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NOTES

New Perspectives in the Classification of the Flavobacteria: Description of *Chryseobacterium* gen. nov., *Bergeyella* gen. nov., and *Empedobacter* nom. rev.

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Our present knowledge concerning the genotypic, chemotaxonomic, and phenotypic characteristics of members of the genus *Flavobacterium* and some related genera, including the genus *Weeksella*, was used to revise the classification of these organisms. The generically misclassified organisms *Flavobacterium balustinum*, *Flavobacterium gleum*, *Flavobacterium indologenes*, *Flavobacterium indoltheticum*, *Flavobacterium meningosepticum*, and *Flavobacterium scophthalmum* are included in a new genus, *Chryseobacterium*, with *Chryseobacterium gleum* as the type species. The generically misclassified organism *Flavobacterium breve* is included in the revived genus *Empedobacter* as *Empedobacter brevis*, whereas the generically misclassified organism *Weeksella zoohelcum* is included in the new genus *Bergeyella* as *Bergeyella zoohelcum*.

The genus *Flavobacterium* was destined to suffer the same fate as many other long-established genera, as its original description relied on parameters which are now considered to have little taxonomic importance. This ill-defined genus comprised a collection of predominantly yellow-pigmented bacteria that were, according to modern genotypic standards, not at all closely related. Throughout its history, the genus *Flavobacterium* has been restricted and redefined many times. Most of the organisms once known as flavobacteria have been reclassified (15). The genus *Flavobacterium* as it is currently defined in *Bergey's Manual of Systematic Bacteriology* comprises seven distinct species (16): *Flavobacterium aquatile* (the type species), *Flavobacterium balustinum*, *Flavobacterium breve*, *Flavobacterium meningosepticum*, *Flavobacterium multivorum*, *Flavobacterium odoratum*, and *Flavobacterium spiritivorum*. The type species has been the subject of many discussions. The single strain which represents this taxon is not the original culture described by Frankland and Frankland (9), and it does not fit the original description, although that description was rather meager. For several reasons this strain is considered unrepresentative of the genus, and therefore Holmes and Owen (15) requested that *F. aquatile* be rejected as a nomen dubium and be replaced with *F. breve* as the type species of the genus. The Judicial Commission of the International Committee on Systematic Bacteriology denied this request as there was no great potential for confusion if *F. aquatile* was retained, nor were strong arguments for rejecting this type species found in the *International Code of Nomenclature of Bacteria* (35). In subsequent taxonomic studies, new *Flavobacterium* species were described, whereas other were removed and included in new genera (8, 14, 17, 21, 24, 29, 34, 37).

The most recent review of the taxonomy of the flavobacteria appears in *The Prokaryotes*, 2nd ed. (13). In this review, flavobacteria are divided into four natural groups, excluding *F. aquatile*. The first group includes *F. balustinum*, *F. breve*, *Flavobacterium gleum*, *Flavobacterium indologenes*, *Flavobacterium indoltheticum*, and *F. meningosepticum*. A second natural group is formed by *F. odoratum*. The third group includes *Flavobacterium mizutae*, *F. multivorum*, *F. spiritivorum*, *Flavobacterium thalpophilum*, and *Flavobacterium yabuuchiae*; these organisms form a group considered to be a separate genus, *Sphingobacterium* (29, 37). Finally, two species, formerly known as Centers for Disease Control groups IIf and IIj, constitute a fourth group, for which a separate genus has been proposed (19, 20); these taxa are now known as *Weeksella virosa*, the type species, and *Weeksella zoohelcum*, respectively (19, 20).

An important, additional problem throughout the history of the genus *Flavobacterium* has been the difficulty of separating this taxon from similar genera, such as *Cytophaga* and *Flexibacter*. Differentiation of these genera relies mainly on ultrastructural features, such as gliding motility and cellular morphology (13, 27). Not surprisingly, these features have turned out to have limited taxonomic value, and genus delineation has remained troublesome (27). Recently, several phylogenetic analyses have provided new insights concerning the taxonomic relationships within this cluster of organisms, which is often referred to as the *Flavobacterium-Cytophaga* rRNA cluster (10, 25, 28). One of the main conclusions of these studies is that the genera *Flavobacterium*, *Cytophaga*, and *Flexibacter* all are polyphyletic and should be redefined and subdivided into several genera. The relationships of these taxa to other members of this rRNA superfamily, such as the genera *Capnocytophaga*, *Ornithobacterium*, *Riemerella*, and *Weeksella*, have been described in several papers (10, 25, 28, 33) and are partially shown in Fig. 1, which is a schematic compilation of previously published DNA-rRNA hybridization results and new data (1, 31). The results obtained for the flavobacteria indicate that

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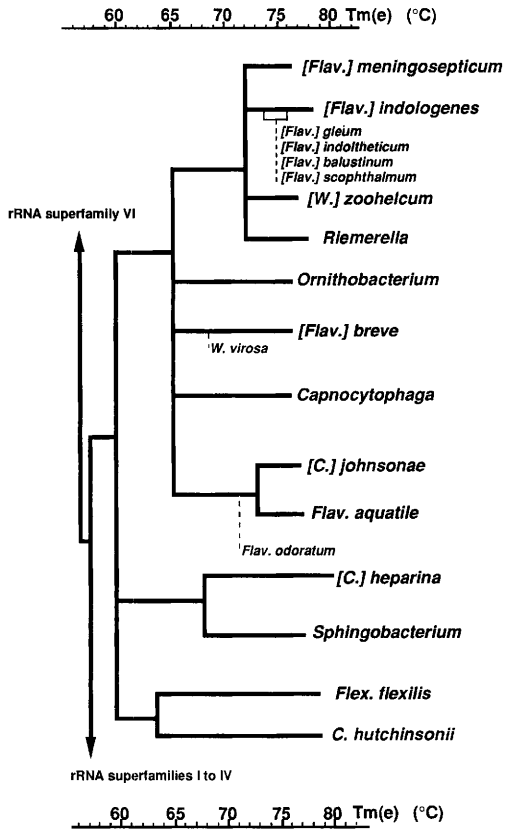

FIG. 1. Simplified rRNA cistron similarity dendrogram for rRNA superfamily V. Abbreviations: *C.*, *Cytophaga*; *Flav.*, *Flavobacterium*; *Flex.*, *Flexibacter*; *W.*, *Weeksella*. Brackets indicate generically misnamed species.

none of the four natural groups described above is closely related to *F. aquatile*.

Within well-characterized genera, differences in melting temperatures [$T_{m(e)}$] for the most part range from 4 to 7°C (7), whereas differences in $T_{m(e)}$ values of up to 12°C are found within bacterial families (32). This implies that, except for *F. odoratum*, all members of the four natural groups sensu Holmes (13) should be excluded from the genus *Flavobacterium* on genotypic grounds, as the name *Flavobacterium* must be retained for the type species. The results of phylogenetic analyses have also established that the genus *Weeksella*, although it contains only two species, is also heterogeneous, as differences in $T_{m(e)}$ values of 12°C were measured (28). Again, the genus name must be retained for the type species, which is *W. virosa*. The genus *Sphingobacterium*, on the other hand, has been found to be genotypically defined, with differences in $T_{m(e)}$ values within this genus of about 8°C (Fig. 1) (28). These data also support the transfer of *F. thalpophilum* and *F. mizutaii* to the genus *Sphingobacterium* as *Sphingobacterium thalpophilum* and *Sphingobacterium mizutae*, respectively; these transfers were based mainly on the results of chemotaxonomic studies (21, 29, 37).

Since a previous report (28), radioactively labeled rRNA probes of the type strains of *F. meningosepticum*, *Flexibacter flexilis*, and *Cytophaga hutchinsonii* were prepared in order to further explore the taxonomic relationships of these taxa. The hybridization results obtained with *F. meningosepticum*, *Flexibacter flexilis*, and *Cytophaga hutchinsonii* rRNA probes will be discussed in detail elsewhere (1, 31). The taxonomic positions of these three taxa within rRNA superfamily V are shown in Fig. 1. From these data it is obvious that the flavobacteria belonging to the first natural group sensu Holmes (13) form a tight rRNA cluster in which *F. meningosepticum* occupies a separate position (Fig. 1). This subdivision into two groups corresponds to the original phenotypic delineation of Centers for Disease Control groups IIa (now *F. meningosepticum* [22]) and IIb (*F. balustinum*, *F. gleum*, *F. indologenes*, *F. indoltheticum*, and numerous unnamed strains [13]). *Flavobacterium scophthalmum*, a recently recognized fish pathogen, belongs to the same rRNA cluster (24) (Fig. 1). The following two additional taxa occupy separate positions at the base level between the two groups mentioned above: *W. zoohelcum* and *Riemerella anatipestifer* (Fig. 1). The genotypic divergence within this rRNA cluster is within the range of divergence of many bacterial genera. Criteria such as chemotaxonomic and classical phenotypic features are decisive for including all or some of these taxa in one genus. An example of such a polyphasic approach is genus delineation in the family *Comamonadaceae* (36). The genera *Acidovorax*, *Aquaspirillum*, *Comamonas*, *Hydrogenophaga*, *Variovorax*, and *Xylophilus* all branch at a base level of about 76°C, which corresponds to a level of divergence of about 5°C. Several of these genera (the genera *Acidovorax*, *Aquaspirillum*, and *Comamonas*) include species that occupy separate positions at the same base level (about 76°C) (36). In such cases, phenotypic criteria are decisive for determining the final genus designation. The present situation with *F. balustinum*, *F. gleum*, *F. indologenes*, *F. indoltheticum*, *F. meningosepticum*, *F. scophthalmum*, *R. anatipestifer*, and *W. zoohelcum* is completely analogous. Obviously, *F. balustinum*, *F. gleum*, *F. indologenes*, *F. indoltheticum*, *F. meningosepticum*, and *F. scophthalmum* are similar in many respects. They share many classical phenotypic features (13, 24), they all contain menaquinone 6 as their major respiratory quinone (5, 6; no data have been published for *F. indoltheticum* and *F. scophthalmum*), and they have similar fatty acid profiles which are characterized by large amounts of 15:0 iso, iso 17:1ω9c, 17:0 iso 3OH, and summed feature 4 (i.e., 15:0 iso 2OH or 16:1ω7t or both [24, 28]). Within this group, *F. meningosepticum* has the most aberrant fatty acid profile (28). *W. zoohelcum*, conversely, is phenotypically very different from these flavobacteria (13, 20) and has a different fatty acid profile (28). Finally, *R. anatipestifer* can be distinguished from its neighbors by several classical phenotypic features, by its capnophilic metabolism, and by its fatty acid and quinone contents (28) (Table 1).

We concluded that separate generic status is warranted for (i) *F. balustinum*, *F. gleum*, *F. indologenes*, *F. indoltheticum*, *F. meningosepticum*, and *F. scophthalmum* (the name *Flavobacterium* must be preserved for the type species, *F. aquatile*); (ii) *W. zoohelcum* (the name *Weeksella* must be preserved for the type species, *W. virosa*); and (iii) *R. anatipestifer*. Below, we propose the name *Chryseobacterium* gen. nov. to include former *Flavobacterium* species as *Chryseobacterium balustinum*, *Chryseobacterium gleum*, *Chryseobacterium indologenes*, *Chryseobacterium indoltheticum*, *Chryseobacterium meningosepticum*, and *Chryseobacterium scophthalmum*. The two oldest species, *Chryseobacterium balustinum* (originally described by Harrison in 1929 [12]) and *Chryseobacterium indoltheticum* (originally described by Campbell and Williams in 1951 [4]), were not chosen as the type species as they have been inadequately characterized and each is currently represented by a single strain (cf. Recommendation 20d of the *International Code of Nomenclature of Bacteria* [23]). *Chryseobacterium gleum* is a well-characterized species, and both its genotypic

TABLE 1. Differentiating characteristics of the genus *Chryseobacterium* and allied bacteria[a]

Characteristic	*Flavobacterium*	*Chryseobacterium*	*Empedobacter*	*Weeksella*	*Bergeyella*	*Riemerella*
G+C content (mol%)	32	33–38	31–33	35–38	35–37	29–35
Respiratory quinone	Menanquinone 6	Menaquinone 6	Menaquinone 6	Menaquinone 6	ND	Menaquinone 7
Habitat	Free living	Free living or parasitic	Free living or parasitic	Parasitic or saprophytic	Parasitic or saprophytic	Parasitic
Pigment production	+ (carotenoid)	+ (flexirubin)[b]	+ (flexirubin)	−	−	−
Saccharolytic metabolism	+	+	+	−	−	+
Capnophilic metabolism	−	−	−	−	−	+
Resistance to penicillin	ND	+	+	−	−	−
DNase activity	ND	+[c]	+	−	−	ND
Gelatinase activity	−	+[d]	+	+	+	+[e]
Urease activity	−	v[f]	−	−	+	v[f]
Production of indole	−	v[g]	+	+	+	−
Hydrolysis of esculin	−	+[h]	−	−	−	ND
Growth at 37°C	−	+	v[i]	+	+	+
Growth at 42°C	−	v[f]	−	+	−[j]	+[e]
Growth on MacConkey agar	−	+[k]	+	+	−	−
Growth on β-hydroxybutyrate	−	+	+	+	−	ND
Acid production from glucose	+	+[l]	v[i]	−	−	v[f]
Acid production from sucrose	+	−	−	−	−	−

[a] Data were obtained from Holmes (13), Holmes et al. (16–20), Mudarris et al. (24), Segers et al. (28), and Yabuuchi et al. (37). +, present in all strains; −, absent in all strains; v, variable (see below); ND, not determined.
[b] Some *Chryseobacterium meningosepticum* strains are nonpigmented.
[c] Present in all *Chryseobacterium* strains studied except 2 of 12 *Chryseobacterium gleum* strains. Not determined for *Chryseobacterium indoltheticum*.
[d] Present in all *Chryseobacterium* strains studied. Not determined for *Chryseobacterium indoltheticum*.
[e] Most *R. anatipestifer* strains are positive for this characteristic.
[f] Variable within and between species.
[g] Strain dependent for *Chryseobacterium meningosepticum*. Present in all other *Chryseobacterium* species except *Chryseobacterium scophthalmum*.
[h] Present in all *Chryseobacterium* strains studied except in 2 of 49 *Chryseobacterium meningosepticum* strains.
[i] Present in six of seven *E. brevis* strains studied.
[j] Present in 1 of 30 *B. zoohelcum* strains studied.
[k] Absent in 7 of 13 *Chryseobacterium indologenes* strains studied and in all *Chryseobacterium scophthalmum* strains tested.
[l] Absent in 7 of 49 *Chryseobacterium meningosepticum* strains studied and in all *Chryseobacterium scophthalmum* strains tested.

structure and phenotypic structure have been studied in detail (17). We therefore propose that *Chryseobacterium gleum* should be the type species of the genus *Chryseobacterium*. *Chryseobacterium meningosepticum*, which is clinically the most important species of this group and has also been well-characterized (2, 3, 30), was not chosen as the type species as it is the most aberrant member of the genus (Fig. 1) (28). We also propose the name *Bergeyella* gen. nov., with *Bergeyella zoohelcum* as the type species.

A similar situation occurs in the rRNA branch comprising *W. virosa* and *F. breve*. The level of genotypic divergence between these taxa is about 6°C (28) (Fig. 1), and the two taxa differ in many biochemical features (13) (Table 1). They have considerably different fatty acid compositions (6) but have the same respiratory quinone content (i.e., menaquinone 6 is the major quinone [6]). Logically, these two taxa should be considered members of different genera. Instead of proposing a new name for *F. breve*, we propose that the name *Empedobacter*, which has been applied previously to the same taxon (26), should be revived. This name was published before 1 January 1980 but was not included on Approved Lists of Bacterial Names (cf. Rule 28a of the *International Code of Nomenclature of Bacteria* [23]). Below, we revive the name *Empedobacter* to include *F. breve* as *Empedobacter brevis*.

Finally, *F. aquatile* is the only member of the genus *Flavobacterium* that remains in this taxon. It has been stated repeatedly that the description of the genus *Flavobacterium* given in *Bergey's Manual of Systematic Bacteriology* (16) is more appropriate for the organisms which we include in the genus *Chryseobacterium* than for *F. aquatile* (13, 15). The description of the genus *Chryseobacterium* given below corresponds in virtually all respects to that description, whereas the description of the genus *Flavobacterium* will have to be revised. This is a consequence of the decision of the Judicial Commission (35). The $T_{m(e)}$ differences for several generically misnamed *Cytophaga* and *Flexibacter* species fall within the generic range of 4 to 7°C when the DNAs of these organisms are hybridized with *F. aquatile* rRNA (1, 28), and these misnamed organisms share many phenotypic characteristics with *F. aquatile*. A revision of the classification and nomenclature of the genus *Flavobacterium*, including the taxonomic status of *F. odoratum*, and the relationships between members of this taxon and the generically misnamed flexibacters and cytophagas are the subjects of a forthcoming paper (1).

Description of *Chryseobacterium* gen. nov. *Chryseobacterium* (Chry.se.o.bac.te'ri.um. Gr. adj. *chryseos*, golden; Gr. neut. n. *bakterion*, a small rod; N. L. neut. n. *Chryseobacterium*, a yellow rod) cells are gram-negative, nonmotile, non-spore-forming rods with parallel sides and rounded ends; typically the cells are 0.5 μm wide and 1 to 3 μm long. Intracellular granules of poly-β-hydroxybutyrate are absent. Aerobic. Chemoorganotrophic. All strains grow at 30°C; most strains grow at 37°C. Growth on solid media is typically pigmented (yellow to orange), but nonpigmented strains occur. Colonies are translucent (occasionally opaque), circular, convex or low convex, smooth, and shiny, with entire edges. Positive for catalase, oxidase, and phosphatase activities. Several carbohydrates, including glycerol and trehalose, are oxidized. Strong proteolytic activity occurs. Esculin is hydrolyzed. Agar is not digested. Resistant to a wide range of antimicrobial agents. Additional features are shown in Table 1.

Branched-chain fatty acids (i.e., 15:0 iso, iso 17:1ω9c, 17:0 iso 3OH, and summed feature 4 [15:0 iso 2OH or 16:1ω7t or both]) are predominant (28). Sphingophospholipids are ab-

sent. Menaquinone 6 is the only respiratory quinone. Homospermidine and 2-hydroxyputrescine are the major polyamines in *Chryseobacterium indologenes*, whereas putrescine and agmatine are minor components (11).

The type species is *Chryseobacterium gleum* comb. nov. The DNA base composition ranges from 33 to 38 mol% guanine plus cytosine. *Chryseobacterium* species are widely distributed in soil, water, and clinical sources.

The descriptions of *Chryseobacterium balustinum* (basonym, *F. balustinum* Harrison 1929), *Chryseobacterium gleum* (basonym, *F. gleum* Holmes, Owen, Steigerwalt, and Brenner 1984), *Chryseobacterium indologenes* (basonym, *F. indologenes* Yabuuchi, Kaneko, Yano, Moss, and Miyoshi 1983), *Chryseobacterium indoltheticum* (basonym, *F. indoltheticum* Campbell and Williams 1951), *Chryseobacterium meningosepticum* comb. nov. (basonym, *F. meningosepticum* King 1959), and *Chryseobacterium scophthalmum* (basonym, *F. scophthalmum* Mudarris, Austin, Segers, Vancanneyt, Hoste, and Bernardet 1994) are the same as the original species descriptions given in references 4, 12, 16, 17, 22, 24, and 37.

Description of *Bergeyella* gen. nov. *Bergeyella* (Ber.gey.el'la.; proper name Bergey; L. dim. suff. *-ella*; N. L. fem. n. *Bergeyella*, in honor of D. H. Bergey, who created, together with his coworkers, the genus *Flavobacterium* in 1923, for his contributions to the taxonomy of the genus *Flavobacterium* and related bacteria).

The description of *Bergeyella* is the same as the description given previously for *Weeksella* (19). In addition, the following features differentiate the genus *Bergeyella* and genuine *Weeksella* species. Urease activity is present. No growth occurs at 42°C, on MacConkey agar, or on β-hydroxybutyrate. Branched-chain fatty acids (15:0 iso, 15:0 iso 2OH, 17:1 iso, 17:0 iso 3OH) are predominant. Sphingophospholipids are absent. The type species is *B. zoohelcum*. The DNA base composition ranges from 35 to 37 mol% guanine plus cytosine. The upper respiratory tracts of dogs and human wounds caused by dog bites are the most frequent sources. Pathogenicity is unknown.

The description of *B. zoohelcum* comb. nov. (basonym, *W. zoohelcum* Holmes, Steigerwalt, Weaver, and Brenner 1986) is the same as the description given previously for *W. zoohelcum* (20).

Description of *Empedobacter* (ex Prévot 1961) nom. rev. *Empedobacter* (Em.pe.do.bac'ter. Gr. adj. *empedos*, fixed; M. L. masc. n. *bacter*, a small rod; M. L. masc. n. *Empedobacter*, nonmotile rod) cells are gram-negative, nonmotile, non-spore-forming rods with parallel sides and rounded ends; typically the cells are 0.5 μm wide and 1 to 2 μm long. Intracellular granules of poly-β-hydroxybutyrate are absent. Aerobic, having a strictly respiratory type of metabolism. Chemoorganotrophic. All strains grow at 30°C; most strains grow at 37°C. Growth on solid media is light yellow. Colonies are circular, low convex, smooth, and shiny, with entire edges. Positive for catalase, oxidase, and phosphatase activities. Indole is produced. Several carbohydrates are oxidized, but glycerol and trehalose are not oxidized. Strong proteolytic activity occurs. Esculin is not hydrolyzed. Agar is not digested. Resistant to a wide range of antimicrobial agents.

Fatty acids 15:0 iso, 16:1ω7c, 16:1ω5c, 16:0, 16:0 3OH, and 17:0 iso 3OH are predominant. Sphingophospholipids are absent. Menaquinone 6 is the only respiratory quinone.

The type species is *E. brevis* comb. nov., which has been isolated from water samples and clinical sources. The DNA base composition ranges from 31 to 33 mol% guanine plus cytosine.

The description of *E. brevis* comb. nov. (basonym, *F. breve* Holmes and Owen 1982 ex Bergey, Harrison, Breed, Hammer, and Huntoon 1923) is the same as the description given previously for *F. breve* (16, 18).

Table 1 shows features that differentiate the genera *Chryseobacterium*, *Bergeyella*, *Empedobacter*, *Flavobacterium*, *Riemerella*, and *Weeksella*.

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