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Phylogenetically, *Cytophaga aprica* and *Cytophaga difluens* occupy independent positions in the flavobacteroides phylum. Both of these organisms are gram-negative rods that are motile by gliding, chemotrophic, and aerobic, degrade several kinds of biomacromolecules, and inhabit marine environments. Their major isoprenoid quinone is menaquinone 7. The G+C content of the DNA of *C. aprica* is 35 to 37 mol%, and the G+C content of the DNA of *C. difluens* is 40 to 42 mol%. In addition to constituting an independent phylogenetic lineage, each species has a distinctive cellular polyamine constitution. *C. aprica* is characterized by possessing cadaverine as its major polyamine, and *C. difluens* is characterized by possessing spermidine, in contrast to most species of the genera *Cytophaga*, *Flavobacterium*, and *Flexibacter* and related organisms, which possess homospermidine. Transfer of *C. aprica* to the genus *Flammeovirga* gen. nov. as *Flammeovirga aprica* comb. nov. and transfer of *C. difluens* to the genus *Persicobacter* gen. nov. as *Persicobacter difluens* comb. nov. are proposed.

The taxonomic overlap among the genera *Cytophaga*, *Flavobacterium*, and *Flexibacter* and related organisms and the heterogeneity within these genera have been described in several chemotaxonomic and phenotypic investigations (4, 5, 9, 17, 26). 16S rRNA cataloging (19) and sequencing (30) have shown that the genera *Cytophaga* and *Flavobacterium*, along with the anaerobic genus *Bacteroides* and other taxa, constitute one phylum in the domain *Bacteria* (31). 16S rRNA and ribosomal DNA sequencing (7, 14–16, 29, 32) and DNA-rRNA hybridization data (1, 2, 24, 25) have revealed that the genera *Cytophaga*, *Flavobacterium*, and *Flexibacter* are all polyphyletic, and the contradiction between phylogenetic relationships and the present classification means that these genera should be divided into several distinct genera. Vandamme et al. (28) proposed the genus *Bergeyella* for *Weeksella zoohelcum*, the genus *Chryseobacterium* for the *Flavobacterium gleum* group, and the genus *Empeobacter* for *Flexibacter breve*. Recently, Bernardet et al. (2) emended the genus *Flavobacterium* to include *Flavobacterium*, *Cytophaga*, and *Flexibacter* species which are characterized by containing menaquinone 6 (MK-6) as the major isoprenoid quinone and by inhabiting soil and freshwater. Nakagawa and Yamasato (16) proposed that the genus *Cytophaga* should be emended and restricted to two species, *Cytophaga hutchinsonii* and *Cytophaga aurantiaca*, which degrade distinctly crystalline cellulose, and that the genus *Marinilabilia* should be established for *Cytophaga agarovorans* and *Cytophaga salmonicolor*, which are distinguished from other members of the genera *Cytophaga*, *Flavobacterium*, and *Flexibacter* and related genera by being facultative anaerobes, inhabiting marine environments, and containing MK-7 as the major isoprenoid quinone and spermidine as the major polyamine. However, many misnamed cytophagas, flavobacteria, and flexibacteria remain to be reclassified.

The phylogenetic relationships among representative taxa of the flavobacteroides phylum are shown in Fig. 1. 16S rRNA and ribosomal DNA sequence data were obtained from previously published studies (3, 7, 14–16, 18, 29, 30, 32) and the DNA Data Bank of Japan database. The phylogenetic analysis procedures used in this study have been described previously (16). The reconstructed phylogenetic tree based on 16S rRNA sequences reveals that the species assigned to the genera *Cytophaga*, *Flavobacterium*, and *Flexibacter* diverge into several phylogenetic lineages which should be assigned to several independent genera (Fig. 1). The genera *Bergeyella*, *Capnocytophaga*, *Chryseobacterium*, *Empeobacter*, *Flavobacterium*, *Oribacterium*, and *Weeksella* constitute a monophyletic group, which is equivalent to the emended family *Flavobacteriaceae* (2), as reported previously (7, 14–16). The genera *Bacteroides*, *Marinilabilia*, *Porphyromonas*, and *Rikenella* belong to the bacteroides subdivision (16, 18, 31). The genus *Sphingobacterium* forms an independent cluster (7, 16). *Flexibacter flexilis*, the type species of the genus *Flexibacter*, is independent of other species. *Microscilla marina*, the type species of the genus *Microscilla*, constitutes an independent phylogenetic lineage. The genera *Flexibacter* and *Microscilla* should each be restricted to...
the species which are closely related to the respective type species of these genera.

*Cytophaga aprica* and *Cytophaga diffluens* occupy distinct positions in this group of bacteria, and both of these taxa are far removed from other previously described genera (Fig. 1). The levels of 16S rRNA sequence similarity between *C. aprica* and other species are less than 89.4% (Table 1). Both *C. aprica* and *C. diffluens* are gram-negative rods that are motile by gliding, chemooorganotrophic, and aerobic, degrade several kinds of biomacromolecules, inhabit marine environments, and contain MK-7 as the major isoprenoid quinone (Table 2). The descriptions of the genera *Flammeovirga* and *Persicobacter* which are given below are taken from the data of Reichenbach (20) and our own data.

**Description of *Flammeovirga* gen. nov.** *Flammeovirga* (Flam- me'o.vir'ga L. adj. flammeus, fire colored; L. fem. n. virga, rod; L. fem. n. Flammeovirga, fire-colored rod). Cells are long and flexible rods that are 0.5 to 0.7 \( \mu \text{m} \) wide and 6 to 30 \( \mu \text{m} \) long. There is no resting stage. Motile by gliding. Gram negative. Cell mass is orange to reddish orange. Oxidase positive and catalase negative. Strict aerobes with a respiratory type of metabolism. Chemoorganotrophs. All strains of the type species decompose alginate, agar, gelatin, and starch but not crys-

**Description of *Persicobacter* gen. nov.** *Persicobacter* (Persi.co.bac'ter. Gr. neut. n. persikon, peach; L. masc. n. bacter, rod; L. masc. n. Persicobacter, peach rod, because the organism is a peach-colored rod). Cells are slender flexible rods that are 0.3 \( \mu \text{m} \) wide and 4 to 30 \( \mu \text{m} \) long. There is no resting stage. Motile by gliding. Gram negative. Cell mass is pink to orange. Oxidase positive and catalase negative. Strict aerobes with a respiratory type of metabolism. Chemoorganotrophs. All

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**FIG. 1.** Phylogenetic tree derived from 16S rRNA sequences for the members of the Flavobacterium-Cytophaga complex and related genera. All of the sequences used are the sequences of the type strains (the strain of *Escherichia coli* is unknown). The brackets indicate generally misclassified bacteria. *Agrobacterium tumefaciens* and *E. coli* were used as the root organisms. The software package Clustal V (10) was used to generate similarity values and \( K_{\text{imm}} \) values (13) and to reconstruct a phylogenetic tree by the neighbor-joining method (23). Scale bar = 0.01 \( K_{\text{imm}} \) in nucleotide sequences. The lengths of the vertical lines are not significant. The total number of nucleotides compared was 903 after elimination of the positions at which secondary structures varied in the strains (16). Confidence limits of less than 60% are not shown.

**Notes**

1. The **Agrobacterium tumefaciens** and **Escherichia coli** were used as the root organisms. The software package Clustal V (10) was used to generate similarity values and **Kimm** values (13) and to reconstruct a phylogenetic tree by the neighbor-joining method (23). Scale bar = 0.01 **Kimm** in nucleotide sequences. The lengths of the vertical lines are not significant. The total number of nucleotides compared was 903 after elimination of the positions at which secondary structures varied in the strains (16). Confidence limits of less than 60% are not shown.

2. The **Agrobacterium tumefaciens** and **Escherichia coli** were used as the root organisms. The software package Clustal V (10) was used to generate similarity values and **Kimm** values (13) and to reconstruct a phylogenetic tree by the neighbor-joining method (23). Scale bar = 0.01 **Kimm** in nucleotide sequences. The lengths of the vertical lines are not significant. The total number of nucleotides compared was 903 after elimination of the positions at which secondary structures varied in the strains (16). Confidence limits of less than 60% are not shown.

3. The **Agrobacterium tumefaciens** and **Escherichia coli** were used as the root organisms. The software package Clustal V (10) was used to generate similarity values and **Kimm** values (13) and to reconstruct a phylogenetic tree by the neighbor-joining method (23). Scale bar = 0.01 **Kimm** in nucleotide sequences. The lengths of the vertical lines are not significant. The total number of nucleotides compared was 903 after elimination of the positions at which secondary structures varied in the strains (16). Confidence limits of less than 60% are not shown.

4. The **Agrobacterium tumefaciens** and **Escherichia coli** were used as the root organisms. The software package Clustal V (10) was used to generate similarity values and **Kimm** values (13) and to reconstruct a phylogenetic tree by the neighbor-joining method (23). Scale bar = 0.01 **Kimm** in nucleotide sequences. The lengths of the vertical lines are not significant. The total number of nucleotides compared was 903 after elimination of the positions at which secondary structures varied in the strains (16). Confidence limits of less than 60% are not shown.

5. The **Agrobacterium tumefaciens** and **Escherichia coli** were used as the root organisms. The software package Clustal V (10) was used to generate similarity values and **Kimm** values (13) and to reconstruct a phylogenetic tree by the neighbor-joining method (23). Scale bar = 0.01 **Kimm** in nucleotide sequences. The lengths of the vertical lines are not significant. The total number of nucleotides compared was 903 after elimination of the positions at which secondary structures varied in the strains (16). Confidence limits of less than 60% are not shown.

6. The **Agrobacterium tumefaciens** and **Escherichia coli** were used as the root organisms. The software package Clustal V (10) was used to generate similarity values and **Kimm** values (13) and to reconstruct a phylogenetic tree by the neighbor-joining method (23). Scale bar = 0.01 **Kimm** in nucleotide sequences. The lengths of the vertical lines are not significant. The total number of nucleotides compared was 903 after elimination of the positions at which secondary structures varied in the strains (16). Confidence limits of less than 60% are not shown.

7. The **Agrobacterium tumefaciens** and **Escherichia coli** were used as the root organisms. The software package Clustal V (10) was used to generate similarity values and **Kimm** values (13) and to reconstruct a phylogenetic tree by the neighbor-joining method (23). Scale bar = 0.01 **Kimm** in nucleotide sequences. The lengths of the vertical lines are not significant. The total number of nucleotides compared was 903 after elimination of the positions at which secondary structures varied in the strains (16). Confidence limits of less than 60% are not shown.
TABLE 1. 16S rRNA sequence similarity matrix for species of the genera Cytophaga, Flavobacterium, and Flexibacter and the related taxa

<table>
<thead>
<tr>
<th>Species</th>
<th>% Similarity</th>
</tr>
</thead>
<tbody>
<tr>
<td>[Flavobacterium] fungineum</td>
<td>92.6</td>
</tr>
<tr>
<td>Flavobacterium aprica</td>
<td>81.2 80.1</td>
</tr>
<tr>
<td>Persicobacter diffens</td>
<td>84.7 83.7 85.1</td>
</tr>
<tr>
<td>Flexibacter aggregans</td>
<td>84.8 83.7 83.9 89.4</td>
</tr>
<tr>
<td>Flexibacter flexilis</td>
<td>83.3 81.7 83.5 86.4 85.7</td>
</tr>
<tr>
<td>Flexibacter elegans</td>
<td>82.8 80.2 82.3 86.3 84.9 86.8</td>
</tr>
<tr>
<td>Microscilla marina</td>
<td>84.8 82.2 83.0 87.2 87.2 85.3 86.2</td>
</tr>
<tr>
<td>Microscilla marina</td>
<td>82.8 81.0 81.6 85.7 84.9 86.6 86.3 90.7</td>
</tr>
<tr>
<td>Sphingobacterium spiritivorum</td>
<td>84.2 80.8 83.9 85.8 84.9 84.6 84.6 85.9 85.2</td>
</tr>
<tr>
<td>Flexibacter canadensis</td>
<td>85.2 82.8 81.8 86.3 87.7 86.7 85.9 85.7 87.8 90.7</td>
</tr>
<tr>
<td>Marinilabilia salmonicolor</td>
<td>84.8 83.0 83.0 87.4 84.8 85.1 85.1 85.4 84.3 86.5 86.7</td>
</tr>
<tr>
<td>Rikenella microfusus</td>
<td>80.6 79.6 82.1 84.2 83.1 83.9 83.5 84.5 83.5 86.3 86.1 88.9</td>
</tr>
<tr>
<td>Porphyromonas asaccharolytica</td>
<td>80.4 80.6 80.5 80.4 78.7 80.3 79.7 83.2 82.1 80.8 82.5 84.7 83.4</td>
</tr>
<tr>
<td>Bacteroides fragilis</td>
<td>82.4 81.1 80.8 84.5 83.0 83.0 81.1 82.2 82.3 82.3 84.2 86.8 85.1 85.6</td>
</tr>
<tr>
<td>Bergeyella zoohelcum</td>
<td>81.5 80.7 80.6 84.4 83.8 83.1 83.9 85.5 84.7 84.8 84.5 85.9 85.6 81.7 83.6</td>
</tr>
<tr>
<td>Chryseobacterium gleum</td>
<td>83.2 82.0 80.7 85.3 83.4 83.3 83.9 85.5 85.2 84.8 84.1 86.1 85.1 81.4 83.2 96.2</td>
</tr>
<tr>
<td>Ornithobacterium rhinotraechale</td>
<td>82.7 83.0 82.4 84.8 84.2 84.1 83.1 83.7 83.3 84.2 84.9 86.3 85.2 81.5 81.0 89.9 90.1</td>
</tr>
<tr>
<td>Empedobacter brevis</td>
<td>83.0 83.5 81.0 84.7 85.1 83.3 83.6 83.1 83.2 84.1 85.1 84.8 83.6 81.0 82.5 89.5 90.0 91.3</td>
</tr>
<tr>
<td>Weeksella virosa</td>
<td>83.7 83.2 80.3 83.1 83.1 83.4 82.1 83.3 83.8 83.8 83.6 84.2 84.1 81.6 82.2 88.7 88.7 90.3 92.4</td>
</tr>
<tr>
<td>Flavobacterium aquatile</td>
<td>83.5 83.3 80.6 83.1 83.5 82.6 81.5 83.6 83.0 83.0 84.2 84.2 83.9 82.1 82.6 86.3 86.8 89.5 88.7 89.5</td>
</tr>
<tr>
<td>Capnocytophaga ochracea</td>
<td>81.5 82.6 80.4 83.0 82.2 82.1 80.3 82.2 81.7 82.5 83.8 84.6 83.3 82.8 82.1 85.5 85.6 87.3 88.5 87.9 90.5</td>
</tr>
<tr>
<td>Escherichia coli</td>
<td>77.1 77.4 77.2 79.4 79.5 78.5 77.0 79.1 76.5 78.1 77.3 77.1 73.0 75.8 76.9 77.0 75.9 78.2 77.6 76.4 76.4 75.3</td>
</tr>
</tbody>
</table>

a The brackets indicate generically misclassified bacteria.

strains of the type species decompose alginate, agar, gelatin, and starch. Marine organisms. The optimum temperature is 25 to 30°C. The optimum pH is around 7.

The major isoprenoid quinone is MK-7. The major polyamine is spermidine. The G+C content of the DNA is 40 to 42 mol%. The type species of the genus Persicobacter diffensus comb. nov. The description of P. diffensus is the same as that given by Reichenbach (20).

TABLE 2. Taxonomic characteristics of the genera Flammeovira and Persicobacter, the emended genera Cytophaga and Flavobacterium, and allied bacteria

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Habitat</th>
<th>Relation to oxygenb</th>
<th>Pigmentation</th>
<th>Sphingolipid</th>
<th>G+C content (mol%)</th>
<th>Polyaminec</th>
<th>Quinone(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flammeovira</td>
<td>Marine</td>
<td>A</td>
<td>+</td>
<td>ND</td>
<td>35-37</td>
<td>Cad</td>
<td>MK-7</td>
</tr>
<tr>
<td>Persicobacter</td>
<td>Marine</td>
<td>A</td>
<td>+</td>
<td>ND</td>
<td>40-42</td>
<td>Spd</td>
<td>MK-7</td>
</tr>
<tr>
<td>Bergeyella</td>
<td>Parasitic, saprophytic</td>
<td>A</td>
<td>-</td>
<td>-</td>
<td>35-37</td>
<td>ND</td>
<td>MK-6</td>
</tr>
<tr>
<td>Capnocytophaga</td>
<td>Parasitic, saprophytic</td>
<td>F</td>
<td>+</td>
<td>ND</td>
<td>33-41</td>
<td>ND</td>
<td>MK-6</td>
</tr>
<tr>
<td>Chryseobacterium</td>
<td>Free-living, parasitic</td>
<td>A</td>
<td>-</td>
<td>-</td>
<td>33-38</td>
<td>Hspd</td>
<td>MK-6</td>
</tr>
<tr>
<td>Cytophaga</td>
<td>Soil</td>
<td>A</td>
<td>+</td>
<td>ND</td>
<td>39-42</td>
<td>Hspd</td>
<td>MK-7</td>
</tr>
<tr>
<td>Empedobacter</td>
<td>Free-living, parasitic</td>
<td>A</td>
<td>-</td>
<td>-</td>
<td>31-33</td>
<td>Hspd</td>
<td>MK-6</td>
</tr>
<tr>
<td>Flavobacterium</td>
<td>Free-living, saprophytic</td>
<td>A</td>
<td>-</td>
<td>-</td>
<td>32-37</td>
<td>Hspd</td>
<td>MK-6</td>
</tr>
<tr>
<td>Flexibacter</td>
<td>Soil, freshwater</td>
<td>A</td>
<td>+</td>
<td>ND</td>
<td>29-48</td>
<td>Hspd</td>
<td>MK-6, MK-7</td>
</tr>
<tr>
<td>Marinilabilia</td>
<td>Marine</td>
<td>F</td>
<td>+</td>
<td>ND</td>
<td>37-41</td>
<td>Spd</td>
<td>MK-7</td>
</tr>
<tr>
<td>Microscilla</td>
<td>Marine</td>
<td>A</td>
<td>+</td>
<td>ND</td>
<td>32-44</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Ornithobacterium</td>
<td>Parasitic</td>
<td>F</td>
<td>-</td>
<td>ND</td>
<td>37-39</td>
<td>ND</td>
<td>MK-6</td>
</tr>
<tr>
<td>Riemerella</td>
<td>Parasitic</td>
<td>M</td>
<td>-</td>
<td>ND</td>
<td>29-35</td>
<td>ND</td>
<td>MK-6</td>
</tr>
<tr>
<td>Sphingobacterium</td>
<td>Free-living, saprophytic</td>
<td>A</td>
<td>+</td>
<td>+</td>
<td>39-45</td>
<td>Hspd</td>
<td>MK-7</td>
</tr>
<tr>
<td>Weeksella</td>
<td>Parasitic, saprophytic</td>
<td>A</td>
<td>-</td>
<td>-</td>
<td>35-38</td>
<td>ND</td>
<td>MK-6</td>
</tr>
</tbody>
</table>

a Data from references 8, 11, 12, 14-17, 20-22, 24, 27-29, and 33.
b A, strict aerobes; F, facultative anaerobes; M, microaerophiles.
c Cad, cadaverine; Spd, spermidine; Hspd, homospermidine.
d ND, not determined.
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nom., the causative agent of septicemia anserum exsudativa, and its phylo-
genetic affiliation within the Flavobacterium-Cytophaga rRNA homology


sp. nov., Sphingobacterium piscium sp. nov., Sphingobacterium heparinum
comb. nov., Sphingobacterium thalophilum comb. nov. and two genospecies
of the genus Sphingobacterium, and synonymy of Flavobacterium yabuchiae

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