associated, with a possible secreted component also involved (Wassenaar, 1997). Blood enhances, but is not essential for, culture. Strains grow on solid media containing 1.0–1.5% ox-bile, 0.02% safranin, 32 mg/l cephalothin, and 0.04% triphenyl-tetrazolium chloride. Reduction of the latter substrate is also observed. Most (~76%) strains are resistant to 100 U/l 5-fluorouracil. As with *C. jejuni* subsp. *jejuni*, the proportion of strains that are resistant to the antibiotics nalidixic acid, tetracycline, chloramphenicol, kanamycin, and erythromycin (and related compounds) may significantly vary. However, in comparison with *C. jejuni*, a greater percentage of *C. coli* strains exhibit resistance to erythromycin. The genetic mechanisms determining these traits have been reviewed by Taylor (1992a, b) and Taylor and Courvalin (1988); several (tetracycline, chloramphenicol, kanamycin) are known to be plasmid borne. Aarestrup et al. (1997) showed that >90% of isolates from humans, pigs, and broiler chickens were sensitive to ampicillin (16 mg/l), apramycin (4 mg/l), carbadox (4 mg/l), chloramphenicol (8 mg/l), colistin (16 mg/l), enrofloxacin (16 mg/l), gentamicin (1 mg/l), nalidixic acid (128 mg/l), neomycin (4 mg/l), olaquinox (8 mg/l), spectinomycin (16 mg/l), spiramycin (128 mg/l), and tetracycline (2 mg/l). Aarestrup et al. (1997) determined that

13.8% and 61.7% of isolates showed resistance to streptomycin and tylosin, respectively, beyond the maximum minimal inhibitory concentration (MIC: 128 mg/l) used. *In vitro* activities of 47 antimicrobial agents toward *C. coli* were determined by Gebhart et al. (1985b).

As with *C. jejuni*, plasmid carriage in *C. coli* demonstrates considerable variation by virtue of plasmid presence in a given population, number, and size range (Tenover et al., 1985). It has been noted that conjugative plasmids conferring resistance to tetracycline, kanamycin, and chloramphenicol are more common in *C. coli* than in *C. jejuni* (Taylor, 1992b).

Differentiating *C. coli* from *C. jejuni* subsp. *jejuni* is difficult. The most common biochemical test used for this purpose is hippurate hydrolysis, for which *C. coli* is negative. However, some strains of *C. jejuni* subsp. *jejuni* also give a negative result. Additional tests that are of use were discussed above.

The taxonomic position of 11 isolates from lesions of proliferative enteritis in pigs was studied by Alderton et al. (1995), who considered the strains to represent a species closely related to both *C. coli* and *C. jejuni*. These authors subsequently proposed the name *Campylobacter hyoilei* for these strains. However, the taxonomic position of *C. hyoilei* was reevaluated by Vandamme et al. (1997c) using a range of phenotypic and genotypic methods, and, crucially, a classical quantitative DNA-DNA hybridization method. These data showed *C. hyoilei* to be indistinguishable from *C. coli*. Vandamme et al. (1997c) proposed that the two species be regarded as synonymous, with *C. coli* taking nomenclatural precedence. It was nonetheless noted that strains originally described as *C. hyoilei* may represent a variant of *C. coli* that is highly adapted for the porcine enteric tract, with pathological consequences for the animal.

Pathogenic. Causes diarrhea, septicemia, and occasionally abortion in humans. May cause diarrhea in pigs and monkeys and abortion in rodents. Has been associated with hepatitis in certain bird species. Certain strains have been associated with proliferative enteritis in pigs.

*The mol% G + C of the DNA is:* 31–35 ( $T_m$ ).

*Type strain:* CIP 7080, ATCC 33559, CCUG 11283, LMG 8847, NCTC 11366.

*GenBank accession number (16S rRNA):* L04312, M59073, L19738.

3. **Campylobacter concisus** Tanner, Badger, Lai, Listgarten, Visconti and Socransky 1981, 442<sup>VP</sup>  
*con.ci'* *sus.* L. part. adj. *concisus* brief, concise.

Cells are small and curved,  $0.5 \times 4 \mu\text{m}$ , with rounded ends. Rapid darting motility by means of a single polar flagellum. A membrane-like polar cap occurs at the ends of the cells. Colonies are convex, translucent, 1 mm in diameter, with entire edges. The agar is not pitted by the colonies. Does not grow microaerobically on common agar bases in an atmosphere without hydrogen. Will not grow in semisolid medium (0.16% agar), in air, or in an atmosphere containing  $\text{O}_2/\text{CO}_2/\text{N}_2$  (5:10:85). Anaerobic growth occurs with formate and fumarate in the medium. Formate is oxidized to hydrogen and  $\text{CO}_2$ ; and fumarate is reduced to succinate, which accumulates in the medium. Growth is stimulated by nitrate, formate, and fumarate. End products of metabolism when grown in a medium with formate and

fumarate are acetate, succinate, and  $\text{H}_2$ . Strains do not grow on MacConkey agar or on media containing 3.5% NaCl, 32 mg/l cephalothin, 64 mg/l cefoperazone, or 0.04% triphenyl-tetrazolium chloride. Most strains (70–80%) produce alkaline phosphatase and grow on media containing 0.032% methyl orange and 0.05% sodium fluoride. A few strains (14–29%) grow in the presence of 0.01% Janus green and 0.005% basic fuchsin.

Minimum inhibitory concentrations of antibiotics are ( $\mu\text{g}/\text{ml}$ ): bacitracin, 128; chloramphenicol, 4.0; clindamycin, 24; colistin, 0.5–1.0; erythromycin, 4.0; gentamicin, 24; kanamycin, 12; metronidazole, 0.5–2.0; minocycline, 2; nalidixic acid, 64–128; neomycin, 16–32; penicillin, 0.5–4.0; polymyxin, 0.25–1.0; rifampin, 16–64; streptomycin, 12; tetracycline, 12; and vancomycin, 128. *C. concisus* strains were shown to be chemotactic toward formate (Paster and Gibbons, 1986). Whole-cell protein electrophoresis and DNA-DNA hybridization experiments (Vandamme et al., 1989; Van Etterijk et al., 1996) revealed that this is a heterogeneous species comprising many protein electrophoretic and several genotypic subgroups. The species is also phenotypically diverse (On et al., 1996), making definitive identification difficult. Found in the gingival crevices of humans with gingivitis, periodontitis, and periodontosis; in normal and diarrhetic feces of humans, in human blood, and in human stomach and esophagus specimens.

*The mol% G + C of the DNA is:* 37–41 ( $T_m$ ).

*Type strain:* FDC 484, ATCC 33237, CCUG 13144, LMG 7788, NCTC 11485.

*GenBank accession number (16S rRNA):* L04322.

4. **Campylobacter curvus** (Tanner, Listgarten and Ebersole 1984) Vandamme, Falsen, Rossau, Hoste, Segers, Tytgat and De Ley 1991a, 98<sup>VP</sup> (*Wolinella curva* Tanner, Listgarten and Ebersole 1984, 279.)

*curv'us.* L. adj. *curvus* curved.

Cells are small and curved,  $0.5\text{--}1 \times 2\text{--}6 \mu\text{m}$ , with rounded or tapered ends. Helical or straight cells also occur. A membrane-like polar cap occurs at the ends of the cells. Rapid darting motility. Motile by means of a single polar flagellum or bipolar flagella. Translucent colonies are produced on blood agar bases. Different colony types are observed: small pinpoint colonies, 1 mm in diameter or spreading colonies up to 5 mm in diameter. Agar pitting is medium dependent; this trait was not seen in anaerobic, 3-d-old cultures on 5% blood agar (On et al., 1996).

Does not grow microaerobically on common agar bases in an atmosphere without hydrogen. Will not grow in air, in a  $\text{CO}_2$ -enriched atmosphere, or in an atmosphere containing  $\text{O}_2/\text{CO}_2/\text{N}_2$  (5:10:85) on common agar bases. Anaerobic growth occurs with formate and fumarate in the medium. Hydrogen and formate are used as energy sources. Formate is oxidized to hydrogen and  $\text{CO}_2$ ; and fumarate is reduced to succinate. Fumarate, nitrate, aspartate, asparagine, and malate serve as electron acceptors. Membrane-bound cytochrome *b*, cytochrome *c*, and CO-binding cytochrome *c*, and soluble cytochrome *c* and CO-binding cytochrome *c* are present. Strains grow in the presence of 0.005% basic fuchsin and 0.04% triphenyl-tetrazolium chloride; reduction of the latter is concurrently seen in many strains (60%). Most strains (80%) will grow on media containing 64 mg/l cefoperazone, 0.1% potassium perman-

ganate, and 0.01% Janus green. Alkaline phosphatase activity has been detected in 40% of strains.

Minimum inhibitory concentrations of antibiotics are ( $\mu\text{g/ml}$ ): bacitracin, >128; chloramphenicol, 2–4; clindamycin, 0.5–1; colistin, 4; erythromycin, 2; gentamicin, 2; kanamycin, 4–8; metronidazole, 1–2; minocycline, 2–4; nalidixic acid, 64–128; neomycin, 4–8; penicillin, 32; polymyxin B, 8; rifampin, 128 to >128; streptomycin, 2; tetracycline, 1; and vancomycin, >128. Strains were isolated from lesions in human oral cavities, from a blood culture, peritoneal fluid, and from normal and diarrheic feces of humans.

*The mol% G + C of the DNA is:* 43–47 ( $T_m$ ).

*Type strain:* VPI 9584, ATCC 35224, CCUG 13146, DSM 6644, LMG 7609.

*GenBank accession number (16S rRNA):* L04313.

5. **Campylobacter gracilis** (Tanner, Badger, Lai, Listgarten, Visconti and Socransky 1981) Vandamme, Daneshvar, Dewhirst, Paster, Kersters, Goossens and Moss 1995a, 151<sup>VP</sup> (*Bacteroides gracilis* Tanner, Badger, Lai, Listgarten, Visconti and Socransky 1981, 442.)

*gr'cil.is.* L. adj. *gracilis* slim, slender, thin.

Cells are small and straight,  $0.4 \times 4\text{--}6 \mu\text{m}$ , with rounded or tapered ends. Nonmotile. Intracytoplasmic, electron-dense inclusions, some membrane-bound, approximately 40 nm in diameter have been observed. Translucent colonies are produced on blood agar bases. Different colony types are observed: small pinpoint colonies, 1 mm in diameter or spreading colonies up to 5 mm in diameter. Agar pitting is medium dependent; this trait was not seen in anaerobic, 3-d-old cultures on 5% blood agar (On et al., 1996).

Optimal growth in anaerobic conditions. Does not grow microaerobically on common agar bases in an atmosphere without hydrogen. Will not grow in air, in a  $\text{CO}_2$ -enriched atmosphere, or in an atmosphere containing  $\text{O}_2/\text{CO}_2/\text{N}_2$  (5:10:85) on common agar bases. Anaerobic growth occurs with formate and fumarate in the medium. Hydrogen and formate are used as energy sources. Formate is oxidized to hydrogen and  $\text{CO}_2$ , and fumarate is reduced to succinate. Fumarate, nitrate, nitrite, neutral red, benzyl viologen aspartate, asparagine, and malate serve as electron acceptors. Membrane-bound cytochrome *b*, cytochrome *c*, and CO-binding cytochrome *c*, and soluble cytochrome *c* and CO-binding cytochrome *c* are present. Strains will grow in the presence of 0.1% potassium permanganate and 0.05% basic fuchsin. Strains do not grow in the presence of 0.04% triphenyl-tetrazolium chloride, or 64 mg/l cefoperazone. A few strains (14%) grow on 0.01% Janus green medium. Alkaline phosphatase activity is not detected.

*C. gracilis* is the only oxidase-negative *Campylobacter* species. However, the pattern of cytochromes found in *C. gracilis* resembles that reported for other *Campylobacter* species in that it possesses cytochromes *b*, *c*, and CO-binding cytochrome *c* and does not possess detectable cytochromes *a* and *d*. Oxidase activity, as determined in the Kovacs test, is associated with cytochrome *c* and oxygen respiration, which is present in all *Campylobacter* species. Possible explanations for the failure to detect oxidase activity may be an incapability of the reagent to penetrate the cellular membranes, or the presence of a low-potential cytochrome *c* that cannot oxidize this reagent.

A group of bile-resistant *C. gracilis*-like organisms was recently reclassified in a novel genus *Sutterella* (Wexler et al., 1996a). This taxon is phylogenetically distinct from the campylobacters. Cellular fatty acid analysis, differences in dehydrogenase enzymes mobilities, and higher resistance to antimicrobial agents are useful to distinguish *Sutterella* strains from *C. gracilis*.

Minimum inhibitory concentrations of antibiotics are ( $\mu\text{g/ml}$ ): bacitracin, >128; chloramphenicol, 2–8; clindamycin, 0.25–0.5; colistin, 0.5–1; erythromycin, 1–2; gentamicin, 2–4; kanamycin, <0.50–2; metronidazole, 0.12–1; minocycline, <0.5–2; nalidixic acid, 16–128; neomycin, 16–32; penicillin, 1–32; polymyxin B, <0.25–1; rifampin, 4–32; streptomycin, 1–2; tetracycline, 1–8; vancomycin, >128, amoxicillin/clavulanate, 0.06–0.5; cefoxitin, 1–16; ceftizoxime, 0.25–1; ceftriaxone, 0.016–0.25; meropenem, 0.03; piperacillin, 2–26; piperacillin/tazobactam, 0.016–4; and ticarcillin/clavulanate, 0.016. In general, *C. gracilis* is very susceptible to antimicrobial agents active against anaerobic bacteria.

Strains have been isolated from gingival crevices and from visceral, head, and neck infections; in soft tissue abscesses; pneumonia; empyema; and an ischial wound in humans. The association of *C. gracilis* with serious deep tissue infection, coupled with a high frequency of antibiotic resistance, suggests that its pathogenic role might be underestimated.

*The mol% G + C of the DNA is:* 44–46 ( $T_m$ ).

*Type strain:* FDC 1084, ATCC 33236, CCUG 27720.

*GenBank accession number (16S rRNA):* L04320.

6. **Campylobacter helveticus** Stanley, Burnens, Linton, On, Costas and Owen 1993a, 398<sup>VP</sup> (Effective publication: Stanley, Burnens, Linton, On, Costas and Owen 1992, 2302.) *hel.ve'ti.cus.* L. adj. *helveticus* referring to Swiss, after the country of first isolation.

Cells are small curved, S-shaped, or helical rods,  $0.2 \times 1.5\text{--}3 \mu\text{m}$ , with rounded ends. Rapid darting motility. Motile by means of single bipolar flagella. Translucent, flat colonies, pinpoint to 0.5 mm in diameter are produced on blood agar bases after 48 h. Swarming may occur on moist agar surfaces. Grows microaerobically in the absence of hydrogen. Will not grow in air or in a  $\text{CO}_2$ -enriched atmosphere. The species is phenotypically, genotypically, and phylogenetically similar to *C. upsaliensis*, also a common inhabitant of domestic pets. *C. helveticus* grows on media containing 1.0–1.5% ox-bile and 100 U/15-fluorouracil, but not on potato starch or MacConkey agars. Sensitive to 32 mg/l cephalothin; some strains (22–44%) resistant to 64 mg/l cefoperazone.

Strains have been isolated from feces of diarrheic and asymptomatic domestic cats, more rarely from dogs. Pathogenicity is unknown.

*The mol% G + C of the DNA is:* 34 ( $T_m$ ).

*Type strain:* ATCC 51209, CCUG 30682, LMG 12638, NCTC 12470.

*GenBank accession number (16S rRNA):* U03022.

7. **Campylobacter hominis** Lawson, On, Logan and Stanley 2001, 658<sup>VP</sup> *hom.in'i.s.* L. gen. n. *hominis* of man, from which the bacterium was first isolated.

Cells are small and straight,  $0.25\text{--}0.5 \times 0.5\text{--}1.8 \mu\text{m}$  (after 10 days of incubation) with blunt ends. Nonmotile. Some isolates produce irregular fimbria-like structures which are  $4\text{--}8 \text{ nm}$  wide and  $>1.0 \mu\text{m}$  long. Gray pinpoint colonies may be convex and entire or spreading and irregular on blood agar base media. No agar pitting is observed. Optimal growth in anaerobic conditions at  $37^\circ\text{C}$ . No growth in anaerobiosis at room temperature,  $25^\circ\text{C}$ , or  $42^\circ\text{C}$ . Poor growth, if any, under microaerobiosis with 2% hydrogen. Will not grow in air, in a  $\text{CO}_2$ -enriched atmosphere, or in an atmosphere containing 5%  $\text{O}_2$ , 10%  $\text{CO}_2$  and 85%  $\text{N}_2$  on common agar bases. Strains grow in the presence of 0.1% sodium fluoride, but not in the presence of 0.04% triphenyltetrazolium chloride. Alkaline phosphatase activity has not been detected. Strains have been isolated from asymptomatic human feces. Pathogenicity, if any, is unknown.

*The mol% G + C of the DNA is:* 32–33 ( $T_m$ ).

*Type strain:* CH001A, LMG 19568, NCTC 13146.

*GenBank accession number (16S rRNA):* AJ251584.

8. **Campylobacter hyointestinalis** Gebhart, Edmonds, Ward, Kurtz and Brenner 1985a, 535<sup>VP</sup> (Effective publication: Gebhart, Edmonds, Ward, Kurtz and Brenner 1985b, 718.) *hy.o.in.tes'tin.al.is*. Gr. n. *hys*, *hyos* a hog; M.L. adj. *intestinalis* pertaining to the intestines; M.L. gen. n. *hyointestinalis* of a hog's intestine.

Cells are loosely spiraled, curved rods with characteristic darting motility due to a single polar flagellum. Occasionally, cells with two flagella at one pole have been observed. Cells are  $0.2\text{--}0.5 \times 1.2\text{--}2.5 \mu\text{m}$ . Filamentous forms, not coccoid bodies, are seen in old cultures. After 48 h of incubation, colonies are  $1.5\text{--}2.0 \text{ mm}$  in diameter, circular, and convex and do not swarm on moist media; they typically have a dirty yellowish color and are slightly mucoid.

When grown on common blood agar bases, only some strains grow microaerobically without hydrogen. All strains grow microaerobically in the presence of hydrogen. Many strains are weakly  $\alpha$ -hemolytic; this is normally accompanied by a greenish hue around the bacterial growth. Strains grow in the presence of 1.0% ox-bile and 0.032% methyl orange. Most strains (~85%) are sensitive to cephalothin (32 mg/l).

Whole-cell protein electrophoretic analysis has revealed considerable protein electrophoretic diversity within this species and it has been suggested that this diversity offers potential for typing studies (Vandamme et al., 1990, 1991b; On et al., 1993). In addition, pulsed-field gel electrophoresis of large genomic fragments was shown to be a useful typing method (Salama et al., 1992b; On and Vandamme, 1997). Plasmids of about 38 mDa and 1.6 mDa in size were reported in some strains by Boosinger et al. (1990). Selective media were developed by different researchers (reviewed by Ohya et al., 1988). On and Vandamme (1997) reported additional groups of *C. hyointestinalis*-like bacteria; the exact taxonomic status of the "subgroup 3" and "subgroup 4" strains is at present unknown.

Minimum inhibitory concentrations of antibiotics are ( $\mu\text{g/ml}$ ): bacitracin,  $>128$ ; chloramphenicol, 2–8; clindamycin, 0.25–0.5; colistin, 0.5–1; erythromycin, 1–2; gentamicin, 2–4; kanamycin,  $<0.5\text{--}2$ ; metronidazole, 0.12–1; minocycline,  $<0.5\text{--}2$ ; nalidixic acid, 16 to  $>128$ ; neomycin, 16–32; penicillin, 1–32; polymyxin B,  $<0.25\text{--}1$ ; rifampin, 4–32; streptomycin, 1–2; tetracycline, 1–8; vancomycin,  $>128$ ,

amoxicillin/clavulanate, 0.06–0.5; cefoxitin, 1–16; ceftizoxime, 0.25–1; ceftriaxone, 0.016–0.25; meropenem, 0.03; piperacillin, 2–26; piperacillin/tazobactam, 0.016–4; and ticarcillin/clavulanate, 0.016. *In vitro* activities of 47 antimicrobial agents toward *C. hyointestinalis* were determined by Gebhart et al. (1985b). Isolated from the intestines of pigs and hamsters, the stomach 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 mol% G + C of the DNA is:* 31–36 ( $T_m$ ).

*Type strain:* 80-4577-4, ATCC 35217, CCUG 14169, LMG 7817, NCTC 11608.

*GenBank accession number (16S rRNA):* M65010, AF097689.

- a. **Campylobacter hyointestinalis subsp. hyointestinalis** (Gebhart, Edmonds, Ward, Kurtz and Brenner 1985b) On, Bloch, Holmes, Hoste and Vandamme 1995, 773<sup>VP</sup> (*Campylobacter hyointestinalis* Gebhart, Edmonds, Ward, Kurtz and Brenner 1985b, 718.)

Morphology and characteristics as for species, except as noted. Strains grow in the presence of 0.01% Janus green. Most strains grow in the presence of 1.5% ox-bile. Alkaline phosphatase activity has not been reported. Isolated from the intestines of pigs and hamsters, and cattle, deer, and human feces. May be associated with porcine proliferative enteritis and diarrhea in animals and humans. Pathogenicity is not known.

*The mol% G + C of the DNA is:* 33–36 ( $T_m$ ).

*Type strain:* 80-4577-4, ATCC 35217, CCUG 14169, LMG 7817, NCTC 11608.

*GenBank accession number (16S rRNA):* M65010, AF097689.

- b. **Campylobacter hyointestinalis subsp. lawsonii** On, Bloch, Holmes, Hoste and Vandamme 1995, 773<sup>VP</sup> *law.so'ni.i*. N.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 *Lawsonia intracellularis*.

Cells are loosely spiraled, curved rods. Cells are  $0.2 \times 1.42 \mu\text{m}$ . Morphology and characteristics as for species, except as noted. Few (11%) strains can grow on 1.5% bile media. Alkaline phosphatase activity has been seen in ~22% of strains. 44% of strains can grow on 0.01% Janus green medium. Isolated from the stomach of pigs. Pathogenicity is not known.

*The mol% G + C of the DNA is:* 31–33 ( $T_m$ ).

*Type strain:* CHY5, CCUG 34538, LMG 14432, NCTC 12901.

*GenBank accession number (16S rRNA):* AF097685.

9. **Campylobacter jejuni** (Jones, Orcutt and Little 1931) Véron and Chatelain 1973, 128<sup>AL</sup> (*Vibrio jejuni* Jones, Orcutt and Little 1931, 861; *Vibrio hepaticus* Mathey and Rissberger 1964 1339; *Campylobacter fetus* subsp. *jejuni* Smibert 1974, 209.) *je.ju'ni*. M.L. gen. neut. n. *jejuni* of the jejunum.

Small, tightly coiled spiral or S-shaped cells (average wavelength  $1.12 \mu\text{m}$  and average amplitude of coils is  $0.48 \mu\text{m}$ ) which transform rapidly to coccoid forms with age, or exposure to toxic concentrations of oxygen (Ng et

al., 1985; Moran and Upton, 1987). Electron microscopic studies reveal a ring-shaped cellular form that may represent an intermediate form between spiral and coccoid cells (Ng et al., 1985). Two types of colonies may be observed (Smibert, 1965, 1969). The first has a low, flat, grayish, finely granular, and translucent appearance with an irregular edge, and a tendency to spread along the direction of the streak, and to swarm and coalesce. The second is round (1–2 mm diameter), raised, convex, smooth, shiny, with an entire, translucent edge and a darker, opaque center. Most strains are weakly hemolytic on blood agar (Arimi et al., 1990; On et al., 1996), but this characteristic may be affected by composition and pH of the base medium used, the gas composition of the atmosphere, and the period and temperature of incubation (Arimi et al. 1990; Misawa et al., 1995). Hemolytic activity has been reported for rabbit, human, cattle, sheep, goat, horse, and chicken blood (Misawa et al., 1995) and appears to be principally cell associated, although a secreted component may also be involved (see Wassenaar, 1997 for a detailed overview). All strains will grow in the presence of 1.0% ox-bile. No growth is observed at 25°C. Strains are motile by means of a single polar flagellum (at one or both ends of the cell) which seems to be an important virulence factor, necessary for colonization of the intestinal tract (Ketley, 1997). In addition, phase and antigenic variation of the flagellar protein may serve as a means of evading the immunogenic response of the host. Variation of the flagellin gene loci (*flaA* and *flaB*) may be detected by PCR-based methods and used in molecular epidemiological studies (Nachamkin et al., 1993; Ayling et al., 1996; Meinersmann et al., 1997). Recombination may affect the stability of the *flaA*-based methods and possibly acts as a mechanism by which the immunogenic repertoire of a given strain is increased (Harrington et al., 1997).

*The mol% G + C of the DNA is:* 28–33 ( $T_m$ ).

*Type strain:* CIP 702, ATCC 33560, CCUG 11284, LMG 8841, NCTC 11351.

*GenBank accession number (16S rRNA):* L04315, M59298.

- a. **Campylobacter jejuni** *subsp. jejuni* (Jones, Orcutt and Little 1931) Véron and Chatelain 1973, 128<sup>AL</sup> (*Vibrio jejuni* Jones, Orcutt and Little 1931, 861; *Vibrio hepaticus* Mathey and Rissberger 1964, 1339; *Campylobacter fetus* *subsp. jejuni* Smibert 1974, 209.)

Cell walls contain D-galactose only, D-galactose and D-glucose, or D-galactose, D-glucose, and D-mannose (Smibert, 1970). Strains grow on solid media containing 1.0–1.5% ox-bile, and 0.02% safranin. Reduction and tolerance of 0.04% triphenyl-tetrazolium chloride is observed in 90% of strains. Most (90–95% respectively) strains grow in the presence of 100 mg/l 5-fluorouracil and 32 mg/l cephalothin. Older literature reports most strains as being sensitive to 16 mg/l nalidixic acid (Karmali et al., 1981b) but increasing fluoroquinolone resistance has been observed and the proportion of resistant strains now varies significantly (Reina et al. 1994; Koenraad et al., 1995; Aarestrup et al., 1997). Similar observations of resistance to other quinolones (ciprofloxacin, enrofloxacin, norfloxacin, etc.) have also been reported. Resistance may be conferred by mutations in the target gene, *gyrA* (Pidcock and Guant, 1996). Strains may also differ in their susceptibility to other antibiotics

such as tetracycline, erythromycin, chloramphenicol, and kanamycin. The genetic mechanisms underlying these traits have been reviewed (Taylor and Courvalin, 1988; Taylor, 1992a, b). Aarestrup et al. (1997) showed that >90% of isolates from humans, cattle, chickens, and pigs were sensitive to ampicillin (16 mg/l), apramycin (2 mg/l), carbadox (0.5 mg/l), chloramphenicol (8 mg/l), colistin (16 mg/l), enrofloxacin (4 mg/l), erythromycin (4 mg/l), gentamicin (1 mg/l), nalidixic acid (32 mg/l), neomycin (1 mg/l), olaquinox (4 mg/l), spectinomycin (64 mg/l), spiramycin (8 mg/l), streptomycin (2 mg/l), tetracycline (1 mg/l), and tylosin (128 mg/l).

Two broad classes of antigens are recognized: heat-stable (HS) or somatic O-antigens, and heat-labile (HL) antigens. These form the basis of two recognized serotyping schemes, described by Penner et al. (1983) for HS antigens, and Lior et al. (1982) for HL antigens. The major component of the HS antigens is generally accepted as being lipopolysaccharide-based (Mills et al., 1992), although some workers have proposed that a capsule may be involved (Chart et al., 1996). The principal component of the HL antigen is traditionally believed to be the flagellar protein, although other somatic antigens appear to be involved in the recognition of HL-based serogroups (Taylor et al., 1988; Alm et al., 1991). However, *flaA* PCR-restriction fragment length polymorphism analysis showed limited correlation with HL serotyping suggesting that flagella may not be the major HL antigen (Mohran et al., 1996).

Considerable variation in the prevalence, number, and size of plasmids found in *C. jejuni* *subsp. jejuni* has been described. Between 19% (Austen and Trust, 1980) and 95% (Lee et al., 1994b) of strains may harbor 1–5 plasmids (Tenover et al., 1985), which range between 2.0 (Tenover et al., 1985) and 208 kb (Lee et al., 1994b) in size. Resistance to the antibiotics kanamycin, tetracycline, and chloramphenicol is often plasmid-mediated (Taylor, 1992b).

Pathogenic. Causes abortion in sheep; abortions in other animals, such as cattle and goats, have also been reported. May cause diarrhea in animals and has been associated with hepatitis in some bird species. In humans it is generally regarded as the most common bacterial cause of gastroenteritis worldwide; it also causes septicemia and abortion. Infection with certain strains of *C. jejuni* *subsp. jejuni* may be a predisposing factor to the development of the neurological disorders Guillain-Barré (GBS) (Kaldor and Speed, 1984; Nachamkin et al., 1998) and Miller-Fisher syndromes (MFS) (Roberts et al., 1987). Molecular mimicry is postulated as the mechanism for pathogenesis of these neuropathies; a trisaccharide moiety that resembles human gangliosides has been found in different HS serotypes recovered from GBS and MFS patients (Salloway et al., 1996). Strains are also found as normal intestinal flora of poultry and other bird species, cattle, sheep, pigs, goats, dogs, rabbits, and monkeys.

*The mol% G + C of the DNA is:* 30–33 ( $T_m$ ).

*Type strain:* CIP 702, ATCC 33560, CCUG 11284, LMG 8841, NCTC 11351.

*GenBank accession number (16S rRNA):* L04315, M59298.

- b. **Campylobacter jejuni** subsp. **doylei** Steele and Owen 1988, 316<sup>VP</sup>

*doylei*. M.L. gen. n. *doylei* in honor of L.P. Doyle, an American veterinarian.

Cells may be spiral, S-shaped or, less frequently, straight rods. Cultures often demonstrate considerable pleomorphism that increases with age. Colonies are pinpoint to 1 mm diameter, grayish, smooth, glistening, and convex after 2–3 days growth on blood agar. Optimal growth temperature is 35–37°C; strains do not grow at 25°C and poorly, if at all, at 42°C. Reduction of, and tolerance to, 0.04% triphenyl-tetrazolium chloride observed in 40% of strains (On et al., 1996). Strains will not grow on solid media containing 0.02% safranin or 32 mg/l cephalothin. Principal tests differentiating this subspecies from *C. jejuni* subsp. *jejuni* are given in Table BXII.ε.1. These taxa can also be distinguished by numerical analysis of both whole-cell protein electrophoretograms (Vandamme et al., 1992a), and *Hae*III restriction digest patterns (Owen et al., 1985).

In disk susceptibility tests, all strains are susceptible to penicillin (2 U), erythromycin (15 µg), and tetracycline (10 µg). Most strains are inhibited by nalidixic acid (30 µg). Pathogenicity unknown; has been isolated from ulcerated gastric tissue, diarrhea, and blood cultures of humans, notably infants (Steele and Owen, 1988; Lastovica, 1996).

*The mol% G + C of the DNA is:* 28–31 ( $T_m$ ).

*Type strain:* 093, CCUG 24567, LMG 8843, NCTC 11951.

*GenBank accession number (16S rRNA):* L14630.

10. **Campylobacter lanienae** Logan, Burnens, Linton, Lawson and Stanley 2000, 870<sup>VP</sup>

*lanienae*. L. n. *lanienae* abattoir, after place of work of human carriers from whom the bacterium was first isolated.

Cells are slender, slightly spiral rods with rounded ends and are 1.2–2.4 µm long. Characteristic darting motility due to a single bipolar flagellum. Pinpoint colonies are visible on blood agar media after three days of incubation at 37°C. The colonies are smooth, entire, and translucent and cause some greening of blood agar through alpha-hemolytic activity. Optimal growth in microaerobic conditions. Growth is weak under anaerobic conditions. Microaerobic growth at 42°C, but not at 25°C. Catalase produced. Nitrate and selenite reduced. No hydrolysis of indoxyl acetate. The 16S rDNA sequence of *C. lanienae*, and thus its phylogenetic position, is remarkably similar to that of *C. hyointestinalis* subsp. *lawsonii* (Fig. BXII.ε.2). A 16S rDNA-based PCR test developed for the specific detection of *C. lanienae* cross-reacts with *C. hyointestinalis* subsp. *lawsonii* (S.L.W. On, unpublished observations). Extensive DNA–DNA hybridization experiments, however, confirmed that *C. hyointestinalis* subsp. *hyointestinalis* and *C. hyointestinalis* subsp. *lawsonii* strains represent a single species distinct from *C. lanienae* (P. Vandamme, unpublished observations). Strains have been isolated from asymptomatic human feces. Pathogenicity, if any, is unknown.

*The mol% G + C of the DNA is:* 36 ( $T_m$ ).

*Type strain:* LMG21527, NCTC 13004.

*GenBank accession number (16S rRNA):* AF043425.

11. **Campylobacter lari** (corrig.) Benjamin, Leaper, Owen and Skirrow 1984, 270<sup>VP</sup> (Effective publication: Benjamin, Leaper, Owen and Skirrow 1983, 237 (*Campylobacter laridis* Benjamin, Leaper, Owen and Skirrow 1984, 270.) *lari*. L. n. *Larus* gull; L. gen. n. *lari* of a gull.

Cells are small, curved, S-shaped, or helical rods, 0.3 × 1.7–2.4 µm, with rounded ends. Rapid transformation to coccoid forms in cultures exposed to air. Rapid darting motility. Motile by means of single bipolar flagella. Translucent, convex colonies, 1–1.5 mm in diameter are produced on blood agar bases after 48 h. Swarming may occur on very moist agar surfaces. Grows microaerobically in the absence of hydrogen. Anaerobic growth is observed in the presence of trimethylamine *N*-oxide hydrochloride. Will not grow in air or in a CO<sub>2</sub>-enriched atmosphere. Strains grow in the presence of 1.0–1.5% ox-bile, 0.05% sodium fluoride, 32 mg/l cephalothin, and 64 mg/l cefoperazone. Most strains (93%) grow on, and reduce, 0.04% triphenyl-tetrazolium chloride medium. No growth on MacConkey agar.

*C. lari* was originally referred to as the group of nalidixic acid-resistant thermophilic campylobacters (NARTC group). These strains are primarily differentiated from other thermophilic *Campylobacter* species by their resistance to nalidixic acid, their anaerobic growth in the presence of trimethylamine *N*-oxide hydrochloride, and later also by the absence of indoxyl acetate hydrolysis. However, nalidixic acid-susceptible strains (NASC strains), urease-producing thermophilic strains (UPTC strains), and urease-producing, nalidixic acid-susceptible strains (UP-NASC strains) were later identified as *C. lari* variants by a variety of methods. Additional quantitative DNA–DNA hybridization experiments are required to establish the relationships between the different subgroups of strains presently classified as *C. lari* variants.

*C. lari* infections can be treated with aminoglycosides, erythromycin, clindamycin, and chloramphenicol; strains are generally resistant to third-generation cephalosporins, vancomycin, penicillin, and trimethoprim-sulfamethoxazole (Simor and Wilcox, 1987). Strains have been isolated from intestinal contents of seagulls and other animals, river water, and shellfish. Occasionally isolated from human diarrheic feces. Pathogenicity is unknown.

*The mol% G + C of the DNA is:* 31–33 ( $T_m$ ).

*Type strain:* ATCC 35221, CCUG 23947, DSM 11375, LMG 8846, NCTC 11352.

*GenBank accession number (16S rRNA):* L04316.

12. **Campylobacter mucosalis** (Lawson, Leaver, Pettigrew and Rowland 1981) Roop, Smibert, Johnson and Krieg 1985a, 191<sup>VP</sup> (*Campylobacter sputorum* subsp. *mucosalis* Lawson, Leaver, Pettigrew and Rowland 1981, 385.)

*muco.salis*. M.L. adj. *mucosalis* pertaining to the (*tunica*) *mucosa* mucous membrane.

Cells are short, irregularly curved, 0.25–0.30 × 1–3 µm. Motile by means of a single, polar flagellum. In old cultures, coccoid cells and filamentous forms 7–8 µm long are seen. Colonies are 1.5 mm in diameter, circular, raised with a flat surface, and have a dirty yellowish color. On moist agar, colonies tend to swarm along the line of inoculation.

Does not grow microaerobically on common agar bases in an atmosphere without hydrogen. Grows anaerobically

in an atmosphere containing hydrogen and fumarate. Requires hydrogen as an electron donor. Formate may replace hydrogen for growth of most strains (Lawson et al., 1981). Anaerobic growth requires fumarate as an electron acceptor. Converts fumarate to succinate. Oxygen utilization by cell suspensions is greatly increased in the presence of hydrogen and formate. Utilization of oxygen with these substrates is unaffected by cyanide. Cells contain large amounts of cytochrome *c*<sub>553</sub>, which is reduced when cell suspensions are incubated with hydrogen or formate. When exposed to air the reduced cytochrome *c* is reoxidized. Lactate, succinate, and NADH give slight reduction of cytochrome *c* while methanol, malate, glutamate, and serine are inactive. It is not affected by cyanide (Lawson et al., 1981). Strains grow on potato starch medium, and on media containing 1.0% ox-bile and 0.032% methyl orange. Most (70–90%) strains grow in the presence of 0.01% Janus green and 0.005% basic fuchsin.

Serological analysis shows that strains of this organism are closely related antigenically (Lawson et al., 1975). Antisera prepared against five strains agglutinated homologous and heterologous cells. When antisera were absorbed with one strain, the antisera reacted only with homologous cells. An antigenic analysis has been reported (Lawson et al., 1977) and three serovars, A, B, and C, have been described (Lawson et al., 1981). These three different serovars were shown to have strikingly distinct whole-cell protein patterns, but a high level of DNA–DNA hybridization was reported between representative strains (Costas et al., 1987; Vandamme et al., 1990). Selective media were developed by different researchers (reviewed by Ohya et al., 1988).

Minimum inhibitory concentrations of antibiotics are (µg/ml): bacitracin, >128; chloramphenicol, 2–8; clindamycin, 0.25–0.5; colistin, 0.5–1; erythromycin, 1–2; gentamicin, 2–4; kanamycin, <0.5–2; metronidazole, 0.12–1; minocycline, <0.5–2; nalidixic acid, 16 to >128; neomycin, 16–32; penicillin, 1–32; polymyxin B, <0.25–1; rifampin, 4–32; streptomycin, 1–2; tetracycline, 1–8; vancomycin, >128, amoxicillin/clavulanate, 0.06–0.5; cefoxitin, 1–16; ceftizoxime, 0.25–1; ceftriaxone, 0.016–0.25; meropenem, 0.03; piperacillin, 2–26; piperacillin/tazobactam, 0.016–4; and ticarcillin/clavulanate, 0.016. *In vitro* activities of 47 antimicrobial agents toward *C. mucosalis* were determined by Gebhart et al. (1985b).

Pathogenicity unknown. Originally believed to be a causal agent of proliferative enteritis in pigs but subsequent studies have identified *Lawsonia intracellularis* as the principal pathogen in this disease. Human infections with this organism have been reported but were shown to be caused by misidentified *C. concisus* strains (On, 1994; Anderson et al., 1996). Isolated from the intestinal mucosa of pigs with porcine intestinal adenomatosis, necrotic enteritis, regional ileitis, and proliferative hemorrhagic enteropathy; also isolated from the porcine oral cavity.

*The mol% G + C of the DNA is:* 36–38 (*T<sub>m</sub>*).

*Type strain:* FS253/72, ATCC 43264, CCUG 6822, LMG 6448, NCTC 11000.

*GenBank accession number (16S rRNA):* L06978.

13. **Campylobacter rectus** (Tanner, Badger, Lai, Listgarten, Visconti and Socransky 1981) Vandamme, Falsen, Rossau, Hoste, Segers, Tytgat and De Ley 1991a, 98<sup>VP</sup> (*Wolinella recta*

Tanner, Badger, Lai, Listgarten, Visconti and Socransky 1981, 441.)

*rect' us.* L. adj. *rectus* straight.

Cells are small and straight, 0.5 × 2–4 µm, with rounded ends. Rapid darting motility. Motile by means of a single polar flagellum. The outer surface is covered with a distinctive array of hexagonal, packed, macromolecular subunits, each about 17 nm in diameter. Translucent colonies are produced on blood agar bases. Different colony types are observed: small pinpoint colonies, 1 mm in diameter, or spreading colonies up to 5 mm in diameter. Agar pitting is medium dependent but most (80%) strains exhibit this trait after 3 d of anaerobic growth on 5% blood agar (On et al., 1996).

Optimal growth in anaerobic conditions. Does not grow microaerobically on common agar bases in an atmosphere without hydrogen. Will not grow in air, in a CO<sub>2</sub>-enriched atmosphere, or in an atmosphere containing O<sub>2</sub>/CO<sub>2</sub>/N<sub>2</sub> (5:10:85) on common agar bases. Anaerobic growth occurs with formate and fumarate in the medium. Hydrogen and formate are used as energy sources. Formate is oxidized to hydrogen and CO<sub>2</sub>; fumarate is reduced to succinate. Fumarate, nitrate, nitrite, neutral red, benzyl viologen aspartate, asparagine, and malate serve as electron acceptors. Membrane-bound cytochrome *b*, cytochrome *c*, and CO-binding cytochrome *c*, and soluble cytochrome *c* and CO-binding cytochrome *c* are present. Strains do not grow in the presence of 0.04% triphenyl-tetrazolium chloride, 0.01% Janus green or 64 mg/l cefoperazone. Alkaline phosphatase is not produced.

*The mol% G + C of the DNA is:* 42–46 (*T<sub>m</sub>*).

*Type strain:* FDC 371, ATCC 33238, CCUG 20446, DSM 3260, LMG 18219.

*GenBank accession number (16S rRNA):* L04317, L06973.

14. **Campylobacter showae** Etoh, Dewhirst, Paster, Yamamoto and Goto 1993, 638<sup>VP</sup>

*sho' wae.* L. n. *showae* referring to Showa University, Japan, where several of the first strains were isolated.

Cells are small and straight, 0.5–0.8 × 2–5 µm, with rounded ends. Motile by means of polar bundles of two to five flagella. Rapid darting motility. Translucent colonies are produced on blood agar base media.

Optimal growth in anaerobic conditions. Does not grow microaerobically on common agar bases in an atmosphere without hydrogen. Will not grow in air, in a CO<sub>2</sub>-enriched atmosphere, or in an atmosphere containing O<sub>2</sub>/CO<sub>2</sub>/N<sub>2</sub> (5:10:85) on common agar bases. Anaerobic growth occurs with formate and fumarate in the medium. Fumarate is reduced to succinate. Fumarate, nitrate, and nitrite serve as electron acceptors. Strains grow in the presence of 0.05% sodium fluoride but not in the presence of 64 mg/l cefoperazone or 0.04% triphenyl-tetrazolium chloride. Alkaline phosphatase activity has not been detected. Strains have been isolated from human dental plaque and from infected root canals. Pathogenicity is unknown.

*The mol% G + C of the DNA is:* 44–46 (*T<sub>m</sub>*).

*Type strain:* SU A4, ATCC 51146, CCUG 30254, LMG 12635.

*GenBank accession number (16S rRNA):* L06974.

15. **Campylobacter sputorum** (Prévot 1940) Véron and Chatelain 1973, 128<sup>AL</sup> emend. Roop, Smibert, Johnson and

Krieg 1986, 348 emend. On, Atabay, Corry, Harrington and Vandamme 1998, 203 (*Vibrio sputorum* Prévot 1940, 85.) *sputorum*. L. n. *sputum* spit, sputum; L. gen. pl. n. *sputorum* of sputa.

Slender, curved or spiral rods,  $0.3\text{--}0.5 \times 2\text{--}4 \mu\text{m}$ . Cells are usually S-shaped or gull-winged in appearance, but comma-shaped and unusually long (8  $\mu\text{m}$ ) cells are also observed. The ends of the cells are usually rounded. Motile with a characteristic darting and corkscrew-like movement by means of a single flagellum. Colonies of 3-d-old cultures on blood agar media are 1–2 mm in diameter, smooth, shiny, low convex, and round. Bacterial growth on blood agar usually shows a greenish hue, and it is accompanied by weak  $\alpha$ -hemolytic activity. Growth in broth is light and easily dispersed. Strains may be cultured under microaerobic or anaerobic gaseous conditions. Anaerobic growth occurs in media containing fumarate only, formate and fumarate, or fumarate in the presence of hydrogen gas. Alkaline phosphatase is not produced. Neither growth nor reduction of triphenyl-tetrazolium chloride medium is detected. Strains will grow on media containing 0.032% methyl orange. Strains do not give reproducible results when tested for the ability to grow on media containing 3.5–4.0% NaCl, or 1.0–2.0% ox-bile.

Strains isolated from the human oral cavity and the genital tract of bulls were initially believed to be related at the subspecies level on the basis of their extensive biochemical similarities, and named *C. sputorum* subsp. *sputorum* and *C. sputorum* subsp. *bubulus* (Véron and Chatelain, 1973), respectively. Subsequent DNA homology studies (Tanner et al., 1981; Roop et al. 1985b) revealed a high level of DNA–DNA relatedness between these two taxa and between these taxa and “*C. fecalis*” (from sheep feces). Limited biochemical variation between these taxa had been noted (catalase production, and growth on 3.5% NaCl and 1.0% ox-bile media). Roop et al. (1985b) therefore proposed that the aforementioned taxa be referred to as source-specific biovars of *C. sputorum* (biovar *sputorum*, biovar *bubulus*, and biovar *faecalis*, respectively). The legitimacy of biovar *bubulus* as a distinct taxon was questioned when the tests used to distinguish biovar *sputorum* from biovar *bubulus* were found to be poorly reproducible, even when using highly standardized conditions for testing (On et al., 1994, 1998). The absolute validity of the “source-specific biovar” concept was also challenged since some *C. sputorum* strains from sheep and pigs cannot be distinguished from those of bovine and human origin (On et al., 1994, 1998). The recent identification of urease-positive isolates of *C. sputorum* from cattle feces resulted in the proposal of a new biovar structure, defined by reactions in two simple and reproducible tests (catalase and urease). The proposed biovar classification also agrees with the results of protein profile analysis (On et al., 1994, 1998).

*Campylobacter sputorum* biovar *sputorum* strains conform to the description of the species *C. sputorum*. Neither catalase nor urease is produced. Found in the oral cavity, feces (normal and diarrheic), and abscesses (and other skin lesions) of humans, the genital tract of bulls, aborted tissue of sheep, and the feces of sheep and pigs. Pathogenicity unknown. The reference strain is VPI S-17 (LMG 7795, NCTC 11528). GenBank accession numbers of the 16S rRNA gene sequences are X67775 (VPI S-17) and L04319 (ATCC 33491).

*Campylobacter sputorum* biovar *faecalis* strains conform to the description of the species *C. sputorum*. Catalase, but not urease, is produced. The biovar name refers to the fecal habitat. Isolated from the feces of sheep and cattle. Pathogenicity unknown. The recommended reference strain is LMG 8531 (CCUG 17761, NCTC 11415).

*Campylobacter sputorum* biovar *paraureolyticus* strains conform to the description of the species *C. sputorum*. Urease, but not catalase, is produced. The biovar name *paraureolyticus* indicates its resemblance to *Bacteroides ureolyticus*, a urease-producing bacterium closely related to other *Campylobacter* spp. Isolated from the feces of cattle and from human diarrhea. Pathogenicity unknown. Recommended reference strains are LMG 11764 (human) and LMG 17590 (CCUG 37579) (bovine). GenBank accession no. of the 16S rRNA gene sequence of strain LMG 17590 is AF022768.

The mol% G + C of the DNA is: 30–33 ( $T_m$ ).

Type strain: VPI S 17, ATCC 35980, CCUG 9728, LMG 7795, NCTC 11528.

GenBank accession number (16S rRNA): X67775.

16. ***Campylobacter upsaliensis*** Sandstedt and Ursing 1991b, 331<sup>VP</sup> (Effective publication: Sandstedt and Ursing 1991a, 42.)

*up.sa.li.en'sis*. L. adj. *upsaliensis* referring to Uppsala, a Swedish city.

Cells are small, curved, S-shaped, or helical rods,  $0.3\text{--}0.4 \times 1.2\text{--}3 \mu\text{m}$ , with rounded ends. Rapid darting motility. Motile by means of a single polar flagellum or bipolar flagella. Transformation to coccoid forms in cultures exposed to air. Translucent, convex colonies, pinpoint to 1–2 mm in diameter are produced on blood agar bases after 48 h. Swarming may occur on very moist agar surfaces.

Grows microaerobically in the absence of hydrogen. Will not grow in air or in a CO<sub>2</sub>-enriched atmosphere. Goossens et al. (1990a) reported that about 20% of 99 strains did not grow at 42°C; it therefore seems appropriate to consider this species as thermotolerant, not thermophilic. Strains grow on potato starch- and charcoal-based media, and on media containing 1.0–1.5% ox-bile and 100 U/l 5-fluorouracil. Strains do not grow on MacConkey agar. A few strains (11%) are resistant to cephalothin (32 mg/l).

A comprehensive overview of our present knowledge on this species was given by Bourke et al. (1998). A physical and genetic map of the genome and the complete sequence of the iron-uptake regulatory gene (*fur*) from the type strain were described by Bourke et al. (1995). Adherence to lipids and intestinal mucin were described by Sylvester et al. (1996). Selective media were reported to enable isolation of thermophilic campylobacters including *C. upsaliensis* strains (Burnens and Nicolet, 1992; Aspinall et al., 1996). A variety of plasmids has been reported in large percentages of strains (89%, Goossens et al., 1990a; 87%, Owen and Hernandez, 1990; 93%, Da Silva Tatley et al., 1992; 60%, Stanley et al., 1994a).

Minimum inhibitory concentrations of antibiotics are ( $\mu\text{g/ml}$ ): bacitracin, >128; chloramphenicol, 2–8; clindamycin, 0.25–0.5; colistin, 0.5–1; erythromycin, 1–2; gentamicin, 2–4; kanamycin, <0.5–2; metronidazole, 0.121; minocycline, <0.5–2; nalidixic acid, 16–128; neomycin, 16–32; penicillin, 1–32; polymyxin B, <0.25–1; rifampin, 4–32;

streptomycin, 1–2; tetracycline, 1–8; vancomycin, >128, amoxicillin/clavulanate, 0.06–0.5; cefoxitin, 1–16; ceftizoxime, 0.25–1; ceftriaxone, 0.016–0.25; meropenem, 0.03; piperacillin, 2–26; piperacillin/tazobactam, 0.016–4; and ticarcillin/clavulanate, 0.016.

Of 99 *C. upsaliensis* strains examined by Goossens et al. (1990a), all were generally susceptible to ampicillin, gentamicin, chloramphenicol, cefoperazone, colistin, vancomycin, rifampin, trimethoprim, and tetracycline; ten strains were resistant to erythromycin. Strains are isolated from

blood specimens of humans, from feces from humans with gastrointestinal illness, and from asymptomatic humans, dogs, and cats; strains associated with a human abortion and a breast abscess were reported. Clinical data presented by Goossens et al. (1990a, b) suggest an enteropathogenic role in humans.

*The mol% G + C of the DNA is:* 32–36 ( $T_m$ ).

*Type strain:* C 231, ATCC 43954, CCUG 14913, DSM 5365, LMG 8850, NCTC 11541.

*GenBank accession number (16S rRNA):* L14628.

#### Other Organisms

1. *Bacteroides ureolyticus* Jackson and Goodman 1978, 199<sup>AL</sup> (*Bacteroides corrodens* Eiken 1958, 415; *Ristella corrodens* (Eiken 1958) Prévot 1966, 118.)

*ur' e.o.ly.ti.cus.* M.L n. *urea urea*; Gr. adj. *lyticus* dissolving; M.L. adj. *ureolyticus urea* dissolving.

Cells are  $0.5 \times 1.5$ –4  $\mu\text{m}$ . Nonmotile. Filaments exceeding 20  $\mu\text{m}$  in length may occur. Cells of some strains have polar tufts of long pili in electron micrographs (Jackson et al., 1971) and exhibit “twitching” motility. The pili sometimes form a bundle and may be mistaken for flagella with light microscopy. Translucent colonies are produced on blood agar bases. Different colony types are observed: small pinpoint colonies, 1 mm in diameter or spreading colonies up to 5 mm in diameter. Agar pitting is medium dependent, but most strains (90%) exhibit this trait after 3 d of anaerobic growth on 5% blood agar (On et al., 1996).

Does not grow microaerobically on common agar bases in an atmosphere without hydrogen. Will not grow in air, in a CO<sub>2</sub>-enriched atmosphere, or in an atmosphere containing O<sub>2</sub>/CO<sub>2</sub>/N<sub>2</sub> (5:10:85) on common agar bases. Anaerobic growth occurs with formate and fumarate in the medium. Fumarate is reduced to succinate; fumarate, nitrate, and nitrite serve as electron acceptors. Strains grow on media containing 3.5–4.0% NaCl and 0.032% methyl orange. As with other preferentially anaerobic *Campylobacter* species, strains are susceptible to a range of antibiotics including cephalothin (32 mg/l), carbenicillin (32 mg/l), cefoperazone (64 mg/l) and 5-fluorouracil (100 U/l). No growth is observed in the presence of 0.05% basic fuchsin. Contains cytochromes *b* and *c* (Jackson and Goodman, 1978).

Menaquinone-6 (2-methyl-3-farnesyl-farnesyl-1,4-naphthoquinone) and a methyl-substituted menaquinone-6 (2, [5 or 8]-dimethyl-3-farnesyl-farnesyl-1,4-naphthoquinone) have been reported as major respiratory quinones (Vandamme et al., 1995a). Strains have been isolated from superficial ulcers and soft tissue infections, nongonococcal, nonchlamydial urethritis, and periodontal disease. Its pathogenicity is difficult to assess because the strains are mostly recovered from mixed infections. Nevertheless, a potential pathogenic role is suggested by its predominance in mixed infections and its strong proteolytic activity, which may enable tissue destruction.

*B. ureolyticus* was included in a polyphasic taxonomic study to elucidate its taxonomic status (Vandamme et al.,

1995a). This species resembles campylobacters in its respiratory quinone content, its DNA base ratio, and most of its phenotypic characteristics; it differs from campylobacters in its fatty acid composition and its proteolytic metabolism. Bootstrapping analysis of the 16S rRNA gene sequence-derived phylogeny separated *B. ureolyticus* from the *Campylobacter* clade in only 61% of trees generated. This organism was not formally reclassified pending the isolation and thorough taxonomic characterization of additional *B. ureolyticus*-like bacteria. The inclusion of *B. ureolyticus* in the genus *Campylobacter* would considerably extend the phenotypic heterogeneity of this genus. Exclusion from the genus *Campylobacter* would entail the creation of a monotypic taxon with the ability to digest casein and gelatin as differential features from the genus *Campylobacter*. *B. ureolyticus*-like oral isolates that were shown to be heterogeneous on the basis of phenotypic and biochemical criteria (Duerden et al., 1989) have been described. The taxonomic structure and position of these and other *B. ureolyticus*-like strains need further investigation.

*The mol% G + C of the DNA is:* 28–30 ( $T_m$ ).

*Deposited strain:* ATCC 33387, DSM 20703, NCTC 10941.

*GenBank accession number (16S rRNA):* L04321.

The *Campylobacter mucosalis*-like strain CCUG 20705 was isolated from a porcine intestine in the United Kingdom and was originally identified as *C. mucosalis*. It occupied a distinct position in a dendrogram derived from DNA–rRNA hybridization experiments (Vandamme et al., 1991a). No significant DNA–DNA hybridization between CCUG 20705 and *C. mucosalis* reference strains (P. Vandamme, unpublished data) was detected although the 16S rRNA gene sequence of this strain (L14629) is about 98% similar to that of the type strain of *C. mucosalis* (Linton et al., 1994a).

*Campylobacter* sp. strain PGC 40-6AT, isolated from a pig stomach, was reported as one of several genetically similar isolates. A number of studies have remarked on its distinct phylogenetic position, suggesting it to represent a novel species. However, a study examining the phylogenetic position and diversity of the 16S rRNA gene from *C. hyointestinalis*, closely clustered PGC 40-6AT with six other sequences derived from reference strains of *C. hyointestinalis* subsp. *lawsonii* (Harrington and On, 1999). Since the latter subspecies is most commonly associated with porcine stomach tissue, these authors considered PGC 40-6AT identified as a strain of *C. hyointestinalis* subsp. *lawsonii*.