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Reclassification of *Bacteroides ureolyticus* as *Campylobacter ureolyticus* comb. nov., and emended description of the genus *Campylobacter*

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The protein profiles, genomic amplified fragment length polymorphism patterns and 16S rRNA and *cpn60* gene sequences of a diverse collection of 26 *Bacteroides ureolyticus* strains, along with published data on their DNA base, respiratory quinone and cellular fatty acid compositions, were used to reassess the taxonomy of this bacterial species. The results demonstrate that this organism is most appropriately allocated in the genus *Campylobacter*. The presence of much higher amounts of 18 : 1ω7*c* in its cellular fatty acid profile and its ability to digest gelatin and casein are the characteristics that differentiate it from present species of the genus *Campylobacter*. Therefore we propose to reclassify this species *incertae sedis* into the genus *Campylobacter* as *Campylobacter ureolyticus* with strain LMG 6451^T (=CCUG 7319^T =NCTC 10941^T) as the type strain.

On the basis of genotypic, chemotaxonomic and phenotypic characteristics, the generically misclassified *Bacteroides gracilis* has been transferred into the genus *Campylobacter* as *Campylobacter gracilis* (Vandamme *et al.*, 1995). In the same study it was unclear whether *Bacteroides ureolyticus* was to be reclassified as a member of the genus *Campylobacter*, or as a representative of a novel genus within the family *Campylobacteraceae*. Hence, it remained a species *incertae sedis* pending the isolation and characterization of additional *B. ureolyticus*-like bacteria. In the present study, the taxonomic status of a collection of 26 human *B. ureolyticus* strains from various clinical sources was re-evaluated using a polyphasic approach.

The strains used and their sources are listed in Supplementary Table S1 (available in IJSEM Online). Bacteriological purity was checked by plating and examining living and Gram-stained cells. The collection of strains examined included four well-characterized reference strains from a previous taxonomic study (LMG 6451^T, LMG 8448, LMG 8449 and LMG 8450) and 22 human isolates (20 from Sweden, two from the USA) obtained between 1977 and 2005 (Supplementary Table S1).

The 26 strains were first analysed by means of whole-cell protein electrophoresis and amplified fragment length polymorphism analysis in order to reveal the taxonomic structure of this taxon. For whole-cell protein SDS-PAGE, all *B. ureolyticus* strains were grown on Mueller–Hinton agar supplemented with 5 % horse blood and incubated at 37 °C for 48 h under micro-aerobic conditions (approx. 4 % O_2, 6.5 % CO_2, 6.5 % H_2, 83 % N_2). The preparation of whole-cell proteins and SDS-PAGE were performed as described by Pot *et al.* (1994). Normalization of densitometric traces was performed using the GelCompar version 4.2 software (Applied Maths). Numerical analysis was performed using the Pearson product moment correlation coefficient and UPGMA with BioNumerics 4.61 software. AFLP-analysis was performed as described by Debruyne *et al.* (2009) using the *Hin*dIII–*Hha*I restriction enzyme combination. One microlitre of the final product was analysed by capillary gel electrophoresis using an ABI 3130XL automated DNA sequencer. For every sample, 0.4 µl of an internal lane standard (LIZ-600, Applied Biosystems) was included. AFLP profiles were collected with the Data Collection software v 3.0 (Applied Biosystems), and the profiles generated were imported, using the CrvConv filter, into BioNumerics version 4.61 (Applied Maths) for normalization and further analysis. Similarity between normalized profiles was determined by the Pearson product moment correlation coefficient and a UPGMA dendrogram was reconstructed.

The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequences of strains LMG 24746, LMG 24747, R-38115, LMG 8448 and R-37890 are FN401323–FN401327, respectively. The accession numbers for the *cpn60* gene sequences of strains LMG 24746, R-37890, LMG 6451^T, LMG 24747, R-38115 and LMG 8448 are FN421436–FN421441, respectively.

Numerical reproductions of whole-cell protein profiles and a corresponding UPGMA dendrogram, a neighbour-joining phylogenetic tree based on *cpn60* gene sequences, a list of *B. ureolyticus* strains examined and their sources, and reciprocal DNA–DNA hybridization results are available with the online version of this paper.

Supplementary Figure S1 shows the result of the numerical comparison of the protein profiles of the 26 strains. As discussed by Taylor *et al.* (1986, 1987) the whole-cell protein profiles of *B. ureolyticus* strains differ mainly in the position of major protein bands in the molecular mass region of 36–52 kDa (Taylor *et al.*, 1987). The same observations have been reported for a range of species of the genus *Campylobacter* (e.g. Vandamme *et al.*, 1990, 1991b, 1992) and different PAGE profile types within *B. ureolyticus* have been described (Taylor *et al.*, 1986, 1987). Nevertheless, high DNA–DNA hybridization values among strains representing such different PAGE profile types have been obtained (Taylor *et al.*, 1986), as for species of the genus *Campylobacter* (e.g. Vandamme *et al.*, 1990, 1991b, 1992). The numerical analysis of the AFLP profiles also revealed considerable diversity among the 26 strains (Fig. 1). Twenty one clinical isolates formed a single but heterogeneous cluster grouping with the type strain and two additional reference strains (Vandamme *et al.*, 1995). A third reference strain (LMG 8448) and a single clinical isolate (R-37787) grouped separately in the dendrogram (Fig. 1); the protein profiles of the latter two isolates, nevertheless, were not aberrant from those of the other strains examined (Supplementary Fig. S1).

We subsequently performed DNA–DNA hybridizations among strains representing four different PAGE profile types (LMG 6451^T, LMG 24746, LMG 24747 and R-37890; marked in Supplementary Fig. S1 and Fig. 1 in bold type). DNA–DNA hybridizations were performed with photobiotin-labelled probes in microplate wells (Ezaki *et al.*, 1989), using an HTS7000 Bio Assay Reader (Perkin Elmer) for the fluorescence measurements. The hybridization temperature was 30 °C. Reciprocal experiments were performed for every pair of strains. The DNA–DNA hybridization values obtained were generally above 70 % (Supplementary Table S2) confirming results by Taylor *et al.* (1986).

One of the key issues for revising the classification of *B. ureolyticus* is its phylogenetic position relative to members of the genus *Campylobacter*. For that reason, we examined the phylogenetic position of strains LMG 6451^T, LMG 8448, LMG 24746, LMG 24747, R-37890 and R-38115 (marked in Supplementary Fig S1 and Fig. 1 with an asterisk) through comparative 16S rRNA and *cpn60* gene sequence analysis. 16S rRNA gene amplification, purification and sequencing were performed as described by Vandamme *et al.* (2006). Sequence assembly was performed using the BioNumerics 4.61 software, and selected sequences representing members of the genus *Campylobacter* and related bacteria were aligned by using CLUSTAL X. Subsequently, the aligned sequences were imported into the BioNumerics software for phylogenetic analyses and bootstrap analysis (500 replicates). Unknown bases were discarded for the analysis and phylogenetic trees were reconstructed by using the neighbour-joining, maximum-likelihood and maximum-parsimony methods. The similarity of the 16S rRNA gene sequences of the six *B. ureolyticus* strains was >99 %; the similarity towards species of the genus *Campylobacter* was in the range of 91–93 %, whereas the similarity towards other representatives of the class *Epsilonproteobacteria* was below 90 %. When varying the number of reference strains included in the phylogenetic analysis, *B. ureolyticus* strains clustered either at the periphery of the *Campylobacter* lineage, or as a deep branching line of descent among the *Campylobacter* species (Fig. 2). This confirms previous observations (Vandamme *et al.*, 1995). When considering the taxonomic position of *B. ureolyticus* in the single 16S rRNA tree harbouring all sequenced prokaryotic type strains of the 'All-Species Living Tree' project (http://www.arb-silva.de/projects/living-tree/), *B. ureolyticus* clusters among the species of the genus *Campylobacter*. When applying maximum-parsimony or maximum-likelihood clustering methods, the *B. ureolyticus* cluster also groups among the *Campylobacter* species (data not shown).

Sequence analysis of protein encoding genes provides a higher taxonomic resolution compared to 16S rRNA gene sequence analysis. In the genus *Campylobacter* and related bacteria, partial *cpn60* gene sequence-based phylogeny correlates with 16S rRNA gene sequence-based phylogeny but provides a better resolution among closely related species (Kärenlampi *et al.*, 2004; Hill *et al.*, 2006; Debruyne *et al.*, 2009). The partial *cpn60* gene sequences (555 bp) of the six strains analysed by 16S rRNA gene sequence analysis were determined as described by Hill *et al.* (2006) and modified by Debruyne *et al.* (2009). Sequencing and further analyses were performed as described above. The similarity of the *cpn60* gene sequences of the five strains was >95 %; the similarity with species of the genus *Campylobacter* was below 83 %. A neighbour-joining tree representing the *cpn60* gene phylogeny is presented in Supplementary Fig. S2. Again, when varying the number of reference strains included in the phylogenetic analysis, *B. ureolyticus* strains clustered either at the periphery of the *Campylobacter* lineage, or as a deep branching line of descent among the *Campylobacter* species.

Several additional characteristics have been determined for *B. ureolyticus* strains. Their DNA base composition was examined in several studies and is in the range of 28–30 mol% (Jackson & Goodman, 1978; Taylor *et al.*, 1986; Vandamme *et al.*, 1991a). Vandamme *et al.* (1995) showed that *B. ureolyticus* ATCC 33387^T (=LMG 6451^T) comprised menaquinone (MK)-5, MK-6, and a methyl-substituted menaquinone-6 [2, (5 or 8)-dimethyl-3-farnesyl-farnesyl-1,4-naphthoquinone] designated *MK-6, the so-called thermoplasmaquinone, as respiratory quinones. The latter was present as a major compound. This overall menaquinone pattern was essentially identical to that of members of the genus *Campylobacter*. The cellular fatty acid composition of *B. ureolyticus* differed primarily from those of the species of the genus *Campylobacter* examined by the presence of much higher amounts of 18 : 1ω7*c*.

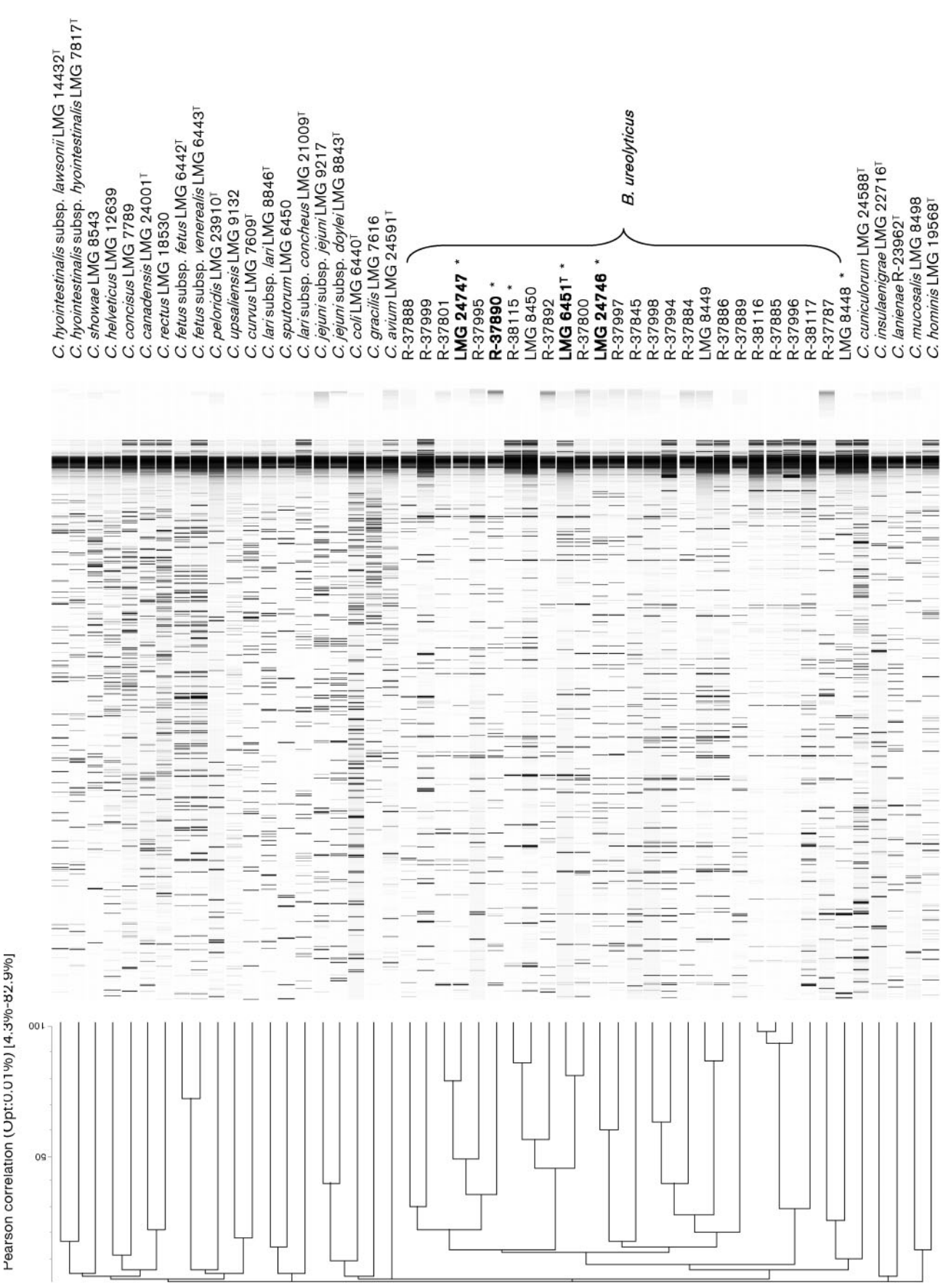

Fig. 1. Numerical reproductions of AFLP profiles and corresponding UPGMA dendrogram including all *B. ureolyticus* strains examined and type or reference strains of established species of the genus *Campylobacter*. Strains selected for 16S rRNA and *cpn60* gene sequence analysis are marked by an asterisk. Strains included in DNA–DNA hybridization experiments are shown in bold type.

The reclassification of *B. ureolyticus* is not straightforward. In the present study, we provide polyphasic taxonomic information on a diverse set of 26 *B. ureolyticus* strains. Two of these (LMG 8448 and R-37787) grouped separately in the AFLP dendrogram, but conformed to the other strains examined in terms of whole-cell protein profile and *cpn60* and 16S rRNA gene sequences. Since the 1995 study, the number of *Campylobacter* taxa with validly published names has nearly doubled and several of the characteristics that then differentiated *B. ureolyticus* from campylobacters are no longer valid. Maximum-likelihood and parsimony analyses of the 16S rRNA gene sequences allocate this organism in the genus *Campylobacter*; neighbour-joining based analyses are equivocal. Its fatty acid composition (the relative proportion of essentially one fatty acid) and the hydrolysis of gelatin and casein (Jackson & Goodman, 1978; Duerden *et al.*, 1989; Taylor *et al.*, 1986) remain the key differential characteristics towards the current *Campylobacter* species. In addition, the presence of urease activity also distinguishes *B. ureolyticus* from most other campylobacters (only some *Campylobacter lari* and *Campylobacter sputorum* strains are urease-positive).

It serves no purpose to preserve the taxonomic status of this organism as a species *incertae sedis*. We feel it is most appropriate to formally reclassify this well-characterized taxon within the genus *Campylobacter* as *Campylobacter ureolyticus* comb. nov.

Emended description of the genus *Campylobacter* Sebald and Véron 1963, 907[AL]

Campylobacter (cam.py′lo.bac.ter. Gr. adj. *kampulos* bent, curved; N.L. masc. n. *bacter* rod; N.L. masc. n. *Campylobacter* a curved rod).

This emended description is based on the data provided by On & Holmes (1995), On *et al.* (1996) and Vandamme *et al.* (2005).

Cells of most species are slender, spirally curved rods, 0.2–0.8 μm wide and 0.5–5 μm long; cells of some species are predominantly curved or straight rods. Rods may have one or more spirals and can be as long as 8 μm; they also appear S-shaped and gullwinged when two cells form short chains. Non-spore-forming. 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 two to three times the length of the cells. Cells of other species are non-motile (*C. 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

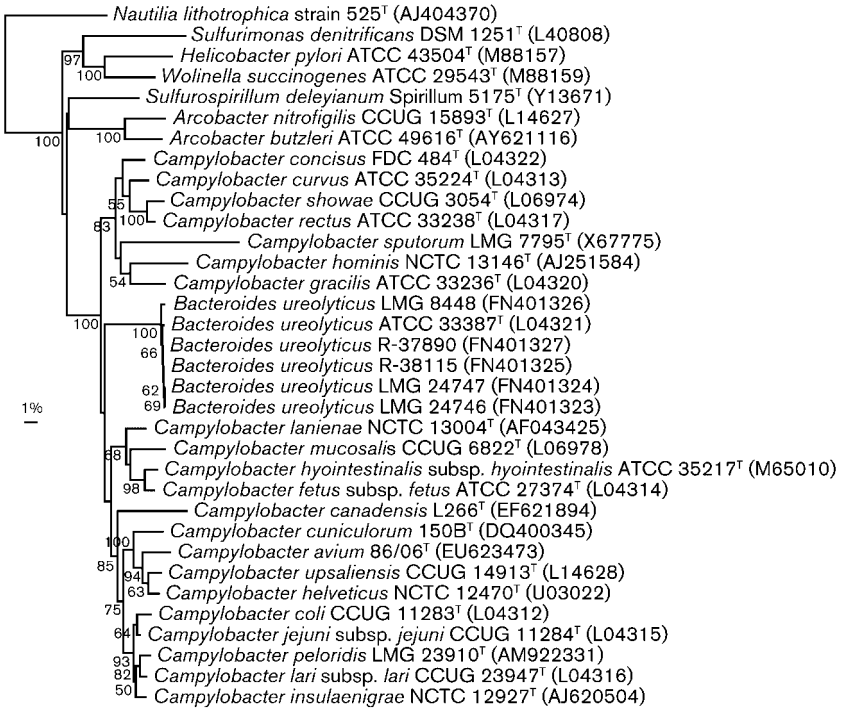

Fig. 2. Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences showing the position of *B. ureolyticus* and related bacteria. Bar, 1 % difference in nucleotide sequence as determined by measuring the length of horizontal lines connecting two species. Bootstrap values are indicated at the nodes; values of less than 50 % are not shown.

grow only microaerobically in the presence of fumarate with formate or hydrogen. Require an oxygen concentration between 3 and 15 % and a carbon dioxide concentration of 3 to 15 %. Grow at 35–37 °C, not at 4 °C. Chemo-organotrophs. 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 from carbohydrates. Starch and tyrosine are not hydrolysed. Typically non-proteolytic, yet *C. ureolyticus* is capable of digesting gelatin and casein (although *C. showae* is able to grow on casein hydrolysis test media, it does not hydrolyse casein). 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 man and animals.

The mol% G+C of the DNA ranges from 29 to 47 (thermal denaturation method). 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. Internal transcribed spacers or intervening sequences occur in the 16S or 23S rRNA genes of strains of several species.

The type species is *Campylobacter fetus* (Smith and Taylor 1919) Sebald and Véron 1963, 907.

Description of *Campylobacter ureolyticus* comb. nov.

Campylobacter ureolyticus [ur′e.o.ly.ti.cus N.L. fem. n. *urea* urea; N.L. masc. adj. *lyticus* (from Gr. masc. adj. *lutikos*), able to loose, able to dissolve; N.L. masc. adj. *ureolyticus* urea dissolving].

Basonym: *Bacteroides ureolyticus* Jackson and Goodman 1978, 199[AL].

The description is mainly based on data for *B. ureolyticus* presented by On & Holmes (1995), On *et al.* (1996) and Vandamme *et al.* (2005). Additional references are provided when appropriate.

Cells are 0.5 μm in diameter and 1.5–4 μm long. Non-motile. Filaments exceeding 20 μm in length may occur. Cells of some strains have polar tufts of long pili in electron micrographs 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 (90 %) strains exhibit this trait after three days of anaerobic growth on 5 % blood agar. Optimal growth in hydrogen-enriched microaerobic conditions. Does not grow microaerobically on common agar bases in an atmosphere without hydrogen. Will not grow in air, in a CO_2-enriched atmosphere, or in an atmosphere containing 5 % O_2, 10 % CO_2 and 85 % N_2 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. Grows at 30 and 37 °C, but not at 25 °C; strain-dependent growth at 42 °C. Grows on media containing 0.1 % trimethylamine-*N*-oxide, 1 % glycine, 0.05 % sodium fluoride, 0.032 % methyl orange or 2–4 % NaCl; no growth in the presence of 1.5–2 % bile, 0.04 % 2,3,5-triphenyl-tetrazolium chloride or 0.05 % basic fuchsin; strain-dependent growth in the presence of 1 % bile, 0.1 % potassium permanganate, 0.02 % sodium arsenite, 0.02 % safranine, 0.0005 % crystal violet or 0.01 % janus green. Most strains grow on nutrient agar and buffered charcoal yeast medium; growth on *Campylobacter* charcoal deoxycholate medium, *Campylobacter* minimal medium and MacConkey agar is strain-dependent.

Oxidase- and urease-activity is present, but no hydrolysis of hippurate, DNase activity, alkaline phosphatase activity, reduction of triphenyl-tetrazolium chloride, or production of hydrogen sulphide in triple-sugar iron medium. Gelatinase activity is present (Jackson & Goodman, 1978). Nitrate is reduced, but not selenite. No pigment production. Alpha-haemolysis and catalase activity of indoxyl acetase are strain-dependent. No hydrolysis of casein or growth on casein medium when performed as described by Cowan (1974); casein hydrolysis is weak (Jackson & Goodman, 1978), as described by Jackson *et al.* (1971), but strain-dependent as described by Taylor & Owen (1984). As with other preferentially anaerobic species of the genus *Campylobacter*, strains are susceptible to a range of antibiotics including cephalothin (32 mg l^{-1}), nalidixic acid (32 mg l^{-1}), carbenicillin (32 mg l^{-1}), cefoperazone (64 mg l^{-1}) and 5-fluorouracil (100 U l^{-1}). Contains cytochromes b and c. 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. The mol% G+C of the DNA is 28 to 30 (thermal denaturation method).

Strains have been isolated from superficial ulcers and soft tissue infections, non-gonococcal, non-chlamydial urethritis, and periodontal disease. Pathogenicity is difficult to assess because strains are mostly recovered from mixed infections.

The type strain is LMG 6451^T (=CCUG 7319^T =NCTC 10941^T).

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